Maternal genetic effects throughout the life of the dam in Pirenaica beef cattle. a random regression model approach

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ABSTRACT

In beef cattle, dams play a crucial role in shaping the pre- and postnatal environment for the growth of their offspring. Acknowledging the substantial impact of maternal influence on the early development of calves, researchers utilize maternal animal models. These models take into account both maternal genetic and permanent environmental effects, operating under the assumption that these influences remain constant throughout the productive life of the cow. Nevertheless, it cannot be ruled out that these genetic and environmental effects may evolve throughout the lifespan of the cows. Therefore, this study aims to describe the changes in genetic and environmental maternal effects over the productive lifespan of cows. To accomplish this goal, we utilized random regression models, incorporating the age of the dam effect, maternal genetic effects, and environmental permanent effects using Legendre orthogonal polynomials. Additionally, the analytical model incorporated a covariate to adjust for the calf's age at recording, a two-level sex effect, a random herd-year-season effect, and an additive direct genetic effect associated linked to the calf. The dataset comprised information from dams aged between 2 and 16 years, resulting in a final database that comprised weight records of 58 332 calves from 21 673 dams. The average weight at 90 days was 135.0 ± 39.3 kg, and the mean age of the dam at calving was 7.03 ± 3.41 years. We evaluated models incorporating 2, 3, 4, 5, and 6 orthogonal polynomials alongside the standard maternal animal model. Afterward, we selected the model with five orthogonal polynomials based on the Akaike Information Criteria. The Restricted Maximum Likelihood estimates within this model indicated a direct heritability of around 0.50, and a maternal heritability ranging between 0.15 and 0.25, exhibiting a consistent increase between 4, 5 to 13 years. The genetic correlation estimates between direct and maternal genetic effects remained stable at approximately −0.55 across the lifespan of the cows. Furthermore, maternal genetic correlations between different ages of the dam decreased to around 0.7 for more distant age points. The maternal permanent correlations were notably lower, occasionally even reaching negative values, suggesting variability in environmental influence on maternal effects over the productive lifespan of the cow. Finally, the model enables the prediction of breeding values for the maternal genetic effects of the cow across its lifespan, providing opportunities for innovative selection strategies on the maternal side.

Implications

The study's findings highlight variations in the genetic and environmental determinism of maternal effects throughout the productive lifespan of the cow. This is evident through the observed increase in maternal heritability between 4, 5 and 13 years and by a correlation between maternal genetic effects at early and older ages of approximately 0.7. Moreover, correlations between maternal environmental effects at different age points were lower and, in some instances, even negative. By accounting for these changes over the cow's lifespan, the proposed model enables the prediction of maternal breeding values for each individual in the population across various ages.

Introduction

In beef cattle, cows play a pivotal role in shaping both prenatal and postnatal environments. This includes providing nutrients for the fetus, the quantity and quality of milk provided to the calf during the preweaning period, as well as offering protection, creating a

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suitable environment, and providing maternal care provided from birth to weaning. Consequently, the genetic variability of weight at early ages is influenced by both the individual and the maternal genotype (Willham, 1963; Koch, 1972). This understanding has led to widespread adoption of the maternal animal model (Meyer, 1992; Waldron et al., 1993; Crews and Wang, 2007), extensively used for modeling early-age weights in beef cattle populations.

The conventional application of the maternal animal model (Crews and Wang, 2007) incorporated several random (direct additive, maternal additive, and maternal permanent environmental effects) and systematic effects, such as age at recording, sex, contemporary group, and age of the dam (Rumph and Van Vleck, 2004). The latter effect accounts for well−known changes in cows' milk production and maternal care, reaching its peak between 6 and 8 years of age and declining thereafter (Kay and M'Candlish, 1929; Lush and Shrode, 1950; Lubritz et al., 1989). Nevertheless, the maternal animal model posits that both the maternal genetic effect and the permanent environmental effects endure unchanged throughout the cow's lifespan. However, a recent study in dairy cattle (Williams et al., 2022) employed random regression models (Schaeffer, 2004; Oliveira et al., 2019) to examine milk yield across multiple lactations. The results indicated a strong pairwise genetic correlation between adjacent parities, but this correlation decreases to levels below 0.7 between distant parities. Considering that the maternal effect in beef cattle is intricately tied to milk production (Miller and Wilton, 1999; MacNeil and Mott, 2006), it can be viewed as a longitudinal trait measured at multiple points throughout a cow's productive life.

Therefore, the primary objective of this study is to describe the progression of maternal genetic and permanent environmental effects throughout the productive life of beef cattle. This will be achieved by employing a random regression model that incorporated the age of the dam, maternal genetic effects, and maternal permanent environmental effects. Moreover, the study aims to compare these results with those obtained from the standard maternal animal model (**SMAM**). The Pirenaica breed was chosen as the model for this investigation.

Material and methods

Dataset

The datasets utilized in this study consisted of phenotypic and pedigree information collected by **CONASPI** (*Confederación Nacional de Asociaciones de Criadores de Raza Pirenaica*). The Pirenaica population is predominantly raised in the vicinity of the Pyrenean Mountain System. The system of production is extensive, although this region is characterized by harsh winter conditions and limited grass availability, necessitating winter housing and supplementation. Calves remain with their dams until weaning at around 5 or 6 months of age. The initial dataset comprises 58 904 BW records of Pirenaica calves, evenly distributed between 46 and 134 days of age. This database underwent filtering to include only calves with dams aged between 2 and 16 years and with BW ranging from 60 to 300 kg. After filtering, the phenotypic dataset included BW records from 58 332 individuals (28 542 males and 29 790 females). There was only one weight recorded per calf, with an average age of 94.65 days and a SD of 24.56 days. The recorded calves were offspring of 21 673 dams, with 14 982 calves also serving as dams for other calves. Among these dams, 13 284 underwent repeated calvings. The average age at parity recorded was 7.03 ± 3.41 years. However, the distribution of dam ages was not homogeneous (see Fig. 1a), because a large proportion of them originated from young cows as a result of culling. Unfortunately, the reasons

of culling are not recorded in the database. The average calf weight was 135.0 ± 39.3 kg and evolved from 120.22 ± 35.23 kg from dams between 2 and 3 years to 141.23 ± 40.01 kg from dams between 8 and 9 years (see Fig. 1b). Additionally, a pedigree comprising 85 670 individual sire-dam entries was utilized. The percentage of unknown sires and dams was 3.94 and 3.26%, respectively. The age of each recorded individual's dam was represented as a linear combination of up to six normalized orthogonal Legendre polynomials (Kirkpatrick et al., 1990; Meyer and Kirkpatrick, 2005), encompassing a range from 2 to 16 years of dam's age.

Model of analysis

Six statistical models were employed to analyze the data, incorporating 1–6 (Np) normalized orthogonal Legendre polynomials to represent the age of dam. It is important to note that the model with 1 polynomial is equivalent to the SMAM. The model of analysis was as follows:

$$y = Xb + Wr + Z_1h + Z_2p + Z_3m + Z_4u + e$$

where y represents a vector of BW, b is a vector of systematic effects encompassing a covariate with the age of recording, a sex effect (two levels) for all models and an age of dam effects (14 levels) for the model with $Np = 1$ (SMAM). The vector r includes the regression coefficients associated with each normalized orthogonal Legendre polynomial, h is a vector of herd year season effects (9 689 levels), p is a vector of random regression coefficients for maternal permanent environmental effects (21 673 levels × Np), m is a vector of random regression coefficients for additive genetic maternal effects (85 670 levels × Np), u is a vector of additive genetic direct effects (85 670 levels), and e is a vector of residuals. Further, X, W, Z_1, Z_2, Z_3 and Z_4 are the corresponding incidence matrices.

The variance of h random variable was given by $var(h) = I\sigma_h^2$, where σ_h^2 is the variance associated with the herd-year-season effects and I is the identity matrix. The variance of the random regression coefficients for the permanent environmental effects (p) was $var(p) = I\otimes P$, where $\otimes$ represents the Kronecker product and P is the $Np \times Np$ matrix of the permanent environmental (co)-variances associated with the normalized orthogonal polynomials, defined as:

$$P = \begin{pmatrix} \sigma_{p(1)}^2 & \sigma_{p(12)} & \cdot & \sigma_{p(1N_p)} \\ \sigma_{p(21)} & \sigma_{p(2)}^2 & \cdot & \sigma_{p(2N_p)} \\ \cdot & \cdot & \cdot & \cdot \\ \sigma_{p(N_p1)} & \sigma_{p(N_p2)} & \cdot & \sigma_{p(Np)}^2 \end{pmatrix}$$

where $\sigma_{p(i)}^2$ represents the permanent environmental variance associated with the ith polynomial and $\sigma_{p(ij)}$ is the covariance between the ith and jth polynomials.

Similarly, the variance of the direct (u) and maternal genetic effects (m) was $var(u, m) = A\otimes G$, where the matrix G is ($Np + 1$) × ($Np + 1$) and represents the genetic (co)variances of the direct genetic effect and the maternal genetic effects linked with the normalized orthogonal polynomials, as follows:

$$G = \begin{pmatrix} \sigma_u^2 & \sigma_{um(1)} & \sigma_{um(2)} & \cdot & \sigma_{um(Np)} \\ \sigma_{um(1)} & \sigma_{m(1)}^2 & \sigma_{m(12)} & \cdot & \sigma_{m(1N_p)} \\ \sigma_{um(2)} & \sigma_{m(21)} & \sigma_{m(2)}^2 & \cdot & \sigma_{m(2N_p)} \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \sigma_{um(Np)} & \sigma_{m(N_p1)} & \sigma_{m(N_p2)} & \cdot & \sigma_{m(Np)}^2 \end{pmatrix}$$

where σ_u^2 is the direct genetic variance, $\sigma_{m(i)}^2$ is the maternal genetic variance associated with the ith polynomial, $\sigma_{um(i)}$ is the covariance
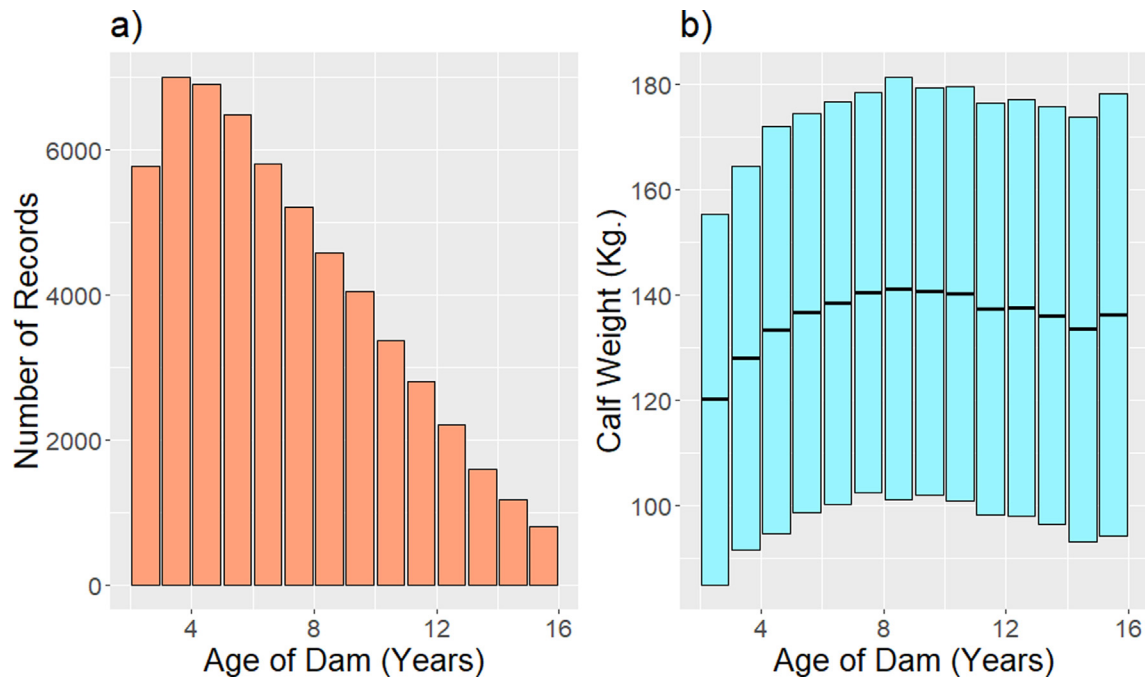
Fig. 1. Number of Records (Fig. 1a) and average ± one SD of calf weight (Fig. 1b) categorized by the dam's age at calving in the Pirenaica population.

between the direct genetic effects and maternal effects associated with the *ith* polynomial, and $\sigma_{m(ij)}$ is the covariance between the maternal effects associated with the *ith* and the *jth* polynomials. It is crucial to note that the dimensions of the **P** and **G** matrices, as well as the *p*, *m*, and *r* vectors, depend on the number of orthogonal polynomials included in the analysis. Finally, the variance of the residuals (**e**) was specified as $var(\mathbf{e}) = \mathbf{I}\sigma_e^2$. The residual variance (σ_e^2) was assumed to be constant across the dam's age, under the assumption that all environmental influences associated with the dams are encompassed by the permanent environmental and genetic maternal effects. Additional possibilities were considered, including modeling direct genetic effects using a random regression approach based on: a) the age of the dam, and b) the age of the calf. However, we opted to exclude the first option under the assumption that direct genetic effects are not influenced by the age of the dam. Furthermore, the relevance of the second option would only emerge if multiple records per individual were accessible.

Six models were implemented by specifying the number of orthogonal regression coefficients (1, 2, 3, 4, 5 and 6). The estimation of the variance components was conducted using the AIREML algorithm (Gilmour et al., 1995) after 100 iterations with the EM algorithm (Dempster et al., 1977). The analysis was conducted using the BLUPF90 + software (Misztal et al., 2018). The four models were compared using the Akaike Information Criterion (**AIC**) (Akaike, 1974).

Once the best model has been selected, the estimates of the age of dam effect ($\widehat{ag}_i$) at the *ith* age are calculated as $\hat{ag}_i = \mathbf{t_i}\hat{\mathbf{r}}'$, where $\mathbf{t_i}$ is a vector containing the orthogonal polynomials calculated at the *ith* age point and $\hat{\mathbf{r}}$ is the vector of solutions for the regression coefficients associated with each polynomial. Additionally, the estimates of the permanent environmental ($\hat{\Psi}_{ii}$) and maternal ($\hat{\Sigma}_{ii}$) variances at the *ith* age point were as follows:

$$\hat{\Psi}_{ii} = \mathbf{t_i}\hat{\mathbf{P}}\mathbf{t'_i} \text{ and } \hat{\Sigma}_{ii} = \mathbf{t_i}\hat{\mathbf{G_m}}\mathbf{t_i}'$$

where $\hat{\mathbf{G_m}}$ is the $Np \times Np$ submatrix of the $\hat{\mathbf{G}}$ matrix associated with the maternal orthogonal coefficients.

Moreover, the permanent environmental covariance ($\hat{\Psi}_{ij}$) and maternal genetic (co) variances ($\hat{\Sigma}_{ij}$) between the *ith* and the *jth* age points were as follows:

$$\hat{\Psi}_{ij} = \mathbf{t_i}\hat{\mathbf{P}}\mathbf{t'_j} \text{ and } \hat{\Sigma}_{ij} = \mathbf{t_i}\hat{\mathbf{G_m}}\mathbf{t_j}'$$

These estimates were used to calculate the permanent environmental ($\widehat{Cor(p)}_{ij}$) and maternal genetic correlation ($\widehat{Cor(m)}_{ij}$) between the *ith* and the *jth* age points as:

$$\widehat{Cor(p)}_{ij} = \frac{\hat{\Psi}_{ij}}{\sqrt{\hat{\Psi}_{ii}\hat{\Psi}_{jj}}} \text{ and } \widehat{Cor(m)}_{ij} = \frac{\hat{\Sigma}_{ij}}{\sqrt{\hat{\Sigma}_{ii}\hat{\Sigma}_{jj}}}$$

The estimated genetic covariance $co\,\hat{v}(u,m)_i$ between the additive genetic effects (u) and the maternal genetic effects at the *ith* age (m_i) was calculated as:

$$co\,v(\hat{u},m)_i = \mathbf{t_i}\hat{\mathbf{g}}'_{1,2:\mathbf{Np+1}}$$

where $\mathbf{t_i}$ represents the normalized orthogonal polynomials at *ith* age, and

$$\hat{\mathbf{g}}'_{1,2:\mathbf{Np+1}} = \begin{pmatrix} \hat{\sigma}_{um(1)} \\ \hat{\sigma}_{um(2)} \\ . \\ \hat{\sigma}_{um(Np)} \end{pmatrix}$$

Given these estimates, the maternal ($\hat{m}_i^2$) and direct heritability ($\hat{h}_i^2$) at the *ith* age point are calculated as:

$$\hat{m}_i^2 = \frac{\hat{\Sigma}_{ii}}{\hat{\Sigma}_{ii} + \sigma_u^2 + co\,\hat{v}(u,m)_i + \hat{\Psi}_{ii} + \sigma_h^2 + \sigma_e^2}$$

$$\hat{h}_i^2 = \frac{\sigma_u^2}{\hat{\Sigma}_{ii} + \sigma_u^2 + co\,\hat{v}(u,m)_i + \hat{\Psi}_{ii} + \sigma_h^2 + \sigma_e^2}$$

and the genetic correlation between the additive genetic effects and the maternal genetic effect at the *ith* age was calculated as:

$$Cor\widehat{(u,m)}_i = \frac{co\widehat{v(u,m)}_i}{\sqrt{\hat{\sigma}_u^2 \hat{\Sigma}_{ii}}}$$

Finally, the breeding values $(\widehat{bv}_{ij})$ for the *ith* individual at the *jth* age were calculated as:

$$\hat{b}v_{ij} = \boldsymbol{t_j m_{i\prime}}$$

where $\boldsymbol{m_i}$ is the vector of the maternal breeding values associated with the orthogonal polynomials for the *ith* individual. The confidence intervals for the effect of the age of dam, variances components, maternal heritability, and the ratio of permanent maternal environment were computed using the procedure proposed by Fischer et al. (2004). This is based on the average information matrix generated by the BLUPF90 + software (Misztal et al., 2018).

Results and discussion

The results of the model comparison, assessed through the AIC (Akaike, 1974) obtained from the BLUPF90 + software, revealed that the model incorporating 5 Legendre orthogonal polynomials (AIC = 537 312.61) provided a superior fit compared to the models with 4 (AIC = 537 371.39) and 6 (AIC = 537 322.19) polynomials. The model with one polynomial (SMAM) showed a poorer fit (AIC = 537 584.60), while models with 2 and 3 polynomials fared even worse (539 040.00 and 537 849.37, respectively). The AIC procedure selects the best model by balancing model complexity with the available information. Consequently, all subsequent results will pertain to the model with five orthogonal polynomials, and it will be compared with the SMAM.

The results of the age of dam effect in the calf weight, along with its corresponding confidence interval, ranging from 2 to 16 years of life, are depicted in Fig. 2. It reveals that the age of the dam effect is lowest in very young dams and rapidly increases
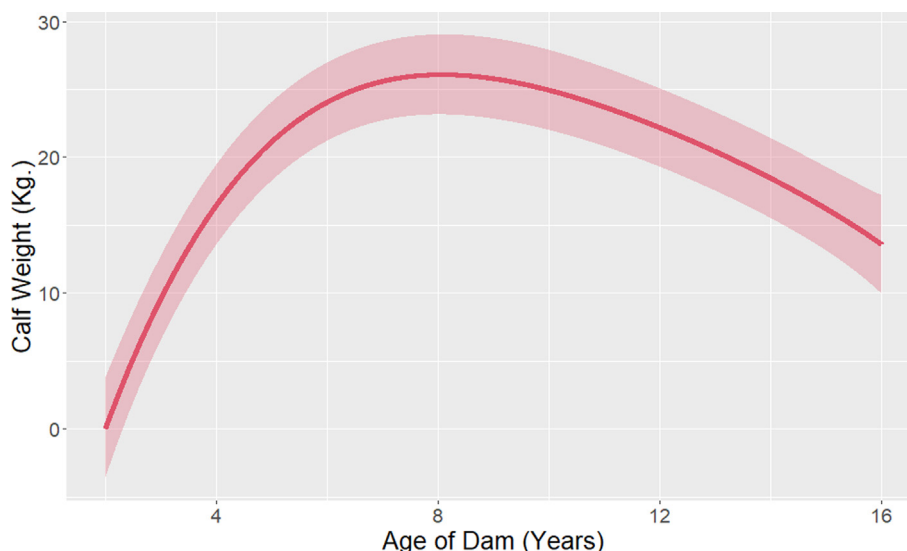

Fig. 2. Estimates of the age of dam effect between 2 and 16 years for weight at 90 days in the Pirenaica population with the model featuring five orthogonal polynomials, along with its 95% confidence interval.

Table 1
Estimates and SE (between brackets) of the permanent environment variances (diagonal) and covariances (upper diagonal) for weight at 90 days in the Pirenaica beef cattle population within the **P** matrix and associated with five orthogonal polynomials.

Item	1 (1st Pol.)	2 (2nd Pol.)	3 (3rd Pol.)	4 (4th Pol.)	5 (5th Pol.)
1 (1st Pol.)	53.93 (6.98)	10.31 (3.94)	−15.31 (3.32)	3.57 (2.58)	−2.51 (2.41)
2 (2nd Pol.)	–	25.58 (3.93)	−4.24 (2.17)	−6.70 (2.17)	−8.89 (1.94)
3 (3rd Pol.)	–	–	9.38 (2.08)	1.13 (1.56)	3.80 (1.46)
4 (4th Pol.)	–	–	–	13.65 (2.14)	−3.33 (1.34)
5 (5th Pol.)	–	–	–	–	8.98 (1.59)

Abbreviations: Pol = Polynomial.

Table 2
Estimates and SE (between brackets) of the genetic variances (diagonal) and covariances (upper diagonal) for weight at 90 days in the Pirenaica beef cattle population within the **G** matrix and associated with five orthogonal polynomials.

Item	1 (Direct)	2 (1st Pol.)	3 (2nd Pol.)	4 (3rd Pol.)	5 (4th Pol.)	6 (5th Pol.)
Direct	411.24 (18.53)	−214.19 (16.56)	−0.10 (8.05)	12.12 (8.45)	18.64 (4.93)	−2.93 (4.69)
1 (1st Pol.)	–	262.07 (19.29)	15.22 (6.83)	−14.30 (7.14)	−16.40 (4.26)	−0.03 (3.95)
2 (2nd Pol.)	–	–	16.72 (3.05)	−5.52 (2.25)	−2.80 (1.36)	−2.96 (1.26)
3 (3rd Pol.)	–	–	–	15.63 (3.02)	−2.35 (1.27)	3.51 (1.28)
4 (4th Pol.)	–	–	–	–	6.27 (1.18)	−1.90 (0.77)
5 (5th Pol.)	–	–	–	–	–	4.20 (0.89)

Abbreviations: Pol = Polynomial.

until reaching a peak at around 8 years, followed by a gradual decline. The difference between the maximum and minimum age of dam effect was over 26 kg., aligning with the phenotypic differences depicted in Fig. 1b. The impact of the age of the dam on the weight at early ages in beef cattle is well-documented in the scientific literature. The results of our study closely align with previous studies in the field (Gregory et al., 1978; Szabó et al., 2006; Morales et al., 2013) and are consistent with estimates of the evolution of the milk yield along the productive life of the cows (Lubritz et al., 1989; Williams et al., 2022).

The Restricted Maximum Likelihood (**REML**) estimates, along with ± SE, for the herd-year-season and residual variance under the model with five orthogonal polynomials were 166.66 ± 3.84 and 169.76 ± 9.36, respectively. In comparison, under the SMAM, these estimates were 170.88 ± 3.91 and 193.92 ± 9.78, respectively. The REML estimates, along with their SE, of the elements of the P and G matrices under the model with five orthogonal polynomials are presented in Tables 1 and 2.

It should be noted that the element (1,1) of the G matrix (411,24 ± 18.53) corresponds to the direct additive genetic variance. Given the REML estimates of P alongside the average information matrix, Fig. 3 illustrates the evolution of the permanent maternal environmental variance and its corresponding confidence interval across the parameter range of 2–16 years, compared with the result of the permanent maternal variance under the SMAM (33.79 ± 5.40).

The highest maternal environmental variance was observed in very young dams. However, it is essential to note that estimates near the boundaries of the parameter range may offer less reliable information, and it is well−known that such estimates tend to be overestimated (Misztal, 2006; Oliveira et al., 2019). The smallest maternal environmental variance was observed around 3 years of life, and subsequently, it increases and remains relatively stable between approximately 5–11 years and reaches a peak around 13–14 years. Under the SMAM, the maternal environmental variance was lower than the ones achieved with the random regression model in most of the parametric space (Fig. 3). The reason behind
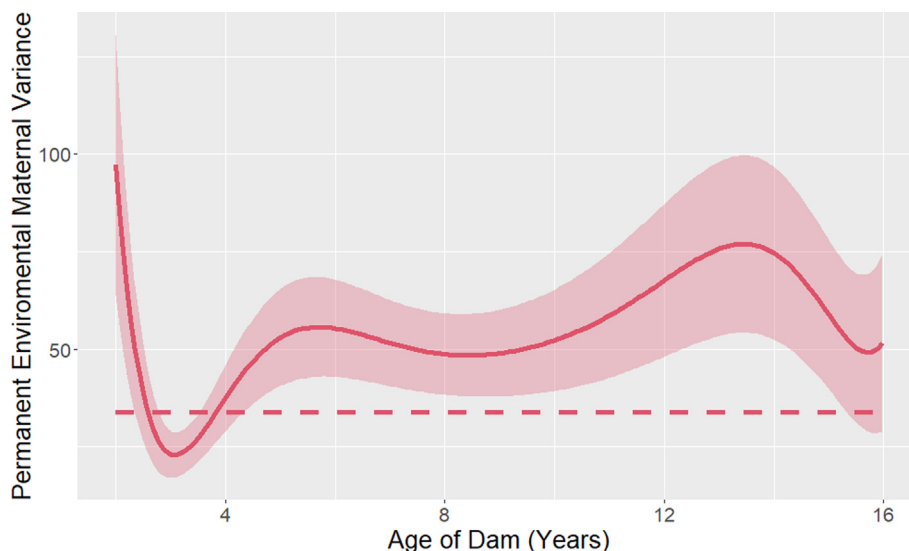

Fig. 3. Estimates of the permanent maternal environment variance for weight at 90 days in the Pirenaica population under the model with five orthogonal polynomials between 2 and 16 years of age, along with its 95% confidence interval and the estimate under the standard maternal animal model (dashed line).
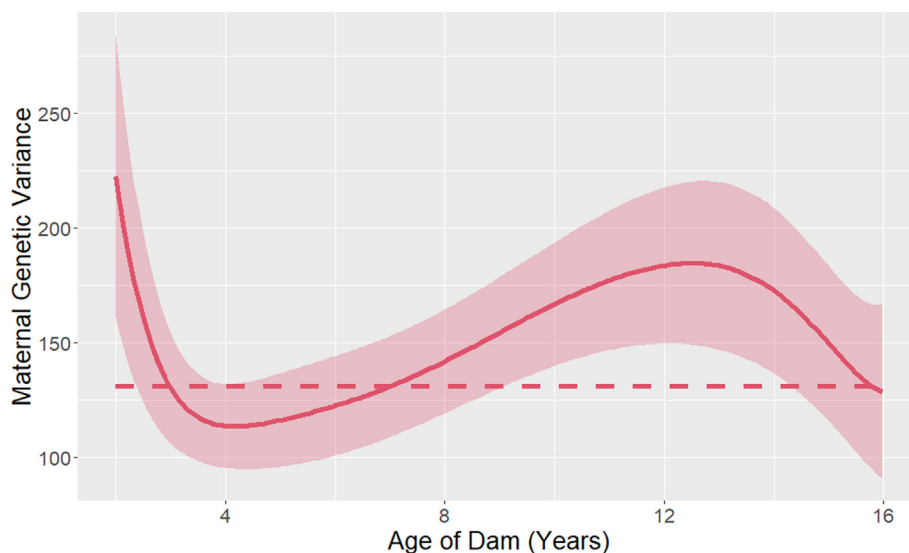

Fig. 4. Estimates of the maternal genetic variance under the model for weight at 90 days in the Pirenaica population with five orthogonal polynomials between 2 and 16 years of age, along with its 95% confidence interval and the estimate under the standard maternal animal model (dashed line).

this lower estimate with SMAM is that it assumes the permanent environmental effects are uniform throughout the productive lifespan, whereas the random regression model merely allows for the possibility of correlation among them. As a result, the permanent maternal environmental component under the SMAM cannot fully account for all the environmental variance associated with the dam.

Fig. 4 illustrates the evolution of the maternal genetic variance and its corresponding confidence interval throughout the productive lifespan of the cows. Despite the extreme values observed at the beginning of the parameter range, it is evident that the maternal genetic variance exhibits a consistent upward trend with the age of the dam. Specifically, it increases steadily from around 4 years to 13 years, and then starts to decline again. The increase in maternal genetic variance with the age of the dam was also reported by Morales et al. (2013) when analyzing the first six par-

ities in the Retinta Population. One potential explanation for these differences in the maternal genetic variability could be that some cows may experience a decline in milk production or maternal ability as they age, while others maintain them at older ages. These differences in performance as they age can be understood as a heritable quantitative trait. Moreover, a large proportion of the cows are culled before reaching 10 or 12 years, and the estimate under the SMAM model aligns better with the estimates in early ages (131.35 ± 13.54).

The changes in the maternal genetic variance with the age of the dam are also apparent in the estimates of the maternal heritability presented in Fig. 5. The average maternal heritability was approximately 0.20, ranging between 0.15 and 0.25 with a consistent increase between 4.5 and 13 years approximately. These estimates were consistent with the findings of previous studies in beef cattle (Meyer, 1992; Robinson, 1996; Gutiérrez et al., 2007). Fig. 5
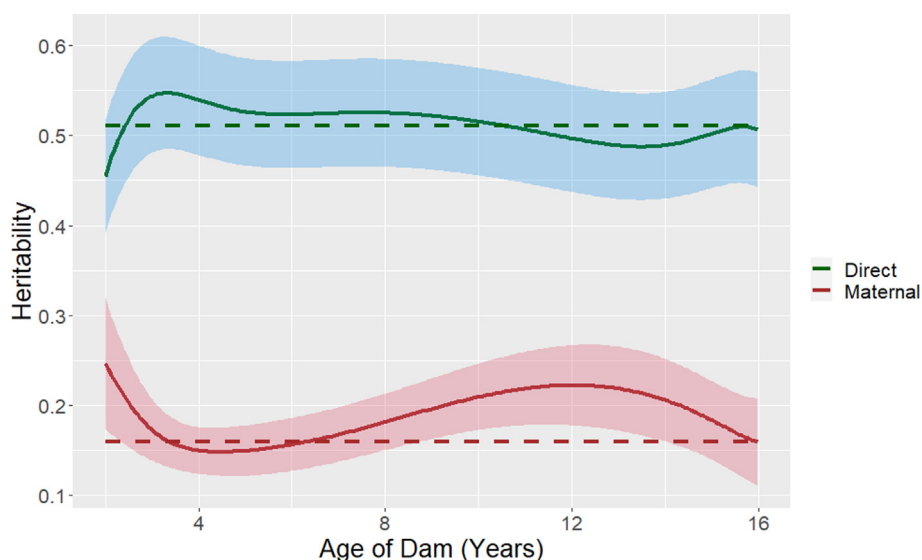

Fig. 5. Estimates of the direct and maternal heritabilities under the model for weight at 90 days in the Pirenaica population with five orthogonal polynomials between 2 and 16 years of age, along with its 95% confidence interval and the estimates under the standard maternal animal model (dashed lines).

Fig. 6. Estimates of the direct-maternal genetic correlation under the model for weight at 90 days in the Pirenaica population with five orthogonal polynomials between 2 and 16 years of age, along with its 95% confidence interval and the estimate under the standard maternal animal model (dashed line).
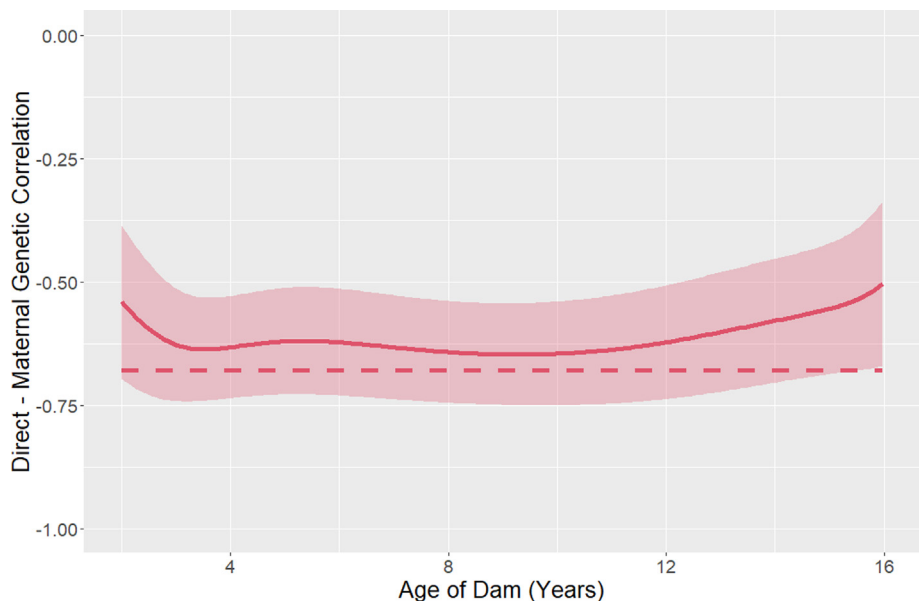
also illustrates the evolution of direct heritability, following a complementary pattern and fluctuating between 0.45 and 0.55, within the upper range of previous estimates of direct heritability for weaning weight (Utrera and Van Vleck, 2004).

The evolution of the direct maternal genetic correlation throughout the productive lifespan of the cows is illustrated in Fig. 6. The estimates of the direct-maternal genetic correlations ranged between −0.50 and −0.65, slightly higher than the estimate under the SMAM model (−0.68). The presence of strong negative genetic correlations between direct and maternal effects is common in beef cattle populations (Robinson, 1996; Bonifazi et al., 2021). In the literature, there are several theories to explain these genetic correlations, including the presence of environmental covariances between the dam and offspring (Quintanilla et al., 1999; Bijma, 2006), sire and herd association (Robinson, 1996), the effect of parent of origin effects (Varona et al., 2015) or data structure (Gerstmayr, 1992; Clément et al., 2001). Here, the results confirm this negative genetic correlation, and no relevant differences were found throughout the productive lifespan of the cows.

Furthermore, Fig. 7 presents a heatmap of the estimates of the permanent maternal correlations across the productive lifespan of the cows. As it is showed in the figure, the permanent maternal correlations decrease to very low values, even turning negative, between distant permanent environmental effects, such as those between the permanent maternal environmental effects at 2 and 14 years. These results indicate that the environmental effects associated with dams are strongly correlated among adjacent parities, but they can become much weaker or even negative between distant parities. In other words, a positive maternal environmental influence from a young dam may transition to a negative one as the

cow ages, and vice versa. Hence, the assumption of a constant permanent environmental effect in the SMAM may be erroneous, potentially introducing bias into the prediction of maternal breeding values. Additionally, as mentioned earlier, the low permanent environmental correlations among different ages of the dam imply that the permanent environmental variance in the standard maternal animal will be significantly lower (see Fig. 3). This is because it is assumed to remain constant throughout the productive life of the cows. They also explain the differences in the estimates of the residual variance (169.76 ± 9.36 in the random regression model and 193.92 ± 9.78 in the standard maternal animal model).

A heatmap of the estimates of the maternal genetic correlations across the productive lifespan of cows is presented in Fig. 8. The genetic correlations among adjacent age points were consistently large and positive, decreasing with the distance between age points. However, in contrast with the permanent environmental correlations, the maternal genetic correlations consistently remained above 0.6, reaching the lowest values between the early age points and older ages. This result aligns with previous findings (Carlén et al., 2004; Williams et al., 2022), which demonstrated that the genetic correlation for milk yield between the first lactation and subsequent ones was lower compared to the correlation between lactations over the second. This difference can be attributed to the fact that cows are not fully mature during their first lactation.

The structure of maternal genetic variances and covariances described above implies that the maternal genetic breeding values of individuals change along the productive lifespan of the cows. Changes in the maternal breeding values across the productive lifespan of the cows imply that the anticipated maternal perfor-
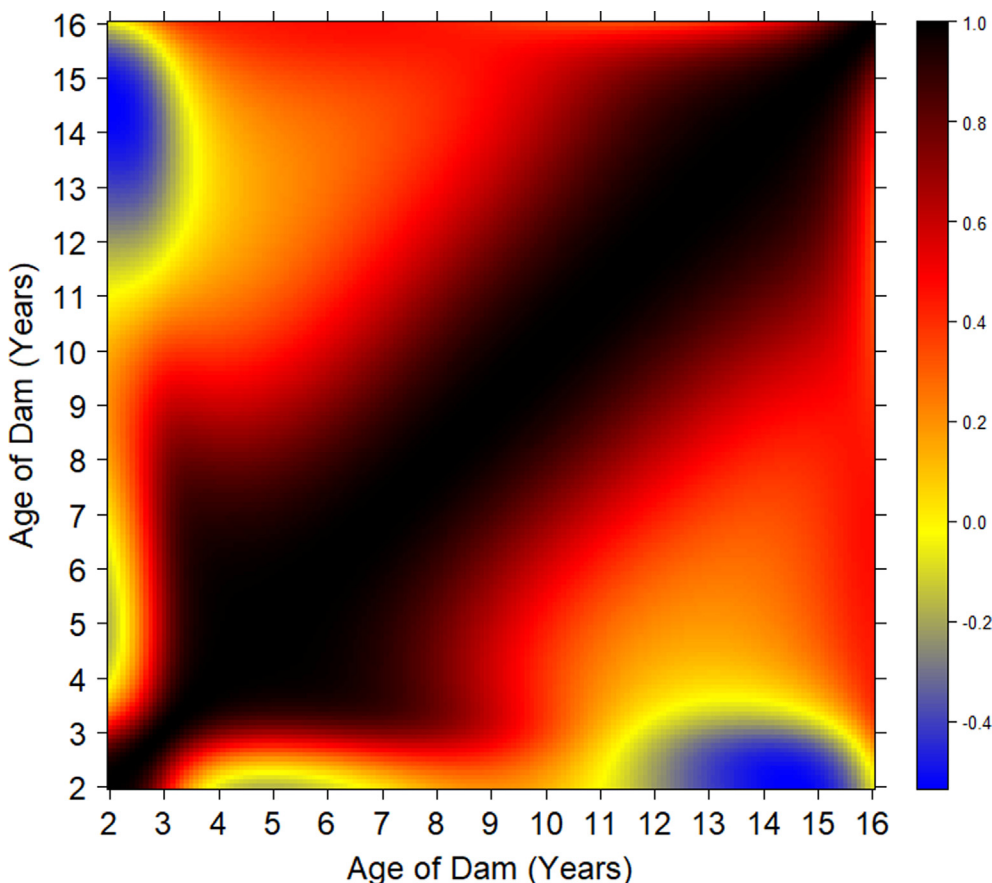

Fig. 7. Heatmap of the estimates of the maternal permanent environmental correlations across the productive lifespan of the cows under the model with five orthogonal polynomials.
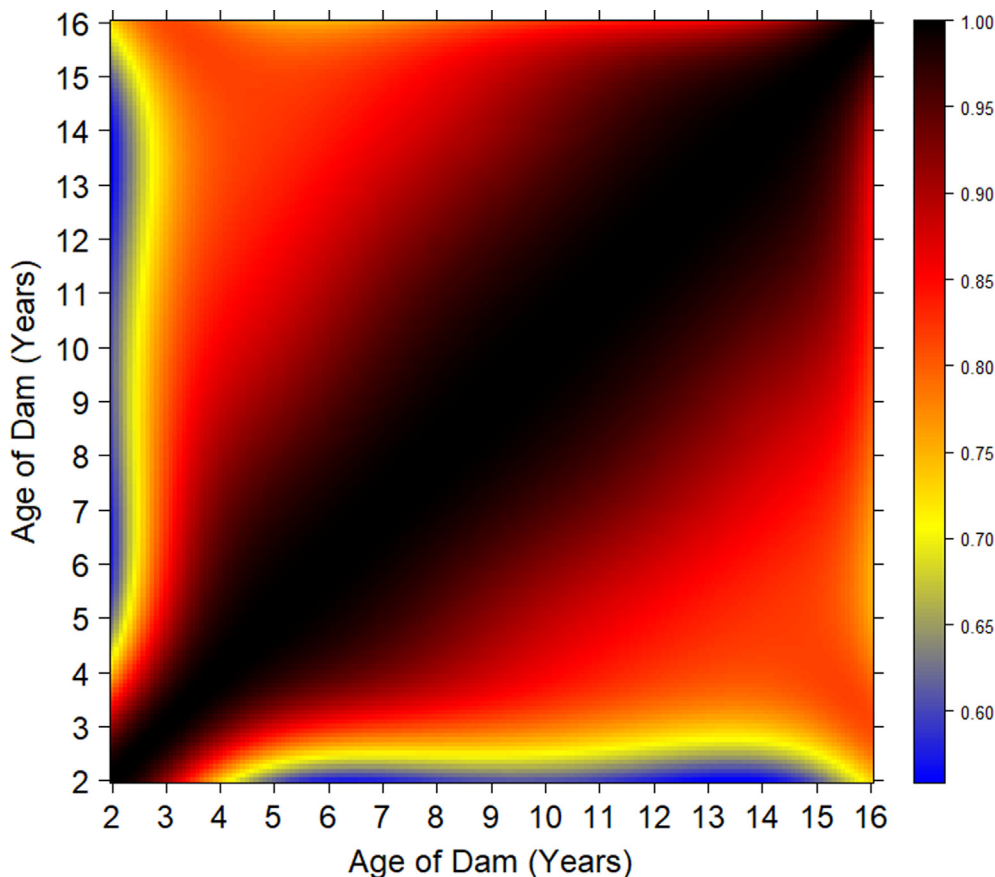
Fig. 8. Heatmap of the estimates of the maternal genetic correlations across the productive lifespan of the cows under the model with five orthogonal polynomials.
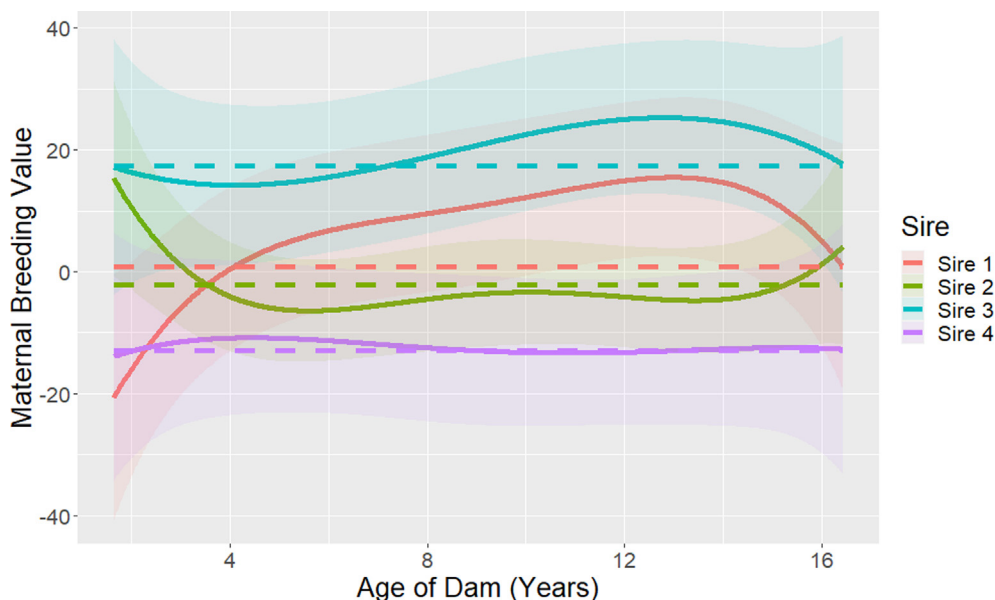

Fig. 9. Evolution of the estimates of the maternal breeding values between 2 and 16 years for four chosen sires of the Pirenaica beef cattle population, along with its 95% confidence interval and the estimates under the standard maternal animal model (dashed lines).

mance can vary, depending on the expected longevity of future cows. One of the crucial aspects in the management of a beef cattle is the definition of culling strategies, which depends on various economic and productive circumstances (Sessim et al., 2020). With this model, selection criteria can be defined based on the expected age structure or cow longevity within the population.

To illustrate this phenomenon, we selected four sires based on the following criteria: 1) the sire with the largest positive difference between maternal breeding values at 3 and 14 years (sire 1), 2) the sire with the most negative difference between maternal breeding values at 3 and 14 years (sire 2), 3) the sire exhibiting the highest maternal breeding values under the SMAM, and 4) the sire

Table 3
Pearson (upper diagonal) and Kendall rank (below diagonal) correlations between the predicted maternal effects for weight at 90 days in the Pirenaica beef cattle population at 3, 6, 9, 12 and 15 years and those from the SMAM in all individuals.

Item	3 yr	6 yr	9 yr	12 yr	15 yr	SMAM
3 yr	–	0.927	0.872	0.868	0.854	0.968
6 yr	0.766	–	0.976	0.949	0.889	0.961
9 yr	0.679	0.858	–	0.983	0.889	0.930
12 yr	0.676	0.795	0.883	–	0.943	0.921
15 yr	0.670	0.699	0.695	0.785	–	0.878
SMAM	0.836	0.866	0.792	0.772	0.708	–

Abbreviations: yr = years; SMAM: Standard Maternal Animal Model.

Table 4
Percentage of concordance within the 10% (upper diagonal) and 25% (below diagonal) sires within the 622 sires with more than 25 recorded progeny at 3, 6, 9, 12 and 15 years and with the standard maternal animal model (SMAM).

Item	3 yr	6 yr	9 yr	12 yr	15 yr	SMAM
3 yr	–	81.3%	72.9%	76.1%	74.8%	87.7%
6 yr	71.0%	–	89.0%	85.8%	78.1%	89.6%
9 yr	64.5%	85.5%	–	93.5%	77.4%	81.9%
12 yr	59.7%	79.0%	90.3%	–	82.6%	81.9%
15 yr	69.4%	69.4%	79.0%	80.6%	–	78.1%
SMAM	77.4%	83.9%	77.4%	72.6%	67.7%	–

Abbreviations: yr = years; SMAM: Standard Maternal Animal Model.

with the lowest maternal breeding values under the SMAM. Fig. 9 displays the predicted maternal breeding values throughout the productive lifespan of the dams with their predicted breeding values under the SMAM.

In the figure, it is evident that some sires (Sire 3 and Sire 4) exhibit minimal variation in their maternal breeding values over the productive lifespan of the cows. Conversely, other sires or individuals may experience significant fluctuations in their predictions across the parameter space, rendering them valuable in specific scenarios. For instance, sires 1 and 2 have predicted breeding values close to 0 under the SMAM. However, they show breeding values nearing 20 kg. for young cows (Sire 2) and older cows (Sire 1). Thus, they could be of interest if cows are culled after a set number of parities (Sire 2) or if cows are expected to maintain productivity into advanced age (Sire 1). The effects of these changes in the prediction of maternal genetic effects across the parameter space, compared to predictions from the SMAM, are illustrated in Table 3. In this table, we calculated Pearson and Kendall rank correlations between the predicted maternal genetic effects at 3, 6, 9, 12, and 15 years and those from the SMAM in all individuals.

As previously mentioned, the prediction of maternal genetic effects under the SMAM primarily relies on data from younger rather than older cows, because the number of dams over 10 or 12 years is considerably lower. The Pearson correlation between the predictions using SMAM was 0.968 and 0.961 for predictions at 3 and 6 years, respectively. This correlation decreased to 0.921 and 0.878 for predictions at 12 and 15 years. However, the Kendall rank correlations were lower, ranging from 0.708 for predictions at 15 years to 0.866 for predictions at 6 years. Lower Kendall figures compared to Pearson correlations were also evident across dam ages, varying from 0.670 between 3 and 15 years to 0.883 between 9 and 12 years. The reduced Kendall rank correlations suggest potentially significant differences between individuals at the extremes of the breeding value distribution. Therefore, selecting top individuals for maternal effects under SMAM may more efficiently enhance maternal ability in younger cows than in older ones, making it potentially suboptimal for farmers aiming to maintain cows in production until advanced ages. To illustrate this, we choose the 622 sires that have more than 25 recorded progeny, and we calculated the degree of concordance within the top 10 and 25%, as well as between the rankings at 3, 6, 9, 12, and 15 years,

and with the ranking under the SMAM. The results are presented in Table 4.

The results align perfectly with the Kendall rank correlations, although it should be noted that the percentage of concordance was lower for the top 10% compared to the top 25% of sires. Similar to the rank correlations, the percentage of concordance is higher between adjacent age points and decreases as the age difference increases. Additionally, the percentage of sires included in the top 10 and 25% with the SMAM model that is also included at each age point is highest at 6 years of age (89.6% for the top 10% and 83.9% for the top 25%) and lowest at 15 years of age (78.1 and 67.7%, respectively). Lastly, it should be highlighted that the low percentage of concordance between the top individuals at 3 years, compared to other age points, is consistent with the lower genetic correlation, as illustrated in Fig. 8.

In summary, the proposed model provides new opportunities to tailor selection strategies to align with farm-specific culling practices. It offers an alternative to the standard SMAM model, which places excessive emphasis on records at early ages due to the limited data from older dams. In contrast, the random regression method calculates breeding values for maternal effects throughout the entire productive lifespan of the cows, relying on the available data. This method will be valuable when selection aims to enhance maternal genetic effects at a specific age of the dams. Furthermore, the proposed model effectively captures the non-genetic variability associated with dams and accurately accounts for environmental covariance between adjacent parities. However, for larger populations, it may require higher computational resources compared to the SMAM. Nevertheless, it is comparable to the widely used random regression test−day models in dairy cattle breeding (Schaeffer, 2004).

Ethics approval

Not applicable.

Data and model availability statement

None of the data were deposited in an official repository. The data used in this study belong to CONASPI (Confederación Nacional

de Asociaciones de Ganado Pirenaico). However, it can be shared by the corresponding author upon reasonable request.

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

During the preparation of this work, the author(s) used Chat-GTP in order to improve the English writing. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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Declaration of interest

None.

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