

## Evaluation of animal models for genetic analysis of growth performance in *Landlly* pigs

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**Abstract:** Selection of the most appropriate animal model for the estimation of genetic parameters for body weight was carried out using restricted maximum likelihood (REML) procedure at birth and thereafter at 3, 6, and 8 weeks of age in *Landlly* pigs. Six different models were fitted for each trait; by inclusion or exclusion of maternal additive genetic effect, maternal permanent environmental effect, and covariance between direct and maternal additive genetic effects. Records on 1968 piglets, born in 4 parities of 131 gilts/sows, sired by 68 boars during a period of 5 years from 2014 to 2018 were used. In order to determine the most appropriate model, Log likelihood values, log the likelihood ratio test and Akaike's information criterion were used. A model including direct additive genetic and maternal permanent environmental effects fitted best to data for birth weight. The best model explaining W3, W6, and W8 included direct additive genetic, maternal genetic and maternal permanent environmental effect with direct and maternal genetic covariance. Total heritability estimates for the body weights were low to moderate across best models.

**Key words:** *Landlly* pig, body weight, genetic parameter, maternal effect, heritability

### 1. Introduction

Livestock rearing plays a significant role in ensuring the livelihood security of the human population all over the world. Pig farming is one of the main enterprises contributing to nutritional security with huge importance in developing nations. Courtesy of a high reproductive life and short gestation interval, pig rearing has recently received a boost in the north and northeastern parts of India. However, pig production suffers due to inadequate and/or inefficient selection and breeding strategies being applied most of the time. Genetic improvement in pigs is scientifically attainable through the introduction of appropriate selection strategies. Selection methods and breeding strategies based on the knowledge of genetic parameters accelerate genetic improvement in various livestock species. Reliable pedigree information and a large dataset across generations is essential component for estimating accurate genetic parameters. Introduction of REML and Bayesian procedures in animal mixed models and advancement in computing capacity have resulted in more accurate parameters.

Body weight is an important trait in pig production and is included in almost all breeding evaluations [1–7]. Important traits in pig production such as preweaning mortality, risk of suffering from hypothermia, crushing,

litter competition, and starvation are directly correlated with birth weight [8]. Piglets with heavier body weight are found to be dominant and acquire more feed either in the form of mother's milk or creep ration [9]. They also have greater capabilities to deal with changes in environment due to weaning [10]. Creep ration is provided to pigs after the third week, which influences the direct additive effect on piglet body weight [11].

Change in growth performance over time is also influenced by genetic with environmental factors. Direct additive genetic, maternal additive genetic, and maternal permanent environmental effects influence piglet weight [4,7,11–13]. Phenotypic expression of offspring on growth is maternally contributed, excluding direct additive gene effect [11]. Maternal effect, which may be genetically and environmentally determined, includes intrauterine environment along with mother's milk production and care. Numerous studies have recommended the inclusion of maternal effects in animal models for piglet weight in different pig breeds [4,7,11–18]. Literature revealed that 6 different animal models were considered mainly for accurate estimation of genetic parameters for body weight in different breeds of pigs [2,4,5,7,13,15,18,19]. Fitting an informative and concise statistical model is essential for accurate estimation of genetic parameters and to decrease

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bias in predicted responses. The objective of this study was to choose the most appropriate animal model for estimation of genetic parameters for body weight at birth and thereafter at 3, 6, and 8 weeks of age in *Landlly* pigs.

**2. Materials and methods**

**2.1. Animals and farm management**

The present study was conducted on *Landlly* (75% Landrace X 25% Ghurrah) crossbred piglets, at Swine Production Farm, Livestock Production and Management Section, ICAR–Indian Veterinary Research Institute (IVRI), Izatnagar, Uttar Pradesh, India; a unit of ICAR–All India Coordinated Research Project (AICRP) on Pigs. To study the performance of exotic breeds of pigs under different agroclimatic conditions, AICRP on pigs was started in 1970. The ICAR–IVRI center came into existence in 1971. This center is situated at an altitude of 564 ft above mean sea level, 28 °N latitude, and 79 °E longitude.

The climate of this place touches both extremes and relative humidity ranges between 45% and 85%. On the basis of temperature and relative humidity over the last 5 years, season was classified into 3 groups. Season 1 (November–February) had low temperature (12–18 °C) and high humidity (0.83–0.96), season 2 (March–June) had high temperature (23–30 °C) and low humidity (0.45–0.83), and season 3 (July–October) had high temperature (25–30 °C) and high humidity (0.85–0.89).

The *Landlly* pig has been developed at ICAR-IVRI as a variety and can be reared in all types of breeding conditions with low cost feed resources. This variety has acceptable performance in North India. This farm follows a controlled mating system and most of the information is being recorded for individual and pedigree. Breeding of pigs starts at 7–8 months of age. The pigs were reared under similar feeding and breeding conditions. The pregnant animals were given a dry concentrate mixture (16% crude protein and 3200 Kcal) for proper growth of the fetus as well as for their own body requirements. At birth, piglets were ear-tagged and information concerning their dam, birth date, and sex were registered. Piglets were injected 1mL iron dextran on the 4th and 14th days after birth. Creep ration rich in protein (protein 21%, lysine 0.89%, and ME 3.36 Mcal/kg) was started from 3rd week onwards and was continued up to weaning age (6 weeks of age). The piglets of each farrowing were maintained in separate pen (Pakka system) with their respective lactating sows. Sufficient space was provided to each individual according to age. Weaning of piglets was done at 6 weeks of age. Weaned piglets were given ad-lib concentrate thereafter. The ration consisted of 20% protein, 0.78% lysine, and 3.17 Mcal/kg ME. Weaned piglets were housed in a group of 10 up to the age of 8 weeks.

**2.2. Data recording and studied traits**

In the present study, records on 1968 piglets born in 4 parities of 131 gilts/sows, sired by 68 boars during a period of 5 years from 2014 to 2018, were collected from pedigree, date of birth, sex, generation, age of dam at farrowing, and parity. Body weight at birth (W0), 3 weeks (W3), 6 weeks (W6), and 8 weeks (W8) of age were collected. The structure of the dataset has been described in Table 1.

**2.3. Statistical analysis**

Variance components for each trait were estimated separately using animal model with a restricted maximum likelihood (REML) algorithm through the WOMBAT program [20]. The model included parity of dam (1–4), sex of piglet (male, female), year of birth (1–5), season of birth (1–3), and generation (1–4) as fixed effects and age of dam at farrowing as a linear covariable. Six different models were fitted for each trait, by inclusion or exclusion of maternal additive genetic effect, maternal permanent environmental effect, and covariance between direct and maternal additive genetic effect.

These models were:

$$y = Xb + Z_1a + e \tag{1}$$

$$y = Xb + Z_1a + Z_2m + e \text{ Cov}(a, m) = 0 \tag{2}$$

$$y = Xb + Z_1a + Z_2m + e \text{ Cov}(a, m) = A\sigma_{am} \tag{3}$$

$$y = Xb + Z_1a + Z_3pe + e \tag{4}$$

$$y = Xb + Z_1a + Z_2m + Z_3pe + e \text{ Cov}(a, m) = 0 \tag{5}$$

$$y = Xb + Z_1a + Z_2m + Z_3pe + e \text{ Cov}(a, m) = A\sigma_{am} \tag{6}$$

Where y is a vector of observations, b is a vector of fixed effects with incidence matrix X, a ~N (0, Aσ<sup>2</sup><sub>a</sub>), and m ~N (0, Aσ<sup>2</sup><sub>m</sub>) are vectors of direct and maternal additive genetic effects with incidence matrices Z<sub>1</sub> and Z<sub>2</sub>, respectively pe ~N (0, Iσ<sup>2</sup><sub>pe</sub>) is a vector of random maternal permanent environmental effect with incidence matrix Z<sub>3</sub>, e ~N (0, Iσ<sup>2</sup><sub>e</sub>) is a vector of random residual effects. Random effects were sampled from a normal distribution with zero mean and variance–covariance matrix of:

$$\text{var} \begin{pmatrix} a \\ m \\ c \\ e \end{pmatrix} = \begin{pmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I\sigma_{pe}^2 & 0 \\ 0 & 0 & 0 & I\sigma_e^2 \end{pmatrix}$$

Where σ<sup>2</sup><sub>a</sub> is the direct additive genetic variance, σ<sup>2</sup><sub>m</sub> is the maternal additive genetic variance, σ<sub>am</sub> is the covariance between direct and maternal additive genetic effects, σ<sup>2</sup><sub>pe</sub> is the maternal permanent environmental variance, σ<sup>2</sup><sub>e</sub> is the residual variance. A is the additive genetic relationship matrix, and I is identity matrix.

The Log likelihood value was estimated for each model. After addition of a random effect to a model, reduction in –2logL (log likelihood ratio test) was also calculated. Additional random effect fitted was considered significant if this reduction was greater than the value of the Chi–

**Table 1.** Description of dataset.

Description/ Trait	W0	W3	W6	W8
No. of piglets	1968	1779	1643	1539
No. of sires	68	68	68	68
No. of dams	131	129	127	126
Minimum weight (kg)	0.4	1.2	2.2	3.8
Maximum weight(kg)	1.7	7.8	14.6	18.8
Average weight(kg)	0.99	4.7	8.62	11.44
Standard deviation	0.24	1.29	2.35	3.15
Coefficient of variation (%)	24.3	27.5	27.3	27.6

W0 = Body weight at birth, W3 = Body weight at 3 weeks, W6 = Body weight at 6 weeks, W8 = Body weight at 8 weeks.

square distribution with 1 degree of freedom ( $P < 0.05$ ). When log likelihood estimates did not differ significantly ( $P > 0.05$ ), the model that had the fewer number of parameters was selected as the most appropriate [21].

$$\Lambda^2 = -2 (\text{Log } L_{\text{reduced model}} - \text{Log } L_{\text{full model}}) \quad (7)$$

Akaike's information criterion (AIC) value was estimated according to [21]. The formula is given below:

$$\text{AIC}_i = -2\log L_i + 2p_i \quad (8)$$

where  $\log L_i$  is the maximized log likelihood of model  $i$  at convergence and  $p_i$  is the number of independently estimated parameters of model  $i$ . The model with the smallest AIC was considered as the most appropriate model.

Log likelihood value, likelihood ratio test, and Akaike's information criterion were used to determine the most appropriate model for estimating (co)variance components for each trait.

Total heritability estimates were calculated using the best model for each trait according to [22]:

$$h_t^2 = (\sigma_a^2 + 0.5 \sigma_m^2 + 1.5 \sigma_{am}^2) / \sigma_p^2 \quad (9)$$

Standard errors (SE) for estimates of heritabilities were approximated using the following formula [23, 24]:

$$\text{SE}(h^2) = 4 \frac{\sqrt{2(1-t)^2[1+(k-1)]^2}}{\sqrt{k(k-1)(s-1)}} \quad (10)$$

where  $t$  is an intraclass correlation,  $k$  is an average number of offspring per sire, and  $s$  is the number of sires.

### 3. Results

AIC values obtained under different models using equation 8 have been summarized in Table 2. The smallest AIC value for W0 was observed in Model 4 having direct additive and permanent maternal environment effects. However, for W3, W6, and W8, the lowest AIC was noted in Model 6 with a direct additive, maternal genetic, permanent maternal environment effect with covariance between direct and maternal genetic effect.

Log likelihood values and LRT values between each of the reduced models and full models have been presented in Table 3. The highest loglikelihood value was observed in Model 4 for W0 and in Model 6 for W3, W6, and W8.

LRT values revealed that maternal genetic effect in Model 2 and maternal permanent environmental effect in Model 4 were significant when they were added in Model 1 having a direct additive effect only. Direct and maternal genetic covariance in Model 3 was nonsignificant when added in Model 2 with direct and maternal genetic effects. The effect of maternal permanent environment in Model 5 was significant when it was added in Model 2. Maternal genetic variance effect was, however, nonsignificant in Model 5 when it was added in Model 4 with additive genetic and maternal permanent environment effects. High negative correlation between direct and maternal genetic effect showed significant difference in Model 6 when direct and maternal genetic covariance was added in Model 5. The results revealed that maternal genetic, maternal permanent environment, and direct and maternal genetic covariance effects are equally important for consideration in the model along with direct genetic effect.

Higher estimate of direct heritability ( $h_d^2$ ) was observed for Model 1 in all body weights when additive genetic effect alone was considered. Estimate for  $h_d^2$  decreased in Model 2 (38%–77%) and Model 4 (40%–75%) when maternal genetic effect and maternal permanent environmental effect was included. Introduction of direct-maternal genetic covariance in Model 3 increased  $h_d^2$  by 11 to 27% as compared to Model 2 for all body weights. Model 5, which included maternal genetic and maternal permanent environmental effects without direct and maternal genetic covariance, had  $h_d^2$  similar to Models 4 for all body weights. The addition of direct maternal genetic covariance, along with genetic and maternal

**Table 2.** Estimates of Akaike's information criterion (AIC) of the 6 models of analysis for body weight in crossbred piglets.

AIC						
Model	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
W0	-3663.80	-3724.10	-3722.40	<b>-3733.96</b>	-3732.51	-3730.85
W3	2544.66	2489.67	2490.99	2480.68	2482.67	<b>2478.42</b>
W6	4184.78	4129.78	4130.41	4129.18	4127.87	<b>4125.13</b>
W8	4652.59	4593.77	4592.13	4593.12	4591.97	<b>4588.49</b>

AIC value of the best model is shown as bold-faced type.

W0 = Body weight at birth, W3 = Body weight at 3 weeks, W6 = Body weight at 6 weeks, W8 = Body weight at 8 weeks.

permanent environmental effects in Model 6 led to higher  $h^2_d$  (22%–36%) as compared to Model 5 for all weights.

Log likelihood values, likelihood ratio tests, and AIC estimates indicated that Model 4, which contained direct additive genetic and maternal permanent environmental effects, performed better for W0 as compared to other models. Model 6 was the most appropriate to explain variation in W3, W6, and W8, which included direct additive genetic, maternal genetic, and maternal permanent environmental effects with covariance between direct and maternal genetic effects. Therefore, Model 4 for W0 and Model 6 for all other body weights was the best fit to the data for estimating variance components and genetic parameters.

Estimates of (co)variance components and heritability estimates for body weights obtained from each univariate model analysis have been presented in Table 4. The best model revealed that direct heritability estimates for W0, W3, W6, and W8 were 0.10, 0.32, 0.37, and 0.34, respectively. Maternal heritability estimate was 0.10 for W3 through the best model. It remained similar for W6 and decreased thereafter for W8 (0.09). Additive and maternal genetic effects (total) in the best model explained 10%, 42%, 46%, and 43% of phenotypic variation for W0, W3, W6, and W8 respectively. Furthermore, direct genetic variance was 2–3.8 times higher than maternal genetic variance across the body weights. Heritability estimates due to permanent environmental effects were 0.18, 0.19, 0.17, and 0.15 for W0, W3, W6, and W8, respectively showing a general trend of decline in estimates over the age. An antagonistic association between direct and maternal genetic effects was illustrated by strong negative genetic correlations (–0.87 to –0.82) for W3, W6, and W8, which declined with advancement in age. Estimates of total heritability ( $h^2_t$ ) for W0, W3, W6, and W8 were 0.10, 0.14, 0.19, and 0.17, respectively indicating an increase up to weaning and a decrease thereafter.

#### 4. Discussion

A likelihood ratio test showed that inclusion of maternal permanent environment with direct genetic effect was significant for W0. Similarly, maternal genetic, maternal permanent environment, and direct and maternal covariance effects were significant when added with direct genetic effect in models for W3, W6, and W8. Literature also reveals that piglet weights are influenced by the direct additive genetic, maternal genetic and maternal permanent environmental effects [4,7,13,15,19]. Exclusion of the maternal genetic effect increases the direct additive genetic effect as some of the maternal genetic variation would appear to be contributed by the direct additive genetic effect [7,15]. Similarly, models which don't consider maternal permanent environment effect underestimate heritability of a trait, as it inflates residual error variance [4].

The highest estimate of direct heritability ( $h^2_d$ ) in Model 1, reported by Mondal et al. [18], was similar to our study. When maternal genetic and common environmental effects were overlooked in models, the largest biased estimates of direct additive genetic variance have been reported [25]. In our investigation, the inclusion of maternal genetic effect in Model 2 and permanent maternal environment effect in Model 4 decreased direct heritability estimates. Mondal et al. [18] reported a reduction of direct heritability in Models 2 (53%–100%) and 4 (51%–100%). These findings were in agreement with our results. Contrary to this investigation, a 2% increase in direct heritability using Model 4 was reported in Mukota pigs [4]. Reduction in direct heritability in the present investigation might be due to proper partitioning of phenotypic variance. Introduction of maternal genetic and maternal permanent environmental effects, without direct and maternal genetic covariance (Model 5), resulted in a direct heritability estimate similar to Model 4 for all body weights. However, a decrease in direct heritability in Model 5 (10%–17%) was reported by Mondal et al. [18].

**Table 3.** Estimates of loglikelihood values (LogL) and likelihood ratio test (LRT) of the 6 models for body weight in crossbred piglets.

Trait	Model	LogL	Compared	LRT	df
W0	Model 1	1833.89	1 vs. 2	62.28*	1
	Model 2	1865.03	2 vs. 3	0.38	1
			2 vs. 5	10.46*	1
	Model 3	1865.22	3 vs. 6	10.42*	1
	Model 4	<b>1869.99</b>	1 vs. 4	72.2*	1
	Model 5	1870.26	4 vs. 5	0.54	1
	Model 6	1870.43	5 vs. 6	0.34	1
W3	Model 1	-1270.3	1 vs. 2	57*	1
	Model 2	-1241.8	2 vs. 3	0.6	1
			2 vs. 5	9*	1
	Model 3	-1241.5	3 vs. 6	14.6*	1
	Model 4	-1237.3	1 vs. 4	66*	1
	Model 5	-1237.3	4 vs. 5	0	1
	Model 6	<b>-1234.2</b>	5 vs. 6	6.2*	1
W6	Model 1	-2090.4	1 vs. 2	57*	1
	Model 2	-2061.9	2 vs. 3	1.4	1
			2 vs. 5	4*	1
	Model 3	-2061.2	3 vs. 6	7.2*	1
	Model 4	-2061.6	1 vs. 4	57.6*	1
	Model 5	-2059.9	4 vs. 5	3.4	1
	Model 6	<b>-2057.6</b>	5 vs. 6	4.6*	1
W8	Model 1	-2324.3	1 vs. 2	60.8*	1
	Model 2	-2294	2 vs. 3	3.8	1
			2 vs. 5	4*	1
	Model 3	-2292.1	3 vs. 6	5.8*	1
	Model 4	-2293.6	1 vs. 4	61.4*	1
	Model 5	-2292	4 vs. 5	3.2	1
	Model6	<b>-2289.2</b>	5 vs. 6	5.6*	1

Loglikelihood value of the best model is shown as bold-faced type.

\*LRT value indicate that fitted additional random effect was considered significant (P < 0.05)

In the present investigation, similar direct heritability estimates in Models 4 and 5 may be due to nonsignificant maternal genetic variance. Mondal et al. [18] reported an increase in direct heritability using Model 6, which was similar to our results. It may be due to significant negative covariance between direct additive genetic effect and maternal genetic effect. A change in 1 parameter may lead to changes in other corresponding parameters when correlated parameters were incorporated in the model [25]. In the case of negligible presence or absence of maternal

and common litter effects, the direct effect model could be appropriate. The practical consequences of the results could be lower genetic gain than expected [13].

In the present investigation, Model 4, which included direct additive genetic and maternal permanent environmental effects, fitted best to data for W0. In contrast to our findings, many reports in different pig breeds revealed that the model that best fit to the data for birth weight included 3 random effects, i.e. litter effect, maternal genetic effect, and direct genetic effect [2,7,13,19].

**Table 4.** Estimates of (co)variance components and genetic parameter estimates ( $\pm$  SE) for growth traits in 75% Landrace from univariate analyses.

Trait	Model	$\sigma_a^2$	$\sigma_m^2$	$\sigma_{am}$	$\sigma_{pe}^2$	$\sigma_e^2$	$\sigma_p^2$	$h_d^2$	$h_m^2$	$r_{am}$	$pe^2$	$h_t^2$
W0	1	0.025	-	-	-	0.04	0.06	0.40 $\pm$ 0.05	-	-	-	0.10 $\pm$ 0.04
	2	0.006	0.014	-	-	0.04	0.06	0.09 $\pm$ 0.05	0.23 $\pm$ 0.04	-	-	
	3	0.007	0.017	-0.002	-	0.04	0.06	0.1 $\pm$ 0.06	0.26 $\pm$ 0.06	-0.23 $\pm$ 0.03	-	
	4	0.006	-	-	0.011	0.04	0.06	0.1 $\pm$ 0.05	-	-	0.18 $\pm$ 0.03	
	5	0.005	0.002	-	0.009	0.04	0.06	0.09 $\pm$ 0.06	0.03 $\pm$ 0.02	-	0.15 $\pm$ 0.05	
	6	0.006	0.003	-0.002	0.009	0.04	0.06	0.11 $\pm$ 0.07	0.05 $\pm$ 0.02	-0.42 $\pm$ 0.05	0.16 $\pm$ 0.05	
W3	1	0.81				0.96	1.78	0.46 $\pm$ 0.06				0.14 $\pm$ 0.05
	2	0.5	0.5			1	1.98	0.25 $\pm$ 0.07	0.24 $\pm$ 0.04			
	3	0.6	0.6	-0.16	-	0.96	1.98	0.29 $\pm$ 0.09	0.30 $\pm$ 0.07	-0.27 $\pm$ 0.23		
	4	0.43			0.34	1.03	1.80	0.24 $\pm$ 0.07			0.19 $\pm$ 0.03	
	5	0.43	0.008		0.33	1.03	1.80	0.24 $\pm$ 0.07	0.005 $\pm$ 0.002		0.19 $\pm$ 0.06	
	6	0.58	0.18	-0.28	0.34	1.01	1.80	0.32 $\pm$ 0.1	0.1 $\pm$ 0.04	-0.87 $\pm$ 0.27	0.19 $\pm$ 0.06	
W6	1	2.82				2.79	5.61	0.50 $\pm$ 0.06				0.19 $\pm$ 0.06
	2	1.97	1.49			2.82	6.28	0.31 $\pm$ 0.07	0.24 $\pm$ 0.04			
	3	2.18	1.85	-0.59		2.71	6.16	0.35 $\pm$ 0.1	0.30 $\pm$ 0.07	-0.29 $\pm$ 0.20		
	4	1.75			1.05	2.94	5.74	0.30 $\pm$ 0.08			0.18 $\pm$ 0.04	
	5	1.78	0.56		0.62	2.91	5.9	0.30 $\pm$ 0.08	0.1 $\pm$ 0.04		0.10 $\pm$ 0.05	
	6	2.10	0.6	-0.92	0.98	2.93	5.7	0.37 $\pm$ 0.10	0.1 $\pm$ 0.06	-0.82 $\pm$ 0.22	0.17 $\pm$ 0.06	
W8	1	3.85				4.9	8.73	0.44 $\pm$ 0.06				0.17 $\pm$ 0.06
	2	2.55	2.39			4.84	9.78	0.26 $\pm$ 0.07	0.24 $\pm$ 0.04			
	3	3.13	3.25	-1.38		4.54	9.54	0.33 $\pm$ 0.09	0.34 $\pm$ 0.07	-0.43 $\pm$ 0.18		
	4	2.22			1.73	5.01	8.97	0.25 $\pm$ 0.07			0.19 $\pm$ 0.04	
	5	2.3	0.92		1	4.95	9.19	0.25 $\pm$ 0.07	0.10 $\pm$ 0.05		0.11 $\pm$ 0.06	
	6	3.09	0.82	-1.29	1.37	5.03	9.02	0.34 $\pm$ 0.1	0.09 $\pm$ 0.08	-0.82 $\pm$ 0.21	0.15 $\pm$ 0.06	

W0 = Body weight at birth, W3 = Body weight at 3 weeks, W6 = Body weight at 6 weeks, W8 = Body weight at 8 weeks,  $\sigma_a^2$  = Direct additive genetic variance,  $\sigma_m^2$  = Maternal additive genetic variance,  $\sigma_{am}$  = Covariance between direct and maternal additive genetic effects,  $\sigma_{pe}^2$  = Maternal permanent environmental variance,  $\sigma_e^2$  = Residual variance,  $\sigma_p^2$  = Phenotypic variance,  $h_d^2 = \sigma_a^2 / \sigma_p^2$  = Heritability of direct genetic effect,  $h_m^2 = \sigma_m^2 / \sigma_p^2$  = Heritability of maternal genetic effect,  $r_{am} = \sigma_{am} / \sigma_a \sigma_m$  = Correlation between direct and maternal genetic effects,  $pe^2 = \sigma_{pe}^2 / \sigma_p^2$  = Maternal permanent environmental variance as a proportion of phenotypic variance,  $h_t^2 = (\sigma_a^2 + 0.5 \sigma_m^2 + 1.5 \sigma_{am}) / \sigma_p^2$  = Total heritability.

Model 6 was the best to describe W3, W6, and W8, which included direct additive genetic, maternal genetic, and maternal permanent environmental effects with direct and maternal genetic covariance. Our results were in agreement with Silio et al. [14] who reported direct and maternal genetic effects and common environmental effects to be considered for the 3-week body weight of Iberian pigs. Solanes et al. [2] also showed that the best model for parameter estimation for the 3-week body weight and weaning weight was an animal model that included permanent maternal environmental effect, maternal genetic effect, direct genetic effect, and a genetic

correlation between the direct and maternal effects. The same trend was also reported by Chimonyo et al. [4] in Mukota; Alves et al. [7] in Canadian-purebred Yorkshire and Landrace pigs; and Kaufmann et al. [11] in Large White and Chimonyo et al. [19], wherein all 3 random effects were included in the best model for weaning weight.

In our investigation, the Model 4 having direct additive and permanent maternal environment effects fits best to the data for W0. Noninclusion of maternal genetic effect in our investigation at birth indicates little variation in uterine nutrient supply and uterine capacity of gilts/sows. However, W3, W6, and W8 were best described by

Model 6 with direct additive, maternal genetic, permanent maternal environment, and direct and maternal genetic covariance effect, suggesting that the maternal care exhibited by the *Landlly* gilts/sows has a genetic component of variation.

Variance components vary due to age, breed, population, and country, and their interpretation, are highly complicated. Direct heritability for W0 was  $0.1 \pm 0.05$  in the present investigation. The literature reported a direct heritability estimate of 0.02–0.15 for birth weight using an animal model with maternal and litter effects [7,11–13,19]. On the contrary, a higher heritability estimate (0.25–0.32) was reported [6,26] in Landrace piglets. A low estimate of direct heritability for birth weight in the present investigation indicated that most of the influence on weight at this point is contributed by the maternal uterine environment of the sow. A higher direct heritability estimate ( $0.32 \pm 0.1$ ) of W3 as compared to W0 was observed in our investigation. This corroborated the hypothesis of Haraldsen et al. [27] indicating an increase in direct genetic effect as the animal gets older. Addition of creep ration could also be the reason for increasing direct additive effect at 3 weeks of age [11]. Solanes et al. [2], Chimonyo et al. [4] and Silio et al. [14], however, reported lower direct heritability estimate ranging from 0.08 to 0.13 in Iberian, Yorkshire and Mukota pigs for 3-week body weight. They concluded that weight at 3 weeks was largely controlled by dam rather than piglet's individual genes. The direct heritability estimate for W6 (weaning weight) was  $0.37 \pm 0.1$  in the present investigation, which was higher to that (0.06) reported [4]. In our investigation, the direct heritability estimate for W8 was  $0.34 \pm 0.1$ . Zhang et al. [28], however, observed lower direct heritability of 0.17 for 8-week piglet weight in the crossbred pig line.

Maternal genetic effects are presumably due to genetically controlled components of uterine nutrient supply, uterine capacity and milk production [11]. The best model in our investigation did not show the importance of maternal genetic effect at birth, indicating little variation in uterine nutrient supply and the uterine capacity of gilts/sows. The best models at 3, 6 and 8 weeks, however, included the maternal genetic component. The maternal heritability estimate was 0.1 at 3 weeks, remained similar at 6 weeks, and declined to 0.09 at 8 weeks. This revealed that maternal genetic influence remained constant up to weaning age and started to decline thereafter. These findings were similar to Chimonyo et al. [4], who reported an increase in maternal genetic influence in Mukota pigs as the pig grows. However, Kaufmann [11] reported a decrease in maternal genetic influence from birth to weaning in Large White pigs. The maternal heritability estimate in Mukota pigs for 3-week body weight reported

by Chimonyo et al. [4] was also similar to our study. However, a higher estimate of the same was reported by Solanes et al. [2] and Silio et al. [14]. Maternal heritability estimate for W6 in this study was in agreement with Solanes et al., [2]. Maternal genetic heritability (0.11) for body weight at 8 weeks was also similar to Zhang et al. [28].

The total genetic effect at birth was similar to that reported by Chimonyo et al. [19]. However, Alves et al. [7], Kaufmann et al. [11], and Roehle [12] reported higher total genetic effect ranging from 0.23 to 0.35, which is almost 2 times higher than the present investigation. The total genetic effect for 3-, 6- and 8-week body weight was almost double that reported in literature [2,4,14,28].

Common litter effect is also important to litter bearing species as they share a common permanent environment which contributes to their resemblance. The origin of common permanent environmental variances among families could be due to similar diet and/or climatic conditions [6,11,17,28]. Heritability estimate due to permanent environmental effect in this study was 0.18, 0.19, 0.17, and 0.15. The estimates showed a slight increase from W0 to W3 and decrease thereafter with lowest estimate for W8. The lowest heritability estimate due to permanent environmental effect after weaning may be due to establishment of new groups [11]. Another reason for the same may be a reduction in maternal permanent effect with advancement of age. Permanent environmental heritability estimates in this study were in agreement with those reported in the literature. It ranged from 0.01 to 0.19 for birth weight [2,7,13,19], from 0.02 to 0.19 for 3-week body weight [2,4,14], 0.21 for 6-week body weight [2] and 0.2 for 8-week body weight [28].

A strong negative genetic correlation ( $-0.81$  to  $-0.87$ ) between direct and maternal genetic effect for W3, W6, and W8 suggests an antagonistic association between direct and maternal genetic effects. Similar negative correlations were also reported in literature [6–7,19,29,30]. Kaufmann et al. [11] and Tomiyama et al. [5] however, observed positive genetic correlation between direct and maternal genetic effects. Explanation for negative genetic correlation is not clear. It can be due to minor difference in management factors [31]. *Landlly* is a crossbred pig population originated from the cross between Landrace and Ghurrah, which had different environmental origins. Therefore, negative genetic correlation may be due to different environmental conditions from where the base generation pigs originated [19]. The strong negative correlation between direct and maternal additive genetic effects led to very low total heritability [32]. Therefore, it is important to consider this effect in genetic evaluation and breeding programs.

Total heritability estimates were low to moderate for all body weights. Total heritability estimate reported by Alves et al. [7] and Su et al. [32] for birth weight in Yorkshire (0.11–0.17) and Landrace piglets (0.11–0.15) were similar to our study.

In conclusion, maximum log likelihood (MLL), likelihood ratio test (LRT) and Akaike's information criterion (AIC) values in the present investigation revealed that maternal genetic and maternal permanent environment effects are equally important for consideration in the model with direct genetic effect for the best prediction of genetic parameters. Model including direct additive genetic and maternal permanent environmental effect was the best fit to data for W0. Inclusion of direct additive genetic, maternal genetic, maternal permanent environmental effect and direct and maternal genetic covariance was observed to be best for W3, W6, and

W8. Total heritability estimates for the body weights were low to moderate through the best models.

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#### Conflict of interest

The authors certify that no conflicts of interest exist with regards to this work.

#### Ethical statement

The manuscript does not contain clinical studies.

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