Estimation of genetic parameters of growth traits for direct and maternal effects in Murrah buffalo

Pooja Joshi1 · G. R. Gowane1 · Rani Alex1 · I. D. Gupta1 · Destaw Worku2 · Linda George1 · Ashish Ranjan1 · Archana Verma1

Received: 28 January 2022 / Accepted: 4 October 2022 © The Author(s), under exclusive licence to Springer Nature B.V. 2022

Abstract
An understanding of genetic principles and environmental factors affecting the growth traits is essential to implement optimal breeding and selection programs. Early growth is an indicator of future success in production and reproduction status of dairy animals. In this study, a total of 18,989 records of body weight were used to estimate genetic parameters of body weight at birth (BW), 3 months (3BW), 6 months (6BW), 9 months (9BW), 12 months (12BW), 18 months (18BW), 24 months (24 BW), 30 months (3BW), and 36 months (36BW) in Murrah buffalo at ICAR-NDRI Karnal, Haryana, for the period 1974–2019. The genetic parameters were estimated using the average information restricted maximum likelihood (AIREML) procedure by excluding or including maternal effects. Six analytical models were fitted in order to optimize the model for each trait. The most appropriate univariate model was selected based on the log likelihood ratio test (LRT). Influencing factors like calf sex, period of birth, season of birth, and dam’s parity were investigated. The results showed that the maternal genetic effects, in addition to direct additive effects, were important for unbiased and accurate genetic parameter estimates of growth traits in Murrah buffaloes. Total heritability estimates $h^2_T$ for BW, 3BW, 6BW, 9BW, 12BW, 18BW, 24BW, 30BW, and 36BW were 0.25, 0.04, 0.14, 0.16, 0.10, 0.15, 0.21, 0.24, and 0.23, respectively. Maternal effect was significant for birth weight and accounted for 13% variation through maternal genetic and 5% variability through maternal permanent environmental effect. Maternal genetic effect was also important for other traits. However, it interfered with the estimates of variance ratios in live weight traits owing to large and negative covariance between direct and maternal genetic effects. Direct genetic correlations between body weight traits were positive and high ranging from 0.10 to 0.94. Results revealed that the Murrah herd has a sizable genetic variability for growth traits and hence, there is sufficient scope for selection for achieving better growth rate if selection in this direction is applied. Owing to higher positive genetic correlation of 6BW with later ages, the scope of indirect selection for optimum growth in later ages can be aimed at by selecting animals for their higher 6-month live weight.

Keywords Animal model · AIREML · Genetic parameters · Growth traits · Maternal effects · Murrah buffalo

Introduction
Growth traits are among the important economic traits of livestock. An animal growing faster commences the reproductive and the productive cycle early, hence maximizes the net economic return (Fleck et al. 1980, Boro et al. 2006; Wattiaux 2011). Higher growth at an early age also indicates more nutritional requirement and higher feed intake; however, long-term growth defines the age at maturity and hence needs to be emphasized in a breeding program of Murrah buffaloes for attaining early maturity and future production as well as reproduction. Decisions about heifer management interact with underlying biological aspects of growth, thereby influencing future profitability of the herd (Mourits et al. 1999). Thus, the growth rates of replacement heifers affect economic returns on dairy farms. Growth traits are affected by the genetic and environmental factors across the livestock sector (Soh et al. 2020). Maternal effect also contributes to the total variance of the growth
traits, and is essential for obtaining the unbiased estimates of genetic parameters (Gowane et al. 2014). The maternal effect refers to the effect of genotypes of animal’s dam influencing the individual’s performance during gestation and nursing. The maternal effects are a social environment which are partially heritable and are of immense breeding interest in livestock industry. The direct additive maternal effect represents the maternal genetic component that is passed down to the animal and represents the ability to be a mother. Maternal permanent environment represents the environment provided by the dam to all its progeny, which is common during gestation and nursing. The knowledge of genetic properties of economic traits is the pre-requisite in establishing the selection program.

India holds the first spot in global market for the highest milk production. Murrah buffaloes contribute more than 50% to the total milk production of the country (FAOSTAT 2020). Murrah buffalo is the dynamic water buffalo breed, belonging to Haryana and Punjab state of the country. This breed is used extensively in upgrading of the non-descript buffaloes in the country and for improved milk production of dairy buffaloes in other countries, viz., Egypt, Bulgaria, and Italy (Mishra et al. 2015). Recent literature reveals genomic population structure (Macciotta et al. 2021) and historical insights on domestication and migration of water buffaloes (Coll et al. 2018) using SNP panels. Riverine buffaloes have always been selected for lactation traits and Murrah takes center stage in all the breeds of riverine buffaloes for milk production. Genetic selection in buffalo is hampered by lack of accurate pedigree information (Rosati and Van Vleck 2002; Ghoreishifar et al. 2020), and the difficult implementation of performance recording due to the farming structure consisting small holders and poor reproductive performance. As a result, the potential of buffalo has not been completely exploited (Mokhber et al. 2018). Current advances in genomic selection help in reducing the generation interval and selecting the best animals at a very early age. In buffaloes, a few efforts for the implementation of genomic selection have been done, where feasibility of genomic selection in the Italian Mediterranean water buffalo was explored (Cesarani et al. 2021), and also inclusion of a single-step method for genomic evaluation of milk production in Egyptian buffalo was also successfully done (Abdel-Shafy et al. 2020) with more reliable estimates of genetic parameters. In India, the initial efforts for genotyping are being made; however, the creation of reference population may result in biased estimation of genetic parameters, if the traits are actually affected by maternal effects. Therefore, the present investigation was undertaken to estimate the variance and covariance components in the growth traits of Murrah buffaloes using the animal model with due consideration of maternal effects. The aim of the study was to estimate the genetic parameters for the growth traits and suggest a possible strategy for futuristic breeding program.

Materials and methods

The study was conducted in ICAR-National Dairy Research Institute, Karnal, during the period extended from year 1974 to 2019. A total of 18,989 body weight records of Murrah buffaloes starting from time of birth up to 36 months of age were used in the present study. The geographical location of NDRI livestock farm is at an altitude of 250 m above the sea level at 29° 42ʹ N and 72° 02ʹ E longitude. Nine different growth traits used for the analysis were birth weight (BW), 3-month weight (3BW), 6-month weight (6BW), 9-month weight (9BW), 12-month weight (12BW), 18-month weight (18BW), 24-month weight (24BW), 30-month weight (30BW), and 36-month weight (36BW). Murrah buffaloes are maintained in a loose housing system in the herd, fed on good-quality green fodder ad libitum, and provided with adequate veterinary health and care. Selective breeding policy was practiced with major emphasis on improved progeny performance for milk production. The selection of female buffaloes is based on expected producing ability (EPA) computed twice in a year. The young elite male buffaloes are selected for future test bulls based on their pedigree, dam’s milk yield, breed characteristics, expected production differences (EPD), and subsequently based on their growth,
libido, semen quality, and semen freezability. Animals were weighed on a regular basis. Birth weight was taken within 24 h of birth of calf, and 3BW, 6BW, 9BW, 12BW, 18BW, 24BW, 30BW, and 36BW were taken on exact dates. Time to influx of germplasm from the field in to the nucleus was also carried out to maintain the genetic diversity in the nucleus. Number of records, number of sire and dam, least squares means, standard deviations, and coefficient of variation for respective traits are summarized in Table 1.

Co(variance) components and heritability estimates were obtained through a single-trait animal model analysis using the average information restricted maximum likelihood (AIREML) approach with various combinations of additive and maternal effects. The log likelihood ratio test (LRT) was used to determine the most suitable model for each trait (Meyer 1992). Least squares analysis of variance was done to identify the fixed effects that will be used further in the genetic analysis of data. For growth traits, statistical model for least squares analysis included effect of period of birth (10 levels; year of birth was used to determine the period of birth), season of birth (4 levels; winter (December–February), summer (March–May), rainy (June–August), and autumn (September–November)), sex of the calf (2 levels), and parity of the dam (9 levels; dam’s parity is the order of parity in which the animals taken in the study were born) as fixed effects. The significance of various fixed effects is shown in Table 1. Only significant effects ($P < 0.05$) were included in the models that were subsequently used for the genetic analysis.

Six different single-trait linear models that account for various combinations of direct and maternal effects were fitted for each trait. Model 1 was the simple animal model with animal additive genetic effect as the only random effect other than residual effect. In Model 2, the maternal additive genetic effect was included as the additional random effect ignoring the covariance between animal direct additive and maternal additive genetic effect ($C_{(a_m,m_o)} = 0$). In Model 3, the maternal additive genetic effect was included as the additional random effect considering the covariance between animal direct additive and maternal additive genetic effect ($C_{(a_m,m_o)} = A\sigma_{am}$). Model 4 included permanent environment effect due to dam as an additional random effect. In Model 5, both maternal additive genetic effect and permanent environment effect due to dam were taken as additional random effect ignoring the covariance between animal direct additive and maternal additive genetic effect ($C_{(a_m,m_o)} = 0$). In the inclusive Model 6, both maternal additive genetic effect and permanent environment effect due to dam were taken as additional random effect accounting for the covariance between animal direct additive and maternal additive genetic effect ($C_{(a_m,m_o)} = A\sigma_{am}$).

$$Y = X\beta + Z_{a}a + e$$ (1)
$$Y = X\beta + Z_{a}a + Z_{m}m + e \text{ with } C_{(a_m,m_o)} = 0$$ (2)
$$Y = X\beta + Z_{a}a + Z_{m}m + e \text{ with } C_{(a_m,m_o)} = A\sigma_{am}$$ (3)
$$Y = X\beta + Z_{a}a + Z_{pe}pe + e$$ (4)
$$Y = X\beta + Z_{a}a + Z_{m}m + Z_{pe}pe + e \text{ with } C_{(a_m,m_o)} = 0$$ (5)

Table 1 Characteristics of the data structure for economic traits in Murrah buffalo

| Trait               | BW  | 3BW | 6BW | 9BW  | 12BW | 18BW | 24BW | 30BW | 36BW |
|---------------------|-----|-----|-----|------|------|------|------|------|------|
| Period              | **  | **  | **  | **   | **   | **   | **   | **   | **   |
| Season              | **  | **  | **  | *    | **   | *    | ***  | **   | **   |
| Sex                 | **  | *   | **  | **   | **   | **   | **   | **   | **   |
| Parity              | **  | *   | **  | **   | **   | **   | **   | **   | **   |
| No. of records      | 3754| 2020| 2088| 1667 | 2013 | 1983 | 1975 | 1764 | 1725 |
| No. of sires with progeny | 371 | 250 | 293 | 287  | 305  | 305  | 300  | 283  | 287  |
| No. of dams with progeny | 1643| 1117| 1182| 1049 | 1210 | 1212 | 1206 | 1115 | 1077 |
| Minimum(kg)         | 11  | 28  | 46  | 90   | 120  | 135  | 160  | 177  | 196  |
| Maximum(kg)         | 50  | 175 | 235 | 294  | 450  | 586  | 596  | 620  | 746  |
| LSM(kg)             | 32.45| 66.68| 110.76| 152.15| 200.23| 277.14| 360.40| 404.35| 458.71|
| S.D.(kg)            | 4.93 | 15.42| 21.01| 32.20| 44.57| 50.71| 56.17| 55.57| 59.87 |
| CV%                 | 14.88| 24.06| 18.96| 21.74| 22.72| 18.80| 16.22| 13.85| 12.80 |

LSM, least squares mean; S.D., standard deviation; CV, coefficient of variation

Birth weight: 3BW, 3-month weight; 6BW, 6-month weight; 9BW, 9-month weight; 12BW, 12-month weight; 18BW, 18-month weight; 24BW, 24-month weight; 30BW, 30-month weight; 36BW, 36-month weight

Figures in superscript within the column indicates significant at $*P < 0.05$ and $**P < 0.01$
\[ Y = X\beta + Z_a a + Z_m m + Z_{pe} pe + e \] with \( \text{Cov}(a_m, m_o) = A \sigma_{am} \) (6)

where \( Y \) represents the vector of records, \( \beta, a, m, pe, \) and \( e \) were the vectors of fixed, direct additive animal genetic, maternal additive genetic, permanent environmental effects of the dam, and residual effects, respectively. The \( X, Z_a, Z_m, \) and \( Z_{pe} \) were association matrices, \( A \) represents a numerator relationship matrix between animals, and \( \sigma_{am} \) referred to the covariance between additive direct and maternal genetic effects.

The average information restricted maximum likelihood (AIREML) algorithm (Johnson and Thompson 1995) was employed for the estimation of (co)variance components using WOMBAT software. A value of \( 10^{-8} \) was used as the convergence criterion for the analysis. A likelihood ratio test (LRT) was used to select the most appropriate univariate model for each trait (Meyer 1992). The model with the highest log likelihood value was considered the best model. Whenever inclusion of one effect increased the log likelihood, compared to the model in which it was ignored, the effect was considered to have a significant influence. Significance was tested at \( P < 0.05 \) by comparing differences in log likelihoods to values for a \( \chi^2 \) distribution with degrees of freedom equal to the difference in the number of (co) variance components fitted for the two models. Genetic, phenotypic, and environmental correlations among all the traits mentioned above were estimated by bivariate analysis with starting values derived from the best selected univariate model.

\[
g_{(xy)} = \frac{\text{Cov}(S_X Y)}{\sqrt{\sigma^2_S(S_X)\sigma^2_Y(S_Y)}}
\]

where

\( X \) and \( Y \) represent two traits in the same individual

\[ \text{Cov} \quad S_{XY} \quad \text{Sire component of the covariance between traits} \quad X \quad \text{and} \quad Y \]

\[ \sigma^2_S \quad \text{Sire component of the variance for traits} \quad X \quad \text{and} \quad Y \quad \text{respectively.} \]

The total heritability estimates were calculated by accounting for the maternal effects using Willham (1972) as \( h^2_{T_1} \) and Eaglen and Bijma (2009) as \( h^2_{T_2}. \)

\[
h^2_{T_1} = \frac{[\sigma^2_A + 1.5(\sigma_{am}) + 0.5(\sigma^2_M)]}{\sigma_p^2}
\]

\[
h^2_{T_2} = \frac{[\sigma^2_A + 2(\sigma_{am}) + (\sigma^2_M)]}{\sigma_p^2}
\]

\( h^2_{T_1} \) and \( h^2_{T_2} \) are the total heritability; \( \sigma^2_A \) is the additive genetic variance, \( \sigma^2_M \) is the additive maternal variance, \( \sigma^2_p \) is the phenotypic variance, and \( \sigma_{am} \) is the covariance between additive genetic and maternal effect.

Genetic trend was estimated by regressing the mean breeding values (BV) on birth year (\( T \)).

\[
\Delta g = b_{BVT}
\]

**Results and discussion**

The data characteristics that include the least squares means along with the standard deviation and percent coefficient of variation for different traits under this study along with the pedigree details are presented in Table 1. The number of progenies per dam for the respective traits was 2.28 (BW), 2.28 (BW), 1.81 (3BW), 1.77 (6BW), 1.59 (9BW), 1.66 (12BW), 1.64 (18BW), 1.64 (24BW), 1.58 (30BW), and 1.60 (36BW), respectively. The least squares mean for various traits was BW = 32.45 ± 0.09 kg; 3BW = 66.68 ± 0.31; 6BW = 110.76 ± 0.52 kg; 9BW = 152.15 ± 0.71 kg; 12BW = 200.23 ± 1.01 kg; 18BW = 277.14 ± 1.23 kg; 24BW = 360.40 ± 1.13 kg; 30BW = 404.35 ± 1.31 kg; and 36BW = 458.71 ± 1.73 kg. The sex of the calf significantly affected all the growth traits except 3BW and 6BW as male calves are heavier than female calves. Season of calving also had a significant effect on all the traits except 6BW where calves born during winter season were heavier compared to those born in other seasons. This may be due to appropriate temperature and good feeding regime during winter season. Furthermore, period of calving had significantly affected all the growth traits. The effect of period of calving reflects year-to-year variability with respect to climate change, management practices, and feeding, apart from the genetic progress that has taken place due to selection in the nucleus. Moreover, in the current study, the effect of dam’s parity was significant on early rearing phase, i.e., BW, 3BW, and 6BW. Birth weight was lower for primiparous dam than those of multiparous. Also, with an increase in parity number, higher birth weight was observed. The effect of dam’s parity on BW and other growth traits may be attributed to the maturity status of dams in their advanced parity; they have adequate body capacity leading to better development of fetus. Non-significant impact of parity on later ages can be attributed to decrease in the maternal environment and expression of the individual’s own phenotype as the dominant entity. From 9BW, expression of the live weight has minimal or no impact of parity of dam.

(Co)variance components and genetic parameters estimated by the most appropriate model in univariate analysis for various traits using LRT (Meyer 1992) are presented in Table 2. As per the log likelihood ratio test, the best model for birth weight (BW) was Model 5, which included direct...
additive and permanent environmental effects of the dam. For 12BW, Model 1 (a simple animal model) was the best that included only direct additive effect. For the rest of the traits (3BW, 6BW, 9BW, 18BW, 24BW, 30BW, and 36BW), Model 3 was best that included direct additive effect of animal, direct additive effect of dam, and covariance between direct additive effects of dam and progeny. We have compared the models and found that for most of the traits, the best models have negative covariance between direct and maternal additive effects, thus inflating the variance components. Hence, to avoid biased interpretation, we have estimated total heritability that corrects for such estimates.

**Birth weight**

Model 1 gave substantially higher estimate of heritability for birth weight than other models, i.e., 0.34 ± 0.03, which reduced to 0.18 ± 0.02 on addition of maternal genetic effect in Model 2. Also, fitting maternal genetic effect resulted in improvement of log likelihood value over Model 1. Direct heritability estimate was increased to 0.24 ± 0.04 when direct additive and maternal permanent environmental effect (c^2) were included in Model 4, however did not increase the log likelihood. Model 5 provided a much better fit to the data for birth weight with a significantly high log likelihood value over all other models for birth weight in Murrah buffaloes; however, it must be cautioned that the selection on the birth weight basis is not effective due to significant maternal influence. Lower h^2 estimates of birth weight 0.10 with maternal additive (m^2) 0.11 and maternal permanent environmental effect (c^2) 0.04 were reported by Thiruvenkadan et al. (2009) in Murrah buffaloes. In the literature available, higher estimates of heritability for birth weight in Murrah buffaloes were found as compared to our results. The possible reason for the difference in the current estimate may lie with the method of estimation and population differences. Pandey et al. (2015) reported similar h^2 estimate (0.18) in Surti buffaloes using paternal half sib method. Higher h^2 estimates (ranging from 0.35 to 0.49) were reported by Yadav et al. (2001), Gupta et al. (2015), and Shahin et al. (2010) in Murrah buffaloes and Soh et al. (2020) in swamp buffaloes using paternal half sib method.

**3-month body weight**

Model 3 was found to be best for the 3-month body weight with estimates for direct additive h^2 0.14 ± 0.05 and m^2 0.18 ± 0.03. There was a negative covariance between direct genetic and maternal effects, which lead to increased estimates of variance components and their ratios. The total heritability after correcting for negative covariance between direct and maternal effects was 0.04, which was low. Direct additive h^2

### Table 2

| Trait | BW | 3BW | 6BW | 9BW | 12BW | 18BW | 24BW | 30BW | 36BW |
|-------|----|-----|-----|-----|------|------|------|------|------|
| Model | 5  | 3   | 3   | 3   | 3    | 1    | 3    | 3    | 3    |
| \(\sigma_a^2\) | 4.70 | 28.61 | 170.40 | 460.79 | 198.30 | 796.27 | 973.64 | 1347.16 | 1002.83 |
| \(\sigma_m^2\) | 3.20 | 19.91 | 81.60 | 189.25 | -     | 258.04 | 81.72 | 302.44 | 191.85 |
| \(\sigma_{am}^2\) | -   | -19.91 | -98.10 | -259.62 | -     | -354.88 | -223.13 | -508.68 | -184.46 |
| \(\sigma_e^2\) | 1.25 | -    | -    | -    | -     | -     | -    | -    | -    |
| \(\sigma_{c_or}^2\) | 15.78 | 175.30 | 301.38 | 668.84 | 1798.40 | 1913.44 | 2372.77 | 1854.61 | 2492.91 |
| \(\sigma_p^2\) | 24.93 | 203.91 | 455.28 | 1059.62 | 1996.71 | 2612.87 | 3204.99 | 2995.53 | 3503.13 |
| \(h^2\) | 0.19 ± 0.03 | 0.14 ± 0.05 | 0.37 ± 0.08 | 0.43 ± 0.11 | 0.10 ± 0.03 | 0.30 ± 0.08 | 0.45 ± 0.10 | 0.12 ± 0.03 | 0.27 ± 0.08 |
| \(m^2\) | 0.13 ± 0.04 | 0.10 ± 0.04 | 0.18 ± 0.05 | 0.18 ± 0.06 | -     | 0.10 ± 0.04 | 0.02 ± 0.03 | 0.10 ± 0.05 | 0.05 ± 0.04 |
| \(c^2\) | 0.05 ± 0.03 | -    | -    | -    | -     | -     | -    | -    | -    |
| \(h^2_{T1}\) | 0.25 | 0.04 | 0.14 | 0.16 | 0.10 | 0.15 | 0.21 | 0.24 | 0.23 |
| \(h^2_{T2}\) | 0.32 | 0.04 | 0.12 | 0.12 | 0.10 | 0.13 | 0.17 | 0.21 | 0.24 |
| Log-L | -7398.70 | -5978.71 | -6885.01 | -6289.53 | -7801.95 | -8162.18 | -8309.17 | -7359.32 | -7362.81 |

\(\sigma_a^2, \sigma_m^2, \sigma_{am}^2, \sigma_e^2, \text{ and } \sigma_{c_or}^2\) are additive direct, additive maternal, additive direct maternal covariance, maternal permanent environment, residual variance, and phenotypic variance respectively. \(h^2\) is the direct heritability, \(m^2\) is the maternal additive effect, \(c^2\) is the \(\sigma_a^2/\sigma_p^2\) and \(h^2_{T1}\), and \(h^2_{T2}\) is the total heritability and log-L is log likelihood for the best model obtained from AIREML.
estimate of 0.07 ± 0.03 in Model 1 was fairly consistent across models. Estimates were 0.06 ± 0.03 \( (h^2) \) and 0.02 ± 0.02 \( (m^2) \) in Model 2 and 0.06 ± 0.03 \( (h^2) \) and 0.04 ± 0.03 \( (m^2) \) in Model 4, respectively. However, the estimates from the inclusive Model 5 were \( h^2 = 0.06 ± 0.03, m^2 = 0.00, \) and \( c^2 = 0.04 ± 0.04. \) This indicated that partitioning the maternal effect into its genetic and environmental component is not easy. Model 6 gave a higher estimate of \( h^2 \) (0.14), \( m^2 \) (0.07), and \( c^2 \) (0.04); however, these estimates were inflated to adjust the negative covariance between direct and maternal additive effect. Our results were in line with those of Neyser et al. (2012) in Brangus cattle and Akhtar et al. (2012) in Nili-Ravi buffaloes for 3-month body weight. Similar estimates in Murrah buffalo where direct \( h^2 \) estimate was 0.19, \( m^2 \) was 0.09, and \( c^2 \) was 0.03 were reported by Thiruvenkadan et al. (2009).

6-month and 9-month body weight

Among six animal models, Model 3 resulted in the highest log likelihood for both 6- and 9-month body weights. High direct heritability estimates were found for both thetraits with \( h^2 \) as 0.37 ± 0.08 and 0.43 ± 0.11 for 6BW and 9BW, respectively. Of the total variance, 18% was explained by the maternal genetic effects for both the traits. However, as the direct additive and maternal covariance was high and negative effect over 12BW. Adding maternal genetic effect (Model 3) partitioned total variance into \( h^2 \), \( m^2 \), and \( c^2 \) estimates 0.10 and 0.05 were reported for 30BW and 36BW (Table 2). The estimate of \( r_{am} \) was significantly higher and negative for all these four traits. This estimate has actually inflated the variance ratios and hence, the higher estimates of the heritability were observed. To account for the maternal effect, we have estimated the total heritability using Willham (1972) as \( h^2 = 0.17 \) and Eaglen and Bijma (2009) as \( h^2 = 0.17 \). The estimates for total heritability \( h^2 \) after correctly accounting for the maternal effects were 0.15, 0.21, 0.24, and 0.23 for 18BW, 24BW, 30BW, and 36BW respectively and \( h^2 = 0.17 \) for 18BW, 0.17, 0.21, and 0.24 for 18BW, 24BW, 30BW, and 36BW, respectively.

Higher heritability estimates in buffaloes of Murrah breed augur the scope for selection for achieving higher weights at later ages, if selection is implemented in this direction. In accordance with our study, the higher \( h^2 \) estimates of 0.73 and 0.77 for 18BW were reported by Tien and Tripathi (1990) and Gurung and Johar (1983) respectively. Similarly, for the 36-month body weight, nearly similar estimate (0.23) using animal model was obtained by Akhtar et al. (2012) in Nili-Ravi buffaloes. We understand that the selection for higher growth at the later ages is of not much significance as the selection age has to be low for effective culling and to avoid expenses on unwanted animals. However, estimates reflect the genetic diversity and scope for indirect selection, if we analyze the genetic correlation for growth in early and later ages.
Correlation estimates

The bivariate analysis for estimation of correlation between different growth traits of Murrah buffaloes was done using the most appropriate models from the single-trait analyses. Results obtained by bivariate analysis are depicted in Table 3 along with the number of animals having phenotype for both traits. The correlation estimates obtained between different economic traits were positive and moderate to high, suggesting that selection of any early trait will have its positive consequence over the other correlated trait at later ages (Table 3). Our results of genetic correlation between body weight traits fall within the range of estimates reported by Pandey et al. (2015) in Nili-Ravi buffaloes.

Estimates for direct genetic correlation ($r_g$) between birth weight and body weight at different ages were low to moderate except very low of 0.03 between BW and 9BW. It ranged from 0.17 between BW and 18BW to 0.61 between BW and 36BW. Our findings were consistent with positive and medium to high genetic correlation estimates of BW with 3BW (0.72), 6BW (0.70), 9BW (0.68), and 12BW (0.52) by Thiruvenkadan et al. (2009). Neyser et al. (2012) also reported high genetic correlation of birth weight with 3BW (0.72), 6BW (0.70), 9BW (0.68), and positive and medium to high genetic correlation estimates between BW and 36BW. Our findings were consistent with 9BW. It ranged from 0.17 between BW and 18BW to 0.61 to moderate except very low of 0.03 between BW and 3BW and body weight at different ages were low between 3 and 24BW, 0.75 between 3 and 30BW, and 0.71 between 3 and 36BW). These results were in agreement with correlation estimates reported by Thiruvenkadan et al. (2009), Neyser et al. (2012), and Pandey et al. (2015). Shahin et al. (2010) reported low correlation estimates between 3BW and other growth traits. Genetic correlations between 6BW and other ages were also high ranging from 0.29 to 0.92, indicating the scope of indirect selection for post-6BW on the basis of 6BW, suggesting that animals with above average 6BW would tend to be above average in genetic merit for 9BW, 12BW, 18BW, 24BW, 30BW, and 36BW too. Similar high genetic correlation estimates were observed between other traits such as 9BW, 12BW, 18BW, 24BW, 30BW, and 36BW (Table 3). Estimates of maternal genetic correlation were high for BW and 6BW (0.89). For other traits, non-reliable maternal correlation estimates were obtained with high standard error. Most of the phenotypic correlation estimates were lesser than their genetic counterparts (Table 3). Phenotypic correlations between all the body weight traits were positive and medium to large. Selecting animals for their live weights is a difficult task, as the optimum live weight gained is expressed at later ages. However, owing to high genetic correlation estimates of 6BW with later age live weight, we suggest the use of 6BW as the criteria for indirect selection for achieving optimum weight at later ages.

Genetic trend of growth trait

The estimates of annual rates of genetic progress for all the growth traits were positive but low (Table 4). For birth weight and 3-month body weight, statistically significant ($P < 0.05$) genetic gain of 9.7 g/year and 11 g/year was

| Trait  | BW  | 3BW | 6BW | 9BW | 12BW | 18BW | 24BW | 30BW | 36BW |
|--------|-----|-----|-----|-----|------|------|------|------|------|
|        | 0.29 ± 0.17 | 0.27 ± 0.03 | 0.24 ± 0.02 | 0.24 ± 0.02 | 0.32 ± 0.03 | 0.45 ± 0.02 | 0.45 ± 0.02 | 0.41 ± 0.02 | 0.41 ± 0.02 |
|        | (1795) | (897) | (1379) | (1337) | (919) | (1357) | (1576) | (1528) | (1525) |
|        | 0.03 ± 0.19 | 0.52 ± 0.28 | 0.53 ± 0.16 | 0.53 ± 0.16 | 0.62 ± 0.01 | 0.72 ± 0.14 | 0.72 ± 0.14 | 0.69 ± 0.01 | 0.66 ± 0.01 |
|        | (1557) | (919) | (1298) | (1337) | (1418) | (1335) | (1275) | (1281) | (1268) |
|        | 0.28 ± 0.19 | 0.63 ± 0.29 | 0.50 ± 0.17 | 0.50 ± 0.17 | 0.80 ± 0.09 | 0.67 ± 0.14 | 0.67 ± 0.14 | 0.80 ± 0.08 | 0.66 ± 0.01 |
|        | (1576) | (904) | (1298) | (1275) | (1705) | (1576) | (1528) | (1620) | (1697) |
|        | 0.17 ± 0.16 | 0.49 ± 0.18 | 0.27 ± 0.10 | 0.37 ± 0.16 | 0.90 ± 0.08 | 0.74 ± 0.10 | 0.88 ± 0.06 | 0.88 ± 0.06 | 0.88 ± 0.06 |
|        | (1528) | (915) | (1148) | (1149) | (1620) | (1506) | (1579) | (1579) | (1507) |
|        | 0.40 ± 0.13 | 0.50 ± 0.16 | 0.23 ± 0.19 | 0.37 ± 0.16 | 0.90 ± 0.08 | 0.74 ± 0.10 | 0.96 ± 0.07 | 0.96 ± 0.07 | 0.89 ± 0.06 |
|        | (1525) | (1132) | (1213) | (1149) | (1620) | (1506) | (1579) | (1579) | (1507) |
|        | 0.38 ± 0.14 | 0.75 ± 0.28 | 0.23 ± 0.19 | 0.39 ± 0.18 | 0.74 ± 0.10 | 0.96 ± 0.07 | 0.96 ± 0.07 | 0.96 ± 0.07 | 0.96 ± 0.07 |
|        | (1403) | (861) | (1213) | (1189) | (1456) | (1507) | (1507) | (1507) | (1507) |
|        | 0.61 ± 0.14 | 0.71 ± 0.27 | 0.23 ± 0.19 | 0.39 ± 0.18 | 0.48 ± 0.17 | 0.48 ± 0.17 | 0.48 ± 0.17 | 0.48 ± 0.17 | 0.48 ± 0.17 |
|        | (1405) | (886) | (1213) | (1189) | (1416) | (1416) | (1416) | (1416) | (1416) |

Value in the parenthesis represents number of animals sharing phenotype for both of the traits.
obtained, respectively. For other growth traits, the genetic trend was found to be non-significant for all the body weight traits with gain of 8 g/year, 19 g/year, 24 g/year, 53 g/year, 74 g/year, 73 g/year, and 110 g/year for 6BW, 9BW, 12BW, 18BW, 24BW, 30BW, and 36BW, respectively. The sluggish genetic gain in all growth traits indicates the negligence of these traits while formulating the breeding strategies in the past. Therefore, the present result shows that we necessarily need to include these economic traits in our breeding goals.

Conclusions

Direct heritability estimates were moderate for all growth traits while direct genetic correlations between the different traits were all positive ranging from moderate to high. Results indicate that the Murrah herd has a considerable amount of genetic variability and hence, there is adequate scope of genetic gain in growth rate if selection is applied in this direction. We could visibly see the impact of maternal influence on the growth traits, especially at the early ages, influencing the estimates of additive genetic variance. Higher genetic correlations of 6BW with other body weights in later ages along with high heritability of 0.37 for 6BW are suggestive of using 6BW as one of the criteria for selection in the Murrah herd. Exclusion of maternal effects in the model resulted in biased estimates of genetic parameters in Murrah buffaloes. Hence, to implement optimum breeding strategies for improvement of Murrah buffalo, maternal effects should be considered.

Acknowledgements The authors are thankful to the Director, ICAR-NDRI Karnal, for providing necessary facilities for successful completion of the work. We deeply acknowledge the support from In-Charge of the record room and livestock production management section for maintaining farm records.

Author contribution Archana Verma elaborated the project and was in charge of the overall direction, supervised the work, and helped in writing of the manuscript; Pooja Joshi designed the experiment; collected, edited, and analyzed the data; and wrote the draft of the manuscript in consultation with authors. G.R. Gowane took the lead in the interpretation of results, and technical details contributed in the analysis. Rani Alex helped in the technical details and analysis, I.D Gupta helped in writing the manuscript, Destaw Worku helped in analysis and manuscript writing, and Linda George and Ashish Ranjan were involved in writing the manuscript. All authors read and approved the final manuscript.

Data availability The data set generated and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Code availability Not applicable.

Declarations

Ethics approval This study is based on animal breeding data and no experiment animal was used. We have obtained proper permission from the office of In-Charge of the record room, ICAR-NDRI, Animal Genetics and Breeding Division, Karnal, Haryana, India. Therefore, use of this data in research does not require ethical clearance.

Consent to participate Not applicable (no case study).

Consent for publications Not applicable (no case study).

Conflict of interest The authors declare no competing interests.

References

Abdel-Shafy, H., Awad, M. A. A., El-Regalaty, H., Ismael, A., El-Assal, S. E., Abou-Bakr, S. 2020. A single-step genomic evaluation for milk production in Egyptian buffalo. Livest. Sci. 234: 103977; https://doi.org/10.1016/j.livsci.2020.103977

Akhtar, P., Kalsoom, U., Ali, S., Yaqoob, M., Javed., Babar, M.E., Mustafa, M.I., Sultan, J.I., 2012. Genetic and Phenotypic parameters for growth traits of Nili-Ravi Buffalo Heifers in Pakistan. The J. Anim. Pla. Sci. 22(3 Suppl.): 347-352 ISSN: 1018-708.

Bouquet A., Juga J., 2013. Integrating genomic selection into dairy cattle breeding programmes: A review. Animal. May;7(5):705-13. https://doi.org/10.1017/S1751731112002248. Epub 2012 Dec 3. PMID: 23200196.

Cesaran, A., Biffani, S., Garcia, A., Lourenco, D., Bertolini, G., Neglia, G., Misztal, I., Macciotta, N. P. P., 2021. Genomic investigation of milk production in Italian buffalo. Italian Journal of Animal Sci. 20: 539-547.

Coll, L., Marco, M., Elia, V. et al. 2018. New Insights on Water Buffalo Genomic Diversity and Post-Domestication Migration Routes From Medium Density SNP Chip Data. Frontiers in Genetics. 9, https://www.frontiersin.org/article/10.3389/fgene.2018.00053

Eaglen, S.A.E., Bijma, P., 2009. Genetic parameters of direct and maternal effects for calving ease in Dutch Holstein-Friesian cattle. J. Dairy Sci., 92: 2229-2237. FAOSTAT, 2020. http://www.fao.org/faostat/en/#home. Accessed 10 Apr 2020.

Filipecic R, Falta D, Kopec T, Chladek G, Vecera M, Reckova Z., 2020. Environmental Factors and Genetic Parameters of Beef Traits in Fleckvieh Cattle Using Field and Station Testing. Animals (Basel),Nov 19;10(11):2159. https://doi.org/10.3390/ani10112159. PMID: 33228243; PMCID: PMC7699527.

Fleck, A.T., Schalles, R.R., Kiracofe, G.H., 1980. Effect of growth rate through 30 months on reproductive performance of beef heifers. J Anim Sci. 51:816-821.
Ghoreishifar, S.M., Moradi-Shahrbabak, H., Fallahi, M.H., Moradi-Shahrbabak, M., Abdollahi-Arpanahi, R., Khansefid, M., 2020. Genomic measures of inbreeding coefficients and genome-wide scan for runs of homozygosity islands in Iranian river buffalo. BMC Genet. 21:16.

Gowane, G. R., Chopra, A., Prakash, V., Prince, L. L. L., 2014. The role of maternal effects in sheep breeding: A review. Indian Journal of Small Ruminant: 20: 1–11.

Gowane, G.R. and Vohra, V., 2022. Advances in Buffalo Breeding: A Journey from Classical Breeding to Genomic Selection. In: Chauhan, M.S., Selokar, N. (eds) Biotechnological Applications in Buffalo Research. Springer, Singapore. https://doi.org/10.1007/978-981-16-7531-7_3.

Gupta, J.P., Sachdeva, G.K., Gandhi, R.S., Chakravarty, A.K., 2015. Developing Multiple-trait prediction models using growth and production traits in Murrah buffaloes. Buffalo Bull.34(3): 347-355.

Gurung, B.S., Johar, K.S., 1983. Genetic architecture of body weights in Murrah buffaloes [India]. Indian Veterinary Journal (India), 60: 365–370.

Hietala, P., Wolfová, M., Wolf, J., Kantanen, J., Juga, J., 2014. Economic values of production and functional traits, including residual feed intake, in Finnish milk production. J. Dairy Sci. 97:1092–1096.

Johnson, D.L., Thompson, R., 1995. Restricted Maximum Likelihood estimation of variance components for univariate animal models using sparse matrix techniques and average information. J. Dairy Sci. 78 :449–456.

Macciotta, N.P.P., Colli, L., Cesari, A. et al., 2021. The distribution of runs of homozygosity in the genome of river and swamp buffaloes reveals a history of adaptation, migration and crossbred events. Genet. Sel. Evol. 53: 20. https://doi.org/10.1186/s12711-021-00616-3

Mehrban, H., Naserkheil, M., Lee, D. H., & Ibanez-Escriche, N., 2021. Genetic parameters and correlations of related feed efficiency, growth, and carcass traits in Hanwoo beef cattle. Animal Bioscience, 34(5), 824–832. https://doi.org/10.5713/ajas.20.0135

Meyer, K., 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. Livestock Production Science.31: 179–204.

Mishra, B. P., Dubey, P. K., Prakash, B., Kathiravan, P., Goyal, S., Sadana, D. K., et al. (2015). Genetic analysis of river, swamp and hybrid buffaloes of north-east India throw new light on phylogeography of water buffalo (Bubalus bubalis). J. Anim. Breed. Genet. 132, 454–466. https://doi.org/10.1111/jbg.12141

Mokhber, M., Moradi-Shahrbabak, M., Sadeghi, M., Moradi-Shahrbabak, H., Stella, A., Nicozzi, E.L., Rahmanninia, J., Williams, J.L., 2018. A genome-wide scan for signatures of selection in Azeri and Khuzestani buffalo breeds. BMC Genomics. 19(1):449.

Mourits, M.C.M., Huirne, R.B.M., Dijkhuizen, A.A., Kristensen, A.R., Galligan, D.T., 1999. Economic optimization of dairy heifer management decisions. Agric. Syst. 61:17–31.

Neyser, F.W.C., Wyk. J.B., Fair. M.D., Lubout. P., Crook. B.J., 2012. Estimation of genetic parameters for growth traits in Brangus cattle. S. Afr. J. Anim. Sci., (Suppl. 1).

Pandey, H., Tomar, A.K.S., Upadhyay, D., 2015. Effect of environmental factors on first lactation milk yield in Murrah buffaloes. Buffalo Bulletin.34(4): 459–60.

Rosati, A., Van Vleck, L.D., 2002. Estimation of genetic parameters for milk, fat protein and mozzarella cheese production for the Italian river buffalo Bubalus bubalis population. Liv Prod Sci. 74(2):185–190.

Shahin, K.A., Abdallah, O.Y., Fooda, T.A., Mourad, K.A., 2010. Selection indexes for genetic improvement of yearling weight in Egyptian buffaloes. Archiv Tierzucht53:436-446.

Soh, S.S., Sailisi, M.S., Saad, M.Z., Goh, Y.M., Yahaya, M.S. Zulkafi H.S., 2020. Heritability Estimation of Birth Weight of Swamp Buffalo in Sabah, Malaysia. J. Buff. Sci. 9: 24-28.

Thiruvenkadan, A.K., Panneerselvam, S., Rajendran, R., 2009. Non-genetic and genetic factors influencing growth performance in Murrah Buffalos. S. Afr. J. Anim. Sci.39: 102-106.

Tien, N.Q., Tripathi, V. N., 1990. Genetic parameters of body weight at different ages and first lactation traits in Murrah buffaloes. Indian Vet. J.67: 821–825.

Watiaux, M.A., 2011. Heifer Raising - Birth to Weaning. Chapter 35: Measuring Growth. The Babcock Institute for International Dairy Research and Development [online].

Willham, R.L., 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. J. Ani Sci. 35:1288–1293.

Yadav, B.S., Yadav, M.C., Ashok, S., Khan, F.H., 2001. Murrah buffaloes - I. Birth weight. Buffalo Bull. 20: 29-31.

Publisher’s note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.