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A multivariate gametic model for the analysis of purebred and crossbred data. An example between two populations of Iberian pigs

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Abstract

Crossbreeding plays a pivotal role within pig breeding programmes, aiming to maximize heterosis and improve reproductive traits in crossbred maternal lines. Nevertheless, there is evidence indicating that the performance of reciprocal crosses between two genetic lines might exhibit variability. These variations in performance can be attributed to differences in the correlations between gametic effects, acting as either sire or dam, within purebred and crossbred populations. To address this issue, we propose a multivariate gametic model that incorporates up to four correlated gametic effects for each parental population. The model is employed on a data set comprising litter size data (total number of piglets born—TNB- and number of piglets born alive—NBA-) derived from a reciprocal cross involving two Iberian pig populations: Entrepelado and Retinto. The data set comprises 6933 records from 1564 purebred Entrepelado (EE) sows, 4995 records from 1015 Entrepelado × Retinto (ER) crosses, 2977 records from 756 Retinto × Entrepelado (RE) crosses and 7497 records from 1577 purebred Retinto (RR) sows. The data set is further supplemented by a pedigree encompassing 6007 individual-sire-dam entries. The statistical model also included the order of parity (with six levels), the breed of the service sire (five levels) and the herd-year-season effects (141 levels). Additionally, the model integrates random dominant and permanent environmental sow effects. The analysis employed a Bayesian approach, and the results revealed all the posterior estimates of the gametic correlations to be positive. The range of the posterior mean estimates of the correlations varied across different gametic effects and traits, with a range between 0.04 (gametic correlation between the paternal effects for purebred and the maternal for crossbred in Retinto) and 0.53 (gametic correlation between the paternal effects for purebred and the paternal for crossbred in Entrepelado). Furthermore, the posterior mean variance estimates of the maternal gametic effects were consistently surpassed those for paternal effects within all four populations. The results suggest the possible influence of imprinting effects on the genetic control of litter size, and underscore the importance of incorporating crossbred data into the breeding value predictions for purebred individuals.

KEYWORDS

crossbreeding, gametic correlation, parent of origin, reciprocal cross

1 | INTRODUCTION

The Iberian pig breed is renowned for its adaptability to the natural Mediterranean ecosystem in Southwestern Spain, as well as its product quality (Lopez-Bote, 1998). Despite the Iberian pigs exhibit slower growth, lower feed efficiency and reduced prolificacy compared to other commercial pig populations, their meat quality (Gilles, 2009) and specialized derivative products contribute to their sustainability. However, in recent decades, the traditional extensive production methods that solely relied on purebred Iberian individuals have been partly replaced by intensive farming practices involving crossbreeding with Duroc pigs. The rationale behind this crossbreeding is to enhance growth and efficiency (Serrano et al., 2008). This shift towards intensive farming has yielded several advantages, such the collection of productive data and the implementation of genetic selection programmes. It is important to note that regulatory norms governing the production of Iberian pig products stipulate that the sow must belong to a pure Iberian lineage. This highlights the importance of improving the reproductive efficiency of Iberian sows to ensure the economic sustainability of the breed.

INGA FOOD S.A. is a Spanish company specializing in the production and distribution of premium pig products. As part of their breeding programme, they have successfully developed a hybrid Iberian sow called CASTUA. This hybrid sow is the result of crossbreeding between the Retinto and Entrepelado populations of the Iberian breed. Through this crossbreeding, the CASTUA hybrid sow exhibit improved litter size traits due to heterosis, as confirmed by Noguera et al. (2019). Furthermore, INGA FOOD S.A. is actively implementing a breeding programme with the aim of further enhancing litter size based on the performance of purebred individuals. The foundation of this programme is built upon the assumption of a positive genetic correlation between the performance of purebred and crossbred pigs (Wientjes & Calus, 2017). This hypothesis finds support in a preceding study (Srihi et al., 2022) that quantified the genetic correlation between the performance of purebred and crossbred animals within the Entrepelado and Retinto populations.

Furthermore, as highlighted by Noguera et al. (2019), variations in the performance of reciprocal crosses suggest that the gametic contribution to genetic variance may diverge when the populations act as either sires or dams in the crossbreeding process (Srihi et al., 2023). While previous literature has employed gametic models to identify differences in parent-of-origin effects (Meyer & Tier, 2012; Varona et al., 2015), to the best of our knowledge, these models have not been previously implemented within the context of crossbreeding. Hence, the goal of this study was to develop a multivariate gametic model encompassing both paternal and maternal gametic effects for purebred and crossbred performance. This framework will enable the estimation of gametic correlations between these effects. Additionally, the model will also incorporate a dominance effect.

2 | MATERIALS AND METHODS

The data set used in this study consisted of a total of 22,402 records for two reproductive traits: total number of piglets born (TNB) and number of piglets born alive (NBA). These records were collected from 4912 sows that were part of a complete diallelic experiment involving two strains of the Iberian pig breed: Retinto (RR) and Entrepelado (EE). Additionally, the data set included their reciprocal crosses: Entrepelado × Retinto (ER) and Retinto × Entrepelado (RE). Along with the phenotypic data, a pedigree containing 6007 individual-sire-dam entries was included for genetic analysis. Table 1 provides a summary of the phenotypic data used in this study.

The data were analysed with the following models:

$$
\begin{aligned}
\boldsymbol{y}_{EE} &= \boldsymbol{X}_{EE}\boldsymbol{b}_{EE} + \boldsymbol{Z}_{EE}\boldsymbol{p}_{EE} + \boldsymbol{W}_{EE}\boldsymbol{m}_{EE} + \boldsymbol{Q}_{EE}\boldsymbol{d}_{EE} + \boldsymbol{H}_{EE}\boldsymbol{r}_{EE} + \boldsymbol{e}_{EE} \\
\boldsymbol{y}_{ER} &= \boldsymbol{X}_{ER}\boldsymbol{b}_{ER} + \boldsymbol{Z}_{ER}\boldsymbol{p}_{ER} + \boldsymbol{W}_{ER}\boldsymbol{m}_{ER} + \boldsymbol{Q}_{ER}\boldsymbol{d}_{ER} + \boldsymbol{H}_{ER}\boldsymbol{r}_{ER} + \boldsymbol{e}_{ER} \\
\boldsymbol{y}_{RR} &= \boldsymbol{X}_{RR}\boldsymbol{b}_{RR} + \boldsymbol{Z}_{RR}\boldsymbol{p}_{RR} + \boldsymbol{W}_{RR}\boldsymbol{m}_{RR} + \boldsymbol{Q}_{RR}\boldsymbol{d}_{RR} + \boldsymbol{H}_{RR}\boldsymbol{r}_{RR} + \boldsymbol{e}_{RR} \\
\boldsymbol{y}_{RE} &= \boldsymbol{X}_{RE}\boldsymbol{b}_{RE} + \boldsymbol{Z}_{RE}\boldsymbol{p}_{RE} + \boldsymbol{W}_{RE}\boldsymbol{m}_{RE} + \boldsymbol{Q}_{RE}\boldsymbol{d}_{RE} + \boldsymbol{H}_{\boldsymbol{RE}}\boldsymbol{r}_{RE} + \boldsymbol{e}_{RE}
\end{aligned}
$$

In the given equations, $\boldsymbol{y}_{JK}$ is the vector of phenotypic records (TNB or NBA) for the $JK = \{EE, ER, RR, RE\}$ population. Here, $J = \{E, R\}$ denotes the paternal population, and $K = \{E, R\}$ denotes the maternal. Additionally, $\boldsymbol{b}_{JK}$ is the vector of systematic effects, including order of parity six levels), breed of service sire (five levels) and herd-year-season (141 levels). Moreover, $\boldsymbol{p}_{JK}$, $\boldsymbol{m}_{JK}$, $\boldsymbol{d}_{JK}$, $\boldsymbol{r}_{JK}$ and $\boldsymbol{e}_{JK}$ are the paternal, maternal, dominance, permanent environmental and residual effects of the JK population respectively. It must be noted that $\boldsymbol{p}_{JK}$ is the vector of the paternal gametic effects of the $J = \{E, R\}$ population in the

TABLE 1 Number of phenotypic records (and number of sows producing them in brackets), mean (± standard deviation) of Total Number Born (TNB) and Number Born Alive (NBA) for Entrepelado (EE), Retinto (RR) and Entrepelado × Retinto (ER) and Retinto × Entrepelado (RE) crosses.

	EE	RR	ER	RE
N[a] (NS[b])	6933 (1564)	7497 (1577)	4995 (1015)	2977 (756)
TNB	8.23 ± 2.14	8.44 ± 2.22	8.55 ± 2.27	8.51 ± 2.28
NBA	7.87 ± 2.11	8.05 ± 2.18	8.27 ± 2.25	8.18 ± 2.25

[a] N: number of phenotypic records.

[b] NS: number of recorded sows.

JK cross, and that $\boldsymbol{m}_{JK}$ is the vector of the $K=\{E, R\}$ maternal gametic effects in the $JK=\{EE, ER, RR, RE\}$ cross. Besides, $\boldsymbol{X}_{JK}$, $\boldsymbol{Z}_{JK}$, $\boldsymbol{W}_{JK}$, $\boldsymbol{Q}_{JK}$ and $\boldsymbol{H}_{JK}$ are the corresponding incidence matrices involved in the equations.

The statistical model was analysed by employing a Bayesian approach with a Gibbs sampler (Gelfand & Smith, 1990). In this analysis, bounded uniform distributions were employed as prior distributions for the systematic effects and variance components. The prior distributions for the gametic, dominance, permanent environmental and residual effects were modelled as multivariate Gaussian distributions, characterized by a zero mean and the following variances:

$$var\begin{pmatrix} p_{EE} \\ p_{RR} \\ p_{ER} \\ p_{RE} \\ m_{EE} \\ m_{RR} \\ m_{ER} \\ m_{RE} \end{pmatrix} = \boldsymbol{T} \otimes \boldsymbol{G},\ var\begin{pmatrix} d_{EE} \\ d_{RR} \\ d_{ER} \\ d_{RE} \end{pmatrix} = \boldsymbol{Q} \otimes \boldsymbol{D},$$

$$var\begin{pmatrix} r_{EE} \\ r_{RR} \\ r_{ER} \\ r_{RE} \end{pmatrix} = \boldsymbol{R} \otimes \boldsymbol{I} \text{ and } var\begin{pmatrix} e_{EE} \\ e_{RR} \\ e_{ER} \\ e_{RE} \end{pmatrix} = \boldsymbol{E} \otimes \boldsymbol{I}$$

where $\boldsymbol{G}$ and $\boldsymbol{D}$ are the gametic and dominance relationship matrix (Smith, 1984), $\boldsymbol{I}$ is the identity matrix and

$$\boldsymbol{T} = \begin{bmatrix} \sigma^2_{P_{EE}} & 0 & \sigma_{P_{EE}P_{ER}} & 0 & \sigma_{P_{EE}M_{EE}} & 0 & 0 & \sigma_{P_{EE}M_{RE}} \\ 0 & \sigma^2_{P_{RR}} & 0 & \sigma_{P_{RR}P_{RE}} & 0 & \sigma_{P_{RR}M_{RR}} & \sigma_{P_{RR}M_{ER}} & 0 \\ \sigma_{P_{EE}P_{ER}} & 0 & \sigma^2_{P_{ER}} & 0 & \sigma_{P_{ER}M_{EE}} & 0 & 0 & \sigma_{P_{ER}M_{RE}} \\ 0 & \sigma_{P_{RR}P_{RE}} & 0 & \sigma^2_{P_{RE}} & 0 & \sigma_{P_{RE}M_{RR}} & \sigma_{P_{RE}M_{ER}} & 0 \\ \sigma_{P_{EE}M_{EE}} & 0 & \sigma_{P_{ER}M_{EE}} & 0 & \sigma^2_{M_{EE}} & 0 & 0 & \sigma_{M_{EE}M_{RE}} \\ 0 & \sigma_{P_{RR}M_{RR}} & 0 & \sigma_{P_{RE}M_{RR}} & 0 & \sigma^2_{M_{RR}} & \sigma_{M_{RR}M_{ER}} & 0 \\ 0 & \sigma_{P_{RR}M_{ER}} & 0 & \sigma_{P_{RE}M_{ER}} & 0 & \sigma_{M_{RR}M_{ER}} & \sigma^2_{M_{ER}} & 0 \\ \sigma_{P_{EE}M_{RE}} & 0 & \sigma_{P_{ER}M_{RE}} & 0 & \sigma_{M_{EE}M_{RE}} & 0 & 0 & \sigma^2_{M_{RE}} \end{bmatrix}$$

where $\sigma^2_{X_{JK}}$ represents the paternal ($X=P$) or maternal ($X=M$) gametic variance in the JK population, JK can represent any of the following combinations *{EE, ER, RR, RE}*. Similarly, $\sigma_{X_{JK}Y_{LM}}$ denotes the covariance between the gametic effects between the paternal (if $X=P$) or maternal (if $X=M$) gametic variance in the *JK* cross with the paternal (if $Y=P$) or maternal (if $Y=M$) gametic variance in the LM cross, where *JK* and *LM* can each be *EE, ER, RR* and *RE* respectively. It is essential to emphasize that in this analysis, the covariances between gametic effects from distinct populations (Retinto or Entrepelado) are explicitly fixed at zero, allowing no correlation between them. Conversely, the model allows for non-null covariance between gametic effects from the same population.

Further,

$$\boldsymbol{Q} = \begin{bmatrix} \sigma^2_{d_{EE}} & 0 & 0 & 0 \\ 0 & \sigma^2_{d_{RR}} & 0 & 0 \\ 0 & 0 & \sigma^2_{d_{ER}} & 0 \\ 0 & 0 & 0 & \sigma^2_{d_{RE}} \end{bmatrix},$$

$$\boldsymbol{R} = \begin{bmatrix} \sigma^2_{r_{EE}} & 0 & 0 & 0 \\ 0 & \sigma^2_{r_{RR}} & 0 & 0 \\ 0 & 0 & \sigma^2_{r_{ER}} & 0 \\ 0 & 0 & 0 & \sigma^2_{r_{RE}} \end{bmatrix}, \text{ and}$$

$$\boldsymbol{E} = \begin{bmatrix} \sigma^2_{e_{EE}} & 0 & 0 & 0 \\ 0 & \sigma^2_{e_{RR}} & 0 & 0 \\ 0 & 0 & \sigma^2_{e_{ER}} & 0 \\ 0 & 0 & 0 & \sigma^2_{e_{RE}} \end{bmatrix}$$

with $\sigma^2_{d_{JK}}$, $\sigma^2_{r_{JK}}$ and $\sigma^2_{e_{JK}}$ are the dominance, permanent environmental and residual variances of the *JK* population respectively.

The inverse of the gametic relationship matrix ($\boldsymbol{G}^{-1}$) was calculated using a FORTRAN program that follows the algorithm proposed by Meyer and Tier (2012). The gametic relationship matrix ($\boldsymbol{G}$) was itself calculated by direct inversion using R software (R Core Team, 2021). Subsequently, the elements of $\boldsymbol{G}$ were employed to derive the elements of the dominance relationship matrix ($\boldsymbol{D}$) according to the following expression:

$$d_{ij} = g_{ipjp}g_{imjm} + g_{ipjm}g_{imjp}$$

Here, d_{ij} represents the dominance relationship between the *ith* and *jth* individuals. Specifically, g_{ixjy} signifies the relationship between the gametes of the *ith* individual (paternal or maternal, depending on *x*) and the *jth* individual (paternal or maternal, depending on *y*).

The implementation of the Gibbs Sampler was conducted using the BLUPF90 suite of programs, specifically with the gibbsf90+ program (Misztal et al., 2018). The analysis involved a single long chain comprising 1,100,000 iterations, with the initial 100,000 iterations discarded to guarantee convergence towards the stationary distribution.

During each iteration, the following parameters were calculated:

Ratios of paternal (p^2_{JK}) or maternal (m^2_{JK}) gametic variances for the JK cross

$$p^2_{JK} = \frac{\sigma^2_{p_{JK}}}{\sigma^2_{p_{JK}} + \sigma^2_{m_{JK}} + 2\sigma_{pJKmJK} + \sigma^2_{d_{JK}} + \sigma^2_{r_{JK}} + \sigma^2_{e_{JK}}}$$

$$m^2_{JK} = \frac{\sigma^2_{m_{JK}}}{\sigma^2_{p_{JK}} + \sigma^2_{m_{JK}} + 2\sigma_{pJKmJK} + \sigma^2_{d_{JK}} + \sigma^2_{r_{JK}} + \sigma^2_{e_{JK}}}$$

Ratio of dominance variance (d^2_{JK}) for the JK cross

$$d^2_{JK} = \frac{\sigma^2_{d_{JK}}}{\sigma^2_{p_{JK}} + \sigma^2_{m_{JK}} + 2\sigma_{pJKmJK} + \sigma^2_{d_{JK}} + \sigma^2_{r_{JK}} + \sigma^2_{e_{JK}}}$$

Broad sense heritability (H^2_{JK}) for the JK cross

$$H^2_{JK} = \frac{\sigma^2_{p_{JK}} + \sigma^2_{m_{JK}} + 2\sigma_{pJKmJK} + \sigma^2_{d_{JK}}}{\sigma^2_{p_{JK}} + \sigma^2_{m_{JK}} + 2\sigma_{pJKmJK} + \sigma^2_{d_{JK}} + \sigma^2_{r_{JK}} + \sigma^2_{e_{JK}}}$$

Gametic correlations ($r_{X_{JK}Y_{LM}}$) between the X (paternal—P- or maternal—M-) gametic effects of the from JK population with the Y (paternal—P- or maternal—M-) gametic effects of the LM population

$$r_{X_{JK}Y_{LM}} = \frac{\sigma_{X_{JK}Y_{LM}}}{\sigma_{X_{JK}}\sigma_{Y_{LM}}}$$

3 | RESULTS AND DISCUSSION

3.1 | Variance components

The posterior means (and standard deviations) of the variance components for TNB and NBA are presented in Tables 2 and 3 respectively.

To begin with, it is important to emphasize that the posterior estimates of paternal and maternal gametic variances in both traits were found to be greater in the crossbred populations (ER and RE) when contrasted with the purebred populations (EE and RR). This discrepancy could potentially be attributed to a scale effect (Falconer & Mackay, 1996), since the phenotypic variance is also higher in the crossbred populations. Another contributing factor to this discrepancy is the model's allowance for covariance between the two gametic effects within the purebred populations, which adds twice the value of $\sigma_{X_{JK}Y_{LM}}$ to the genetic variance.

Nevertheless, the outcomes of our analysis demonstrate that both paternal and maternal gametic effects contribute to the phenotypic variability of litter size traits, as evidenced by their posterior distributions significantly deviating from zero. However, it is important to acknowledge

TABLE 2 Posterior means (and standard deviations) of the permanent environmental (σ^2_r), paternal (σ^2_p), maternal (σ^2_m), dominance (σ^2_d) and residual (σ^2_e) variance components for Total Number Born (TNB) in the Entrepelado (EE), Entrepelado × Retinto (ER), Retinto × Entrepelado (RE) and Retinto (RR) populations.

Population	σ^2_r	σ^2_p	σ^2_m	σ^2_d	σ^2_e
EE	0.18 (0.07)	0.14 (0.06)	0.28 (0.07)	0.14 (0.07)	3.50 (0.07)
RR	0.11 (0.04)	0.14 (0.04)	0.20 (0.05)	0.10 (0.04)	4.08 (0.07)
ER	0.14 (0.06)	0.26 (0.09)	0.36 (0.09)	0.13 (0.07)	4.13 (0.09)
RE	0.16 (0.07)	0.15 (0.06)	0.38 (0.10)	0.14 (0.07)	4.17 (0.12)

TABLE 3 Posterior means (and standard deviations) of the permanent environmental (σ^2_r), paternal (σ^2_p), maternal (σ^2_m), dominance (σ^2_d) and residual (σ^2_e) variance components for Number Born Alive (NBA) in the Entrepelado (EE), Entrepelado × Retinto (ER), Retinto × Entrepelado (RE) and Retinto (RR) populations.

Population	σ^2_r	σ^2_p	σ^2_m	σ^2_d	σ^2_e
EE	0.19 (0.07)	0.13 (0.05)	0.24 (0.06)	0.11 (0.06)	3.47 (0.07)
RR	0.11 (0.04)	0.14 (0.04)	0.19 (0.05)	0.11 (0.04)	3.86 (0.07)
ER	0.13 (0.06)	0.26 (0.08)	0.33 (0.08)	0.12 (0.06)	4.01 (0.09)
RE	0.16 (0.07)	0.16 (0.07)	0.35 (0.09)	0.14 (0.06)	3.96 (0.11)

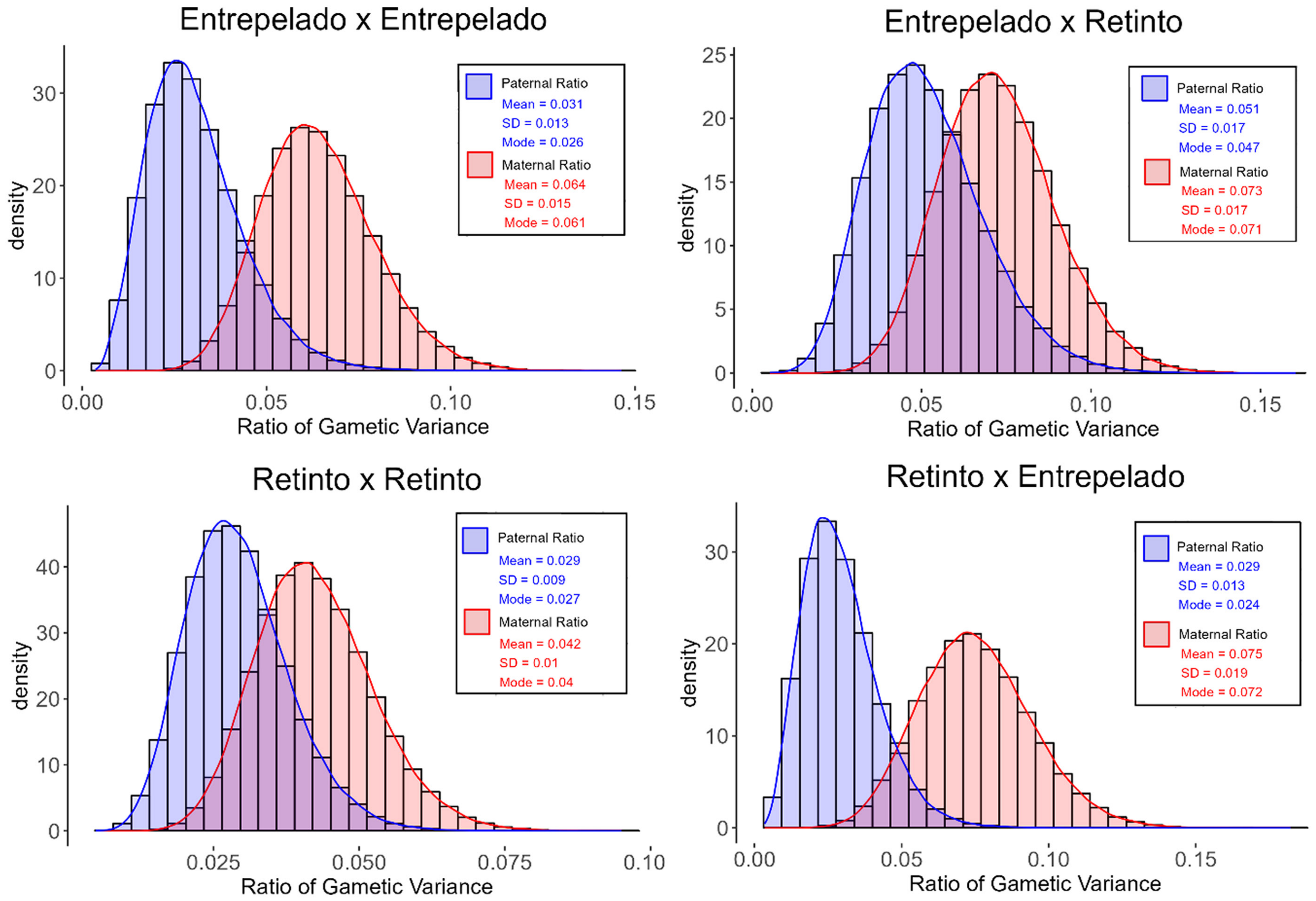

FIGURE 1 Posterior distributions of the ratios of paternal and maternal gametic variances in the Entrepelado × Entrepelado, Entrepelado × Retinto, Retinto × Entrepelado and Retinto × Retinto populations for Total Number Born.

that the variances of maternal gametic variances consistently surpass those of paternal gametic effects. This suggests that the alleles inherited from the mother exert a more pronounced influence on the phenotypic variation of litter size. These findings are further illustrated by the ratios of paternal to maternal gametic variance, visually depicted in Figure 1 for TNB and Figure S1 for NBA.

These findings align with those obtained by Stella et al. (2003) in white pigs, suggesting a similar trend. One plausible explanation for this phenomenon is the potential existence of paternal genomic imprinting (Reik & Walter, 2001), a mechanism ensuring certain alleles are only expressed upon heritance from either the mother or father. Numerous theories have been proposed to elucidate the evolutionary origins of genomic imprinting, comprehensive reviewed by Patten et al. (2014). One of the most prominent being the parental investment theory (Moore & Haig, 1991). In accordance with this theory, imprinting arises due to a conflict between the evolutionary interest of the alleles inherited from the father and those inherited from the mother. Within mammalian reproduction, the evolutionary success of the alleles inherited from the father is associated with augmented foetal growth, while the success of the alleles inherited from the mother is linked with offspring number. This theory finds support in the identification of numerous imprinted genes governing diverse facets of mammalian development (Thamban et al., 2020), encompassing growth, behaviour and placental function (Fowden et al., 2011). Additionally, a growing body of evidence indicating the presence of imprinted genes in the pig genome (Coster et al., 2012; Wu et al., 2020; Zhang et al., 2012) is available.

It is important to underline that the paternal and maternal gametic variances exhibited higher values in the crossbred populations when compared to the purebred populations. As mentioned earlier, this divergence could stem from a scale effect or from the inclusion of covariances between the paternal and maternal gametic effects within the purebred populations. Consequently, the covariance between these effects also contributes to the overall genetic variation. Notably, the posterior distributions of the broad-sense heritabilities showed similar patterns across all purebred and crossbred populations, as there are weighted by the increase of phenotypic variation in crossbreds. The posterior mean estimates spanned from 0.125 in the RR population to 0.160 in the EE population for TNB, and from 0.125 (RR) to 0.149 (EE) for NBA, as depicted in Figure 2 for TNB and Figure S2 for NBA.

These figures also present the posterior distribution of the ratios of dominance variance, featuring posterior mean estimates ranging from 0.021 in RR to 0.031 in EE for TNB, and from 0.024 in RR to 0.029 in RE for NBA. In general, the ratios of dominance variance were modest, indicating that the implementation of a mate allocation procedure (González-Diéguez et al., 2020; Toro & Varona, 2010) to capture favourable dominance effects may yield limited or insignificant results, even if genotyping information were available.

3.2 | Gametic correlations

The proposed model provides the estimates of the gametic covariances and correlations between four gametic effects stemming from each parental population (paternal for purebred, maternal for purebred, paternal for crossbred and maternal for crossbred). Figures 3 and 4 display the posterior distributions of gametic correlations among these four gametic effects for TNB in the Entrepelado and Retinto populations respectively. Furthermore, Figures S3 and S4 provide the posterior distributions of gametic correlations for NBA.

Every posterior mean estimates of the gametic correlations were positive, spanning from 0.04 (paternal gametic effects for purebred and maternal gametic effects for crossbred in Retinto) to 0.53 (paternal gametic effects

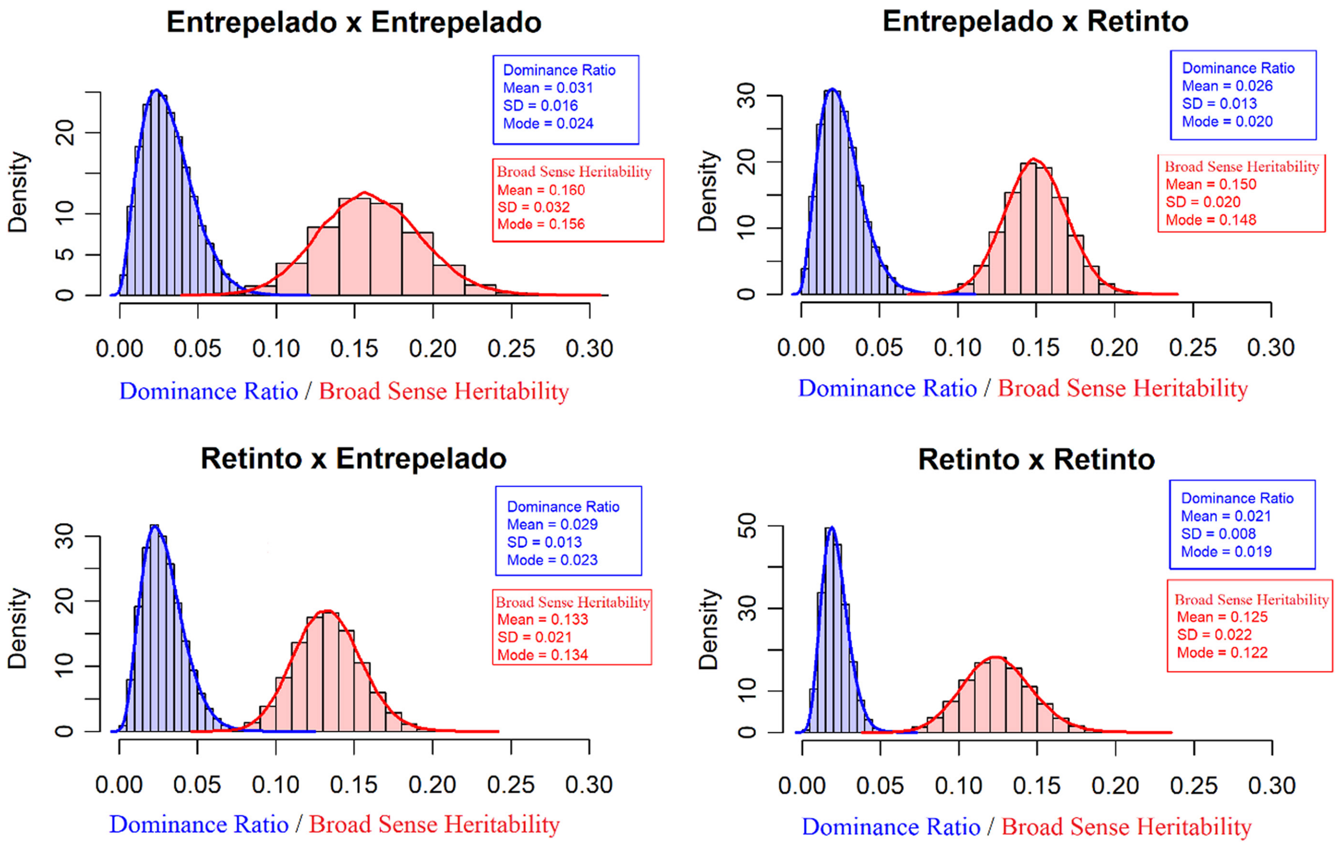

FIGURE 2 Posterior distributions of the broad-sense heritabilities and ratios of dominance variance in the Entrepelado × Entrepelado, Entrepelado × Retinto, Retinto × Entrepelado and Retinto × Retinto for Total Number Born.

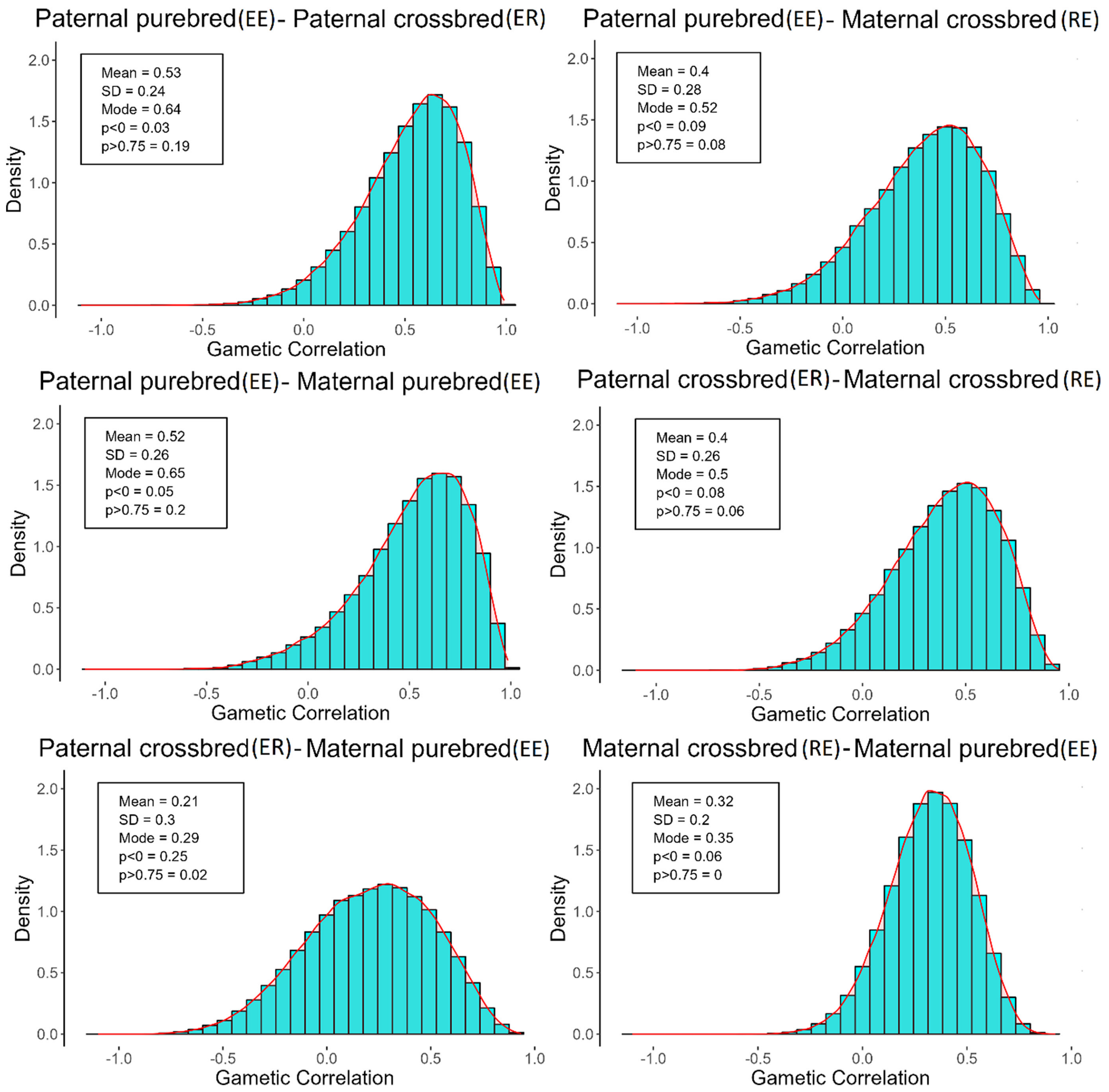

FIGURE 3 Posterior distribution of the correlations between the four gametic from each parental population (paternal for purebred—EE-, maternal for purebred—EE-, paternal for crossbred—ER- and maternal for crossbred—RE-) in the Entrepelado population for Total Number Born.

for purebred and paternal gametic effects for crossbred in Entrepelado). As far as we know, there are no existing estimates of gametic correlations between purebred and crossbred performance available in the literature. However, our estimates fall within the lower range of the genetic correlation estimates for a wide spectrum of traits available in the literature and reviewed by Wientjes and Calus (2017). It is noteworthy that the posterior probability of a gametic correlation surpassing 0.75 was consistently remained below 0.20 for all the gametic correlations. This suggest that selection in the purebred populations might not yield optimal outcomes in the crossbred population. These results differ from those obtained by Srihi et al. (2022); however, it is important to recognize that their study was conducted with a notably smaller data set.

Furthermore, it is interesting to observe that the pattern of gametic correlations differs between purebred and crossbred performance in both populations. Within the Entrepelado population, the gametic effects acting as the sire in the purebred context (paternal for purebred)

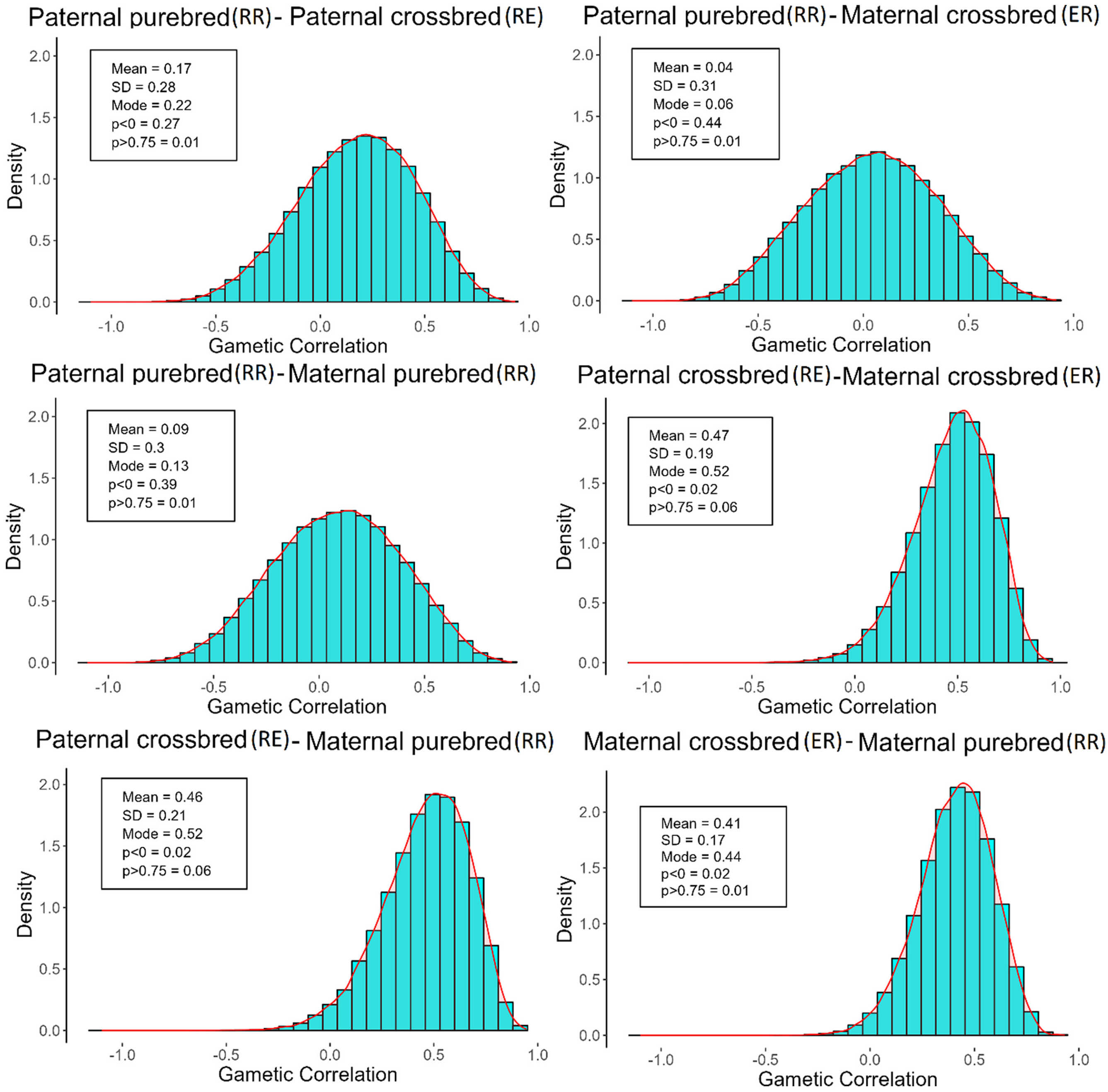

FIGURE 4 Posterior distribution of the correlations between the four gametic from each parental population (paternal for purebred—RR-, maternal for purebred—RR-, paternal for crossbred—RE-, and maternal for crossbred—ER-) in the Retinto population for Total Number Born.

exhibit relatively high correlations with performance within the crossbred population, whether as a sire (posterior mean of 0.53 with paternal for crossbred) or as a dam (posterior mean of 0.40 with maternal for crossbred). Conversely, the correlations involving the gametic effects when acting as the dam within the purebred population (maternal for purebred) were lower with performance in the crossbred population, both as a sire (posterior mean of 0.21 with paternal for crossbred) and as a dam (posterior mean of 0.32 with maternal for crossbred). In contrast, the scenario in the Retinto population was reversed. The correlations between the gametic effects acting as the sire within the purebred population (paternal for purebred) showed lower correlations with the crossbred population (posterior mean of 0.17 with paternal and 0.04 with maternal gametic effects in the crossbred), whereas the gametic effects acting as the dam (maternal for purebred) displayed elevated correlations (posterior mean of 0.46 with paternal and 0.41 with maternal gametic effects in the crossbred).

These findings reinforce the importance of using crossbred data to predict the breeding values of purebred individuals and confirm the need to evaluate them for both purebred and crossbred performance. By doing so, balanced selection strategies can be optimized for crossbreeding purposes. Moreover, the observed diversity in the correlation between gametic effects also suggest the potential influence of imprinting effects, which should be considered in genetic evaluation. These results open up alternative strategies for crossbreeding selection and breeding programme design.

The populations that contribute as sires or dams in crossbreeding should be selected based on the prediction of their gametic effects when performing as sires or dams in the crossbred population respectively. In the example provided, the CASTUA population is commercially produced by crossing Retinto sires with Entrepelado dams. Hence, the selection of the Retinto population should rely on gametic prediction of paternal gametic effects for crossbred, while the Entrepelado population should be selected for maternal gametic effects for crossbred.

In the proposed model, the performance within the purebred populations contributes to the prediction of gametic effects in crossbreeding via gametic covariances (or correlations). Nonetheless, it should be noted that the covariances (or correlations) between gametic effects from different populations (Retinto or Entrepelado in this example) were assumed to be zero. Future research is required to develop a model that integrates genomic information and accounts for potential covariances among these gametic effects, potentially through adaptations of the metafounders analysis (Xiang et al., 2017).

The findings of this study can be summarized as follows: 1) maternal gametic effects consistently exhibit greater variances that paternal gametic effects, indicating a stronger influence of alleles inherited from the mother on litter size, and 2) distinct patterns of gametic correlations were observed between purebred and crossbred performances within the Entrepelado and the Retinto pig populations. These results suggest the potential impact of imprinting effects on the genetic regulation of litter size and underscore the importance of including crossbred data in breeding value predictions for purebred individuals.

AUTHOR CONTRIBUTIONS

Conceptualization: Luis Varona; methodology: Houssemeddine Srihi, David López-Carbonell and Luis Varona; software: Houssemeddine Srihi and Luis Varona; validation: Houssemeddine Srihi, David López-Carbonell and Luis Varona; formal analysis: Houssemeddine Srihi and David López-Carbonell; investigation: Houssemeddine Srihi; resources: Noelia Ibáñez-Escriche and Joaquim Casellas; data curation: Sara Negro, Pilar Hernández and Noelia Ibáñez-Escriche; writing—original draft preparation: Houssemeddine Srihi and Luis Varona; writing—review and editing: Noelia Ibáñez-Escriche, Pilar Hernández and Joaquim Casellas; visualization: David López-Carbonell and Houssemeddine Srihi; supervision: Luis Varona; project administration: Noelia Ibáñez-Escriche and Joaquim Casellas; funding acquisition: Noelia Ibáñez-Escriche and Joaquim Casellas. All authors have read and agreed to the published version of the article.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data set used in this study will be available upon reasonable request to the corresponding author (lvarona@unizar.es).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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