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Comprehensive analysis of inbreeding depression across growth, fertility, and survival traits in Limousine beef cattle

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ABSTRACT

The Italian Limousine cattle population, with approximately 100 000 registered animals in the national herd book, plays a crucial role in the country's national beef industry, being one of the most widely spread breeds in Italy. Maintaining genetic diversity is essential to prevent the negative consequences of inbreeding, which can reduce animal performance for economically important traits such as growth, fertility, and longevity. Traditional pedigree-based inbreeding estimates have been previously used, but genomic tools offer the possibility of greater precision. This study evaluated the effects of inbreeding and inbreeding depression on key performance traits in Limousine cattle, considering both pedigree- and genomic-based inbreeding coefficients. Phenotypic comparisons between animals with low and high inbreeding levels revealed a negative effect of inbreeding on growth traits, including birth weight, weaning weight, yearling weight, and average daily gain. These effects were observed regardless of the inbreeding estimation method. Fertility traits were largely unaffected, except for age at first calving, which increased with higher inbreeding. Longevity, measured by the probability of survival across parities, was significantly reduced in inbred animals. Genomic inbreeding showed a greater impact on animals' fertility and longevity. Notably, when separating recent and ancient genomic inbreeding, the former had a more pronounced effect on growth traits. Similarly, recent inbreeding primarily impacted animal longevity. Genomic inbreeding coefficients provided more granular insights into inbreeding depression, allowing for a better identification of individuals at higher risk of performance reduction. The results highlight the detrimental effects of inbreeding on growth, fertility, and longevity in Limousine cattle, which could have implications for herd productivity and genetic diversity. The study underscores the importance of genomic tools to monitor and manage inbreeding levels. Implementing strategies to control inbreeding accumulation is vital for maintaining genetic variability and ensuring the long-term sustainability of beef cattle populations.

Implications

Maintaining genetic diversity is essential for sustainable beef production. This study assessed how inbreeding affects growth, fertility, and longevity in Limousine beef cattle using pedigree and genomic data. Results showed that inbreeding, particularly recent genomic inbreeding, reduces growth performance, delays reproductive maturity, and shortens herd life. These findings are important for breeders and industry stakeholders, as they highlight the need for managing genetic diversity. Using genomic inbreeding measures, breeders can make informed mating decisions to avoid closely related pairings, reduce inbreeding depression, and preserve herd productivity. Strategic genetic management is essential to safeguard the long-term cattle sustainability.

Introduction

Limousine is a cosmopolitan beef cattle breed originating from France and has been extensively exported worldwide. In Italy, the Limousine population is widely distributed across the country, with approximately 100 000 animals raised on more than 2 500 farms. The breed is continuously expanding in population size and is now one of the most important beef breeds reared in Italy (Fabbri et al., 2024), playing a key role in the national beef industry being the fourth bovine population in the country (Sistema

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Informativo Veterinario, https://www.vetinfo.it/j6_statistiche/index.html#/). As selective breeding becomes more widespread to enhance herd productivity, there is a growing concern about the potential negative impact of inbreeding. Therefore, monitoring and analysing the genetic diversity of the Italian Limousine population is crucial in understanding its genetic background, managing inbreeding-related risks, improving productivity and profitability, and ensuring sustainable breeding practices for the future.

The inbreeding coefficient is a key indicator to assess genetic diversity and evaluate the potential impact of inbreeding depression on economically important traits in livestock populations. It can quantify the probability that an individual carries alleles that are identical by descent relative to a base population where all alleles are assumed to be unrelated (Wright, 1922). Alternatively, it can be defined as the correlation between homologous alleles resulting from the mating of related individuals (Wright, 1922). Both the inbreeding and relatedness coefficients play a crucial role in breeding programmes, as they facilitate the characterisation and efficient management of mating strategies within a population.

Inbreeding within cattle populations poses significant challenges to the breeding industry, as it can lead to a loss of genetic diversity, changes in effective population size and structure, and increased genetic drift. Specifically, increasing inbreeding is generally associated with a reduction in effective population size, as it reflects a decrease in the number of breeding individuals contributing genetically to the next generation (Lozada-Soto et al., 2022). These factors undermine the efficiency and long-term sustainability of breeding programmes (Meuwissen et al., 2020; Curik et al., 2014; Charlesworth and Willis, 2009). As inbreeding accumulates, the mean phenotypic value of selected traits may shift in a negative direction due to inbreeding depression, which directly impacts herd profitability and productivity (Hill and Mackay, 2004; Hedrick and Garcia-Dorado, 2016). These phenotypic changes are primarily driven by the accumulation of deleterious homozygous variants at key loci. This accumulation, in turn, leads to a decline in the population mean when heterozygotes deviate from the average value of two homozygotes (Doekes et al., 2021). For breeders, these challenges require close monitoring and careful management to balance genetic diversity with the selection of desirable traits, ensuring the long-term success of breeding programmes (Mota et al., 2024).

Pedigree-based inbreeding coefficients ($\boldsymbol{F_{PED}}$) are widely used in breeding programmes to monitor inbreeding levels, assess inbreeding depression, and guide mating strategies. These coefficients estimate the probability of alleles being identical by descent based on pedigree records. However, the accuracy depends on the completeness and depth of pedigree data, which can be diminished by unknown parentage or recording errors. Additionally, pedigree-based estimates do not account for Mendelian sampling variation and may underestimate inbreeding levels depending on the number of generations considered (Meuwissen et al., 2020). With the adoption of genomic selection in livestock breeding, genomic data enhance breeding value prediction and accelerates genetic progress by reducing generation intervals (Meuwissen et al., 2016). The availability of single-nucleotide polymorphism (**SNP**) data enables direct estimation of inbreeding, providing a more precise assessment than pedigree-based methods (Meuwissen et al., 2001; Maltecca et al., 2020). SNP-based measures capture homozygosity more effectively, account for Mendelian sampling variation, and distinguish individuals with similar recorded ancestry (Doekes et al., 2021; Keller et al., 2011). Moreover, they allow inbreeding estimation in populations with incomplete or missing pedigree records. Depending on population structure and study objectives, genomic approaches based on marker- or segment-based inbreeding can be used to assess inbreeding depression.

Inbreeding and inbreeding depression have been widely studied, though most genomic-based analyses have focused on dairy cattle. The slower adoption of genomic selection in beef cattle, in contrast to dairy, can be attributed to industry-specific challenges, such as difficulties in phenotype collection for selection candidates, the prevalence of sex-limited traits, and the common use of crossbreeding (Meuwissen et al., 2016). Nevertheless, genomic selection is becoming increasingly prevalent in beef cattle. For instance, routine genomic evaluations have been implemented in the American Angus breed since 2009 (Lozada-Soto et al., 2021). While genomic selection enhances breeding programmes, it also raises concerns about the accumulation of inbreeding over generations. Genomic prediction can control generational inbreeding rates by accounting for Mendelian sampling through SNP data, but it also reduces generation intervals, leading to an increase in the annual rate of inbreeding (Daetwyler et al., 2007). In fact, yearly and generational rates of pedigree and genomic inbreeding have increased in almost all dairy cattle breeds (Doekes et al., 2019; Lozada-Soto et al., 2022; Doublet et al., 2019).

Furthermore, the impact of inbreeding varies, and not all forms necessarily result in inbreeding depression. The timing of inbreeding plays a crucial role, as ancient inbreeding potentially undergoes multiple generations of purging selection, which helps eliminate harmful alleles. In this context, inbreeding can be classified according to age, allowing for a comparative assessment of the effects of recent versus old inbreeding on inbreeding depression. For example, in Canadian Holsteins, authors found that recent inbreeding is more deleterious for milk production, reproduction, and health-related traits (Makanjuola et al., 2020). A study investigating inbreeding depression in U.S. dairy cattle reported that recent inbreeding measured through both pedigree and genomic was associated with a higher risk of reproductive diseases, especially metritis (Lozada-Soto et al., 2024). In contrast, ancient inbreeding either had no effect or reduced the probability of reproductive disease(s). Similarly, in beef cattle, Lozada-Soto et al. (2021) reported that recent genomic inbreeding was more harmful to growth compared to ancient inbreeding.

Production, longevity, and fertility are key traits influencing the efficiency and profitability of beef cattle systems. These traits directly influence herd productivity, replacement, and costs. Longevity and survival contribute to the economic sustainability of beef herds by reducing the need for frequent replacements and improving overall farm efficiency. Fertility, in particular, plays a crucial role in herd sustainability, as it directly impacts reproductive performance and provides potential indirect indicators for early selection of longevity in breeding programmes (Callegaro et al., 2024). However, inbreeding can negatively affect production, fertility, and longevity traits by prolonging calving intervals, delaying puberty, and ultimately reducing reproductive efficiency and lifetime productivity. Understanding these associations is essential for optimising genetic diversity, refining selection strategies, and ensuring herd sustainability. Few studies in beef cattle have confirmed the detrimental effects of increased inbreeding on productive and reproductive performance (Mota et al., 2024; Lozada-Soto et al., 2021; Pereira et al., 2016; Sumreddee et al., 2019; Santana et al., 2010). The objectives of our study were to (1) characterise the Italian Limousine population in terms of pedigree and genomic inbreeding levels; (2) evaluate the impact of inbreeding on growth, fertility, and longevity traits in Limousine beef cattle by comparing phenotypic performance across varying inbreeding levels; (3) differentiate the effects of recent and ancient inbreeding, quantifying their respective contributions in Limousine population.

Material and methods

Animals and data

All data for this study were provided by the National Italian Association of Limousine and Charolais Breeders. The raw pedigree file for the Limousine breed included 526 887 animals, comprising 15 025 sires and 123 701 dams. Pedigree statistics, such as the number of complete generations, complete generation equivalents, and pedigree completeness index, were calculated using the optiSel R package (Wellmann, 2019). The mean number of complete generations was 2.03, with a maximum of 6. The complete generation equivalents represents the sum of $(\frac{1}{2})^n$ known ancestors for every individual, where n is the number of generations separating the individual from a given ancestor. This metric quantifies pedigree depth by summing the contributions of known ancestors. The pedigree completeness index algorithm, as defined by MacCluer et al. (1983), is the harmonic mean of the pedigree completeness of an individual's parents and reflects the percentage of known ancestors over multiple generations. These pedigree metrics were used to filter individuals based on pedigree completeness to minimise potential biases in estimating inbreeding coefficients. Animals with number of complete generations <= 3, complete generation equivalents <= 5, and a pedigree completeness index lower than 0.90 when considering four generations were excluded from further analysis. Although a higher threshold of filtering for complete generation equivalents is commonly used in literature, our pedigree depth was lower, with a maximum complete generation equivalents of 8.02. Using a stricter threshold would have excluded a large portion of the animals. In addition, was considered a pedigree completeness index lower than 0.90 that takes four generations into account, as this approach is consistent with previous studies (Lozada-Soto et al., 2021) and allows for a balance between completeness and sample size. After applying these criteria, 109 241 animals met the pedigree completeness thresholds and were retained for the study. The final pedigree dataset had an average number of complete generations of 3.54 complete generations, an average complete generation equivalents of 5.57 equivalent generations, and an average pedigree completeness index of 0.97. The final average values for complete generation equivalents and the number of complete generations reflect a common scenario in beef cattle populations, which often present less complete pedigree records compared to dairy breeds (Gutiérrez et al., 2003; Nyman et al., 2022).

Before the statistical analysis, genotyped individuals were imputed with a multistep pipeline. A total of 421 sires, used as reference population, were genotyped using a panel of 119 854 SNPs (GeneSeek GGP Bovine 150 K; Illumina Inc., San Diego, CA), while 8 482 individuals were genotyped with a panel of 28 299 SNPs (GeneSeek GGP Bovine LD v3; Illumina Inc.). The two panels had 13 984 SNPs in common. In the first step, individuals genotyped with the GeneSeek GGP Bovine LD v3 panel were imputed to the GeneSeek GGP Bovine 150 K panel, leveraging the common set of 13 984 SNPs shared between the two panels. In the second step, an additional 13 670 non–overlapping SNPs present on the GeneSeek GGP Bovine LD v3 panel were also imputed and integrated with the initial imputed set of 119 854 SNPs. This resulted in a total of 131 805 SNPs. Genotype imputation was carried out using FImpute v.3 with default parameters (Sargolzaei et al., 2014). The quality metrics of the imputation showed a high squared correlation (r^2) between allele frequencies across panels with a value of 0.99, indicating higher accuracy between imputed and true genotypes. After imputation, the Mendelian error rate increased slightly to 0.42%, and 98% of SNPs were retained after quality control filtering. The minor allele frequency remained stable, with 94–98% of SNPs exhibiting a minor allele frequency below 0.05. For subsequent animal analyses, SNPs with minor allele frequency of 0.05 and individuals with the largest genotype changes (>1%) were removed to ensure data consistency. To further assess the accuracy of imputation, a validation step was performed. Specifically, a subset of genotyped markers was randomly masked and subsequently re-imputed using the same pipeline. The results of this masked-marker imputation, including quality metrics, are presented in the Supplementary Table S1.

For these analyses, quality control procedures were implemented to ensure data reliability. Individuals with a call rate below 90% and SNPs with a minor allele frequency below 0.05 and a call rate below 90% were removed. Additionally, SNPs located on non-autosomal chromosomes (e.g., sex chromosomes) were excluded. Following these filtering steps, the final dataset comprised 8 198 genotyped individuals and 116 124 SNP markers. Quality control was performed using preGSf90 software (Aguilar et al., 2014). The main regression analyses were conducted using imputed genotype data. To assess the consistency of the results, the same regression analyses were performed using SNP data from the low-density panel (GeneSeek GGP Bovine LD v3 array). This allowed for a direct comparison between the estimated low-density genotypes and the imputed data, indicating that imputation had minimal impact on the findings of the investigation. To maintain a fair comparison, the same 8 482 animals were included in both analyses.

Animals' traits

Growth traits

The traits analysed in this study were birth weight (**BiW**, kg), weaning weight (**WW**, kg), yearling weight (**YW**, kg), and average daily gain (**ADG**, g/d). BiW was recorded within a range of 30–50 kg, while WW and YW were measured at ages between 170 and 250 and 290–440 days, respectively, in the Limousine population. These traits were selected due to their economic importance and their role in evaluating growth performance in beef cattle. Data were collected from animals born between 1991 and 2024, raised in herds distributed across the national territory. Contemporary groups were defined by combining herd information and birth year, and contemporary groups with fewer than five animals were removed. Additionally, phenotypic records outside the range of mean ±3.5 SD were excluded. After editing, the final dataset consisted of 47 598 records for ADG, 72 282 for BiW, 21 928 for WW, and 14 595 for YW. Only animals with known sire and dam were retained. Descriptive statistics, including the number of animals, mean values, median, SD, farm ID, number of sires and dams for each growth trait, and the number of genotyped animals, are presented in Table 1.

Stayability and fertility traits

Stayability (**STAY**) is a key trait influencing farm profitability, reflecting herd efficiency and costs. It is defined as the probability of a cow remaining in the herd and producing until a specified age, provided that animals have the opportunity to reach that age. STAY is commonly expressed as a binary trait (1 = success, 0 = failure), based on the presence or absence of a calving record for each parity (Hudson and Van Vleck, 1981). In this study, STAY was assessed from the second to the fourth calving, with fourth cumulative binary traits assigned per cow (STAY2, STAY3, STAY4). Data editing retained only cows with age at first calving between 700 and 1 400 days. Calving intervals outside the range of 290–550 days were excluded, and twin parities were considered as a single calving event. Records were censored if the last recorded calving occurred within 550 days of data extraction, as subsequent calvings

Table 1
Descriptive statistics and number of genotyped Limousine cattle for growth and fertility traits.

Descriptive statistics							
Traits	Number of animals with records	mean	SD	Herd	Sires	Dams	Genotyped
Growth traits[1]							
ADG, kg/d	47 598	1.00	0.27	1 975	3 552	21 503	5 321
WW, kg	21 928	254.20	46.23	1 617	2 823	13 589	2 490
YW, kg	14 595	335.40	62.28	1 553	2 571	10 504	1 891
BiW, kg	72 282	38.08	3.65	2 199	4 231	29 880	5 931
Fertility traits[2]							
AFC, days	38 188	1 026	143.79	2 471	6 194	28 482	2 298
FCI, days	25 526	405.70	60.87	2 042	4 958	19 887	1 880

[1] ADG, average daily gain; WW, weaning weight; YW, yearling weight; BiW, birth weight.
[2] AFC, age at first calving; FCI, first calving interval.

could not be confirmed. Censored records were treated as missing data in the model.

Data on fertility traits were extracted from records of cows from the STAY dataset. Fertility traits considered were first calving interval, days) and age at first calving (days) and were treated as continuous responses. Values of first calving interval averaged 405.7 d (± 60.87 SD) and values of age at first calving averaged 1 026 d (± 143.69 SD), respectively. A summary of fertility traits is presented in Table 1. The number of cows and incidence of survival according to the number of records for each STAY are reported in Table 2. Data processing and editing for STAY and fertility traits followed the procedures described in Callegaro et al. (2024). In addition, descriptive statistics and incidence of survival rates for each STAY trait are comprehensively reported in Callegaro et al. (2024).

Estimation of inbreeding measures

Different approaches were employed to assess the accumulation of inbreeding and its effect on production in the Italian Limousine population over time. These included inbreeding coefficients derived from pedigree data as well as genomic estimates, specifically those based on the genomic relationship matrix (**GRM**) using marker-by-marker ($\boldsymbol{F_{GRM}}$) and runs of homozygosity (**ROH**) calculated with segment-based approaches ($\boldsymbol{F_{ROH}}$). Genomic-based inbreeding measures were calculated using imputed SNPs.

Pedigree inbreeding measure

The F_{PED} was estimated using the INBUPGF90 program v1.47 from the BLUPF90 family (Aguilar and Misztal, 2008). This method uses a recursive algorithm and iterates to convergence based on minimal changes in inbreeding values across rounds. F_{PED} were estimated using the method proposed by Meuwissen and Luo (1992). The pedigree dataset used for these computations included 109 241 Limousine animals that met completeness criteria, as described in the previous animals and data section, to ensure accurate inbreeding estimates.

Genomic-based inbreeding measures

The first estimator of genomic-based inbreeding (F_{GRM}) was calculated using the diagonal elements of GRM computed following VanRaden's first method (VanRaden, 2008):

$$\mathrm{GRM} = \frac{ZZ'}{\sum_{j=1}^{m} 2p_j(1-p_j)}, \quad (1)$$

where $Z = X - 2p_j$, X is the $n \times m$ matrix of the genotypes coded as the number of the second allele, n is the number of genotyped animals, m is the number of markers, and p_j is the frequency of the second allele at locus j. The denominator represents the scaling factor. The F_{GRM} for individual i was taken as $\mathrm{diag}(G_{ii}) - 1$, where G is the SNP-derived GRM. BLUPF90 family programs (Aguilar et al., 2019) were used for the calculations of GRM.

The minor allele frequency of the markers used in GRM estimation does not accurately represent that of the base population due to the limited sample size in this study. Consequently, genomic inbreeding coefficients were computed under the assumption of a fixed allele frequency of 0.50. Several studies (VanRaden et al., 2011; Bjelland et al., 2013; Forni et al., 2011) have demonstrated that fixing allele frequencies at 0.50 enhances the concordance between F_{GRM} and pedigree- or ROH-based inbreeding estimates, and that was the reason behind our choice. Additionally, fixing allele frequencies at 0.50 helps centre SNP values in the GRM constructions, mitigating biases from rare alleles or unrepresentative sample frequencies. Rare alleles (close to 0 or 1) can disproportionately influence relationship estimates, potentially biasing the computation of genomic relationships and inbreeding coefficients.

Autozygosity across chromosomal regions was assessed through ROH, which were then used to obtain the proportion of the genome residing in ROH (F_{ROH}). To detect ROH segments from SNP data, the R package detectRUNS v. 0.9.5 was employed (Biscarini et al., 2018), implementing a sliding window method to prevent overestimation of shorter ROH segments (Purcell et al., 2007). The parameters used for ROH detection were as follows: (1) a minimum of 20 SNPs in a window (–homozyg-

Table 2
Number of Limousine cows and incidence of survival across parities for stayability (STAY)[1].

Trait	Definition	N[2]	N of cows survived	Incidence (survival %)
STAY1	Stayability as a first parity = 1; failed = 0	38 188	38 188	100.00
STAY2	Stayability as a second parity = 1; failed = 0	33 209	25 526	66.84
STAY3	Stayability as a third parity = 1; failed = 0	30 105	18 764	49.14
STAY4	Stayability as a fourth parity = 1; failed = 0	27 978	14 381	37.66

The total number of genotyped cows for STAY analyses was 2 062.
[1] STAY, Continuity in herd until the subsequent parity (Success = 1; Failure = 0).
[2] N, Total number of cows, including both those that survived and were culled.

window-snp), (2) a minimum SNP density of 1 SNP per 1 000 kb (–homozyg-density), (3) a maximum gap of 1 megabases (Mb) between consecutive homozygous SNPs (–homozyg-gap), (4) a minimum base pair length of 1 000 kb (–homozyg-kb), and (5) a maximum of 2 opposite homozygous genotype allowed within the window (–homozyg-window-het).

The proportion of the autosomal genome covered by ROH is calculated as:

$$F_{ROH} = \frac{L_{ROHi}}{L_{Genome}}, \quad (2)$$

where L_{ROHi} is the length of the i^{th} ROH segment identified for each animal (in base pairs) and L_{Genome} is the total length of the autosomes covered by the markers. This formula is used to calculate the inbreeding coefficient based on ROH (F_{ROH}). The length of an ROH segment provides insight into the age of inbreeding, with shorter segments generally indicating more ancient inbreeding. However, the exact length of an ROH segment originating from a specific generation can vary. To account for this, F_{ROH} was also estimated across four ROH length categories: 1–2 Mb (F_{ROH1-2}), 2–4 Mb (F_{ROH2-4}), 4–8 Mb (F_{ROH4-8}), and >8 Mb ($F_{ROH>8}$), following criteria used in previous studies (Mota et al., 2024; Lozada-Soto et al., 2021).

Inbreeding depression for growth, fertility, and longevity traits

The impact of inbreeding on fertility, longevity, and growth traits was assessed separately for each trait using the different inbreeding coefficients described. Inbreeding depression was estimated by regressing phenotypic values on inbreeding coefficients and calculated as the effect of a 1% increase in pedigree and genomic inbreeding coefficients on the mean of the phenotype measured. Considering pedigree measure, inbreeding depression results were analysed using F_{PED} estimates from two datasets: a full-dataset including all animals with phenotype information, and a reduced-dataset limited to genotyped animals. This approach allows for consistency checks, ensuring that restricting the analysis to genotyped animals does not significantly alter the results. Comparing pedigree-based estimates between the full and genotyped datasets can reveal the impact of pedigree completeness. Additionally, stronger inbreeding depression effects observed with genomic measures would suggest that this better captures recent or cryptic inbreeding.

In addition, to assess the expected phenotypic differences between animals with varying levels of inbreeding, we estimated predictions for growth and fertility traits using a Gaussian-linear model, while for STAY, predicted probabilities were obtained using a threshold-liability model. This approach allowed for a comparison between animals with high and low inbreeding levels, providing a more direct insight into the effects of inbreeding on growth, fertility, and functional longevity. Additionally, to quantify realised phenotypic depression in the Limousine population, we calculated the projected losses in growth traits (ADG, BiW, WW, YW), fertility (AFC), and STAY. These losses were estimated by comparing animals in the 10th percentile (low inbreeding) and 90th percentile (high inbreeding) for both pedigree- and genomic-based inbreeding coefficients. The difference between these groups was also computed to quantify the magnitude of inbreeding depression across these traits. Only traits showing statistically significant inbreeding depression were considered for the estimation of the expected phenotypic differences.

Since ROH detection is influenced by SNP density (Ferenčaković et al., 2013a,b; Villanueva et al., 2021), analyses were conducted using genotypes from imputed data. In addition, analyses with a low-density panel were performed to evaluate whether the patterns observed in the imputed data panel were consistent with those obtained using a low-density dataset. To assess the effect of SNP density on ROH estimation and validate our findings, the same analyses were conducted in both imputed and non-imputed data. Results from low-density genotypes were compared to those from the imputed ones to determine whether inbreeding depression patterns remained consistent. The results from these two scenarios were similar, and therefore, low-density data will be presented in the supplementary material.

Genetic analyses

For growth traits, the model was defined as follows:

$$y = \beta_0 + Xb + \beta_1 F + Za + Wp + e, \quad (3)$$

where y was the vector of phenotypic values of ADG, BiW, WW and YW; β_0 is the intercept; b is the vector of fixed effects of the sex, age of animals, and age of dam; F is a vector of inbreeding coefficients for F_{PED}, F_{GRM}, or F_{ROH}; β_1 is the linear regression coefficient for the regression coefficient, a is the vector of the random additive genetic effect, following $a \sim N(0, A\sigma_a^2)$, where A is the numerator relationship matrix; p is the vector of the random effect of the contemporary group (herd-year), following $p \sim N(0, I\sigma_p^2)$, where I is an identity matrix; e is the random residual, following $e \sim N(0, I\sigma_e^2)$; and X , Z, and W are the incidence matrices for the fixed and random effects. When BiW and WW were modelled in model 3, the maternal permanent environment effect was added, following $mpe \sim N(0, I\sigma_{mpe}^2)$.

Fertility traits and STAY were analysed by fitting a univariate linear and threshold animal model. The fixed effects considered were the same:

$$y = \beta_0 + Xb + \beta_1 F + Za + Wp + e, \quad (4)$$

$$\lambda = \beta_0 + Xb + \beta_1 F + Za + Wp + e, \quad (5)$$

where y is the linear vector of fertility traits (age at first calving, first calving interval) while λ represents the unobserved liability for threshold models for STAY traits; β_0 is the intercept; b is the vector associated with the fixed effects of year of calving (48 levels); β_1 is the linear regression coefficient for the inbreeding coefficient; a is the vector of animal additive genetic effects following $a \sim N(0, A\sigma_a^2)$, where A is the numerator relationship matrix; p is the vector associated with the random effect of herd, following $p \sim N(0, I\sigma_p^2)$, where I is an identity matrix; e is the vector associated with the random residual error following $e \sim N(0, I\sigma_e^2)$; and X , Z, and W are incidence matrices for the fixed and random effects.

The variance components for STAY traits were fixed at values estimated from the single-step GBLUP assessed in the previous work in STAY on Limousine and Charolais beef cattle (Callegaro et al., 2024). For the growth and fertility traits, the variance components from models 3 and 4 are shown in Supplementary Table S2. The (co)variance components were estimated using the Gibbs sampling algorithm implemented in the BLUPF90 family software (Aguilar et al., 2019). Convergence was assessed by visual inspection of trace plots and throughout Geweke's test using the package coda (Plummer et al., 2006) in R. Models, where STAY traits were the response variables, were run using the THRGIBBS1F90 program, and those in which the response variable was a growth and fertility trait were run using the GIBBS3F90 program. All analyses were run for 100 000 cycles with a burn-in of 50 000 samples, and every 10th sample was stored for a total of 5 000 samples used for subsequent inference.

Best Linear Unbiased Estimates of the intercept and inbreeding slopes were used to estimate predictions for growth and fertility

traits and predicted probabilities for STAY on the liability scale values across different inbreeding levels. Our predicted values were obtained from the regression equations using the solutions for the fixed effects obtained at each round of iterations to the phenotypic means. For STAY, predictions on the liability scale were converted to the probability scale by applying the inverse probit transformation (with the pnorm function in R), using the formula: $P_i = \Phi(p_i)$, (6) where Φ is the standard cumulative distribution function and p_i is the i_{th} predicted value of STAY on the liability scale. These predictions allowed us to assess the impact of inbreeding on trait values, providing insights into inbreeding depression across different levels of inbreeding.

Results

Inbreeding coefficients

The mean F_{PED} in the Limousine population was 1.99% (SD = 5.68%). Genomic inbreeding, estimated as F_{GRM} averaged 0.01 (SD = 0.03), while the mean of F_{ROH} was 0.19 (SD = 0.02), indicating a higher proportion of autozygosity captured by ROH. The mean partial inbreeding coefficients derived from ROH segments were 0.045 (SD = 0.029) for F_{ROH1-2}, 0.029 (SD = 0.028) for F_{ROH2-4}, 0.018 (SD = 0.028) for F_{ROH4-8}, and 0.021 (SD = 0.034) for $F_{ROH>8}$. These values reflect the contribution of ROH segments of different lengths to the overall inbreeding estimates. The mean complete generation equivalents and the number of complete generations for the Limousine breed were 5.60 and 3.70, respectively. Furthermore, all animals included in the analyses had a pedigree completeness index exceeding 90%, ensuring high data accuracy. The distributions of pedigree and genomic inbreeding coefficients are shown in Supplementary Figure S1. Over time, F_{PED} exhibited an increasing trend from the first to the last birth year considered. In contrast, genomic inbreeding measures (F_{GRM} and F_{ROH}) remained relatively stable throughout the study period. Suggesting that genomic diversity may have remained relatively stable over time, possibly due to low selective pressure. Additionally, F_{GRM} reflects the average genomic similarity across individuals and depends on allele frequencies and population structure, whereas F_{ROH} captures the proportion of the genome in homozygous segments and is more sensitive to recent inbreeding. These differences may explain why their temporal trends sometimes are not fully aligned. Annual trends for each inbreeding measure are presented in Supplementary Figure S2.

Pearson's correlation coefficients among all inbreeding measures are visualised in a heatmap (Fig. 1). F_{PED} showed moderate to strong correlations with both F_{GRM} and F_{ROH}, with values ranging from 0.69 to 0.71. The highest correlation with F_{PED} was observed for F_{GRM} and F_{ROH4-8} (0.71), whereas the correlation between F_{PED} and F_{ROH} was slightly lower (0.69). Correlations between F_{PED} and short-segment F_{ROH} estimates (F_{ROH1-2} and F_{ROH2-4}) were also high (0.70), with values remaining stable across increasing segment lengths. Genomic inbreeding measures (F_{GRM} and F_{ROH}) showed consistently high correlations. Specifically, the correlation between F_{ROH} and F_{GRM} was 0.89, confirming the strong agreement between these two genomic inbreeding estimators. Correlations between F_{GRM} and different ROH segment classes ranged from 0.85 to 0.89, with a slight decline as segment length increased. This expected trend reflects the fact that shorter ROH segments capture more ancient inbreeding, whereas longer segments indicate more recent inbreeding events. While F_{GRM} correlates strongly with ROH-based measures, it captures homozygosity without explicitly distinguishing between recent and ancient inbreeding. Likewise, correlations among different F_{ROH} segments remained consistently high (0.95–0.99), with the strongest correlations generally

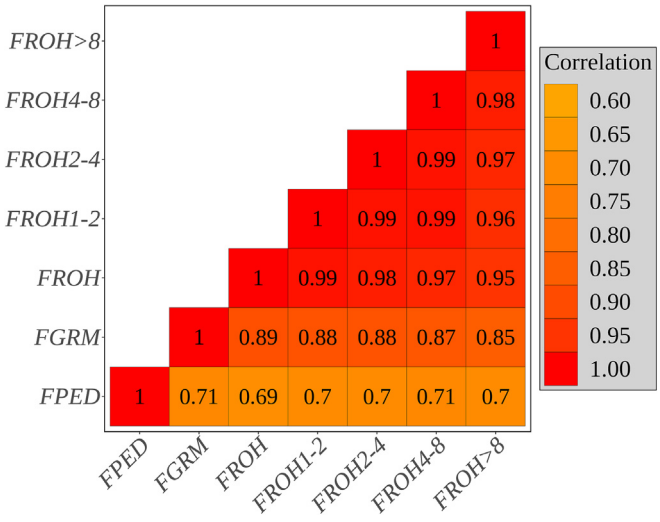

Fig. 1. Pearson correlations between inbreeding measures in Limousine cattle. The plot shows the strength and direction of the correlation between inbreeding measures with darker colours indicating a stronger correlation (F_{PED} = total pedigree inbreeding; F_{GRM} = relationship matrix derived inbreeding; F_{ROH} = runs of homozygosity calculated with segment-based approaches; ROH of different length classes 1–2, 2–4, 4–8, and >8 Mb).

observed between segments of similar lengths, particularly between adjacent categories such as F_{ROH1-2} and F_{ROH2-4}.

The distribution of ROH across 100 randomly selected animals revealed distinct patterns corresponding to different inbreeding timeframes (Fig. 2a). While the accumulation of inbreeding persists across generations, ancient inbreeding segments have fragmented into shorter lengths over time. In our case, short ROH segments (1–2 Mb, 2–4 Mb) made up the largest proportion of the genome, suggesting that inbreeding accumulation has not accelerated dramatically in the last generations. In contrast, longer ROH segments (4–8 Mb, >8 Mb), associated with more recent inbreeding, accounted for a smaller proportion. Fig. 2b shows the distribution of ROH across chromosomes, further confirming that short ROH segments (1–2 Mb, 2–4 Mb) are more frequent, indicating a higher prevalence of ancient inbreeding events. Regression analyses comparing genome-based inbreeding coefficients derived from imputed and non-imputed (low-density panel) data are presented in Supplementary Figure S3. The estimated regression coefficients for F_{GRM} and F_{ROH} from imputed data against their counterparts from the low-density panel ranged from 0.93 to 0.96 for F_{GRM} and F_{ROH}, respectively, showing a high degree of concordance.

Pedigree and genomic inbreeding depression

We quantified the effect of pedigree and genomic inbreeding on four growth traits (BiW, WW, YW, and ADG) in the Italian Limousine population. Furthermore, we estimated inbreeding depression for fertility and survival traits to provide a more comprehensive assessment of its impact. Fertility traits included age at first calving and first calving interval, while longevity was evaluated using STAY, specifically the probability of cows surviving from second to fourth parity (STAY2, STAY3, and STAY4). Inbreeding depression was estimated for all inbreeding measures, with effects expressed by a 1% increase in F_{PED}, F_{GRM}, and F_{ROH} in phenotypic units. The results are summarised in Table 3.

Across all measurements, inbreeding had a negative effect on growth performance, fertility, and longevity, though the magnitude of the effect varied depending on the inbreeding metric used.

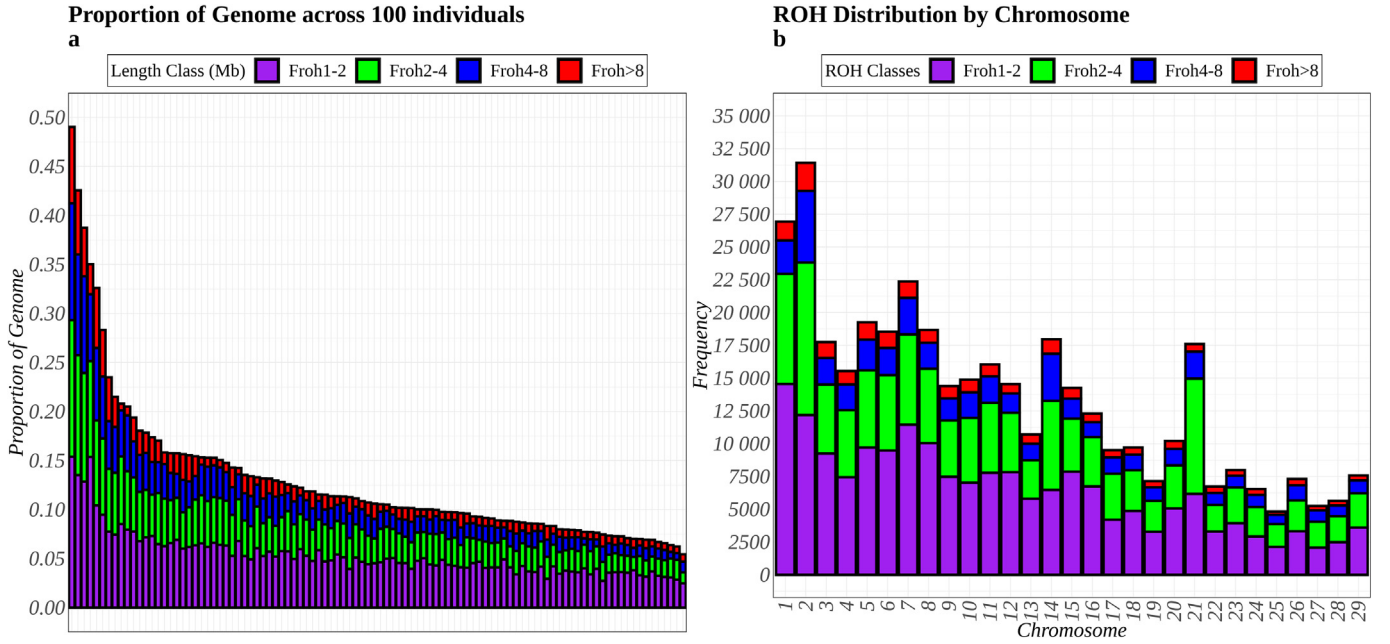

Fig. 2. Runs of homozygosity (ROH) distribution and coverage in Limousine cattle. (a) Proportion of the genome covered by ROH of different length classes (1–2, 2–4, 4–8, >8 Mb) in 100 randomly sampled individuals. (b) Frequency distribution of the number of ROH per chromosome in different length classes (F_{ROH} = runs of homozygosity calculated with segment-based approaches).

Table 3
Inbreeding depression estimates for growth, fertility and stayability traits in Limousine cattle, expressed as change in the phenotype per 1% increase in inbreeding level.

Trait	F_{PED} full-dataset		F_{PED} reduced-dataset		F_{GRM}		F_{ROH}	
	Slope (β)	95% HPDI	Slope (β)	95% HPDI	Slope (β)	95% HPDI	Slope (β)	95% HPDI
Growth traits[1]								
ADG, g/d	−1.20	(−1.65; −0.75)	−4.03	(−7.31; −0.76)	−3.19	(−5.55; −0.83)	−1.56	(−2.98; −0.13)
WW, kg	−0.25	(−0.34; −0.17)	−0.92	(−1.57; −0.27)	−0.93	(−1.77; −0.09)	−0.41	(−0.69; −0.13)
YW, kg	−0.19	(−0.32; −0.06)	−0.65	(−1.77; 0.48)	−1.16	(−2.50; 0.17)	−0.27	(−1.10; 0.57)
BiW, kg	−0.016	(−0.021; −0.012)	−0.06	(−0.10; −0.02)	−0.07	(−0.13; −0.02)	−0.05	(−0.08; −0.02)
Fertility traits[2]								
AFC, days	0.57	(0.22; 0.93)	−0.07	(−1.73; 1.60)	2.51	(1.19; 3.83)	1.30	(0.30; 2.20)
FCI, days	0.15	(−0.08; 0.39)	0.45	(−0.46; 1.36)	0.16	(−1.48; 1.80)	0.05	(−0.91; 1.01)
Stayability traits[3]								
STAY2	−0.015	(−0.020; −0.010)	−0.032	(−0.053; −0.012)	−0.070	(−0.110; −0.024)	−0.043	(−0.068; −0.018)
STAY3	−0.014	(−0.019; −0.010)	−0.016	(−0.041; 0.008)	−0.056	(−0.088; −0.024)	−0.025	(−0.052; 0.003)
STAY4	−0.011	(−0.015; −0.007)	0.000	(−0.036; 0.038)	−0.063	(−0.104; −0.023)	−0.025	(−0.054; 0.004)

Abbreviations: F_{PED}, total pedigree inbreeding; F_{GRM}, relationship matrix derived inbreeding; F_{ROH}; runs of homozygosity calculated with segment-based approaches; HPDI, high posterior density interval.
[1] ADG, average daily gain; WW, weaning weight; YW, yearling weight; BiW, birth weight.
[2] AFC, age at first calving; FCI, first calving interval.
[3] STAY2, stayability2; STAY3, stayability3; STAY4, stayability 4.

This variation was expected given the differences in mean inbreeding values among methods. Table 3 also reports F_{PED}-based inbreeding depression estimates for both the full-dataset and the reduced-dataset. Comparing these estimates ensures that restricting the analysis to genotyped animals does not significantly alter the results. Additionally, this comparison allows for evaluating whether genomic inbreeding measures capture greater variance in inbreeding depression effects than pedigree-based measures.

Inbreeding depression negatively affected all growth traits (BiW, WW, YW, and ADG) in the breed, although the magnitude varied depending on the inbreeding measure (Table 3). A 1% increase in F_{PED} reduced BiW by 0.016 kg in the full dataset and by 0.06 kg when considering only genotyped animals. Similarly, BiW decreased by 0.07 kg for F_{GRM} and 0.05 kg for F_{ROH}. For WW, the reduction ranged from –0.25 kg (F_{PED}) to –0.93 kg (F_{GRM}), with F_{ROH} showing an intermediate effect (–0.41 kg). A similar trend was observed for YW, with reductions between –0.19 kg (F_{PED}, full-dataset) and –1.16 kg (F_{GRM}), although the only significant estimate was for F_{PED} in the full dataset; other estimates were not significantly different from zero. Finally, ADG decreased by –1.20 g/d for F_{PED} (full-dataset), –4.03 g/d for F_{PED} (reduced-dataset), –3.19 g/d for F_{GRM}, and –1.56 g/d for F_{ROH}. Overall, genomic-based inbreeding measures predicted a greater reduction in growth performance with increasing inbreeding. Moreover, the non-random subset of genotyped animals and the imputation process may have contributed to a slight inflation of genomic estimates.

The effects of pedigree-based and genomic inbreeding on female fertility and longevity traits are presented in Table 3. For fertility traits, no significant inbreeding depression was detected

for first calving interval, with none of the four regression coefficients differing significantly from zero. In contrast, for age at first calving, an increase in inbreeding levels was associated with a delay in the onset of reproduction. This was evident from the positive regression coefficients for age at first calving, indicating that inbred animals took longer to conceive. Specifically, a 1% increase in inbreeding resulted in an increase in days to pregnancy of 0.57 days for F_{PED}, 2.51 days for F_{GRM}, and 1.30 days for F_{ROH}. However, when F_{PED} was estimated using only genotyped animals, the effect was not significant. Notably, genomic inbreeding measures showed a greater impact on inbreeding depression for age at first calving than pedigree-based estimates.

For longevity, analysed using a threshold model, an increase in inbreeding level had a notable impact on STAY traits, specifically on the probability of a cow remaining in the herd for subsequent parities. Given that longevity is a key factor for farm profitability, estimating inbreeding depression for this trait is essential for developing effective breeding strategies. An 1% increase in F_{PED} was reported in Table 3 and resulted in a decrease in STAY liability for all the traits, indicating a reduction in the probability of survival of the cow at the next parity. When considering F_{PED} for the reduced dataset, a significant effect was observed only for STAY2, with an estimate of −0.032. For both genomic inbreeding measures, the probability of cows failing to remain in the herd for the next parity increased more markedly compared to pedigree-based estimates. The effects of inbreeding depression per 1% increase in genomic inbreeding measures using the low-density panel are presented in Supplementary Table S3. The inbreeding depression estimates for F_{GRM} and F_{ROH} from non-imputed data were consistent with those obtained in Table 3 using the imputed panel.

Phenotypic depression differences between high and low inbreeding groups

To visualise the realised phenotypic depression in the studied population, we estimated the projected loss in growth traits for animals with low and high levels of pedigree and genomic inbreeding. To ensure direct and easy readability of results, inbreeding coefficients were scaled to pedigree inbreeding (%) to allow for direct comparison between pedigree and genomic inbreeding (F_{GRM} and F_{ROH}) in the same figures (Fig. 3 and Fig. 4). Using predictions, we modelled the expected values of growth traits across different levels of pedigree and genomic inbreeding (Fig. 3). For the ADG, predicted values showed a sharp decline as inbreeding levels increased. A similar trend was evident for WW and YW, with higher inbreeding levels leading to substantial reductions in BW. In contrast, BiW also declined with increasing inbreeding, though the reduction was less pronounced compared to other growth traits.

We also evaluated the projected impact of inbreeding on fertility and longevity traits, using the same approach. For age at first calving, we applied predictions, whereas for STAY, a threshold trait, probability marginal predictions were used (Fig. 4a and Fig. 4b, respectively). An increase in inbreeding was associated with a clear increase in the predicted age at first calving, indicating a negative effect on fertility. The strongest inbreeding depression effects on age at first calving were observed for genomic inbreeding measures, with calving age increasing from approximately 1 022 to 1 065 days for F_{GRM} and from 1 022 to 1 060 days for F_{ROH}. F_{PED} (reduced-dataset) displayed no effect, while F_{PED} (full-dataset) exhibited the mildest increase in age at first calving. These results suggest that genomic measures more accurately capture the adverse effects of inbreeding on fertility. For STAY, increasing inbreeding led to a consistent decline in the probability of survival to subsequent parities, confirming inbreeding depression in longevity. The reduction in STAY was most pronounced for F_{GRM} and F_{ROH}, followed by F_{PED} (reduced-dataset), while the least severe decline was observed for F_{PED} (full-dataset). Specifically, for F_{GRM}, the probability of survival decreased from 0.98 to 0.80 for STAY2, from 0.92 to 0.72 for STAY3, and from 0.84 to 0.52 for STAY4. Similarly, for F_{ROH}, survival probability declined from 0.98 to 0.77 for STAY2, from 0.92 to 0.76 for STAY3, and from 0.84 to 0.61 for STAY4.

To further investigate phenotypic depression, we compared growth traits between animals with low (10th percentile) and high (90th percentile) inbreeding levels (Table 4). Inbreeding had the greatest impact on WW, YW, and ADG, while BiW was the least affected. WW declined by up to 9.25 kg (F_{PED}, reduced-dataset), YW by 6.64 kg (F_{PED}, reduced-dataset), and ADG by 43.44 g/d (F_{PED}, reduced-dataset). The other most pronounced reductions were observed for genomic inbreeding measures, with F_{GRM} decreasing WW by 3.91 kg, YW by 5.18 kg, and ADG by 13.82 g/d. In contrast, BiW showed a modest decline, with reductions of less than 0.4 kg across all inbreeding metrics.

Similarly, the projected impact of inbreeding on fertility and longevity traits was assessed by comparing lowly (10th percentile) and highly (90th percentile) inbred animals (Table 4). For age at first calving, inbreeding increased the trait values, particularly for genomic measures, rising from 1 021 to 1 031 days (F_{GRM}) and from 1 021 to 1 030 days (F_{ROH}). In terms of STAY, survival probabilities showed a decline across all inbreeding metrics, with the strongest effects for genomic inbreeding. For STAY2, the probability dropped from 0.98 to 0.95 (F_{GRM}, F_{ROH}), while STAY3 declined from 0.93 to 0.88 (F_{GRM}) and from 0.93 to 0.89 (F_{ROH}). The most substantial reduction was observed for STAY4, where survival probability decreased from 0.85 to 0.77 (F_{GRM}) and from 0.84 to 0.79 (F_{ROH}). Overall, the strongest inbreeding depression effects were observed when inbreeding was measured using F_{GRM} and F_{ROH}, particularly for fertility and longevity traits.

Impact of recent and ancient inbreeding

We evaluated the effects of recent and ancient genomic inbreeding on growth and longevity traits. As expected, recent inbreeding had a stronger and more detrimental impact on the studied traits compared to ancient inbreeding. The inbreeding depression estimated from homozygous segments was greater for longer segments (F_{ROH4-8} and $F_{ROH>8}$), which indicates more recent inbreeding, compared to shorter segments (F_{ROH1-2} and F_{ROH2-4}), which reflect more ancient inbreeding. The effects of a 1% increase in recent and ancient genomic inbreeding depression on growth and STAY traits are shown in Fig. 5a and Fig. 5b, respectively. The figures also display the highest posterior density intervals, which indicate the statistical significance of inbreeding depression estimates.

For growth traits, both recent and ancient inbreeding were significantly associated with phenotypic reductions in BiW, WW, and YW, while no significant effects were observed for ADG. Specifically, a 1% increase in recent inbreeding (F_{ROH4-8} and $F_{ROH>8}$) reduced BiW by 0.055 kg and 0.070 kg, respectively, whereas an equivalent increase in ancient inbreeding (F_{ROH1-2} and F_{ROH2-4}) led to reductions of 0.045 kg and 0.048 kg, respectively. For both WW and YW, inbreeding depression was more pronounced for recent inbreeding than for ancient inbreeding. A 1% increase in $F_{ROH>8}$ reduced WW by 0.90 kg and YW by 0.93 kg, while the effect of ancient inbreeding (F_{ROH1-2}) was smaller, with reductions of 0.53 kg for WW and 0.36 kg for YW. Notably, F_{ROH1-2} had no significant effect on YW.

For fertility traits, including age at first calving and first calving interval, no significant associations were detected for either recent or ancient inbreeding. These results are therefore not displayed in

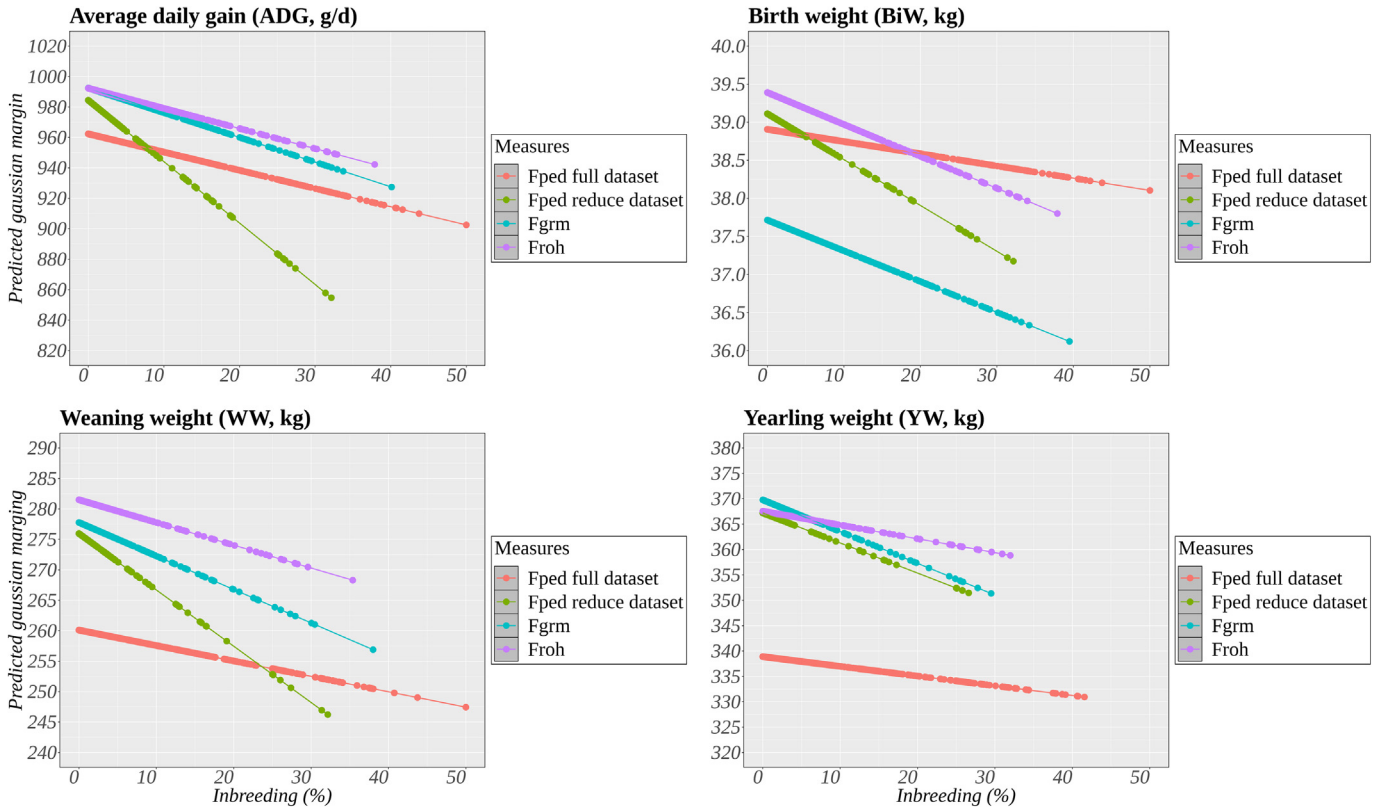

Fig. 3. Expected phenotypic comparisons for growth traits between Limousine cattle with higher and lower inbreeding levels (gaussian prediction) (F_{PED} = total pedigree inbreeding; F_{GRM} = relationship matrix derived inbreeding; F_{ROH} = runs of homozygosity calculated with segment-based approaches).

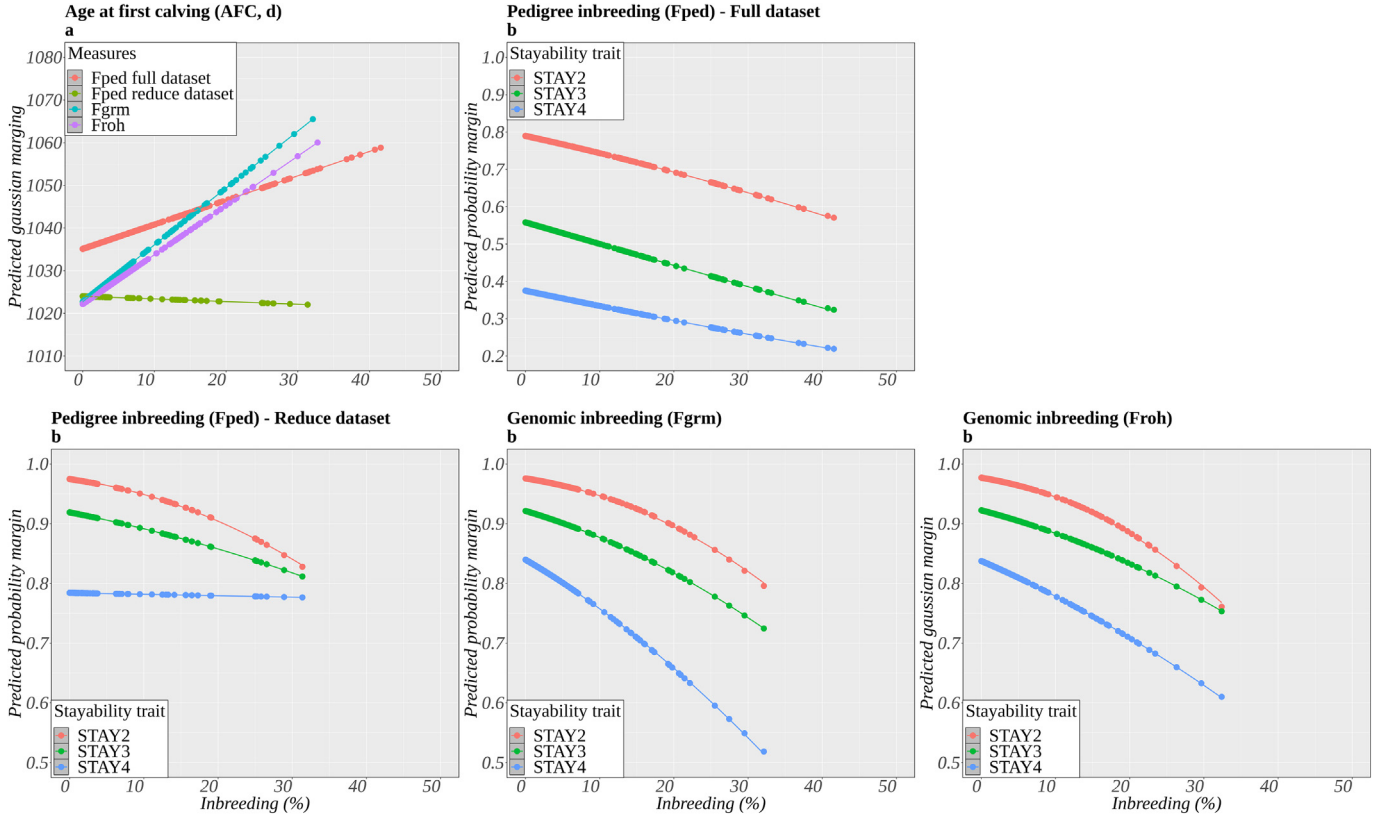

Fig. 4. Predicted effects of inbreeding on age at first calving (AFC) and stayability (STAY) in Limousine cattle. (a) Predictions for AFC. (b) Probability marginal predictions for STAY (F_{PED} = total pedigree inbreeding; F_{GRM} = relationship matrix derived inbreeding; F_{ROH} = runs of homozygosity calculated with segment-based approaches).

Table 4
Projected phenotypic depression in growth, fertility, and stayability traits for low (10th percentile) and high (90th percentile) inbreeding levels in Limousine cattle.

Trait	F_{PED} full-dataset			F_{PED} reduced-dataset			F_{GRM}			F_{ROH}		
	Low	High	Difference (95% HPDI)	Low	High	Difference (95% HPDI)	Low	High	Difference (95% HPDI)	Low	High	Difference (95% HPDI)
Growth traits[1]												
ADG, g/d	962.33	943.13	19.02 to 19.37	984.05	940.61	41.00 to 45.88	994.53	980.71	12.94 to 14.69	993.79	982.75	10.34 to 11.74
WW, kg	260.10	256.00	4.04 to 4.15	275.95	266.70	8.48 to 10.03	273.25	269.34	3.55 to 4.27	281.87	279.03	2.57 to 3.10
YW, kg	330.85	327.47	3.33 to 3.43	364.98	358.34	6.00 to 7.30	368.52	363.34	4.60 to 5.75	371.78	370.77	0.90 to 1.11
BiW, kg	38.91	38.64	0.267 to 0.271	39.11	38.45	0.62 to 0.69	37.77	37.45	0.30 to 0.34	39.43	39.08	0.33 to 0.38
Fertility traits[2]												
AFC, days	1 035	1 039	−3.97 to −3.86	1 024	1 023	0.35 to 0.40	1 021	1 031	−11.43 to −9.38	1 021	1 030	−9.81 to −8.08
Stayability traits[3]												
STAY2	0.79	0.76	0.031 to 0.035	0.97	0.95	0.020 to 0.023	0.98	0.95	0.0234 to 0.0246	0.98	0.95	0.0286 to 0.0290
STAY3	0.56	0.52	0.038 to 0.042	0.92	0.90	0.021 to 0.025	0.93	0.88	0.0433 to 0.0436	0.93	0.89	0.0334 to 0.0338
STAY4	0.38	0.35	0.027 to 0.030	0.83	0.82	0.001 to 0.005	0.85	0.77	0.0765 to 0.0771	0.84	0.79	0.0545 to 0.0551

Abbreviations: F_{PED}, total pedigree inbreeding; F_{GRM}, relationship matrix derived inbreeding; F_{ROH}; runs of homozygosity calculated with segment-based approaches; HPDI, high posterior density interval.
[1] ADG, average daily gain; WW, weaning weight; YW, yearling weight; BiW, birth weight.
[2] AFC, age at first calving.
[3] STAY2, stayability2; STAY3, stayability3; STAY4 staybility4.

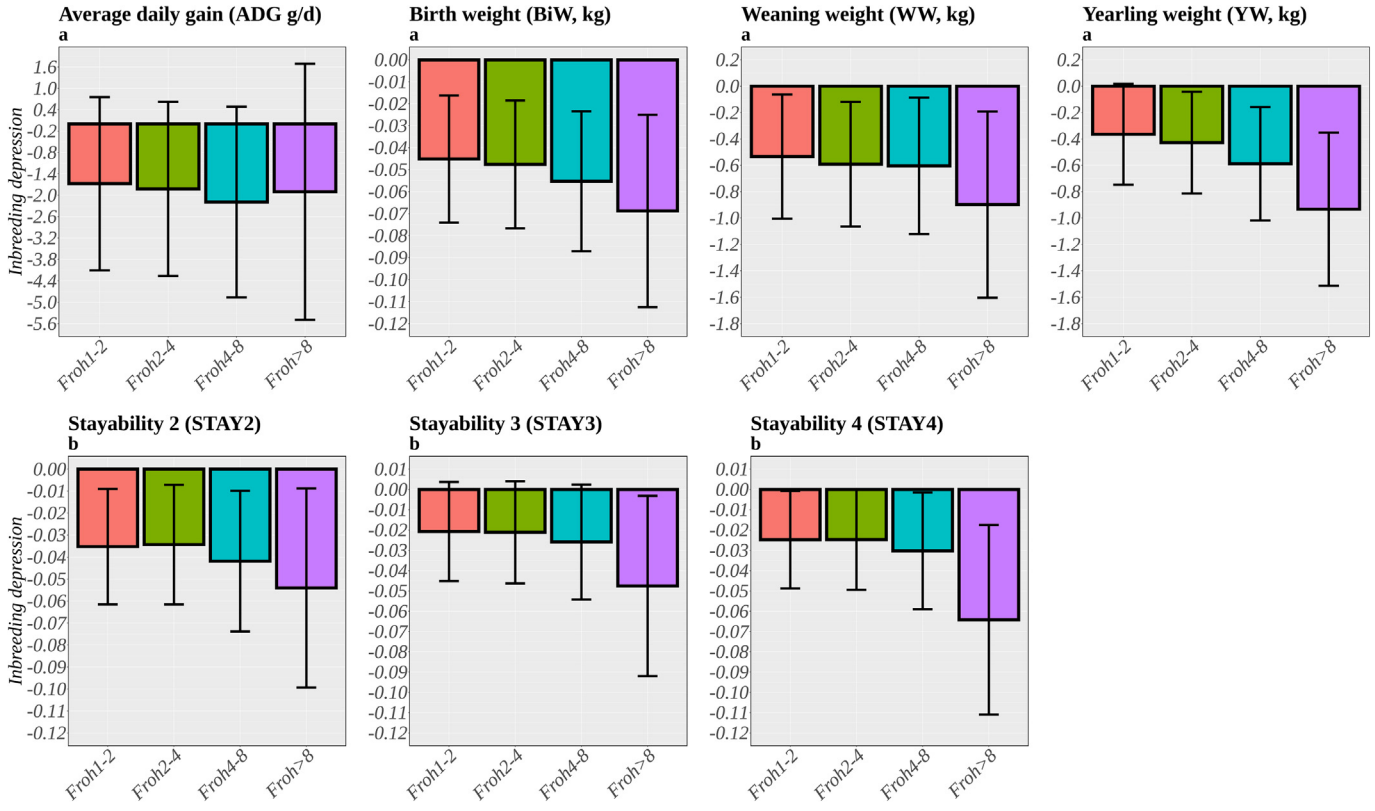

Fig. 5. The effects of 1% increase in recent and ancient genomic inbreeding based on runs of homozygosity calculated with segment-based approaches (F_{ROH}) on (a) growth and (b) stayability traits in Limousine cattle. The range of highest posterior density interval (HPDI) is shown.

Fig. 5. Regarding longevity, recent inbreeding significantly reduced the probability of survival to the next parity for all STAY traits. A 1% increase in inbreeding decreased the probability of survival by 0.054 for STAY2, 0.047 for STAY3, and 0.064 for STAY4 for recent inbreeding ($F_{ROH>8}$). In contrast, an increase in ancient inbreeding (F_{ROH1-2} and F_{ROH2-4}) had a smaller effect, reducing the probability of survival by 0.035 and 0.034 for STAY2 and by 0.025 for STAY4, while no significant effect was observed for STAY3. These results

confirm the greater negative impact of recent inbreeding on longevity traits in Limousine cattle, with the strongest and cumulative effects observed in later parities.

Additional analyses using low-density SNP panel data are reported in Supplementary Figure S4. To further illustrate the phenotypic consequences of recent and ancient inbreeding, we estimated the projected losses in growth and STAY traits for animals with high versus low genomic inbreeding levels. These predictions over the inbreeding levels are shown in Fig. 6a for growth traits and Fig. 6b for STAY traits. The results confirm that phenotypic losses were more pronounced in animals with high levels of recent inbreeding (F_{ROH4-8} and $F_{ROH>8}$) than in those with high levels of ancient inbreeding (F_{ROH1-2} and F_{ROH2-4}).

Discussion

Inbreeding coefficients

In general, the mean F_{PED} observed in this study was slightly lower than values reported by Mota et al. (2024) in Nellore cattle

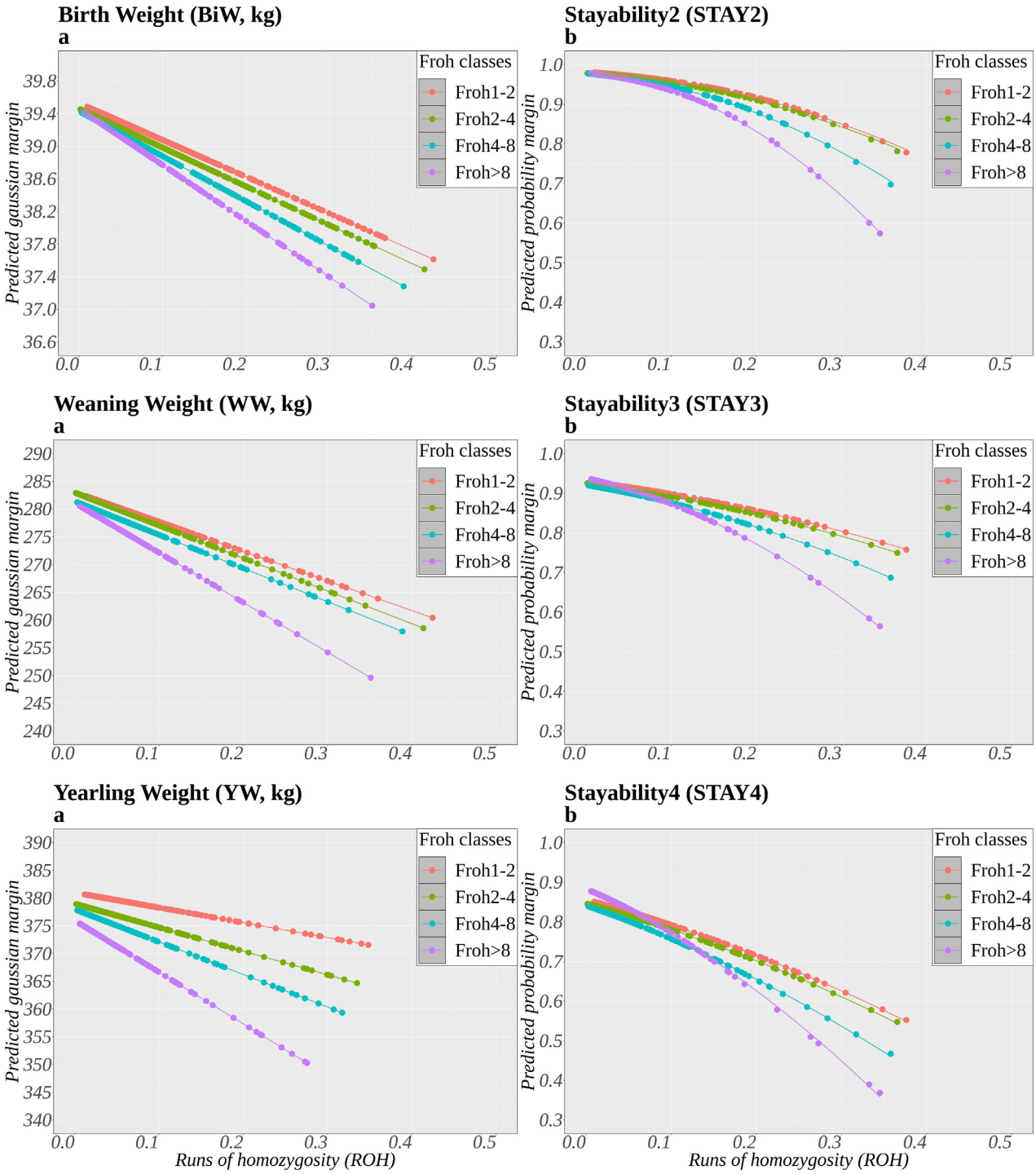

Fig. 6. Projected phenotypic losses due to recent and ancient genomic inbreeding based on runs of homozygosity calculated with segment-based approaches (F_{ROH}) in Limousine cattle. (a) Growth traits (Gaussian predictions). (b) Stayability traits (probability predictions).

and by Pereira et al. (2016) for Zebu breeds. The mean F_{PED} was also slightly lower than the value reported for American Angus cattle under genomic selection (Lozada-Soto et al., 2021). However, it aligned closely with findings from Santana et al. (2010), Peripolli et al. (2018) and Mulim et al. (2025) that reported values below 2%. Notably, the F_{PED} in our study was substantially lower than that reported for Line 1 Hereford cattle (29.2%) (Sumreddee et al., 2019) and Japanese black cattle (9.3%) (Nishio et al., 2023). It is not unexpected that pedigree inbreeding levels are higher in Line 1 Herefords compared to the Italian Limousine, given that the former have been maintained as a closed breeding line for over 85 years, originating from just two closely related bulls (paternal half-brothers) and 50 foundation cows (Sumreddee et al., 2019). The descriptive statistics for complete generation equivalents and the number of complete generations further support the pedigree depth and completeness in our dataset, ensuring reliable estimates of inbreeding depression. However, partial incompleteness of pedigree information may have led to some underestimation of F_{PED}. When using genomic inbreeding measures, the mean F_{GRM} in our population was very similar to values reported in Nellore and Brazilian Angus cattle (Mota et al., 2024; Mulim et al., 2025). The mean F_{ROH} in our study was comparable to that estimated in American Angus cattle (Lozada-Soto et al., 2021) but higher than those observed in Nellore, Japanese black, and Brazilian Angus cattle (Mota et al., 2024; Nishio et al., 2023; Mulim et al., 2025). However, F_{ROH} estimated in the Hereford cattle was higher (23%) (Sumreddee et al., 2019).

Correlations between F_{PED} and genomic inbreeding measures (F_{GRM}, F_{ROH}) have been widely studied in different species. Specifically, some research found F_{PED}-F_{GRM} correlations ranging from 0.33 to 0.64, which were slightly lower than those reported in our study. Conversely, many other studies found F_{PED}-F_{ROH} correlations in the range 0.64–0.71, consistent with our findings. These studies were assessed across multiple beef and dairy cattle populations (Lozada-Soto et al., 2021; Doekes et al., 2019; Sumreddee et al., 2019; Nishio et al., 2023; Martikainen et al., 2017). Zhang et al. (2015) also documented correlations of 0.47 to 0.82 between F_{PED} and F_{ROH} in three dairy cattle breeds. In general, the observed correlations align with literature, with variation influenced by pedigree quality and ROH length. Pedigree depth and ROH segment length are key factors affecting F_{PED}-F_{ROH} correlations, which tend to increase with deeper pedigree records (Sumreddee et al., 2019; Ferenčaković et al., 2013a,b). Additionally, VanRaden et al. (2011) found that fixing minor allele frequency at 0.50 improved F_{GRM}-F_{PED} correlations.

Our findings for genomic inbreeding measures align with previous studies, where strong correlations between F_{GRM} and F_{ROH} (0.81–0.97) have been reported in beef and dairy cattle (Lozada-Soto et al., 2021; Doekes et al., 2019; Bjelland et al., 2013; Forutan et al., 2018). However, lower correlations (0.62–0.66) were observed in Holstein and Jersey cattle (Pryce et al., 2014), likely due to differences in population structure and breeding history. Overall, our results are consistent with the literature, which reports moderate to high correlations between F_{GRM} and F_{ROH} in both beef and dairy cattle populations, as mentioned before. Contrary to our results, Mulim et al. (2025) reported negative correlations among F_{GRM} and F_{ROH} measures. This discrepancy may be explained by methodological aspects of F_{GRM} estimation, which relies on allele frequencies. When these frequencies diverge from those of the founder population, the estimation of inbreeding may become biased (Nishio et al., 2023). Such discrepancies are more likely to emerge at the genomic level, where allele frequency changes can be more pronounced, leading to reduced or even negative correlations between inbreeding coefficients (Villanueva et al., 2021; Mulim et al., 2022). Finally, as expected, F_{ROH} classes representing recent inbreeding showed stronger correlations with each other than with those reflecting ancient inbreeding, and vice versa, a trend also observed in American Angus and Nellore cattle (Mota et al., 2024; Lozada-Soto et al., 2021).

Considering F_{ROH} and the trend observed in the distribution of ROH segments (Fig. 2), both within and across chromosomes, aligns with expectations that recombination progressively breaks down long homozygous segments over generations. The observed inter-individual variability suggests differences in inbreeding history within the population. The higher contribution of short ROH segments supports the hypothesis that inbreeding has accumulated over multiple ancestral generations rather than from recent mating of close relatives. The inter-chromosomal variability suggests that different chromosomes have experienced varying inbreeding histories. The higher prevalence of short ROH segments across chromosomes further supports the hypothesis that inbreeding has accumulated over multiple ancestral generations, rather than being a result of recent close relative matings.

Pedigree and genomic inbreeding depression

The use of genomic measures of autozygosity as an estimator of inbreeding has gained significant interest in livestock genetics. However, research on inbreeding depression based on genomic inbreeding coefficients remains limited, mainly due to the limited availability of genotyped animals across various species. This knowledge gap is particularly evident in beef cattle, since most studies on inbreeding effects have focused on dairy breeds (Bjelland et al., 2013).

In our study, the depressive effects of inbreeding were more pronounced for WW and YW compared to BiW. Similar trends were observed in American Angus cattle, where both pedigree-based and genomic-based inbreeding led to decreased growth from birth to postweaning (Lozada-Soto et al., 2021). While some studies on Hereford and Angus reported no significant F_{PED} effects on BiW (Sumreddee et al., 2019; Davis and Simmen, 2010), they did detect depressive effects on WW and other postweaning traits, consistent with our findings. In American Angus, inbreeding depression was greater than in our study, with reductions of 0.03 kg in BiW (for both males and females) and 0.47 kg in WW for females and 0.50 kg for males (Lozada-Soto et al., 2021). Other studies in beef cattle suggest that a 1% increase in F_{PED} reduces BiW by 0.02–0.06 kg and WW by 0.19–0.44 kg (Carolino and Gama, 2008; Carrillo and Siewerdt, 2010). In Hereford, although no significant effects were found for BiW or WW, YW decreased by 1.06 kg per 1% F_{PED} increase, a larger effect than in our study (Sumreddee et al., 2019). This study also reported a significant reduction in ADG (0.006 kg/d), similar to what was reported in our results.

Although genomic inbreeding research in growth traits is limited, studies in beef populations such as Hereford, American Angus, and Nellore have reported inbreeding depression. In Herefords, a 1% increase in F_{GRM} was associated with a 0.53 kg decrease in WW, which is smaller than the effect observed in our study. For YW, the depression of −0.92 kg is similar to our findings. However, while a depressive effect was observed for YW using F_{GRM}, no significant depression was detected for F_{ROH} in the studied population. In contrast to our results, no depressive effects were found on BiW due to F_{GRM} or F_{ROH}, nor any effect on WW due to F_{ROH}. Regarding ADG, reductions similar to our findings were reported in Herefords, with values ranging from −0.003 to −0.006 kg/d for both F_{GRM} and F_{ROH} (Sumreddee et al., 2019). In American Angus, Lozada-Soto et al. (2021) found depressive effects of genomic inbreeding on growth, with BiW decreasing by 0.04–0.05 kg in both males and females. For WW, authors observed smaller decreases (0.61 kg in males and 0.59 kg in females) per 1% increase in F_{GRM}, but similar depression was observed with F_{ROH}. Finally, Garcia-Baccino et al. (2020), using homozygous SNPs (F_{HOM}) as a

measure related to F_{GRM}, found a similar depressive effect of inbreeding on growth, reporting a decrease of 0.05 kg for BiW and 1.02 kg for WW.

Inbreeding depression for reproductive traits in both beef and dairy cattle has been well documented. However, contrary to our results, studies on Japanese Black cattle have reported no significant inbreeding depression, either using pedigree or genomic measures, for age at first calving (Nishio et al., 2023). Similarly, in Hereford cattle, no inbreeding depression for age at first calving was detected (Sumreddee et al., 2019). Conversely, studies in Alentejana cattle and Zebu, using pedigree and genomic inbreeding measures, have shown an increase in age at first calving, calving intervals, and days open (Pereira et al., 2016; Carolino and Gama, 2008). In comparison, in our results, genome-based inbreeding coefficients tended to yield larger estimates of inbreeding depression for fertility traits than pedigree-based measures. This discrepancy may be attributed to several factors, such as errors in pedigree records, pedigree depth, expected versus actual identical by descent, and the number of records. Previous studies in dairy and beef cattle (Pryce et al., 2014; Nishio et al., 2023) suggested that F_{PED} might underestimate the inbreeding depression for female fertility traits.

Few studies have evaluated the impact of inbreeding on longevity and survival in beef cattle. A study on Alentejana cattle found that increased inbreeding levels were associated with reduced longevity (Carolino and Gama, 2008). Similarly, a meta-analysis by Doekes et al. (2021), reviewing 154 studies across multiple livestock species, reported that a 1% increase in inbreeding led to an average reduction of 0.13% in trait mean values, including survival-related traits. This analysis also highlighted that genomic inbreeding measures were more effective in detecting inbreeding depression than pedigree-based estimates. Thompson et al. (2000) in dairy cattle found an increase in the level of inbreeding associated with a decrease in survival and concluded that survival and production represent a major challenge to the genetic programmes of the US dairy industry. Additionally, a study on dairy cattle found that inbreeding had a statistically significant association with functional longevity (Sewalem et al., 2006). Our results, which highlight the detrimental effect of inbreeding depression on STAY traits, are consistent with those findings, as genomic inbreeding measures were more effective in detecting inbreeding depression in the Limousine population.

Inbreeding depression had a more harmful effect on fertility and longevity traits. Differences observed in pedigree-based estimates between the full and the reduced dataset may reflect the influence of pedigree completeness. Meanwhile, stronger genomic inbreeding depression effects suggest that genomic measures offer a more accurate representation of inbreeding depression. Indeed, inbreeding depression is population-specific (Howard et al., 2017), and its extent varies depending on factors such as population structure, the method used to estimate inbreeding and inbreeding depression, allele frequencies, the strength of directional selection, and the marker panel density (Sumreddee et al., 2019; Reverter et al., 2017).

Our findings on inbreeding depression derived from imputed genotypes and the low-density panel align with Reverter et al. (2017), who consistently observed a negative impact of both marker- and segment-based genomic inbreeding on BW in tropical cattle across marker panels of varying densities. This suggests that even with a lower-density marker panel, genomic inbreeding remains a reliable predictor of inbreeding depression in this context.

Phenotypic depression differences between high and low inbreeding groups

Our results indicate a clear phenotypic depression in growth traits associated with increased inbreeding. Across all inbreeding measures, animals in the high inbreeding group exhibited lower predicted performance compared to those in the low inbreeding group, confirming the detrimental effects of increased homozygosity on production and reproductive traits. Among growth traits, the most pronounced effects were observed for ADG, WW, and YW, while BiW showed a milder decline. The strong depressive effect was found on ADG and the associated reductions in WW and YW, likely stemming from a loss of heterozygosity at loci controlling postnatal growth. In contrast, BiW was less affected, possibly due to its lower environmental sensitivity compared to postnatal growth stages. BiW is strongly influenced by maternal effects (Carrillo and Siewerdt, 2010), which may buffer the impact of inbreeding depression. This is consistent with findings in American Angus cattle, where postweaning traits exhibited greater phenotypic depression than BiW (Lozada-Soto et al., 2021).

Similarly, our analysis of fertility and longevity traits reveals clear phenotypic depression associated with increased inbreeding levels. Inbreeding was linked to delayed sexual maturity, as indicated by the increase in age at first calving among the group of highly inbred animals. This delay in first calving, often leading to prolonged calving intervals, increases the risk of involuntary culling, negatively impacting reproductive efficiency (Parland et al., 2007). The strongest inbreeding depression effects were observed for genomic inbreeding measures (F_{GRM} and F_{ROH}), which showed the highest increase in age at first calving. This may reflect the ability of genomic metrics to better capture the realised homozygosity at deleterious loci compared to pedigree-based measures, particularly in populations with shallow pedigrees. However, it is important to consider that the estimation of inbreeding depression using genomic data in addition might be influenced by the non-random selection of genotyped animals and the imputation process. However, several studies have highlighted the advantages of genomic-based measures in estimating inbreeding depression with respect to pedigree inbreeding (Keller et al., 2011; Howard et al., 2017). For longevity, increasing inbreeding levels were associated with reduced survival probability across parities, reinforcing the negative impact of inbreeding on long-term reproductive success. The decline in STAY was particularly evident for later parities (STAY3 and STAY4), suggesting the cumulative effect of inbreeding over time. The mildest reduction in survival probability was seen for F_{PED}, indicating that pedigree-based inbreeding measures may underestimate the long-term consequences of inbreeding on longevity. This aligns with studies showing that inbreeding depression in longevity becomes more pronounced as animals age, likely due to the accumulation of deleterious alleles affecting survival and reproduction (Parland et al., 2007; Leroy, 2014).

The difference between lowly and highly inbred animals was more evident when using genomic inbreeding measures (F_{GRM} and F_{ROH}) compared to F_{PED}. The stronger effects observed with genomic inbreeding measures likely reflect their ability to capture actual homozygosity rather than relying on expected values from pedigree calculations (Nishio et al., 2023). Our findings indicate that the accumulation of pedigree and genomic inbreeding in the Italian Limousine population is detrimental to growth performance, particularly ADG, as well as fertility and longevity, with age at first calving and STAY being the most affected traits. Therefore, careful monitoring of genetic diversity and inbreeding levels in the Limousine breed is essential to mitigate these negative effects and ensure sustainable productivity.

Impact of recent and ancient inbreeding

As expected, our results confirm the largely unfavourable effects of recent inbreeding on animal weight, highlighting its substantial impact on performance. Previous studies in beef cattle have reported that recent inbreeding (estimated from pedigree,

ROH, and HBD segments) has a greater negative effect on BiW, WW, and postweaning gain than ancient inbreeding (Lozada-Soto et al., 2021). Similarly, another study focusing on growth and carcass traits found that recent ROH-based inbreeding was more detrimental to beef cattle growth than ancient inbreeding (Mota et al., 2024). In dairy cattle, recent genomic inbreeding (measured through ROH and HBD) has also been shown to have stronger negative effects on production traits compared to ancient inbreeding (Doekes et al., 2019; Makanjuola et al., 2020). In another study in the German Holstein, the authors found that, for productive traits, the unfavourable effect of a 1% increase in inbreeding was larger when inbreeding was estimated using short ROH compared to longer ROH segments (Mugambe et al., 2024).

In our study, no significant effects of inbreeding were detected for fertility traits in the Italian Limousine population. This aligns with findings in American Angus cattle, where no significant effects of either recent or ancient inbreeding were observed for heifer pregnancy (Lozada-Soto et al., 2021). In dairy cattle, studies have yielded mixed results: some found no significant effects of recent or ancient inbreeding on fertility traits (Doekes et al., 2019) while others reported that recent pedigree and genomic inbreeding were more detrimental to fertility than ancient inbreeding (Maltecca et al., 2020; Makanjuola et al., 2020).

The observed negative effects of inbreeding on longevity traits (STAY) in the Limousine population align with the documented detrimental impact of inbreeding depression. However, our study provides novel insights by distinguishing the effects of recent and ancient inbreeding on functional longevity in beef cattle. Our findings demonstrate that recent inbreeding had a significantly stronger negative impact on STAY traits than ancient inbreeding, suggesting that recent inbreeding may lead to the fixation of recessive deleterious alleles with stronger detrimental effects on survival and reproductive longevity. The absence of significant associations between ancient inbreeding and STAY3 further supports this hypothesis, as purging mechanisms may have eliminated the most harmful alleles affecting survival beyond early parities. The stronger inbreeding depression observed in later parities (STAY4) suggests a cumulative effect, where increased homozygosity progressively reduces an animal's ability to remain productive in the herd. This pattern is consistent with previous studies showing that inbreeding depression tends to intensify in traits related to fitness and survival over time (Parland et al., 2007). While no prior research has directly compared recent and ancient inbreeding for STAY traits, studies on inbreeding depression in fertility and survival traits in both beef and dairy cattle have consistently reported stronger effects of inbreeding on reproductive performance and longevity-related traits (Pryce et al., 2014). Given that STAY is influenced by both reproductive success and survival, it is reasonable to infer that recent inbreeding may reduce reproductive resilience, increasing the likelihood of early culling.

The stronger detrimental effects of recent inbreeding compared to ancient inbreeding in this study underscore its significant impact on both reproductive and production traits in the Limousine breed. Our results align with previous findings in beef and dairy cattle, where recent inbreeding was found to have more severe consequences than ancient inbreeding across various traits (Mota et al., 2024; Lozada-Soto et al., 2021; Doekes et al., 2019; Makanjuola et al., 2020). The stronger detrimental effects of recent inbreeding can be attributed to the progressive elimination of harmful alleles over multiple generations. Both natural and artificial selection play a role in decreasing the prevalence of deleterious alleles in older generations (Leroy, 2014). Conversely, longer ROH segments, indicative of recent inbreeding, are more likely to carry recessive or harmful alleles due to fewer recombination events, thus amplifying their negative impact on phenotypic traits (Charlesworth and Willis, 2009). Our findings highlight the importance of distinguishing between recent and ancient inbreeding when monitoring inbreeding trends in beef cattle populations.

Conclusions

Our findings confirm that inbreeding has a negative impact on the traits studied, leading to reduced reproductive efficiency and decreased lifetime productivity. Both pedigree and genomic inbreeding depression for growth were observed, with the depressive effects on growth becoming more pronounced from birth to weaning and continuing through postweaning weight and ADG. Furthermore, recent genomic inbreeding had a more detrimental effect on growth compared to inbreeding accumulated over more ancient periods.

Inbreeding also reduced the probability of cows remaining in the herd for the next parity, as indicated by its impact on STAY. Fertility was similarly affected, with inbreeding depression particularly evident in the age at first calving. This reduction in longevity and survival negatively impacts herd sustainability by increasing replacement rates and production costs. Our results suggest that inbreeding negatively influences functional longevity, likely due to the expression of deleterious recessive alleles affecting health and fertility. Moreover, recent genomic inbreeding was found to have a more harmful effect on longevity than inbreeding accumulated over more ancient periods. Therefore, genetic management strategies that control inbreeding levels, especially recent genomic inbreeding, are essential for maintaining longevity and reproductive efficiency in beef cattle populations.

In addition to the potential loss of genetic diversity, inbreeding can reduce the mean fitness of individuals, exacerbating inbreeding depression. These findings underscore the need to manage genetic diversity and refine selection strategies to mitigate the negative effects of inbreeding, ensuring sustainable beef production. Specifically, genomic inbreeding coefficients may better reflect the depressing effects of realised inbreeding than pedigree-based methods. This allows breeders to implement more effective mating strategies and avoid pairing closely related animals, ultimately supporting sustainable breeding practices and the long-term productivity of livestock.

Supplementary material

Supplementary Material for this article (https://doi.org/10.1016/j.animal.2025.101672) can be found at the foot of the online page, in the Appendix section.

Ethics approval

The National Italian Association of Limousine and Charolais Breeders provided phenotypic, pedigree, and genomic information. The data used in this study were obtained from a pre-existing database; therefore, approval from the Animal Care and Use Committee was not required.

Data and model availability statement

The datasets generated and/or analysed during the current study are not publicly available due to being owned by a third party, ANACLI, Associazione Nazionale degli Allevatori delle razze bovine Charolaise e Limousine Italiane (https://www.anacli.it/) but are available from the corresponding author on reasonable request.

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

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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Declaration of interest

The authors declare that they have no competing interests.

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