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Integrating three genetic dimensions relating to piglet birth weight: direct and maternal effects on the mean and genetic control of residual variance

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ABSTRACT

The uniformity of production traits is desired for different traits in livestock species, including the uniformity of within-litter birth weight (**BW**) in piglets. In pigs, BW is associated with increased vitality and survival until weaning. However, as the uniformity of the BW increases, the importance of the initial weight decreases as competition between piglets decreases. The aim of this study was to estimate the direct and maternal genetic components of BW, jointly with the maternal genetic component of the residual variance for within-litter BW, and their genetic correlations. We used two distinct datasets of Swiss Large White pigs: (1) an experimental farm dataset, and (2) a commercial farm dataset, comprising 43 135 and 23 313 records of individual piglet BW, respectively. A heteroscedastic model was used for the statistical analysis. This model assumes that both the mean BW and the residual variance are affected by systematic and random effects, with the residual variance being heterogeneous and partially under genetic control. In the most complex models, which included both genetic effects for the mean trait, the results indicated that direct genetic effects or correlations with such effects were negligible. The genetic component of the residual variance for BW ranged from 0.0712 to 0.1246 for the experimental farm and from 0.0371 to 0.0994 for the commercial farms. The genetic correlation between the mean BW and BW variability was always positive, ranging from 0.1492 to 0.3069 for the experimental farm and from 0.2197 to 0.5892 for the commercial farms. Thus, it is sufficient to model mean BW and BW variability by including only the maternal genetic effect for both traits. In addition, although moderate genetic correlations existed between the within-litter mean BW and BW variability, focusing on BW uniformity within litters would be preferable in simultaneously creating a selection index for both traits.

Implications

Monitoring within-litter birth weight variability is important for efficient piglet production and welfare. Our findings suggest that maternal genetic effects are sufficient to model mean birth weight and birth weight variability as genetic components of residual variance. For both traits, direct genetic variance and its correlations with other components are negligible. However, because of the moderate genetic correlations between the mean birth weight and birth weight variability, it is preferable to focus selection solely on within-litter birth weight uniformity rather than combining both traits in the selection index. This approach simplifies breeding strategies while maintaining the goal of improving piglet welfare.

Introduction

Uniformity is an important quality of various economically significant traits in livestock production, one of which is piglet birth

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weight (**BW**). In pigs, BW is associated with increased vitality (Rutherford et al., 2013) and survival until weaning (Kapell et al., 2011; Knol et al., 2010). However, as the within-litter BW becomes more uniform, the importance of the initial weight diminishes because the competition between piglets decreases (Andersen et al., 2011; Canario et al., 2010). Cross-fostering can be used to avoid issues related to a high number of piglets nursed by one sow and to obtain a homogenised BW across piglets within litters (Baxter et al., 2013). This practice increases preweaning survival and, therefore, farm productivity (Putz et al., 2015); however, it also increases labour costs and poses immunity concerns (Baxter et al., 2013).

Selection for increased uniformity of within-litter BW can be implemented to avoid intervention practices such as cross-fostering. For this purpose, estimating the variance components of BW variability is a priority. BW variability can be studied by the heterogeneity of residual variance of the trait of interest, which was previously investigated in pigs by Sell-Kubiak et al. (2015a) and Sell-Kubiak et al. (2015b) and in mice by Formoso-Rafferty et al. (2016). In addition, in their experiments on mice, Formoso-Rafferty et al. (2019) and Formoso-Rafferty et al. (2022) reported that selecting animals with reduced residual variance in BW is possible and can lead to more robust and feed-efficient animals. Thus, selection for uniformity in within-litter BW can lead to more efficient and ethical livestock production because it results in litters that are easier to manage (Rutherford et al., 2013) and piglets that are more likely to survive until weaning (Damgaard et al., 2013). Furthermore, the application of a canalising selection model (SanCristobal-Gaudy et al., 1998) provides a framework to better understand and model the genetic and environmental factors underlying BW variability. This model allows the residual variance to vary across individuals depending on genetic and environmental influences and includes a specific genetic effect on BW variability, thereby accounting for the model's heterogeneous residual variance. Notably, mean BW and BW variability are considered maternal traits (Sell-Kubiak et al., 2015a,b; Damgaard et al., 2013; Nielsen et al., 2013; Canario et al., 2010), and sows differ from each other in their sensitivity to environmental disturbances (Rönnegård et al., 2010). Although successful selection for reduced residual variance in BW can be performed by assuming that these traits are maternal (Formoso-Rafferty et al., 2016), there is evidence of a direct genetic component in the mean BW (Alves et al., 2018; Kaufmann et al., 2000). Thus, this study aimed to estimate the direct genetic and maternal genetic components of BW jointly with the maternal genetic component of the residual variance for within-litter BW and their genetic correlations in two datasets collected from two types of farms in Switzerland.

Material and methods

Animals

The study used two distinct datasets: (1) a Swiss experimental farm dataset comprising 43 135 records of BW from 3 163 litters of 986 sows collected between 2004 and 2022 and pedigree data for 45 737 individuals; and (2) a Swiss commercial farm dataset comprising 23 313 BW records from 1 748 litters of 813 sows and 27 285 individuals in the pedigree from two different farms collected between 2005 and 2021. The descriptive statistics of both datasets are presented in Tables 1 and 2. In Switzerland, free farrowing has been required by law since 2008 (Swiss Animal Protection Ordinance, 2008, Article 50). This means that farrowing pens must be designed such that the sow can turn freely; thus, farrowing crates are not allowed.

The experimental farm at Agroscope Posieux maintains a dam line of the Swiss Large White breed and has a self-replacement system, recruiting replacement gilts exclusively from its own breeding herd. Thus, all sows in this dataset were from the Large White dam line. Sows were kept in groups of 8–14 animals in pens of approximately 43 m^2. The sows in the same group were inseminated and gave birth at the same time (farrowing batches). Between the 110th day of gestation and the 26th day of lactation, the sows were housed in individual 7.1 m^2 pens (5.9 m^2 solid concrete floor and 1.2 m^2 slatted concrete floor). The piglets had exclusive access to a separate covered area (0.8 m^2) heated with infrared lamps, which was not accessible to the sow. The pen was equipped with an automatic feeder (Schauer Spotmix, Agrotonic GmbH, Prambachkirchen, Austria), allowing the provision of predefined amounts of feed. Piglets were individually weighed within 24 h of farrowing by trained piggery staff via scales with 5 g precision. Before weighing, all piglets in one litter were placed in a box warmed by an infrared lamp, and each piglet was removed individually for measurement. The scales automatically accounted for movement by recording multiple weight measurements over a set period and averaging them. Stillborn piglets were also included in the BW analysis and were taken into account to compute the litter size effect included in the models.

Two nucleus farms operated by the breeding company SUISAG were also included in this study. Both farms inseminated Large White sows with Large White (sire and dam lines) and Landrace boars. The litters were primarily purebred Large White, F1 crosses, a small number of crossbred Large White, and other unknown crosses. Sows were kept in groups of 7–14 animals in waiting pens before being transferred to farrowing pens on day 110 of gestation. Sows were kept in the farrowing pens for 26–30 days during lactation. Each farrowing pen provided 0.8 m^2 of space for the born piglets and was equipped with infrared heating lamps. After 24 h from birth, the piglets born in a litter were placed in the scale box together (Mettler Toledo with a precision of 5 g). Each piglet was then removed one by one, and the decrease in weight was recorded as the individual BW. Stillborn piglets were not included in the BW analysis but were taken into account to compute the litter size effect included in the models.

Statistical analysis

The systematic effects considered in the models and curated in the datasets were the mother's age (from 300 to 1 956 days, commercial farm) or the number of parturitions (10 levels, experimental farm), sex, two levels for commercial farm and four levels for the experimental farm (male, female, hermaphrodites, and unknown), litter size including 16 levels (1–5, 6, 7… 20–25) for the commercial farm and 17 levels (1–6, 7… 20, 21, 22–27) for the experimental farm, a comparison group that included combinations of farm-month years for commercial farm (75 levels) and 357 batches for the experimental farm, and the male breed that included four levels (commercial farm). The litter effect was included as a random effect and included 1 755 and 3 165 levels for commercial and experimental farms, respectively.

Homoscedastic model

To begin, we implemented a classical animal model assuming homoscedastic residual variance. This model is referred to as **HO**:

$$y_i = \mathbf{x}'_i\mathbf{b} + \mathbf{v}'_i\mathbf{a} + \mathbf{z}'_i\mathbf{m} + \mathbf{w}'_i\mathbf{c} + e_i$$

In this model, y_i is the individual BW of animal i, $\mathbf{b}$ is a vector of systematic effects, $\mathbf{a}$ is the vector of direct additive animal genetic effects (individual), $\mathbf{m}$ is a vector of maternal genetic effects, $\mathbf{c}$ is a

Table 1
Number of individual piglet birth weight (BW) records, mean, SD, minimum, and maximum for the analysed traits in the experimental farm dataset.

Item	Mean BW (kg)	SD (kg)	Minimum (kg)	Maximum (kg)	Number of records
All	1.42	0.38	0.24	3.00	43 135
Sex					
Male	1.45	0.39	0.30	3.00	22 522
Female	1.40	0.37	0.24	2.93	20 571
Hermaphrodites	1.28	0.28	0.79	1.66	11
Unknown	1.26	0.35	0.45	2.20	31
Litter size					
1 (<7)	1.82	0.40	0.30	2.80	762
2 (7)	1.75	0.37	0.54	2.56	511
3 (8)	1.61	0.44	0.43	2.80	616
4 (9)	1.67	0.39	0.39	2.78	1 008
5 (10)	1.57	0.37	0.26	2.65	1 613
6 (11)	1.60	0.38	0.41	2.79	2 332
7 (12)	1.50	0.36	0.39	2.73	3 289
8 (13)	1.49	0.37	0.40	2.93	4 205
9 (14)	1.45	0.35	0.32	2.62	5 006
10 (15)	1.39	0.36	0.32	2.76	5 188
11 (16)	1.38	0.36	0.32	3.00	5 563
12 (17)	1.32	0.34	0.31	2.69	4 573
13 (18)	1.32	0.35	0.28	2.39	3 222
14 (19)	1.27	0.35	0.37	2.38	2 488
15 (20)	1.25	0.35	0.24	2.50	1 344
16 (21)	1.24	0.34	0.31	2.26	756
17 (22–27)	1.17	0.34	0.35	2.20	659
Number of parturitions					
1	1.34	0.34	0.26	2.73	12 624
2	1.49	0.38	0.31	3.00	9 271
3	1.47	0.40	0.32	2.76	7 065
4	1.45	0.39	0.24	2.73	5 376
5	1.44	0.38	0.40	2.79	3 885
6	1.41	0.39	0.30	2.44	2 504
7	1.40	0.38	0.43	2.41	1 334
8	1.38	0.41	0.35	2.51	631
9	1.41	0.43	0.42	2.63	299
10 (>9)	1.46	0.42	0.59	2.49	146

Table 2
Number of individual piglet birth weight (BW) records, mean, SD, minimum, and maximum for the analysed traits in the commercial farm dataset.

Item	Mean BW (kg)	SD (kg)	Minimum (kg)	Maximum (kg)	Number of records
All	1.55	0.36	0.40	2.70	23 313
Breed					
Breed 1	1.52	0.35	0.40	2.66	12 530
Breed 51	1.50	0.31	0.61	2.65	755
Breed 99	1.48	0.31	0.43	2.28	1 014
Breed 104	1.61	0.37	0.41	2.70	9 014
Sex					
Male	1.57	0.36	0.43	2.70	12 016
Female	1.53	0.35	0.40	2.67	11 297
Litter Size					
1 (<7)	1.79	0.33	0.83	2.55	172
2 (7)	1.85	0.35	0.94	2.65	168
3 (8)	1.77	0.37	0.60	2.58	239
4 (9)	1.75	0.32	0.80	2.70	419
5 (10)	1.72	0.35	0.68	2.65	669
6 (11)	1.70	0.35	0.43	2.67	1 229
7 (12)	1.63	0.35	0.47	2.66	1 874
8 (13)	1.63	0.33	0.48	2.55	2 260
9 (14)	1.57	0.34	0.45	2.65	2 928
10 (15)	1.52	0.34	0.44	2.57	3 216
11 (16)	1.52	0.35	0.43	2.61	2 734
12 (17)	1.48	0.35	0.40	2.52	2 775
13 (18)	1.48	0.35	0.50	2.55	1 935
14 (19)	1.43	0.33	0.42	2.47	1 145
15 (20)	1.45	0.34	0.53	2.63	746
16 (21–25)	1.34	0.34	0.46	2.50	804

vector of litter effects, e_i is the residual, and $\mathbf{x'_i}$, $\mathbf{z'_i}$ and $\mathbf{w'_i}$ are incidence matrices for systematic, animal, maternal, and litter effects, respectively.

Heteroscedastic model

The heteroscedastic (or canalising selection) model assumes that both the mean BW level and the residual variance are affected by systematic and random effects, with the residual variance being heterogeneous and partially under genetic control. The more complex heteroscedastic model included direct animal genetic and maternal genetic effects for BW, and maternal genetic effects for BW variability:

$$y_i = \mathbf{x}_i'\mathbf{b} + \mathbf{v}_i'\mathbf{a} + \mathbf{z}_i'\mathbf{m} + \mathbf{v}_i'\mathbf{c} + e^{\frac{1}{2}\left(\mathbf{x}_i'\mathbf{b}^* + \mathbf{z}_i'\mathbf{m}^* + \mathbf{v}_i'\mathbf{c}^*\right)}\varepsilon_i$$

where y_i is the individual BW of animal i; * indicates the parameters associated with the residual variance, that is, the variability of BW; **b** and $\mathbf{b^*}$ are vectors of the systematic effects; **a** is a vector of direct additive animal genetic effects; **m** and $\mathbf{m^*}$ are vectors of maternal genetic effects; **c** and $\mathbf{c^*}$ are vectors of litter effects; $\mathbf{x'_i}$, $\mathbf{z'_i}$, and $\mathbf{w'_i}$ are incidence matrices for systematic, animal, maternal, and litter effects, respectively; e is the base of the exponential function, and ε_i is the standardised error. The vectors of genetic effects **a**, **m**, and $\mathbf{m^*}$ are jointly distributed and are assumed to be Gaussian, as follows:

$$\left.\begin{pmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{m}^* \end{pmatrix}\right| \sigma_a^2, \sigma_m^2, \sigma_{m*}^2, \mathrm{A}, \rho_{am}, \rho_{am^*}, \rho_{mm^*}$$

$$\mathrm{N}\left(\begin{pmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{pmatrix}, \begin{pmatrix} \sigma_a^2 & \rho_{am}\sigma_a\sigma_m & \rho_{am^*}\sigma_a\sigma_{m*} \\ \rho_{am}\sigma_a\sigma_m & \sigma_m^2 & \rho_{mm^*}\sigma_m\sigma_{m*} \\ \rho_{am^*}\sigma_a\sigma_{m*} & \rho_{mm^*}\sigma_m\sigma_{m*} & \sigma_{m*}^2 \end{pmatrix} \otimes \boldsymbol{A}\right)$$

where **A** is the additive genetic relationship matrix; σ_a^2 is the direct additive genetic variance for BW; σ_m^2 is the maternal additive genetic variance for BW; σ_{m*}^2 is the maternal additive genetic variance affecting the residual variance for BW; ρ_{am}, ρ_{am^*} and ρ_{mm^*} are genetic correlation coefficients between them; and $\otimes$ denotes the Kronecker product.

The litter effects **c** and $\mathbf{c^*}$ are jointly distributed and are assumed to be Gaussian, as follows:

$$\left.\begin{pmatrix} \mathbf{c} \\ \mathbf{c}^* \end{pmatrix}\right| \sigma_c^2, \sigma_{c^*}^2, I, \ \rho_{cc^*}, \rho_{cc^*} \ \mathrm{N}\left(\begin{pmatrix} \mathbf{0} \\ \mathbf{0} \end{pmatrix}, \begin{pmatrix} \sigma_c^2 & \rho_{cc^*}\sigma_c\sigma_{c*} \\ \rho_{cc^*}\sigma_c\sigma_{c*} & \sigma_{c*}^2 \end{pmatrix}\right)$$

The heteroscedastic models (Table 3), referred to as **HE**, included different combinations of random effects and correlations between them:

- Model HE_1 included the maternal genetic effect for the mean BW (**m**) and BW variability ($\mathbf{m^*}$), their genetic correlation, ρ_{mm^*}, and the litter effect for the mean BW (**c**) and BW variability ($\mathbf{c^*}$) without correlation between them.
- Model HE_2 included the same effects as HE_1 and the correlation between both litter effects (ρ_{cc^*}).
- Model HE_3 included the direct additive genetic effect for the mean BW (**a**), the maternal genetic effect for the mean BW (**m**) and BW variability ($\mathbf{m^*}$), and the genetic correlation between them, ρ_{am}, ρ_{am^*} and ρ_{mm^*}. The litter effect was fitted only for BW variability ($\mathbf{c^*}$).
- Model HE_4 included the direct additive genetic effect for the mean BW (**a**), the maternal genetic effect for the mean BW (**m**) and BW variability ($\mathbf{m^*}$), and the genetic correlation between them, ρ_{am}, ρ_{am^*}, and ρ_{mm^*}. The litter effect was fitted only for the mean BW (**c**).
- Model HE_5 was the most complex model, including the direct additive genetic effect for the mean BW (**a**), the maternal genetic effect for the mean BW (**m**) and BW variability ($\mathbf{m^*}$), and the genetic correlation between them, ρ_{am}, ρ_{am^*}, and ρ_{mm^*}. The litter effect was fitted for the mean BW (**c**) and the BW variability ($\mathbf{c^*}$). Additionally, the correlation between litter effects was included (ρ_{cc^*}).
- Model HE_6 included the same effects as HE_5, except for the maternal genetic effect for the mean BW (**m**) and associated genetic correlations.
- Model HE_7 was the same as HE_5 but without a correlation between the two litter effects.
- Model HE_8 was the same as HE_5 but did not include litter effects for the mean BW and BW variability.

The Akaike information criterion (**AIC**) and Bayesian information criterion (**BIC**) were used to compare the models and select those that best fit the data.

Since the HE models' residual variance is heterogeneous by default, a residual variance can also be estimated for a particular level of systematic effects. A global residual variance was estimated in the HE models by adding the averages of the estimates of all levels within the systematic effects. To maintain the estimability of the corresponding linear combination, the solutions for all levels of each of the other systematic effects were averaged and added to the solution for a particular desired level of the systematic effect. The global heritability (h^2) for the mean trait and each level of systematic effect was subsequently computed (Formoso-Rafferty et al., 2017). ASReml 4.2 (Gilmour et al., 2015) was used to estimate the variance components for the heteroscedastic and homoscedastic models. GSEVM software (Ibáñez-Escriche et al., 2010) was used to obtain solutions for systematic effects and BW heritabilities via the HE_1 model. Note that the HE_1 model was chosen because the GSEVM does not allow for the inclusion of more than one additive genetic effect.

The residual variance, phenotypic variance, and direct and maternal heritabilities were computed for all models solved with ASReml. We computed these using the combination of systematic effects with a higher amount of data and computed the influence

Table 3
Different variance components included in the tested animal models (HO, homoscedastic model; HE, heteroscedastic model) for piglet birth weight (BW).

Model	Var(a)	Var(m)	Var(m*)	Var(c)	Var(c*)	Var(e)	Cov(am)	Cov(am*)	ρmm*	ρam	ρam*	ρcc*
HO	X	X		X		X	X			X		
HE_1		X	X	X	X				X			
HE_2		X	X	X	X							X
HE_3	X	X	X		X		X	X	X	X	X	
HE_4	X	X	X	X			X	X	X	X	X	
HE_5	X	X	X	X	X		X	X	X	X	X	X
HE_6	X		X	X	X			X		X		X
HE_7	X	X	X	X	X		X	X	X	X	X	
HE_8	X	X	X				X	X	X	X	X	

Abbreviations: Var = variance, Cov = covariance, a = direct genetic effect, m = maternal genetic effect, c = litter effect, ρ = correlation, e = residual.
* indicates the parameters associated with the residual variance, that is, the variability of BW.

of the covariate “age” using its average value in the commercial farm dataset. Note that this is not the residual variance; rather, it is the variance in a unique combination of the levels of the systematic effects. Thus, it was not possible to obtain the SE of the parameter. The models took less than 3 min to solve with ASReml, whereas 12–17 h was needed to solve them with GSEVM using a standard PC (i7 3.60 GHz and 16 GB RAM).

Results

Systematic effects for birth weight

Fig. 1 shows the magnitude of the systematic effects on BW via the HE_1 model in the experimental farm dataset. On average, males were heavier than females, and hermaphrodites were lighter than females. The BW decreased with litter size. It increased considerably from the first to the second parturition, remained similar to the second at the third parturition, and then gradually decreased in subsequent parturitions. Similar results were found with the commercial farm dataset (Fig. 2). Here, the age of the sow was positively related to BW; that is, older sows produced piglets with a higher BW. We also found differences in BW depending on the breed in the commercial farm data set, with one paternal breed resulting in slightly heavier piglets than the other three breeds.

Estimates of variance components, heritabilities, and accuracies

Tables 4 and 5 show the estimates of variance components and correlations between them in the different models applied to both datasets. The results of the HO model indicated that the maternal genetic variance was greater (0.0286 and 0.0233 in the experimental and commercial farms, respectively) than the direct additive genetic variance (0.0126 and 0.0045 in the experimental and commercial farms, respectively). Heritabilities for BW were 0.0952 (± 0.0194) for the direct genetic component and 0.2165 (± 0.0221) for the maternal genetic component in the experimental farm. By contrast, lower values were found in the commercial farms, with values of 0.0375 (± 0.0137) and 0.1948 (± 0.0261) for the direct and maternal effects, respectively. The HE_1 model (including maternal effects only) yielded a genetic residual variance of 0.0747 for BW in the experimental farm dataset compared with 0.0372 in the commercial farm dataset. The individual genetic variance for BW was close to 0 when the maternal genetic effect was added to the HE model. When the maternal genetic effect was excluded, the variance explained was not absorbed by the direct additive genetic effect (Model HE_6), even though the variance of this effect slightly increased. The magnitude of the litter effect was greater for the BW variability than for the mean BW.

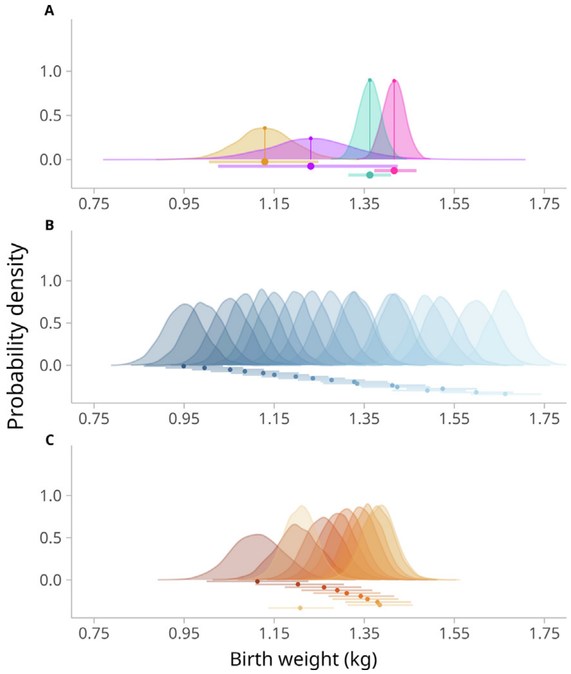

Fig. 1. Probability density of the posterior distributions of the solutions for the systematic effects of sex (A), litter size (B), and number of parturitions (C) on piglet birth weight in the experimental farm dataset. A: turquoise – female, pink – male, purple – hermaphrodite, orange – sex unknown. In B and C, darker colours indicate larger litter sizes and greater numbers of parturitions, respectively.

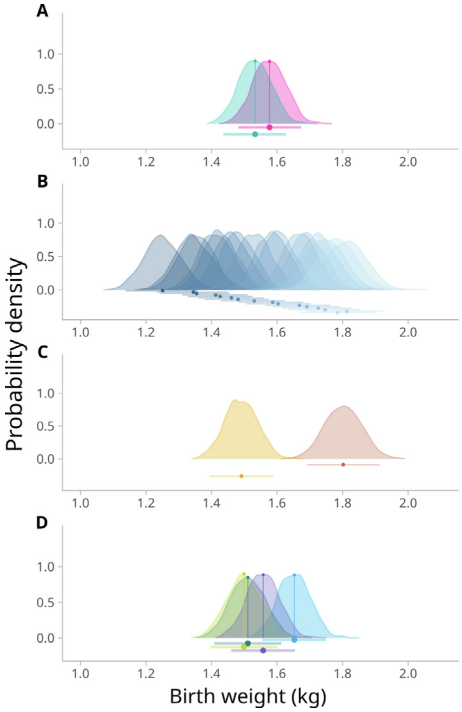

Fig. 2. Probability density of the posterior distributions of the solutions for the systematic effects of sex (A), litter size (B), sow age (C), and sire breed (D) on piglet birth weight in the commercial farm dataset. A: turquoise – female, pink – male. B: darker colours indicate larger litter sizes. C: darker colours indicate greater sow age. D: sires’ breed.

Figs. 3 and 4 show the heritabilities for BW depending on the level of systematic effect using the HE_1 model in the experimental farm and commercial farm datasets. At the experimental farm, females presented higher heritability than males; for litter size, intermediate values were less consistent, and the BW variability increased with parity number. Female piglets had more consistent BW than male piglets in the commercial farm dataset, despite having lower weights, and litter sizes greater than nine piglets had greater variation than smaller litters. The age of the sow positively affected the mean BW but increased the degree of the BW variability. The expected global maternal heritability for BW was 0.2080 (± 0.0205 SD of the marginal posterior distribution) in the commercial farm dataset, and 0.2143 (± 0.0289) in the experimental farm dataset. The genetic trend for the mean BW and BW variability over time is also presented in the Supplementary material (Figs. S1 and S2). It indicates a substantial difference between the experimental farm dataset, which showed a stable for both traits, and the commercial farm dataset. The latter showed an increase in mean BW and BW variability in recent years, indicating a positive yet unfavourable correlation. We also assessed the accuracies

Table 4

Estimates (mean ± SE) of variance components and correlations in the different models for piglet birth weight (BW) applied to the experimental farm dataset (HO, homoscedastic model; HE, heteroscedastic model).

Parameter	HO	HE_1	HE_2	HE_3	HE_4	HE_5	HE_6	HE_7	HE_8
Var(a)	0.0126 ± 0.0026			0.0027 ± 0.0006	0.0015 ± 0.0007	0.0007 ± 0.0004	0.0131 ± 0.0012	0.0006 ± 0.0004	0.0045 ± 0.0009
Var(m)	0.0286 ± 0.0032	0.0282 ± 0.0019	0.0283 ± 0.0019	0.0355 ± 0.0024	0.0276 ± 0.0024	0.0279 ± 0.0023		0.0277 ± 0.0023	0.0356 ± 0.0026
Var(m*)		0.0747 ± 0.0098	0.0743 ± 0.0097	0.0712 ± 0.0094	0.1307 ± 0.0114	0.0736 ± 0.0097	0.0941 ± 0.0117	0.0739 ± 0.0098	0.1246 ± 0.0109
Cov(am)	−0.0062 ± 0.0028			−0.0006 ± 0.0015	0.0002 ± 0.0015	0.0002 ± 0.0013		0.0003 ± 0.0013	−0.0017 ± 0.0018
Cov(am*)				−0.0029 ± 0.0027	−0.0035 ± 0.0037	−0.0031 ± 0.0025	0.0100 ± 0.0028	−0.0032 ± 0.0025	−0.0034 ± 0.0039
Cov(mm*)		0.0072 ± 0.0031	0.0123 ± 0.0032	0.0093 ± 0.0034	0.0099 ± 0.0037	0.0139 ± 0.0034		0.0087 ± 0.0033	0.0099 ± 0.0039
Var(c)	0.0106 ± 0.0006	0.0081 ± 0.0005	0.0081 ± 0.0005		0.0074 ± 0.0005	0.0078 ± 0.0005	0.0168 ± 0.0007	0.0078 ± 0.0005	
Var(c*)		0.0932 ± 0.0074	0.0969 ± 0.0074	0.0875 ± 0.0071		0.0982 ± 0.0075	0.1187 ± 0.0081	0.0941 ± 0.0074	
Cov(c,c*)			−0.0082 ± 0.0014			−0.008 ± 0.0014	−0.0105 ± 0.0018		
Var(e)	0.0866 ± 0.0014	0.0872	0.0867	0.0836	0.0839	0.0847	0.0822	0.0852	0.0812
Var (p)	0.1323 ± 0.0020	0.1235	0.1231	0.1187	0.1201	0.1215	0.1121	0.1219	0.1178
h^2_a	0.0952 ± 0.0194			0.0227	0.0122	0.0057	0.1166	0.0048	0.0382
h^2_m	0.2165 ± 0.0221	0.2282	0.2299	0.2991	0.2301	0.2298		0.2274	0.3022
ρ_{mm^*}		0.1567 ± 0.0659	0.2693 ± 0.0674	0.1844 ± 0.0676	0.1655 ± 0.0607	0.3069 ± 0.0722		0.1915 ± 0.0712	0.1492 ± 0.0571
ρ_{am}	−0.3266 ± 0.1196			−0.0647 ± 0.1535	−0.0287 ± 0.2462	0.0360 ± 0.3033		0.0685 ± 0.3277	−0.1361 ± 0.1401
ρ_{am^*}				−0.2091 ± 0.1954	−0.2500 ± 0.2680	−0.4343 ± 0.3636	0.2858 ± 0.0784	−0.4800 ± 0.3984	−0.1429 ± 0.1658
ρ_{cc^*}			−0.2921 ± 0.0466			−0.3023 ± 0.0469	−0.2359 ± 0.0392		
AIC		13 488.65	12 941.69	13 640.61	17 580.27	12 912.08	13 133.08	13 452.93	17 306.63
BIC		13 554.14	13 016.54	13 724.81	17 664.48	13 015.00	13 207.93	13 546.49	17 381.48

Abbreviations: Var = variance, Cov = covariance, a = direct genetic effect, m = maternal genetic effect, c = litter effect, e = residual, p = phenotypic, h^2 = heritability, ρ = correlation, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion.

[*] indicates the parameters associated with the residual variance, that is, the variability of BW.

Table 5

Estimates (mean ± SE) of variance components and correlations in the different models for piglet birth weight (BW) applied to the commercial farm dataset (HO, homoscedastic model; HE, heteroscedastic model).

Parameter	HO	HE_1	HE_2	HE_3	HE_4	HE_5	HE_6	HE_7	HE_8
Var(a)	0.0045 ± 0.0017			0.0052 ± 0.0009	0.0020 ± 0.0010	0.0003 ± 0.0007	0.0053 ± 0.0012	0.0002 ± 0.0007	0.0084 ± 0.0014
Var (m)	0.0233 ± 0.0033	0.0230 ± 0.0022	0.0232 ± 0.0022	0.0399 ± 0.0033	0.0224 ± 0.0030	0.0225 ± 0.0028		0.0223 ± 0.0028	0.0400 ± 0.0036
Var (m*)		0.0372 ± 0.0094	0.0401 ± 0.0095	0.0438 ± 0.0099	0.0938 ± 0.0115	0.0400 ± 0.009	0.0415 ± 0.0101	0.0371 ± 0.0094	0.0994 ± 0.0117
Cov (am)	−0.0012 ± 0.0033			−0.0010 ± 0.0023	0.0003 ± 0.0023	0.0006 ± 0.0019		0.0007 ± 0.0020	−0.0021 ± 0.0028
Cov (am*)				−0.0016 ± 0.0035	−0.0036 ± 0.0049	−0.0015 ± 0.0032	0.0079 ± 0.0026	−0.0013 ± 0.0032	−0.0044 ± 0.0053
Cov (mm*)		0.0118 ± 0.0032	0.0170 ± 0.0034	0.0153 ± 0.0042		0.0177 ± 0.0037		0.0123 ± 0.0035	0.0138 ± 0.0047
Var (c)	0.0100 ± 0.0008	0.0128 ± 0.0009	0.0128 ± 0.0009		0.0117 ± 0.0089	0.013 ± 0.0009	0.0253 ± 0.0012	0.0127 ± 0.0009	
Var (c*)		0.1191 ± 0.0112	0.1218 ± 0.0112	0.1049 ± 0.0108		0.1224 ± 0.0112	0.1305 ± 0.0117	0.1195 ± 0.0113	
Cov (c,c*)			−0.0090 ± 0.0023			−0.0091 ± 0.0023	−0.0055 ± 0.0027		
Var (e)	0.0832 ± 0.0011	0.0911	0.0913	0.0960	0.0931	0.0914	0.0878	0.0912	0.0966
Var (p)	0.1197 ± 0.0022	0.1270	0.1273	0.1391	0.1297	0.1280	0.1184	0.1279	0.1408
h^2_a	0.0375 ± 0.0137			0.0375	0.0154	0.0026	0.0444	0.0019	0.0600
h^2_m	0.1948 ± 0.0261	0.1814	0.1820	0.2869	0.1729	0.1760		0.1740	0.2838
ρ_{mm^*}		0.4027 ± 0.1059	0.5564 ± 0.1054	0.3662 ± 0.0979	0.2949 ± 0.0869	0.5892 ± 0.1159		0.4291 ± 0.1181	0.2197 ± 0.0731
ρ_{am}	−0.1166 ± 0.2561			−0.0725 ± 0.1593	0.0417 ± 0.3406	0.2088 ± 0.7703		0.3246 ± 1.0189	−0.1141 ± 0.1465
ρ_{am^*}				−0.1073 ± 0.2337	−0.2631 ± 0.3568	−0.4064 ± 0.9604	0.5364 ± 0.1677	−0.4345 ± 1.2269	−0.1525 ± 0.1813
ρ_{cc^*}			−0.2275 ± 0.0562			−0.2322 ± 0.0565	−0.0955 ± 0.0479		
AIC		6 712.08	6 444.69	7 084.36	9 852.27	6 468.79	6 706.46	6 716.41	9 605.62
BIC		6 773.30	6 514.66	7 163.07	9 930.99	6 565.00	6 776.43	6 803.86	9 675.58

Abbreviations: Var = variance, Cov = covariance, a = direct genetic effect, m = maternal genetic effect, c = litter effect, e = residual, p = phenotypic, h^2 = heritability, ρ = correlation, AIC = Akaike Information Criterion, BIC = Bayesian Information Criterion.

[*] indicates the parameters associated with the residual variance, that is, the variability of BW.

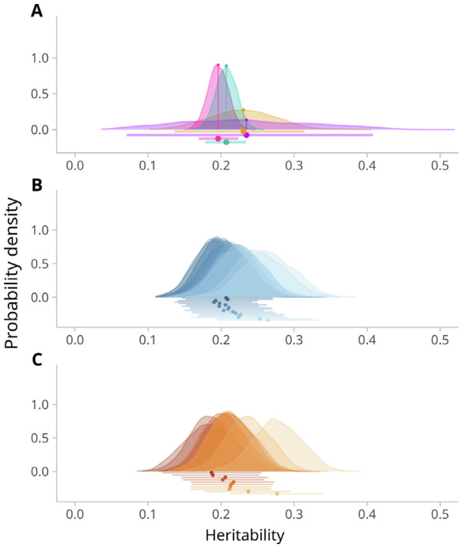

Fig. 3. Posterior distributions of heritability estimates for piglet birth weight at different levels of systematic effects for sex (A), litter size (B), and sow parturition number (C) in the experimental farm dataset. A: turquoise – female, pink – male, purple – hermaphrodite, yellow – sex unknown. B: darker colours indicate larger litter sizes. C: darker colours indicate higher parturition numbers.

of the breeding values using the HE_1 model for the experimental farm dataset. The average accuracies were 0.57 for the mean BW and 0.47 for the BW variability, when the whole pedigree was used, whereas the values were 0.88 and 0.71, respectively, for animals with their own performance. For the commercial farm dataset, the accuracies were 0.47 for the mean BW and 0.33 for the BW variability, when the entire pedigree was used, and 0.80 and 0.56, respectively, for animals with their own performance.

Genetic correlations between mean birth weight and its variability

The model that fitted best was HE_5 in the experimental farm and HE_2 in the commercial farm. Including correlations between both litter effects, that is, for the mean BW and its variability, improved the model's fit to the data, but it also increased the genetic correlations between the mean BW and BW variability (Tables 4 and 5). The genetic correlation between the mean BW and BW variability was always positive and ranged between 0.1492 and 0.3069 for the experimental farm and between 0.2197 and 0.5892 for the commercial farms (Fig. 5). This indicates that with selection pressure for increased BW, the BW variability will also increase. Negative genetic correlations were observed between the direct genetic effect on BW and the maternal effect on BW variance in both datasets and across models, except for HE_6. This finding indicates that, genetically, the increase in BW is linked to a decrease in within-mother variation in her offspring's BW. The genetic correlations between the two genetic effects (direct and maternal) for BW were negative, except in HE_5 and HE_7 for the experimental dataset and in HE_4, HE_5, and HE_7 for the commercial dataset. However, the correlations involving the direct genetic effect on the mean BW and BW variability levels had high SE. In both datasets, the best-fitting model was HE_5, which included both genetic effects for BW, the same random effects for the mean BW and BW variability, and correlations between litter random effects in both datasets.

Discussion

This study aimed to describe the genetic variation in within-litter BW uniformity in two populations of Swiss Large White pigs.

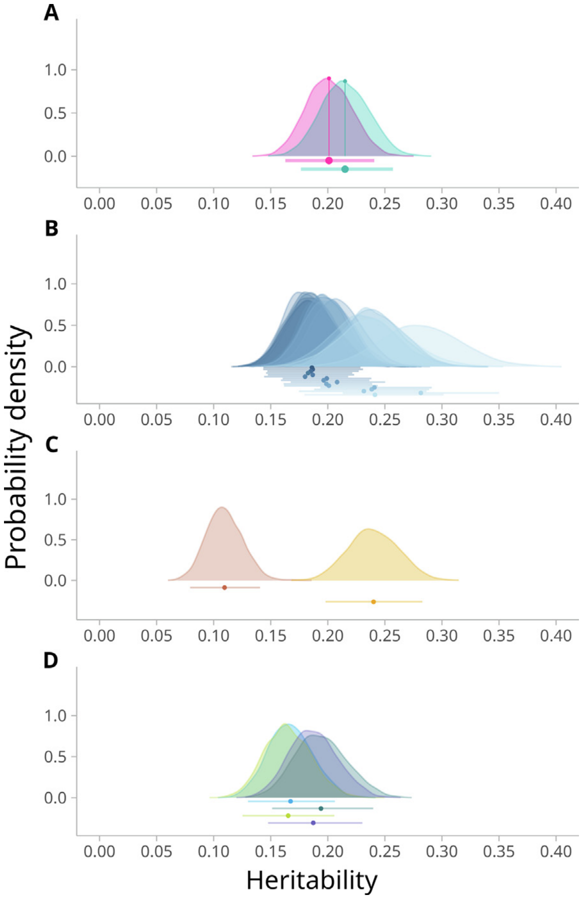

Fig. 4. Posterior distributions of heritability estimates for piglet birth weight at different levels of systematic effects for sex (A), litter size (B), sow age (C), and sire breed (D) in the commercial farm dataset. A: turquoise – female, pink – male. B: darker colours indicate larger litter sizes. Cdarker colours indicate greater sow age. D: sires' breed.

To our knowledge, this is the first time that a heteroscedastic model that includes two correlated genetic effects affecting the mean of a trait has been used together with the genetic component on the residual variance.

Importance of birth weight uniformity

In pigs, BW affects not only piglet survival at birth and until weaning (Moreira et al., 2020; Rutherford et al., 2013; Kapell et al., 2011; Knol et al., 2010) but also the entire production life of the pig (Beaulieu et al., 2010; Quiniou et al., 2002; Lopez-Bote, 1998). Additionally, high within-litter variation can also cause issues during birth (e.g. obstruction of the birth canal by the largest piglets) and lactation (e.g. smaller piglets have lower chances of reaching functional teats) and can increase the overall competition between piglets until weaning (Andersen et al., 2011; Canario et al., 2010). Uniform within-litter BW has also been linked to a reduced occurrence of intrauterine growth retardation, thereby improving piglet prenatal survival (Riddersholm et al., 2021; Matheson et al., 2018). Long-term experiments on two divergent lines of mice have shown that selection for high uniformity of within-litter BW is possible and can lead to increased survival of individuals at birth and until weaning. Additionally, uniformity has been linked to greater embryonic and foetal survival, resulting in animals with greater overall robustness (Formoso-Rafferty et al., 2016, 2022). In the mouse selection experiments, litter size at birth

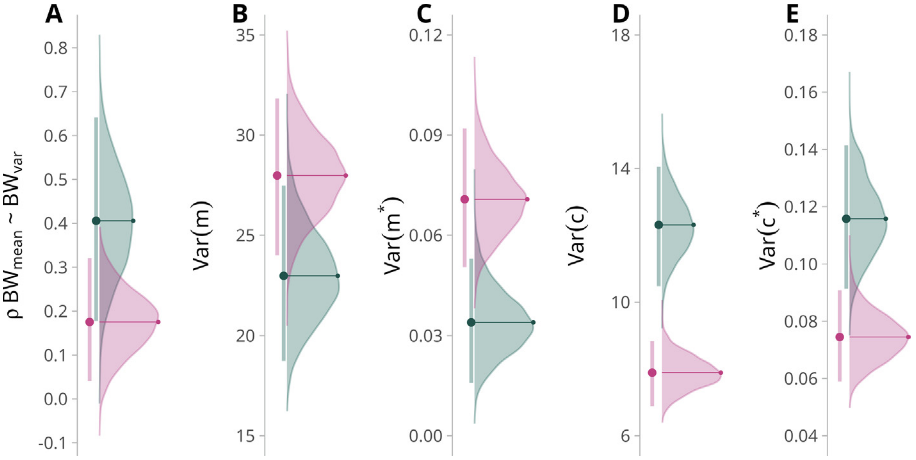

Fig. 5. Genetic parameters of piglet birth weight and birth weight variability on the experimental (pink) and commercial (green) farms. A: genetic correlation between mean birth weight and its variability ($\rho BW_{mean} \sim BW_{var}$), B: maternal genetic variance for the mean BW (Var(m)), C: maternal genetic variance of BW variability (Var(m*)), D: litter effect variance for the mean BW (Var(c)), E: litter effect variance of BW variability (Var(c*)). The axes of B and D are expressed in kg^2x1000.

and weaning was greater in the line selected for increased within-litter BW uniformity than in the line selected for BW heterogeneity and compared with an unselected control line. This finding shows that by selecting for uniformity, it is possible to increase litter size without detrimental effects on BW uniformity (Formoso-Rafferty et al., 2020).

Influence of systematic effects

Our findings indicate that the variability in BW increased with litter size in both datasets (lower heritabilities showed greater residual variance). Litter size has greatly increased in pig populations in recent decades through selection (Knap et al., 2023). However, this has led to high variability in piglet BW within litters (Moreira et al., 2020), thus creating a competitive environment where the smallest individuals lose and die (Riddersholm et al., 2021; Damgaard et al., 2013; Quiniou et al., 2002). The heterogeneity of BW increased with the number of parturitions (experimental farm) and the age of the sow (commercial farms). This has also been observed by Riddersholm et al. (Riddersholm et al., 2021), who reported that BW variability increased after the 5th parturition compared with the 2nd to 4th parturition. For commercial farms, an increase in residual variance with age was observed. With respect to sex, females are born with lower weights than males, which contributes to the heterogeneity (Wittenburg et al., 2011), but females are more homogeneous than males, as shown by the higher heritability estimates. In the case of paternal crossbreeds, we found differences in mean BW and BW variability; the Swiss Large White cross with service sires of other breeds had piglets with higher BW than purebred pigs. In the literature, the crossbreed effect has been shown to be important regarding mean BW and BW variability (Boonkum et al., 2025; Miller et al., 1979). Additionally, hyperprolific lines are more prone to having lower uniformity within-litter BW (Knap et al., 2023; Riddersholm et al., 2021); thus, increasing litter size alone would not be advisable (Sell-Kubiak, 2021).

Genetics of birth weight

In this study, we jointly estimated the direct and maternal genetic effects on piglet BW, which are correlated and contribute to the trait mean. In previous studies, direct heritability varied from 0.01 to 0.13, whereas maternal heritability ranged from 0.16 to 0.28 (Kapell et al., 2011; Knol et al., 2010; Su et al., 2008; Roehe, 1999). In our study, the inclusion of direct additive genetic variance improved the model fit in the experimental farm, but its contribution to the total variance in BW was negligible. Similarly, paternal effects were ignored in our analysis, as previous studies indicated very low variance due to the sire effect on BW (Cieleń and Sell-Kubiak, 2024; Formoso-Rafferty et al., 2023). In both datasets, the additive genetic variance became insignificant when the complete model (HE_5) was fitted, even though the AIC and BIC improved. Thus, we can conclude that the additive genetic effect on BW is negligible compared to the maternal genetic effect on BW. Additionally, the correlations involving the direct effect were not different from 0. These findings allow for the use of a simpler model in the future evaluation of BW.

Genetics of birth weight uniformity

The results of our study show that the within-litter variation in BW in Swiss pigs is very similar to that reported in previous studies on other breeds of pigs (Sell-Kubiak et al., 2015a; Sell-Kubiak et al., 2015b; Kapell et al., 2011; Knol et al., 2010; Su et al., 2008; Roehe, 1999). Most importantly, this trait contains a genetic component that is maternal additive genetic variance, as has been shown previously in pigs (Sell-Kubiak et al., 2015a) and mice (Formoso-Rafferty et al., 2023; Pun et al., 2013). The direct genetic effect on BW variance was not included because repeated records per piglet would be needed to obtain accurate estimates of variance components for BW variability, and the literature indicates issues with including this effect (and corresponding correlations) in the heteroscedastic model (Pun et al., 2013). As reported by us and others (Sell-Kubiak et al., 2015a; Sell-Kubiak et al., 2015b; Kapell et al., 2011; Knol et al., 2010; Su et al., 2008; Roehe, 1999), there is a moderate genetic correlation between the maternal additive effect on mean BW and BW variance. Our study also revealed a difference in this correlation between commercial and experimental farms, which might be due to the timing of piglet weighing; BW data that were not collected 24 h after birth yielded BW levels that were affected by postnatal conditions. However, from a genetic standpoint, the difference in the correlations between the experimental and commercial farm datasets might be due to selection for increased BW on the commercial farms, affecting the magnitude of correlations between mean BW and BW variance.

The positive genetic correlation between the mean BW and BW variability is undesirable, as it will lead to smaller piglets if selection for decreased BW variability is implemented. However, the estimated level of correlation allows for the possibility of selecting for increased mean BW while simultaneously selecting for greater uniformity with the appropriate selection index. This requires the simultaneous selection of both traits. Based on the aforementioned findings in mice, selection for BW uniformity alone appears to be both practical and potentially beneficial to animal welfare. Although such selection may lead to a smaller average BW, the resulting homogeneity within litters could increase survival rates until weaning. Thus, combining selection for greater within-litter uniformity with selection for greater survival at birth—a practice already implemented by breeding companies—could improve piglet survival and robustness, in line with societal demands (EFSA Panel on Animal Health and Welfare (AHAW) et al., 2022).

It is important to mention the greatest difference between the two datasets—handling the information on stillborn piglets. On both farms, stillborn piglets were included in estimating litter size; however, only on the experimental farm was the BW included in the analysis. Stillborn piglets are defined as fully formed animals that died shortly before, during, or shortly after birth. Therefore, accounting for such cases is highly important in BW variability analysis because those piglets develop fully and take up space in the uterus, affecting the amount of space for the growth of other foetuses. However, often due to the specifics of the management of commercial farms in general, the data on the BW of stillborn piglets are not recorded. This crucial difference between datasets could have caused differences in phenotypes of the mean BW and the BW variability estimation, as well as variance components estimation for both traits. For example, heritability estimated based on direct or maternal additive genetic variance was higher in the experimental farm dataset than in the commercial farm dataset. This could indicate that accounting for stillborn piglets in the mean BW provides a better correction for the environmental effects, hence higher heritability. However, running the HE_1 model with the experimental farm dataset but excluding the data on stillborn piglets had a very limited effect on maternal genetic variance. This parameter changed from 0.0747 to 0.0693 after additional data edits (data not shown). Therefore, the difference in handling the data of stillborn piglets did not affect the study results, although it is better to mimic commercial farm procedures regarding such piglets.

Conclusion

Our results suggest that modelling mean BW and BW variability as genetic components of residual variance, while including only the maternal genetic effect for both traits, can yield accurate estimates of BW variability for breeding programmes. This simplification is supported by the fact that the direct additive genetic effect plays a limited role in explaining BW variability. Additionally, despite moderate genetic correlations between the mean and the variance of BW, focusing only on the selection for uniformity in within-litter BW is recommended rather than trying to include both traits simultaneously in the selection index.

Supplementary material

Supplementary Material for this article (https://doi.org/10.1016/j.animal.2025.101651) can be found at the foot of the online page, in the Appendix section.

Ethics approval

The experimental procedure was approved by the Swiss Office for Food Safety and Veterinary Affairs (national licence number 36304), and all procedures were conducted in accordance with the Swiss Ordinance on Animal Protection and the Ordinance on Animal Experimentation.

Data and model availability statement

None of the data were deposited in an official repository. Data are available from the corresponding author upon request and subject to institutional approval.

Declaration of generative AI and AI-assisted technologies in the writing process

The first draft of the manuscript was created without the use of AI. During the revision process, the authors used DeepL and ChatGPT to improve the style and grammar of individual sentences, making the text more concise. The authors then reviewed and edited the content as needed. The authors took full responsibility for the content of the publication.

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Declaration of interest

NK is an employee of Suisag, which provided part of the data and supported its collection, and AL was also employed at Suisag during data preparation. Suisag had no role in the analysis or interpretation of the results. All authors declare no competing interests.

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