

Animal Research Paper

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Abstract

Growth data on Jersey crossbred calves, maintained at ICAR-National Dairy Research Institute, Eastern Regional Station, Kalyani, Nadia, West Bengal, India, were collected and analysed to assess the influence of maternal effects on growth traits of calves. Traits considered for this study were birth weight (BW) and weights at 3 months (W3M), 6 months (W6M), 9 months (W9M) and 12 months (W12M) of age. Least-squares analyses were employed to obtain the effects of non-genetic factors on the traits of interest. Determination of influence of maternal effects on growth traits was estimated by fitting three univariate animal models (including or excluding maternal effects) using Bayesian approach. The most appropriate model for each trait was selected based on Deviance Information Criterion. Direct heritability (h^2) estimates for BW, W3M, W6M, W9M and W12M were 0.31 ± 0.08 , 0.26 ± 0.10 , 0.48 ± 0.10 , 0.44 ± 0.11 and 0.39 ± 0.14 , respectively, under the best model. Permanent environmental maternal effects (c^2) varied from 0.04 to 0.12 for all traits. Existence of maternal effects for all ages reflects the importance of maternal components for these traits. Moderate to high heritability estimates for growth traits indicate the possibility of modest genetic progress for these traits through selection under prevalent management system.

Introduction

Evaluation of the growth performance traits in beef cattle is crucial to ascertain the potentiality of the beef breeds and to formulate the appropriate breeding programme for genetic improvement of the breed (Pires *et al.*, 2016). Early growth traits of calves are influenced not only by calf's own genetic potential but also maternal effects including maternal genetic and permanent environmental effects, which represent the dam's milk production and mothering ability (Meyer, 1992). Maternal effects are especially important in early life but also may have carry-over effects later in life. According to Robison (1981), the importance of maternal influence on the growth of young mammals has been recognized since the earliest attempts to improve livestock production. Willham (1972) stated that though the maternal effect is strictly of environmental origin relative to offspring, phenotypic differences among dams for the maternal effects reflected in the phenotypic values of offspring.

Body weights are often recorded at a relatively early age, so explained variance of these traits due to maternal effects needs to be quantified for optimizing breeding programmes. Published literature (Aziz *et al.*, 2005; Ríos-Utrera *et al.*, 2011; Martinez *et al.*, 2016) showed that both direct and maternal effects play an important role on animal growth. Later in life, the maternal influence diminishes and direct effects of the genes that influence growth assume primary importance. Several authors (Meyer, 1992; Rumph *et al.*, 2002) reported that if the maternal genetic effects are important for any early expressing traits, but not included in the model, then it yielded upward and bias estimation of direct heritability and decreased the selection efficiency of the trait. With the advancement of latest statistical methodology for estimation of variance components, it became possible to partition the variance into direct and maternal effects for growth traits. The reported heritability estimates for growth traits of dairy cattle breeds in India are mostly based on variance components obtained by sire model, where maternal effects are ignored (Sahin *et al.*, 2012). Therefore, accurate estimation of the size of effects of maternal lineage is required to assess the impact of their effects on genetic evaluations of growth traits. Hence, the aim of the present study was to estimate the (co)variance components and genetic parameters due to direct and maternal effects for growth traits in Jersey crossbred cattle.

Materials and methods

Animals and data

Data on birth weight and weights at 3, 6, 9 and 12 months of age of Jersey crossbred calves were collected for a period of 39 years (1983–2021) and 9 years (2013–2021), respectively,

for the present study. In this study, the crossbred animals were produced from the mating of two *Bos indicus* breeds, Tharparkar and Red Sindhi by outcrossing using imported semen of Jersey breed. A total of 12 genetic groups having different levels of Jersey inheritance produced in the breeding programme were used in this study. The details of experimental animals as well as location and climatic conditions of the farm have been described by Koloï and Mandal (2020) and Kumar and Mandal (2021). Briefly, the animals in this farm were generally maintained under loose and open housing system assuring adequate air exchange and exercise. Animals were kept separately according to their age groups and physiological stages. Calves up to 3 months of age are reared in separately constructed calves' shed. The calves of more than 3 months to 1 year of age and heifers from 2 years to conception were kept in different open paddocks with sheds. Pregnant animals are generally separated from dry animals and kept in different sheds. Both calves and dams were weighed at calving and calves are tagged after birth. Just after birth, colostrum is fed to each calf thrice in a day up to 3 days. After 3 days, calves are fed with whole milk twice in a day (morning and evening) using sterile bottle based on their body weight (at 10% body weight). Calves were provided the whole milk for a period of 3 months. Calves are generally dehorned during the first month of life. The lactating animals of the farm were provided with a standard ratio of concentrate and *ad libitum* green fodder. Standard prophylactic measures were followed as a routine for all animals. The calving date, sex and birth type of each calf were recorded. Calves were weighed at 15-day intervals from birth to 3 months of age and thereafter at monthly intervals up to 12 months of age.

Records of 2022 calves, descended from 609 dams and 71 sires, were available for this investigation. Data on postnatal weights were not collected over the entire 39 years, yielding dissimilar numbers of records for different traits. Traits considered for the present study were weight at birth (BW), 3 months (W3M), 6 months (W6M), 9 months (W9M) and 12 months of age (W12M). The characteristics of data and pedigree structure for the traits under study are summarized in Tables 1 and 2, respectively.

Statistical analysis

Estimates of (co)variance components and genetic parameters for the traits were performed through the Gibbs sampling method in

Table 1. Characteristics of data structure for body weights (kg) of Jersey crossbred cattle

Item	Traits				
	BW	W3M	W6M	W9M	W12M
No. of records	2022	521	422	364	329
Mean	23	53	86	119	152
Standard deviation	4.0	9.4	15.3	21.1	23.9
CV (%)	17.6	17.7	17.8	17.7	15.7
Recording period (years)	39	09	09	09	09

BW, birth weight; W3M, weight at 3 months; W6M, weight at 6 months; W9M, weight at 9 months; W12M, weight at 12 months.

a single trait analysis by fitting a series of univariate animal models by Bayesian approach implemented in BLUPF90 software (Misztal, 1999). Initially, the factors affecting the growth traits were tested using least-squares analysis of variance (Harvey, 1990). The fixed effects considered in the initial model were birth year, season of birth, dam's parity and sex of calves. The significant effects for each trait were included in the final mixed models used for genetic analysis. The Gibbs chains of 200 000 iterations, with a burn-in of the initial 20 000 samples, and a sampling interval of 100 iterations were generated. Therefore, for each analysis, 1800 samples of (co)variance components were available and genetic parameters were estimated as the average ratio of sample variances. The convergence diagnostic of the chains generated by the Gibbs sample chains was undertaken using Geweke test algorithm (Smith *et al.*, 2007). Convergence was tested for all parameters using effective sample size from the program POSTGIBBSF90 (Misztal *et al.*, 2014).

To assess the impact of maternal effects on estimation of variance components and genetic parameters of growth traits, the following three univariate animal models, including or excluding maternal effects, were employed for each trait:

$$\text{Model 1: } \mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{a} + \mathbf{e}$$

$$\text{Model 2: } \mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_3\mathbf{c} + \mathbf{e}$$

$$\text{Model 3: } \mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{e} \text{ with } \text{Cov}(\mathbf{a}, \mathbf{m}) = 0$$

where \mathbf{y} is the $n \times 1$ vector of observations for each trait and \mathbf{X} is the incidence matrix that relates data to the unknown vector of fixed effects $\boldsymbol{\beta}$. Incidence matrices, \mathbf{Z}_1 and \mathbf{Z}_2 relate unknown vectors of direct (\mathbf{a}) and maternal (\mathbf{m}) breeding values, respectively, to \mathbf{y} . The incidence matrix \mathbf{Z}_3 relates an unknown additional

Table 2. Characteristics of the pedigree structure of the data used for the study

Item	Traits				
	BW	W3M	W6M	W9M	W12M
Total no. of animal in pedigree	2269	770	673	610	569
No. of animals with records	2022	521	422	364	329
No. of sires with progeny	71	15	14	14	13
No. of dams with progeny	602	223	199	188	177
No. of dams with records and progeny	503	127	110	101	93
Avg. no. of progeny per sire	28.5	34.7	30.1	26.0	25.3
Avg. no. of progeny per dam	3.4	2.3	2.1	1.9	1.9
Average inbreeding coefficient	0.46	0.45	0.41	0.41	0.39

BW, birth weight; W3M, weight at 3 months; W6M, weight at 6 months; W9M, weight at 9 months; W12M, weight at 12 months.

random vector of permanent maternal environmental effects (\mathbf{c}) to \mathbf{y} . The unknown vector \mathbf{e} contains random residuals due to environmental effects peculiar to individual records. It was assumed that $V(\mathbf{a}) = \mathbf{A}\sigma_a^2$, $V(\mathbf{m}) = \mathbf{A}\sigma_m^2$, $V(\mathbf{c}) = \mathbf{I}_d\sigma_c^2$, and $V(\mathbf{e}) = \mathbf{I}_n\sigma_e^2$ where \mathbf{A} is the numerator relationship matrix, and \mathbf{I}_d and \mathbf{I}_n are the identity matrix with dimension equal to the number of dams and number of records, respectively, and σ_a^2 , σ_m^2 , σ_c^2 and σ_e^2 are direct additive genetic, maternal additive genetic, maternal permanent environmental and residual variances, respectively. Estimated variance and covariance components were used to obtain direct heritability ($h^2 = \sigma_a^2/\sigma_p^2$), maternal heritability ($m^2 = \sigma_m^2/\sigma_p^2$), maternal permanent environmental variance as a proportion of phenotypic variance ($c^2 = \sigma_c^2/\sigma_p^2$). σ_p^2 is the phenotypic variance of the trait. For estimation of expected response to selection, the heritability of the total genetic contribution to a maternally influenced trait was calculated as: $h_t^2 = h^2 + 0.5m^2 + 1.5mr_{am}h$ (Willham, 1972) and the total maternal effect was calculated as: $t_m = \frac{1}{4} h^2 + m^2 + c^2 + mr_{am}h$ to estimate the repeatability of dam performance, m and h are the square root of h^2 and m^2 , respectively.

The Deviance Information Criterion (DIC; Spiegelhalter *et al.*, 2002), which is a Bayesian version of the classical deviance for model evaluation, was used for model comparison and to choose the best model for each trait. The DIC is estimated as follows: $DIC = \bar{D}(\theta) + P_D = 2\bar{D}(\theta) + D(\bar{\theta})$ where $\bar{D}(\theta) = E_{0|y} = [\bar{D}(\theta)|0]$ is the posterior expectation of Bayesian deviance and $D(\theta) = -2\log(y|0)$ corresponds to the goodness of fit of the model (Spiegelhalter *et al.*, 2002). A significant difference between the two models exists when their DIC difference is greater than 7

and the model with smaller DIC value was chosen as the best-fitted model (Sadeghi *et al.*, 2020).

Results

Numbers of observations and descriptive statistics including phenotypic mean, standard deviation and coefficient of variation for body weights traits studied for Jersey crossbred calves have been depicted in Table 1. In this dataset, the male and female calves represented approximately 0.50 of the data. Coefficients of variation for body weights of calves at different ages ranged from 15.7% (W12M) to 17.8% (BW) in this study.

Environmental effects

The least-squares means for body weights of Jersey crossbred calves at birth, 3, 6, 9 and 12 months of ages were 22.7 ± 0.19 , 54 ± 1.4 , 87 ± 4.3 , 122 ± 5.9 and 156 ± 6.0 kg, respectively (Table 3). In our study, effect of period of birth was significant ($P < 0.05$) for all growth traits of Jersey crossbred calves. All growth traits except W12M were significantly influenced by season of birth of calves. Calves born in winter season showed significantly ($P < 0.05$) higher body weights from birth to 9 months of age than those born in either summer season or rainy seasons. Parity of dam had a significant ($P < 0.01$) influence only on birth weight of Jersey crossbred calves, such that the calves born from first parity of dam were lighter at birth compared to those born from older cows. Also, male calves significantly ($P < 0.05$) excelled in body weights at birth, 3 and 6

Table 3. Least-squares means \pm standard errors of different body weights (in kg) in Jersey crossbred cattle

Effects	Traits				
	BW	W3M	W6M	W9M	W12M
Overall mean	22.7 \pm 0.19 (2022)	54 \pm 1.4 (521)	87 \pm 4.3 (422)	121 \pm 5.9 (364)	156 \pm 6.0 (329)
Period/year of birth	*	*	**	**	**
Genetic group of calves	**	*	NS	NS	NS
Season of birth	*	**	**	**	NS
Winter (Nov–Feb)	22.8 \pm 0.24 (618)	57 \pm 1.6 (163)	89 \pm 4.5 (140)	121 \pm 6.1 (119)	152 \pm 6.4 (89)
Summer (Mar–Jun)	22.8 \pm 0.23 (714)	51 \pm 1.5 (194)	83 \pm 4.5 (145)	117 \pm 6.2 (110)	157 \pm 6.3 (114)
Rainy (Jul–Oct)	22.3 \pm 0.23 (690)	54 \pm 1.6 (164)	88 \pm 4.5 (137)	126 \pm 6.1 (135)	157 \pm 6.3 (126)
Parity of dam	**	NS	NS	NS	NS
1	20.9 \pm 0.24 (576)	52 \pm 1.6 (153)	86 \pm 4.5 (126)	117 \pm 6.2 (115)	152 \pm 6.4 (100)
2	22.3 \pm 0.25 (450)	53 \pm 1.6 (113)	87 \pm 4.5 (102)	120 \pm 6.3 (74)	155 \pm 6.6 (67)
3	23.1 \pm 0.38 (328)	54 \pm 1.7 (91)	89 \pm 4.6 (73)	121 \pm 6.3 (69)	155 \pm 6.5 (66)
4	23.1 \pm 0.31 (232)	54 \pm 1.9 (57)	89 \pm 4.8 (40)	118 \pm 6.8 (33)	152 \pm 7.2 (33)
5	22.9 \pm 0.35 (171)	56 \pm 2.0 (45)	90 \pm 4.9 (36)	129 \pm 6.7 (33)	157 \pm 7.9 (20)
6	23.0 \pm 0.41 (113)	56 \pm 2.4 (23)	84 \pm 5.4 (19)	126 \pm 7.7 (16)	162 \pm 8.0 (18)
≥ 7	23.1 \pm 0.37 (152)	52 \pm 2.1 (38)	83 \pm 5.2 (26)	118 \pm 7.3 (24)	155 \pm 7.6 (25)
Sex of calves	**	**	*	NS	NS
Male	23.4 \pm 0.21 (1015)	56 \pm 1.5 (236)	89 \pm 4.4 (158)	123 \pm 6.2 (107)	159 \pm 6.5 (65)
Female	21.9 \pm 0.22 (1007)	52 \pm 1.5 (285)	85 \pm 4.4 (264)	119 \pm 5.9 (257)	152 \pm 6.0 (264)

Values in parenthesis indicate number of observations.

NS represents non-significant; * and ** represent the significance at $P < 0.05$ and $P < 0.01$ level, respectively.

months of ages than their female counterparts. Further, birth weight and 3-month weight of calves were significantly influenced by genetic groups of animals in this study.

Model comparisons and genetic parameter estimates

Estimates of (co)variance components and genetic parameters for all growth traits for each analysis under three different models along with their DIC value are summarized in Table 4. The converged parameter chains of additive genetic variance were used to obtain variance components of all growth traits under different relationship matrices by Bayesian inference (Gibbs sampling), according to the Geweke diagnostic (the ratio between the first half and second half of the samples should be <1). The heritability estimates showed relevant variation in different growth traits (Table 4).

Birth weight

Estimates of direct heritability (h^2) for BW rely upon the model used, varying from 0.18 to 0.44. Model 1, which ignored maternal effects, resulted in overestimation of direct heritability. Incorporating the permanent environmental maternal (c^2) effect into model 2 caused a decline in additive direct heritability by 31% as compared to model 1, and this effect was estimated as 0.12. Further, addition of c^2 effect in model 2 significantly decreased the DIC value in comparison with model 1. Fitting the maternal genetic (m^2) effect instead of c^2 effect in model 3 resulted in a further decrease of additive direct heritability by 41% than model 2, and this model explained the maternal genetic variance as 0.19 to the total phenotypic variance. Based on the lowest DIC value, the model which included only direct and maternal permanent environmental effects (model 2) was the best-fitted model for birth weight in Jersey crossbred calves in the present dataset. Estimates of the total heritability (h_t^2) for this trait under different models ranged from 0.27 to 0.44 with the estimate of 0.30 under the best model. The estimate of total maternal effect (t_m) on birth weight, which comprises of both total maternal and dam transmitted additive genetic effects, was found to be 0.20 under the best model, and ranged from 0.11 (model 1) to 0.24 (model 3).

Weight at 3 months

Ignoring maternal effects (model 1) produced higher estimates of direct h^2 than other models. Fitting a permanent environmental maternal (c^2) effect (model 2) decreased both the estimates of σ_a^2 and h^2 to the tune of 18 and 16%, respectively, for this trait (Table 4). Model 3, which included both the direct and maternal additive (m^2) effects, yielded an estimate of m^2 (0.16) with a corresponding reduction of the estimates of direct heritability to 0.14. Hence, model 2 which included only direct genetic and maternal permanent environmental effects was considered as the most suitable model for W3M in Jersey crossbred cattle. Estimates of h_t^2 and t_m for W3M varied from 0.22 to 0.32 and 0.08 to 0.20, respectively, under the three different models with the corresponding estimates of 0.26 and 0.14 under the best-fitted model (Table 4).

Weights at 6, 9 and 12 months

In model 1, where all sources of maternal effects were disregarded, the direct heritability estimates were 0.50, 0.44 and 0.41 for W6M,

W9M and W12M, respectively. Introducing the maternal permanent environmental (c^2) effect in model 2 produced the similar or slight reduction of direct heritability for W6M (0.48), W9M (0.44) and W12M (0.40) as compared to model 1. The c^2 effects for these traits were detected as 0.04, 0.05 and 0.05, respectively. In comparison to model 1, there was significant improvement in DIC values for W6M, W9M and W12M. Fitting maternal genetic (m^2), along with direct genetic effect in model 3, explained a low proportion (0.10) of the total phenotypic variance for body weight traits from 6 to 12 months of age in Jersey crossbred calves. Therefore, the model which included only direct genetic and maternal permanent environmental effects (model 2) was the most preferred model to describe the body weights at 6, 9 and 12 months of age in this study. The total heritability (h_t^2) estimates for W6M, W9M and W12M varied from 0.47 to 0.50, 0.44 (for all three traits) and 0.14 to 0.42, respectively, under different models in Jersey crossbred calves and the corresponding estimates were of 0.48, 0.44 and 0.40, respectively, under the best-fitted model. Further, the total maternal effect (t_m) of weights at 6, 9 and 12 months of age was 0.16, 0.16 and 0.15, respectively, under the most appropriate model (Table 4).

Discussion

In the present study, the coefficients of variation for body weights of calves at different ages were within the range of reported values for other cattle breeds (Eler *et al.*, 1995; Abera *et al.*, 2012; Lopes *et al.*, 2013). This study showed that various environmental factors had a significant influence on most of the growth traits in Jersey crossbred calves. The significant effects of period of birth on birth weight (Khan *et al.*, 2019; Gessesse *et al.*, 2021; Setiaji *et al.*, 2022), 3-month weight (Rahman *et al.*, 2015; Sagar *et al.*, 2017), 6-month weight (Nahar *et al.*, 2016; Sagar *et al.*, 2017), 9-month weight (Nahar *et al.*, 2016) and 12-month weight (Nahar *et al.*, 2016; Khan *et al.*, 2019; Setiaji *et al.*, 2022) were observed in different cattle breeds and their crosses, which aligned with the findings of the present study. The significant influence of period of birth on all growth traits in our study may be due to variations in management practices of the farm, use of differential sires as well as fluctuations of environmental conditions such as temperature, precipitation and humidity over the years. The significant variations of body weights at birth, 3, 6, and 9 months of age in calves born in different seasons, as observed in the current study, were well in agreement with the findings of Sagar *et al.* (2017), Khan *et al.* (2019) and Gessesse *et al.* (2021) in Vrindavani, Simmental \times Angus \times Charolais \times Hereford and Fogera cattle, respectively. In our study, winter-born calves had higher birth weight than calves born in summer or rainy season because pregnant dams of winter-born calves were exposed to favourable climatic conditions, i.e. rainy season when the availability of feeds and fodders is abundant, and as a result, pregnant dams receive sufficient amounts of feeds and fodders for the development of her foetus as well as mammary glands and ultimately it results in heavier birth weight of the calves. As observed in the current study, the significant effects of parity of dam on birth weight of calves were reported by Abera *et al.* (2012) in Horro crossbred and Cortes-Lacruz *et al.* (2017) in Parda de Montaña cattle. The lower birth weight of calves obtained from cows of first parity in this study may be resultant of relative competition for nutrients between the still growing cows and developing foetus during pregnancy period of animals. Similar to the present findings, the significant effects of genetic group on body weights were

Table 4. Estimates of (co)variance components (kg^2) and genetic parameters for growth traits along with their posterior standard deviation in Jersey crossbred cattle

Traits	Model	Parameters										Geweke diagnostic	DIC
		σ_a^2	σ_m^2	σ_c^2	σ_e^2	σ_p^2	h^2	m^2	c^2	h_t^2	t_m		
BW	1	8 ± 1.2	–	–	9.7 ± 0.77	17.2 ± 0.72	0.44 ± 0.055	–	–	0.44	0.11	–0.02	10 832.11
BW	2	5 ± 1.4	–	2.0 ± 0.53	9.6 ± 0.84	16.8 ± 0.73	0.31 ± 0.075	–	0.12 ± 0.032	0.30	0.20	0.07	10 806.32
BW	3	3 ± 1.2	3.2 ± 0.65	–	10.7 ± 0.81	16.9 ± 0.75	0.18 ± 0.068	0.19 ± 0.035	–	0.27	0.24	–0.00	10 862.04
W3M	1	31 ± 11.2	–	–	66 ± 8.1	97 ± 7.3	0.31 ± 0.099	–	–	0.32	0.08	–0.06	3789.11
W3M	2	25 ± 11.1	–	7 ± 4.2	65 ± 8.4	96 ± 7.3	0.26 ± 0.102	–	0.07 ± 0.043	0.26	0.14	0.03	3785.89
W3M	3	14 ± 8.5	16 ± 5.9	–	68 ± 7.0	97 ± 7.4	0.14 ± 0.082	0.16 ± 0.055	–	0.22	0.20	–0.01	3791.71
W6M	1	129 ± 32.6	–	–	127 ± 21.2	257 ± 22.1	0.50 ± 0.096	–	–	0.50	0.12	0.01	3395.89
W6M	2	124 ± 32.6	–	10 ± 7.8	124 ± 21.1	257 ± 21.8	0.48 ± 0.098	–	0.04 ± 0.030	0.48	0.16	0.03	3392.21
W6M	3	112 ± 35.1	26 ± 13.2	–	127 ± 21.6	265 ± 23.3	0.42 ± 0.108	0.10 ± 0.047	–	0.47	0.20	–0.01	3399.47
W9M	1	214 ± 66.3	–	–	272 ± 45.9	486 ± 43.9	0.44 ± 0.109	–	–	0.44	0.11	0.02	3193.01
W9M	2	219 ± 69.0	–	25 ± 19.3	252 ± 48.3	496 ± 43.9	0.44 ± 0.111	–	0.05 ± 0.038	0.44	0.16	–0.03	3178.82
W9M	3	202 ± 72.8	50 ± 28.5	–	263 ± 46.3	514 ± 50.9	0.39 ± 0.116	0.10 ± 0.051	–	0.44	0.19	0.02	3189.77
W12M	1	266 ± 104.1	–	–	378 ± 73.1	644 ± 62.2	0.41 ± 0.133	–	–	0.14	0.1	0.03	2978.66
W12M	2	264 ± 108.6	–	33 ± 25.9	358 ± 76.9	655 ± 65.6	0.40 ± 0.137	–	0.05 ± 0.039	0.40	0.15	0.02	2971.12
W12M	3	253 ± 113.2	69 ± 41.8	–	362 ± 73.4	683 ± 71.1	0.36 ± 0.138	0.10 ± 0.057	–	0.42	0.18	0.00	2976.55

σ_a^2 , direct additive genetic variance; σ_m^2 , maternal additive genetic variance; σ_{am} , direct-maternal genetic covariance; σ_c^2 , maternal permanent environmental variance; σ_e^2 , residual variance; σ_p^2 , phenotypic variance; h^2 , direct heritability; m^2 , maternal heritability; r_{am} , direct-maternal genetic correlation; c^2 , σ_c^2/σ_p^2 ; h_t^2 , total heritability; t_m , repeatability of the dam performance; DIC, Deviance Information Criteria.
The model in bold represents the most appropriate model.

noticed by Bitew *et al.* (2010), Haile *et al.* (2011) and Gessesse *et al.* (2021) in different crossbred cattle. Our study obtained higher body weights of males than females from birth to 6 months of age. Homologous results were inferred by Gessesse *et al.* (2021) in Fogera cattle, Cortes-Lacruz *et al.* (2017) in Parda de Montaña cattle and Setiaji *et al.* (2022) in Bali cattle. Non-significant differences of body weights at 9 and 12 months of age between males and females, as observed in this study, were also reported by Bitew *et al.* (2010) in Fogera and Holstein Friesian cattle and Nahar *et al.* (2016) in Red Chittagong cattle. The heavier body weights of males than females at different ages might be due to differences in sexual chromosomes (X vs. Y) and hormones between males and females.

Our estimate of direct heritability (h^2) of birth weight for Jersey crossbred calves (0.31, Model 2) was similar to those reported for purebred (Wasike *et al.*, 2009; Chud *et al.*, 2014; Ramirez *et al.*, 2020) and crossbred (Haile *et al.*, 2011; Chen *et al.*, 2012) cattle. However, lower (Sagar *et al.*, 2017; Almasri *et al.*, 2020; Carvalho *et al.*, 2020) and higher (Martinez *et al.*, 2016; Cortes-Lacruz *et al.*, 2017) estimates of direct h^2 for this trait have been reported in various breeds of cattle. The estimated moderate heritability of birth weight in this study suggests that there is ample scope of improving this trait genetically through selection. However, selection for this trait should be performed with caution, due to the relationship of birth weight with dystocia and stillbirth in cows. The explained proportion of phenotypic variance of birth weight by permanent environmental maternal effect ($c^2 = 0.12$) from model 2 was well in agreement with the study of Ríos-Utrera *et al.* (2011) in Limousin cattle (0.11), Chud *et al.* (2014) in Nellore cattle (0.10) and Lopez *et al.* (2020) in Hanwoo cattle (0.12). However, c^2 estimates reported by several authors (Sahin *et al.*, 2012; Chud *et al.*, 2014; Carvalho *et al.*, 2020) in different purebred/crossbred cattle were lower than the present estimate. In comparison to our study, higher c^2 estimates (0.24) for this trait were observed by Haile *et al.* (2011) in Boran cattle. In our study, lower c^2 effect for birth weight clearly indicates the existence of large environmental influence on milk production of animals. The moderate total heritability estimate for birth weight (0.30) was within the range of other estimates as reported by various researchers (Meyer, 1992; Shi *et al.*, 1993) in various cattle breeds. The obtained value of t_m for birth weight in the current work showed a high similarity across the models (in a range of 0.11–0.24; Table 4) indicating the consistency in estimating the repeatability of dam performance across the different statistical mixed linear models fitting the maternal effects. The estimated total heritability (h^2_t) and repeatability of dam performance (t_m) for birth weight were substantial and moderate in magnitude (≥ 0.20), indicating the potential genetic and phenotypic progress is expected through selection of this trait.

The estimate of direct heritability for 3-month weight (0.26) of Jersey crossbred calves from the most appropriate model (model 2) was well comparable with the findings of Haile *et al.* (2011) in Boran \times HF crosses, Cortes-Lacruz *et al.* (2017) in Parda de Montaña cattle, Sagar *et al.* (2017) in Vrindavani cattle. However, several workers (Choi *et al.*, 2005; Dezfuli and Mashayekhi, 2009; Almasri *et al.*, 2020) have reported the lower estimates in different breeds/crosses of cattle, ranging from 0.03 to 0.13, for this trait. Higher estimates than our study were also reported by Aziz *et al.* (2005) in Japanese Black cattle (0.53), Haile *et al.* (2011) in Boran cattle (0.43), Afroz *et al.* (2011) in Red Chittagong cattle (0.49), Rahman *et al.* (2015) in HF

crossbred (0.46) and Lopez *et al.* (2020) in Hanwoo cattle (0.51). The moderate heritability estimate for 3-month weight in our investigation might be due to ideal nutritional status of dam and management practices resulting in a minute environmental discrepancy. In our study, permanent environmental maternal effect (c^2 effect) for 3-month weight under the best model was detected as 0.07. Similar estimates of c^2 effect for 3-month body weight were observed by Hwang *et al.* (2008) in Hanwoo cattle (0.06) and Hussein *et al.* (2022) in Friesian cattle (0.04). On the contrary, higher (Choi *et al.*, 2005; Haile *et al.*, 2011) and lower (Dezfuli and Mashayekhi, 2009; Haile *et al.*, 2011) estimates of c^2 have been reported for this trait.

In our study, high direct heritability estimates for W6M (0.48), W9M (0.44) and W12M (0.39) were observed in Jersey crossbred cattle (Table 4). Several researchers have reported high h^2 estimates for 6-month (Aziz *et al.*, 2005; Gutiérrez *et al.*, 2007; Rabeya *et al.*, 2009; Afroz *et al.*, 2011), 9-month (Aziz *et al.*, 2005; Rabeya *et al.*, 2009; Afroz *et al.*, 2011) and 12-month weight (Schiermiester *et al.*, 2015; Martinez *et al.*, 2016; Rezende *et al.*, 2022) in various cattle breeds, which were well comparable with our findings. However, Chen *et al.* (2012), Sagar *et al.* (2017) and Majoya *et al.* (2022) reported lower estimates of direct h^2 for 6-month body weight than our findings. Lower estimates for 9-month weight (Wasike *et al.*, 2006, 2009) and 12-month weight (Wasike *et al.*, 2009; Ríos-Utrera *et al.*, 2011; Majoya *et al.*, 2022) than our study have been observed in different breeds of cattle. The permanent environmental maternal effects (c^2) for W6M, W9M and W12M in this study were low (0.04–0.05) in magnitude, and were in agreement with the reports of several published literature (Aziz *et al.*, 2005; Wasike *et al.*, 2006; Haile *et al.*, 2011; Ríos-Utrera *et al.*, 2011). The considerable heritability estimates for weights at 6, 9 and 12 months of age in our study reflected the presence of substantial additive genetic variances associated with these traits. This implies that there is a significant potential for enhancing the body weights of Jersey crossbred calves at these ages through genetic selection within the prevailing management system. Low proportion of phenotypic variation explained by the permanent environmental maternal effect (c^2) observed for these weight traits illustrates that there is an indication of limited intervention of environmental influence on these traits of the calves. The estimated total heritabilities (h^2_t) for all growth traits under consideration were moderate to high, which was consistent with reported results for the other cattle breeds (Meyer, 1992; Shi *et al.*, 1993; Waldron *et al.*, 1993), reflecting that simultaneous consideration of both direct and maternal effects in the genetic evaluation programmes could be effective for optimum genetic progress of these traits.

Conclusion

The results of the present study revealed that several non-genetic factors had a substantial effect on most of the growth traits of Jersey crossbred calves; therefore, effective strategies (e.g. feeding pattern and management practices) should be taken into consideration for managing the herd. The study further confirmed the usefulness of applying the appropriate model for estimation of variance–covariance components and genetic parameters for growth traits of crossbred calves. If maternal effects are important for the trait of interest and not included in the models, it may lead to overestimation of direct heritability of the trait. Though the permanent environmental maternal effects decrease with advancement of age, this factor still has some impact on growth

in later ages. So, both direct and maternal components should be taken into consideration in formulating the effective breeding programme for improving these traits genetically.

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