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Estimation of genetic parameters and breeding values for growth traits using random regression model in Landrace × desi crossbred pigs

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ABSTRACT

The experiment was conducted to estimate genetic parameters and breeding value of pre-weaning and post-weaning growth traits in Landrace × Desi (indigenous) crossbred pigs. Random regression model (RRM) with fixed effects, random effects of direct additive, maternal genetic, maternal permanent environmental and individual permanent environmental effects and a heterogeneous residual variance structure over growth measurement at different time point was applied to estimate the genetic parameters. Among different order of Legendre polynomial fitted, RRM with heterogeneous error variance (RRM–HET) with fourth order fit for direct genetic, maternal genetic and maternal permanent environmental effect and third order fit for individual permanent environmental effect was found as the best model. The direct genetic heritability estimates were 0.299±0.021 at birth, which was low (0.011±0.006) at W12 and high at W36 (0.582±0.03). The first eigenvalue accounted for more than 98% variation in body weight and the corresponding trajectories had positive values displaying almost linear pattern till weaning and then increased rapidly in post weaning age. This showed that the selection of pigs on the basis of mean body weight at early age can also result in higher body weight in post-weaning stages. The average breeding value for the birth weight, W8 and W32 was 0.951 kg, 10.162 kg and 49.598 kg, respectively. The 42.86% of sire population at W12 and 56.76% at W24 had breeding value higher than the population's mean breeding value indicating existence of genetic variation and thus the scope for increasing the selection pressure.

Key words: Breeding value, Crossbred pigs, Genetic parameters, Growth traits, Random regression model

About 36% of the world meat consumption is derived from pork and pork products. Developing countries like India were facing the challenge to address the food security for its exploding population growth. Piggery can address the growing demand for animal protein due to its better growth performance, FCR, high litter size and ability to convert kitchen waste, hotel waste and other non-conventional feed resources into valuable nutritious meat. In India, per animal productivity was low and in order to improve the productivity of desi pigs, Landrace × Desi (*indigenous*) crossbred pigs were developed in Swine production farm, ICAR–IVRI.

The Random Regression Model (RRM) can accommodate traits having repeated records which vary over time period and it do not require any assumptions about constancy of variances and correlations. RRM also incorporates the heterogeneous variances and covariances along time (Schaffer and Dekkers 1994, Prakash *et al.* 2017). It has the advantage of estimating variance components for any point in trajectory of growth curve and also facilitates modeling of growth data over a range of ages and environments. RRM has been utilized to study growth traits in pigs (Wetten *et al.* 2012, Huynh-Tran *et al.* 2017). Though random regression model has emerged as a method of choice for studying growth traits, there are no reports available for genetic evaluation of growth performance of Indian pig population using random regression model. Further, the genetic parameters are model dependent and population specific and there are no defined models available for evaluation of Indian pig breed/population. Hence the present study was framed to identify the most suitable RRM to estimate genetic parameters and breeding value of pre-weaning and post-weaning body weights of Landrace × Desi crossbred pigs.

MATERIALS AND METHODS

Source of data: Total of 10,792 growth pertaining data from 4,231 Landrace × Desi synthetic strain of crossbred

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pigs were collected from swine production farm at ICAR–Indian Veterinary Research Institute (IVRI), Bareilly, India. The individual weights at different time points for both pre–weaning from birth (W0), till 8 weeks (W1, W2, W3, W4, W5, W6, W7 and W8) as well as post weaning at 12 weeks (W12), 20 weeks (W20), 22 weeks (W22), 24 weeks (W24), 28 weeks (W28) and 32 weeks (W32) were collected. The pig farm has a semi–arid climate with a high range of temperature (4–47°C). Standard feeding, breeding and management practices were followed at the Swine production farm (Mondal *et al.* 2014).

Data classification and random regression model: Data were classified according to seasons (2 levels of summer (April– September) and winter (October–March)), periods of birth (4 levels of 4 years duration), litter size group (3 levels, i.e. up to 5, 6–9 and ≥10) and sex (2 levels). Single trait random regression model was fitted. Season, period, litter size group and sex had significant effect on body weight at different ages and therefore were included in RRM. Additionally, age of the piglet was fitted as covariate to model for the mean growth using Legendre polynomial of order 4 (Venkataramanan 2016). Different RRM used with details of order of fit for various random effects and information criterion are presented in Table 2.

The RRM fitted could be described as:

$$Y_{ij}=Xb+\sum_{k=0}^{k_{s-1}} Z_a a_k+\sum_{k=0}^{k_{m-1}} Z_m m_k+\sum_{k=0}^{k_{p-1}} Z_p p_k+\sum_{k=0}^{k_{w-1}} Z_w W_k+e$$

where, Y_{ij}, body weight of i^{th} animal at j^{th} week of age; Xb, fixed effects of season, period of birth, litter size group, sex, covariate regression of age of order k=3, associated with the Y_{ij}, independent of the time scale (age); a_k, m_k, p_k and w_k are sets of n values (n=number of animals) of k random regression coefficients corresponding to direct, maternal genetic and individual permanent environment effects, with order of fit k_a, k_m, k_p and k_w respectively.

The elements of the different Z matrices are Z_i-Φ_i–A_i (t_{ij}), for which A_i are the coefficients of Legendre polynomial, and t_{ij} are the ages standardized between –1 and +1, derived as,

$$t_{ij}=\left(2\times\frac{T-T_{min}}{T_{max}-T_{min}}\right)-1$$

where, T_{min} is the earliest date (youngest age) and T_{max} is the latest date (oldest age) represented in the data. T is the age in original scale for which t_{ij} is calculated; e are the random residual heterodastic error variances. Heterogeneous residual variance (RRM-HET) was assumed to be constant for body weight records within, but different (heterogeneous) between the followings 16 growth period classes.

Mixed model equations for the effects included in these models were:

$$\begin{bmatrix} X'X & X'Z_a & X'Z_m & X'Z_p & X'Z_w \\ Z_aX & Z_aZ_a+A^{-1}U\otimes K_a^{-1} & Z_aZ_m+A^{-1}U\otimes K_{am}^{-1} & Z_aZ_p & Z_aZ_w \\ Z_mX & Z_mZ_a+A^{-1}U\otimes K_{ma}^{-1} & Z_mZ_m+A^{-1}U\otimes K_m^{-1} & Z_mZ_p & Z_mZ_w \\ Z_pX & Z_pZ_a & Z_pZ_m & Z_pZ_p+I_pU\otimes K_p^{-1} & Z_pZ_w \\ Z_wX & Z_wZ_a & Z_wZ_m & Z_wZ_p & Z_wZ_w+I_wU\otimes K_w^{-1} \end{bmatrix} \begin{matrix} b \\ a \\ [m] = \\ p \\ w \end{matrix} \begin{bmatrix} X'y \\ Z'_ay \\ Z'_my \\ Z'_py \\ Z'_wy \end{bmatrix}$$

where, A is the numerator relationship matrix, × is the Kronecker's product, and Ki is the (co)variance matrix of the random regression coefficients of the effects indicated in subscript. The best model was decided based on lowest BIC values.

Estimation of eigen value: The Eigen values (λi) and their associated Eigen vectors of the genetic regression coefficients matrix were used to analyse the patterns of variation existing in growth over ages (Kirkpatrick *et al.* 1990). The genetic (co)variance between ages were estimated by the general expression (Jamrozik *et al.* 1997).

$$Gx = \Phi xjKxj\Phi' xj$$

where, Gx is the (co) variance matrix for x-additive, maternal genetic, maternal permanent environment or individual permanent environment; Φxj, vector of Legendre polynomials for the random effect of x and j^{th} age group.

Estimation of breeding value: Estimated breeding values (EBV) for any point j in the age curve between 1 and 36 weeks were estimated from the k^i random solutions obtained for i^{th} animal and Legendre polynomial corresponding to the j^{th} age group.

$$EBV = \Phi_j a'_i$$

where, Φ_j is the Legendre polynomial for the j^{th} age group and a'_i is the transpose of vector of random solutions for the i^{th} animal. All analyses for RRM were done using Wombat software (Meyer 2007). Eigen function for j^{th} age and i^{th} Eigen value of random regression coefficient matrix were calculated as $\Phi_j e_i$, where e_i is the Eigen vector for the i^{th} Eigen value.

RESULTS AND DISCUSSION

Descriptive statistics for body weight traits are presented in Table 1. Body weight has increasing trend up to 36th week of age except at 24th week age, where it declined as compared to 22nd week age. It may be due to managemental practices of culling obese pigs from future breeding stock at 22nd week. The analysis in the present study was started with order of 3 for all random effects and then various combinations were applied and finally increased to order 4. On the basis of BIC values, model (4434) with fourth order fit for direct genetic, maternal genetic and maternal permanent environmental effects and third order fit for individual permanent environmental effect was found best. Beyond this, convergence problems were encountered. This could probably be due to data structure (Arango *et al.* 2004). Meyer (1999) also used RRM to analyze monthly weights of cows and concluded that orders of fit of n = 3 and n = 4 were appropriate for Herefords and Wokalups cows, respectively. While modeling growth records of Nilgiri sheep, Venkataramanan (2016) found Legendre polynomials (of age) of fourth order for all four random effects as best fitting.

The estimates of genetic and phenotypic variances showed a constant increasing trend over age. However maternal genetic, maternal permanent environmental and individual permanent environmental variances showed

Table 1. Descriptive statistics and data structure for growth data across different time period

Particulars of data	W0	W1	W2	W3	W4	W5	W6	W7	W8	W12	W20	W22	W24	W28	W32
Pigs (N)	4231	3009	2891	2847	2807	2784	2701	2516	2348	1530	1355	1189	497	1174	841
Boars (N)	145	139	137	137	137	137	135	132	130	112	105	95	37	99	76
Sows (N)	394	355	348	348	348	348	340	332	326	273	253	228	96	234	174
Mean±SE (kg)	0.95± 0.22	1.92± 0.43	3.11± 0.72	4.33± 1.09	5.58± 1.30	6.70± 1.57	7.97± 1.87	8.92± 2.13	10.17± 2.80	15.68± 4.28	23.42± 6.07	32.79± 7.74	29.78± 6.27	43.39± 8.59	51.73± 8.38
CV (%)	23.58	22.78	23.15	23.32	23.35	23.53	23.55	23.96	27.60	27.32	25.95	23.62	21.06	19.80	16.22

Table 2. Order of fit for the Legendre polynomial and information criterion for different models (heterogenous) for body weight records

Model	Order of fit					Information criterion		
	D	M	IPE	MPE	R	Log L	AIC	BIC
3333	3	3	3	3	16	–12612.183	25280.366	25515.65
3334	3	3	3	4	16	–12172.378	24402.756	24646.44
3343	3	3	4	3	16	–12132.837	24323.674	24567.36
3344	3	3	4	4	16	–12132.805	24325.61	24577.7
3433	3	4	3	3	16	–11340.269	22744.538	23013.43
3434	3	4	3	4	16	–11301.564	22669.128	22946.42
3443	3	4	4	3	16	–11319.893	22705.786	22983.08
3444	3	4	4	4	16	–11298.96	22665.92	22951.62
4333	4	3	3	3	16	–11924.438	23906.876	24150.56
4334	4	3	3	4	16	–11857.636	23775.272	24027.36
4343	4	3	4	3	16	–11836.873	23733.746	23985.83
4344	4	3	4	4	16	–11850.086	23762.172	24022.66
4433	4	4	3	3	16	–11313.233	22692.466	22969.76
4434	4	4	3	4	16	–11272.89	22613.78	22899.48
4443	4	4	4	3	16	–11297.271	22662.542	22948.24
4444	4	4	4	4	16	–11808.789	23681.578	23950.47

increasing trend with minor fluctuations at later stages of growth. These changes in variances over time found for body weights showed same pattern as reported by Wetten *et al.* (2012). The contribution of individual permanent environmental variance was high and found to increase with age till weaning age with fluctuations in later stages (Table 3). Maximum estimate of individual permanent environmental variance ratio was observed for W3, whereas it was lowest at W36. The phenomenon of 'end effect of polynomial' could be a possible cause for the over estimation at higher ages (Meyer 2005).

The additive genetic, permanent environmental and residual variances were utilized for estimation of heritability/variance ratios (Table 4). The direct genetic heritability (SE) estimates were 0.299±0.021 at birth and low (0.011±0.006) at W12 and high (0.582±0.03) at W36. This increasing trend of direct heritability towards later ages observed in the study was in agreement with other reports (Fischer *et al.* 2004, Ghafouri-Kesbi *et al.* 2008). Comparing estimates from other studies using RRM for growth in pigs, our results were in agreement with findings of Wetten *et al.* (2012) who reported that estimated heritability for adult body weights for Duroc was 0.35 and for Landrace was 0.25. Arango *et al.* (2004) reported inadequacy of RRM to model genetic variability at later ages, which could address the increase in heritability estimate in later age group with reduced data size.

Table 3. Heritability/Variance ratio estimates for body weights at different ages in crossbred pigs from best model

Trait	h^2 (S.E.)	m^2 (SE)	c^2 (SE)	p^2 (SE)
W0	0.299 (0.021)	0.273 (0.023)	0.015 (0.006)	0.149 (0.012)
W1	0.139 (0.015)	0.145 (0.017)	0.037 (0.009)	0.461 (0.016)
W2	0.084 (0.014)	0.138 (0.021)	0.095 (0.015)	0.553 (0.018)
W3	0.059 (0.013)	0.163 (0.025)	0.133 (0.018)	0.573 (0.02)
W4	0.043 (0.011)	0.193 (0.028)	0.153 (0.02)	0.556 (0.022)
W5	0.032 (0.01)	0.224 (0.03)	0.163 (0.021)	0.536 (0.023)
W6	0.024 (0.009)	0.248 (0.031)	0.163 (0.021)	0.510 (0.022)
W7	0.019 (0.008)	0.263 (0.031)	0.156 (0.02)	0.482 (0.022)
W8	0.014 (0.007)	0.251 (0.029)	0.135 (0.017)	0.422 (0.018)
W12	0.011 (0.006)	0.282 (0.029)	0.112 (0.015)	0.412 (0.018)
W20	0.037 (0.01)	0.287 (0.028)	0.094 (0.014)	0.404 (0.019)
W22	0.06 (0.013)	0.303 (0.029)	0.101 (0.015)	0.417 (0.02)
W24	0.097 (0.017)	0.319 (0.031)	0.112 (0.017)	0.426 (0.023)
W28	0.213 (0.023)	0.292 (0.031)	0.123 (0.02)	0.346 (0.022)
W32	0.415 (0.029)	0.221 (0.03)	0.132 (0.022)	0.204 (0.019)
W36	0.582 (0.03)	0.157 (0.026)	0.131 (0.023)	0.104 (0.016)

In present study, estimates of maternal heritability were high at birth (0.273±0.023) followed by lowest at W1 and increasing trend with highest m^2 (0.319±0.031) at W24. In previous study by Mondal *et al.* (2014) on this population using univariate animal model, the maternal genetic heritability was highest (0.16±0.07 to 0.18) at the age of weaning (W8) and the lowest for BW (0.04±0.03). Maternal effect was important in modeling growth traits and excluding dam effect may result in inflated values for heritability. Chimonyo *et al.* (2008) also reported that estimate of maternal heritability and direct heritability increased with advancement of age. In contrast, studies using RRM showed that the influence of maternal effect started to wade off at an earlier age (Molina *et al.* 2007, Ghafouri-Kesbi *et al.* 2008). In contradiction, Solanes *et al.* (2004) reported that maternal effect decreased for body weights at weaning as compared to BW in Large White piglets.

Maximum value of maternal permanent environmental variance ratio (c^2) was obtained for the W5 (0.163) and W6 (0.163). The values of c^2 at other post weaning ages were comparatively low. Most studies reported similar decrease of maternal permanent environmental effect as time lapses post weaning (Molina *et al.* 2007, Ghafouri-Kesbi *et al.* 2008). However, in present study the variance ratio for maternal permanent environmental effect (c^2) was carried over for post weaning weights. The genetic correlations among traits under investigation were close to unity because of dependency of recorded traits on preceding growth trait.

Eigen functions, estimated from the eigen vectors of the genetic (co)variance matrix (Kirkpatrick *et al.* 1990), provide an insight into the effects of selection across the growth trajectory. The trajectories for first eigen function, accounting for more than 98% genetic variation showed uniform trend with positive values and slight increase with age till weaning and then rapid increase in post weaning age (Fig. 1). Selection on these factors will improve weight at all ages, with more response at later ages after weaning. A straight-line function parallel to the age axis for pre weaning weights indicated that selection at any age results in an equal response. Our function instead increases with post weaning increasing age, which means selected animals during post weaning stage would reach mature weight faster. This implies genetic selection for post weaning growth traits would be successful. The rate of response to that selection depends on the relative magnitude of the leading eigen value of the genetic (co)variance matrix compared with the leading eigen value of the phenotypic (co)variance matrix. In contrast, response to selection based on the function associated with the 2nd, 3rd and 4th eigen values (fourth order polynomial) would be both small and slow as each account for little of the additive genetic variation. Eigen functions 2, which accounted for lesser genetic variation, were high at birth and there was steep decrease during pre-weaning age and up to 12 weeks of age. After this, eigen function increased up to 28W and then steep decline till 36W. Eigen functions 3, showed interesting patterns, where selection for this variable increased weight at pre weaning ages till 12W and decreased weight at later ages. Eigen functions 4 showed that selection on the basis of this variable will lead to increase in weight till 5W followed by decline in body weight till 24W and then again rapid increase. However, in our study Eigen function 3 and 4 were responsible for very little variation in body weight traits.

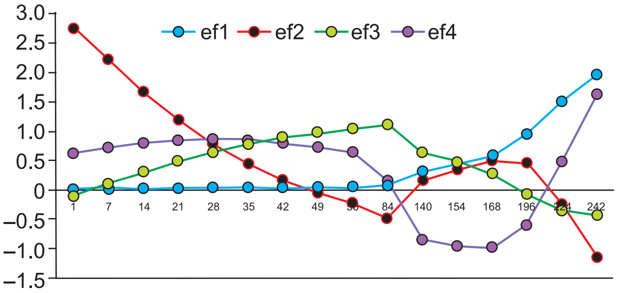

Fig. 1. Eigen functions of the random regression genetic covariance matrix of body weight traits

Table 4. Average, minimum, maximum breeding values (kg) for different growth traits

Trait	Average BV (minimum–maximum)	Number of boars above Average BV (% of boars)
Wo	0.951 (0.639–1.411)	64 (44.14)
W1	1.931 (1.507–2.549)	62 (44.6)
W2	3.118 (2.593–3.882)	61 (44.53)
W3	4.336 (3.734–5.211)	61 (44.53)
W4	5.589 (4.928–6.549)	61 (44.53)
W5	6.715 (6.006– 7.770)	61 (44.53)
W6	7.976 (7.226–9.071)	60 (44.44)
W7	8.928 (8.139–10.095)	58 (43.94)
W8	10.162 (9.332–11.422)	57 (43.85)
W12	15.647 (14.408–17.565)	48 (42.86)
W20	23.335 (18.904–30.112)	46 (43.81)
W22	32.613 (26.668–41.870)	42 (44.21)
W24	26.427 (21.623–32.925)	21 (56.76)
W28	42.898 (29.684–63.684)	43 (43.43)
W32	49.598 (30.153–68.680)	33 (43.42)

ef1= Eigen functin1, ef2= Eigen function 2, ef3 = Eigen function 3, ef4= Egien function 4.

The breeding value estimates for body weights had similar trend like phenotypic value. As the age of the animal increased the average breeding value increased. The mean, maximum and minimum breeding value for pre-weaning and post-weaning body weights has been depicted in Table 4. The average breeding value for the birth weight was 0.951 kg, which improved to 10.162 kg at W8 and 49.598 kg at W32. There was large variation in the breeding value and sizeable population ranging from 42.86% sire at W12 to 56.76% sire at W24 having breeding value higher than the mean breeding value of population. In the post weaning phase influence of maternal effects on piglets are minimal and the true genetic worth of individual is reflected on growth performance. This may have resulted in large differences of breeding values between piglets after 8W.

This indicated existence of animals with high genetic merit in the population and scope of future selection for superior sires based on post weaning performance for genetic improvement. Pattern of variation observed in body weight across the growth curve showed that the growth curves differ significantly between individuals, which could be utilized in a pig breeding system, where selection is based on the growth curve parameters. Growth curve parameters are not currently used directly in the pig evaluation programme. Growth curve models do result in more accurate breeding value estimates because differences in the initial and final weight from the test periods, impact breeding values to a lesser degree when compared with the model currently used to evaluate average daily gain (Koivula *et al.* 2008).

Growth curve of Landrace × Desi crossbred pigs was analyzed using RRM. Based on the BIC values best RRM model with heterogeneous variance was identified as the best model for estimation of variance, covariance, genetic parameters and breeding values in these pig populations. The estimates of genetic and phenotypic variances showed a constant increasing trend over the age. On the other hand, maternal variances, maternal permanent environmental variances and individual permanent environmental variances also showed increasing trend but with fluctuations at later stages of growth. The direct genetic heritability estimates for different body weight traits ranged from moderate to high. The trajectories for first Eigen functions for body weight traits, which accounted more than 98% genetic variation, showed positive trend with slight increase till weaning and then rapid increase in post weaning ages suggesting selection based on this will yield more response at later ages after weaning. Substantial variation in breeding value was found for all growth stages especially after the weaning period. This information can be utilized for selection of animals based on post weaning performance.

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