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Uncovering genetic parameters and environmental influences on fertility, milk production, and quality in autochthonous Reggiana cattle

E. Mancin,[1]* G. Gomez Proto,[1] B. Tuliozi,[1] G. Schiavo,[2] S. Bovo,[2] L. Fontanesi,[2] C. Sartori,[1] and R. Mantovani[1]
[1]Department of Agronomy, Food, Natural Resources, Animals and Environment, University of Padova, Viale dell'Università, 16, 35020 Legnaro (PD), Italy
[2]Department of Agricultural and Food Sciences, Division of Animal Sciences, University of Bologna, Viale Giuseppe Fanin 46, 40127 Bologna, Italy

ABSTRACT

Reggiana is a local cattle breed from northern Italy known for its rusticity and profitability, due to the production of branded Parmigiano Reggiano cheese. To ensure the persistence of such profitability in the long term, an adequate breeding program is required. To this aim, in the present study we estimate the genetic parameters of the main productive and reproductive traits, and we evaluate the effect of genotype by environment interaction (GxE) on these traits using 2 environmental covariates: (1) productivity and (2) temperature-humidity index (THI). Milk, fat, protein, and casein yield were considered as daily production traits, whereas protein, fat, casein percentage, casein index, and somatic cell score were considered as milk quality traits. Finally, reproductive traits such as the number of inseminations, days open, calving interval, and calving-to-first-insemination interval were evaluated. Reggiana cattle produce an average of 19 kg of milk per day with 3.7% fat and 3.4% protein content and have excellent fertility parameters. Compared with other breeds, they have slightly lower heritability for production and quality for production traits (e.g., 0.12 [0.09; 0.15] for milk yield), but similar heritability for fertility traits. Milk, protein, and fat daily yields are highly correlated but negatively correlated with the percentage of protein, fat, and casein, whereas fertility traits have an unfavorable genetic correlation with daily production traits. When considering productivity, a consistent amount of variability due to GxE was observed for all daily production traits, somatic cell count, and casein index. A modest amount of GxE was observed for fertility parameters, while the percentage of solid content showed almost no GxE effect. A similar situation occurred when considering the THI, but no GxE interaction was observed for reproduction traits. In conclusion, this study provides useful information for the implementation of accurate selection plans in this local breed, accounting for environmental plasticity measured through the consistent GxE interaction observed.

Key words: animal genetic resource, milk yield, fertility, GxE, selection programs

INTRODUCTION

Autochthonous breeds are animal populations that have been selectively bred for a long time in specific and limited regions (Hiemstra et al., 2010). These breeds have evolved unique traits due to long-term natural and artificial selection, which has allowed them to adapt to specialized production systems and environments (Marsoner et al., 2018; Bertolini et al., 2020). Conserving and farming local breeds is crucial for sustaining food production in their respective areas of origin and can provide valuable ecosystem and socio-cultural services (Teston et al., 2022). To effectively conserve autochthonous breeds, optimizing their economic viability is the most effective approach (Sponenberg et al., 2018). This can be achieved by improving the agricultural system in low-input farming areas or by establishing a marketing connection between the local breed and its products (Gandini et al., 2010). By doing so, a premium price can be obtained due to consumer recognition of the quality and unique characteristics of the breed's products (Gandini et al., 2010).

The Reggiana is a local Italian cattle breed that is a successful example of this link between product and breed. The breed-branded product linked to Reggiana cattle is the world-famous Parmigiano Reggiano cheese, a protected designation of origin (**PDO**). Despite their lower milk productivity compared with other specialized breeds, Reggiana cows remain economically competitive due to the strong value and niche specialization of this product, which has ensured a premium price for their

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*Corresponding author: enrico.mancin@unipd.it

milk (Gandini and Hiemstra, 2021; www.razzareggiana.it, updated on February 12, 2023).

However, sole reliance on marketing strategies cannot be sufficient to ensure long-term competitiveness of Reggiana and other local breeds; it is also essential to develop appropriate genetic evaluation and selection plans. Such plans should not only consider production and fitness aspects but also preserve functional and identity traits specific to the breed, while maintaining genetic diversity (Biscarini et al., 2015).

Incorporating in the breeding program traits such as dairy quality, measured as casein production and SCS, in addition to fertility, can help maintain the traditional rusticity, functionality, and cultural heritage of the breed (Krupová et al., 2016; Mancin et al., 2021). Although these traits have been introduced in the selection indexes of specialized breeds (Miglior et al., 2005), they have not been widely considered in local breeds.

Moreover, effective genetic evaluation plans in Reggiana should also consider the proportion of genotype by environment (**GxE**) interaction. In local breed such as Reggiana considering GxE can indirectly quantify the resilience of animals (Mulder, 2016), which is particularly relevant as it provides the opportunity to select for this critical trait in breeding programs. Furthermore, a high degree of GxE can result in a reduced selection response when related individuals are recorded in different environments (Mulder, 2016), necessitating the redesign of breeding plans.

The GxE models, unlike classical animal models, take into account that breeding values (EBV) for a specific animal and trait are not only determined by the animal's genetic makeup (G), but also by the environmental conditions in which the animal is located (E) and by the effect of environmental factors that are, in turn, regulated by the animal's genetic makeup (GxE); thus, EBV = G + GxE + E (Tiezzi and Maltecca, 2022). Apart from the considered traits, the effect of GxE can vary based on various other factors, such as the type of environment descriptor (E) under consideration. In our study, we employed 2 environmental descriptors: (1) farm productivity and (2) temperature-humidity index (**THI**). An indicator of farm productivity we used the effect of herd-year-season on daily milk yields, as there are significant differences observed in production systems among breeders of the Reggiana, with some adhering to traditional methods and others using advanced technology. Moreover, this variability is further amplified by the year and season effects, which collectively encompass both seasonal or chronological changes in the production systems and weather effects on milk yields. Therefore, with this indicator we aimed to estimate if productive environments have positive effect on the animals' genetic makeup for milk production/quality and reproduction traits.

The second indicator, THI, is widely used to track the capability of the breed to be constant in its genetic expression under variable and potentially hostile environmental conditions. For the Reggiana breed—as for many other local breeds—the most hostile climate for production is represented by high THI, as in the Reggio Emilia area summer temperatures can get higher than 35°C. Warming conditions caused by climate change can represent a serious threat to local breeds living in limited-sized regions, as intense and long bouts of very hot weather can have disastrous consequences for production. Our inclusion of THI as an indicator of climate conditions thus serves 2 purposes: to estimate the resilience of the breed to varying climate, and to map in detail its effect on the expression of key reproduction and production traits. Indeed, the effect of climate conditions on traits linked to the qualities of the milk would be of particular importance in Reggiana, given that its main product Parmigiano Reggiano relies on a specific and delicate balance of milk components for its production.

With all this in mind, to develop an effective selection plan for the Reggiana breed, our study estimated the genetic parameters (i.e., heritability and genetic correlations) of fertility, milk production, and quality traits using test-day repeatability models. In addition, we investigated the presence of GxE interaction in these traits by using herd-year-season and THI as environmental covariates.

MATERIALS AND METHODS

No human or animal subjects were used, so this analysis did not require approval by an Institutional Animal Care and Use Committee or Institutional Review Board.

Study Subject

Reggiana is a cattle breed of medium-large size, with a distinctive coat color that ranges from dark cherry red to a lighter shade of red with white markings on the face, legs, and belly (Forabosco et al., 2011). Reggiana cows have a strong and sturdy build, with a deep and broad chest, well-developed udders, and strong legs. An example of a Reggiana animal is reported in Figure 1B. The breed is known for its rusticity and adaptability to a wide range of environmental conditions, making it well-suited to extensive farming systems. In addition, the breed has a good temperament, making it easy to manage and handle.

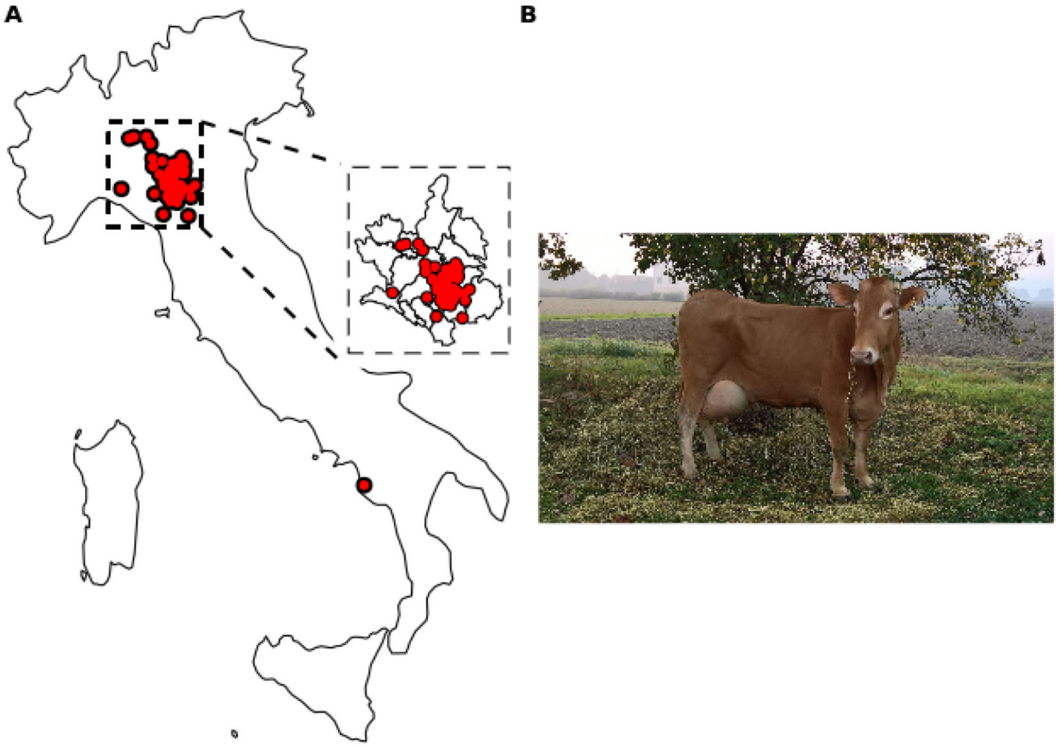


Figure 1. Figure depicting the geographic distribution of Reggiana breed breeders (A) and a female specimen of the Reggiana breed (B).

The origins of the Reggiana breed date back to the barbarian invasions in 568, where the invaders brought with them red cattle originating from southern Russia and the Pannonia regions, that efficiently adapted to new plain environment of the Po Valley.

The ancient Reggiana was a rustic and triple aptitude breed with good milk production, and the cheese produced by Reggiana was the precursor of the current Parmigiano Reggiano. Around the ninth century, the presence of Reggiana cattle was reported in Parma and Reggio Emilia by monks. The breed at that time was a main player in the agricultural and livestock context of the area. The breed reached its peak in 1954 with 139,695 heads. However, the postwar Italian agricultural policy, aimed at increasing agricultural production, led to the replacement or cross of local Reggiana cows with more specialized breeds (Serpieri and Mortara, 1934). As with many other local breeds, there has been a decline in animal numbers since the 1960s, reaching less than 1,000 cows in the 1980s. However, this negative trend was reverted during 1990s, when the high-quality branded-breed Parmigiano Reggiano cheese was trademarked (Parmigiano Reggiano delle Vacche Rosse). The strong niche specialization of this product has ensured, over time, a premium price for the milk of Reggiana cows, balancing the lower milk productivity in comparison to other specialized breeds (www.razzareggiana.it, update: 12 February 2023; Gandini and Hiemstra, 2021). Currently, the Reggiana populations consists of about 4,000 cows of the breed, mostly located in a limited area of the province of Reggio Emilia (Figure 1A).

Data Editing

All data were provided by the National Association of Reggiana Cattle Breeders Association (ANABoRaRe, Mancasale Reggio Emilia, Italy, www.razzareggiana.it/en/), obtained under the official national milk recording system.

Milk Dataset. Before quality control the test-day dataset contained 301,537 records routinely collected from 1991 to 2021, belonging to 13,467 Reggiana cattle. The milk dataset includes information on milk yield (MILK_y, kg/d), percentage of fat (FAT_p, %), protein (PRT_p, %), casein (CAS_p, %), and SCC (no./mL). Similar data editing for the other Italian local breeds was performed as in Mazza et al. (2016), Sartori et al. (2018), and Mancin et al. (2021).

At first data editing, records with DIM outside the interval of 5 d and 305 d were removed. Cows with age at calving outside the following intervals were removed: 21 to 44 mo for first calving, 23 to 60 mo for the second, 44 to 76 mo for the third, and 56 to 87 mo for the fourth, and 59 to 110 mo for the fifth. Records outside the mean ± 4 standard deviations within lactation number and lactation phase (considering 15-d intervals) were also removed from the dataset. Additionally, only lactations with at least one test day starting before 45 d and at least 4 test-day records were retained for further analysis. Lastly, only records belonging to herd-test day with at least 2 observations were maintained.

Then, SCC were normalized in SCS according to Ali and Shook (1980), as $\text{SCS} = 3 + \log_2(\text{SCC}/100{,}000)$. Fat, protein, and casein yields were also derived from MILK_y, FAT_p, and CAS_p, respectively. Casein index was also calculated as the ratio between CAS_p and PRT_p. After this data editing approximately 50% of data were discarded.

This was due to a combination of factors, chiefly attributable to a different structure of the dataset with respect to the more cosmopolite breeds. For example, a significant proportion of the test-day data belonged to animals in parity orders greater than 5, reflecting the long lifespan of Reggiana cows. Another reason is the organization of Reggiana farms, as to obtain robust estimate of herd effects it was necessary to discard data that belonged to herds with few animals in the same lactation class during the test-day. In fact, Reggiana, similar to many local breeds, is characterized by a small-scale farming system where the number of animals per herd is limited compared with Holstein. However, the use of stringent editing criteria is in line with other local breed studies (Sartori et al., 2018; Mancin et al., 2021) and this test data editing method was agreed upon with the breed association. The final dataset used for genetic analysis contained 115,432 test-day records belonging to 16,134 lactation and 6,921 cows. The average number of records per each cow was 16.8 ± 9.9. Information of records in each lactation and distribution of records per each lactation and DIM was reported in Supplemental Table S1 and Supplemental Figure S1 (https://doi.org/10.6084/m9.figshare.24619254.v1).

Fertility Dataset. Fertility traits were analyzed using 2 data sources: the insemination dataset and the test-day dataset. The insemination dataset contained data on insemination events for 11,936 cows collected between 1986 and 2020 (n = 53,201). The test-day dataset was filtered to remove lactations in which animals spent time in 2 or more herds because we cannot attribute 2 different "herd effects" for the same lactation.

The 2 datasets were first merged and then cleaned according to Mancin et al. (2020). Four fertility traits were considered in this study: days open (**DO**), calving interval (**CINT**), calving-to-first-insemination interval (**CFI**), and the number of inseminations to achieve pregnancy (**N_INS**). Days open is the interval between the date of calving and the insemination in which pregnancy was achieved. Calving interval is the difference between 2 consecutive dates of calving. Calving-to-first-insemination interval is the number of days between the calving and first insemination date. Number of inseminations to achieve pregnancy is the count of inseminations necessary to achieve the pregnancy, that is considered a categorical trait with each number of inseminations representing a category, with inseminations ≥5 considered a unique group (Tiezzi et al., 2012). The DO and N_INS records in the last lactation of still alive animals (therefore, lactations without any subsequent ones) were at first considered censored information. However, since censored records were only 2% of the phenotypes, they were removed from the final dataset for a matter of simplicity. Note that the data sets for each phenotype had a different consistency: CINT dataset had the least amount of data (13,826), because 2 consecutive calving dates are needed for a record; DO and CFI dataset contained 17,350 phenotypes, and N_INS dataset contained more phenotypes than all other data sets (22,535), because it was also possible to calculate the number of inseminations also on heifers.

Statistical Analysis

Model Effects. Three different models, in terms of considered effects, were used for (1) dairy traits (both production and quality traits), (2) fertility, and (3) the environmental gradient used as covariate in the GxE analysis.

Dairy Trait Model. The following animal model was used to estimate the variance components for the test-day records of MY, PRT_y, FAT_y, CAS_y PRT_p, FAT_p, CAS_p, CAS_I, and SCS:

$$y_{ijklmno} = \text{HTD}_i + LN_j + GL_k + \sum_{r=1}^{3} \varphi r \times AP\left(LN\right)_l + \sum_{r=1}^{3} \omega r \times MP\left(LN\right)_m + Pe_n + a_n + e_{ijklmno}, \quad [1]$$

where $y_{ijklmno}$ was the individual test-day record of the nth cow; HTD_i was the cross-classified fixed effect of herd-test day (17,628 levels); LN_j was the cross-classified fixed effect of lactation number (5 levels, corresponding to the first 5 lactations); GL_k was the cross-classified fixed effect of the kth gestational status class (18 classes including the absence of gestation and further classes accounting for 15-d intervals, spanning from 1 to 240 d after conception); $AP(LN)_l$ was the cross-classified fixed effect of the lth age at calving within lactation (42 classes in total); $MP(LN)_m$ was the cross-classified fixed effect of the mth month of calving (36 classes, corresponding to single months of a year within 3 lactations). The random effects were represented by the permanent environmental component (Pe_n) and the additive genetic effect (a_n), both sampled from a normal distribution with different co-variances structure, as described below, where $ijklmno$ refers to the observation that belonged to ith HYD class, jth LN class, kth class of GL, lth class AP, mth class of month parity, and nth animal. Residuals were also sampled from a homogeneous normal distribution.

To describe the form of lactation curve, fourth-order Legendre polynomials were used as covariates on the effect of $AP\text{-}LN_l$ and $MP\text{-}LN_m$, and φ and ω in Equation 1 were coefficients for the polynomial of order r varying between 0 and 3 degrees.

Fertility Trait Model. Single-trait analysis for fertility traits (CINT, DO, CFI, N_INS) were carried out with the following animal model:

$$y_{ijklm} = H_i + YM_j + LN_k + a_l + Pe_l + e_{ijklm}, \qquad [2]$$

where y_{ijkl} was one of the 4 fertility traits; H_i was the cross-classified fixed effect of the herd, which levels changed according to the trait considered (from 201 in CINT to 235 for N_INS); YM_j was the year-month cross-classified fixed effect extracted from the date of calving (86 to 92 levels); LN_k was the lactation number (6 levels). The random genetic additive effect a_l, Pe_l, and the residual term e_{ijklm} were sampled as described below.

Environmental Gradient Estimation

Herd-Year-Month Milk Production. To account for the GxE interaction, we calculated an environmental gradient from the solutions of the cross-classified effect herd-year-month (**HYM**, i.e., the combination of herd years and months of the test day) for the MY (kg/d). The following repeatability test-day animal model was used:

$$y_{ijklmno} = HYM_i + LN_j + GL_k + \sum_{r=1}^{3} \varphi r \times AP\left(LN\right)_l + \sum_{r=1}^{3} \omega r \times MP\left(LN\right)_m + Pe_n + a_n + e_{ijklmno}. \qquad [3]$$

The model is similar to Equation 1 except for the replacement of HTD_i with HYM_i. To avoid bias and inaccurate estimation of the environmental gradient, at least 4 records for each level of HYM_i were considered. The best linear unbiased estimator of HYM was used as linear environmental covariate.

Temperature-Humidity Index. The THI was estimated using the formula proposed by Bohmanova et al. (2007). The relative humidity and maximum temperature required for calculating the environmental covariate were collected using an in-house Python code (https://github.com/enmancio/web-scraping-animal-selection). Given the date and municipality of the farms, information about humidity and temperature was obtained by scraping data from the OpenStreetMap website (https://openstreetmap.org) and NASA weather stations (https://power.larc.nasa.gov). For milk traits, THI was considered at the time of the test-day, whereas for fertility traits, the average THI between calving and first insemination was used.

Model Assumption

Single-trait models were employed to determine (1) heritability and variance components, whereas (2) bivariate (bi-trait) models were used to estimate the genetic correlations and, finally, the GxE was estimated using reaction norm. Assumption of these 3 models are described as follows.

Single Traits. Single trait models were represented in this matrix notation:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Wpe} + \mathbf{Za} + \mathbf{e}, \qquad [4]$$

where $\mathbf{y}$ represents the target phenotype, all phenotypes were considered continuous traits (i.e., generated from a normal probability function), except for N_INS that was considered categorical; N_INS was sampled from a truncated normal distribution bounded by a T delimiter based on the values of the observed variable (y). For example, assuming that the random y was composed by n levels ($T = \{t_0, t_1, \ldots, t_n, t_{n+1}\}$), and assuming a liability scale of $l_i = Xb + e$, the threshold conditional probability of y under one of the categories of T (l) became

$$P(yi = j \mid \beta, T) = P(tj - 1 < l \leq t \mid \beta, T) = \Phi\left[Tj - X\beta\right] - \Phi\left[Tj - 1 - X\beta\right], \qquad [5]$$

$\Phi(.)$ was the standard cumulative normal distribution function, where j is one specific category and Tj is the traits in that category). Note that in this case Xb referred to all the fixed and random effects used in the models. **X** is the incidence matrix of all "fixed" effect assumed in the models for the respective traits, and **b** is the vector of that effect. **W** is the incident matrix that related each phenotype to each animal, so we considered every animal as an independent permanent environment effect, and **pe** is the vector of permanent environmental effects. $\mathbf{Z}$ is the incidence matrix of additive genetic effect, and $\mathbf{a}$ is the vector additive effect. $\mathbf{e}$ is the vector of residuals.

Bounded uniform priors were assumed for all fixed effects ($\mathbf{b}$), whereas zero means and normal distributed priors were used for permanent environment ($\mathbf{pe}$), additive genetic ($\mathbf{a}$), and residual effects ($\mathbf{e}$), with this matrix notation:

$$\boldsymbol{a} \sim N\left(0, \mathbf{G} \otimes \mathbf{A}\right); pe \sim N\left(0, \mathbf{Pe} \otimes \mathbf{I}\right); \mathbf{e} \sim N\left(0, \mathbf{R} \otimes \mathbf{I}\right), \quad [6]$$

where $\mathbf{A}$ was the relationship matrix obtained from pedigree, and $\mathbf{I}$ was an identity matrix. In single trait models, $\mathbf{G}$, $\mathbf{Pe}$, and $\mathbf{R}$ were represented by scalars $\left(\sigma_a^2, \sigma_{pe}^2, \sigma_e^2\right)$ representing additive genetic variances, permanent environment variances and residuals, respectively.

Bivariate Models. Genetic correlations between all the considered phenotypes were estimated by using bivariate models as follows:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{W}_1 & 0 \\ 0 & \mathbf{W}_2 \end{bmatrix} \begin{bmatrix} \mathbf{pe}_1 \\ \mathbf{pe}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix}, \quad [7]$$

where $\mathbf{y}_1$ and $\mathbf{y}_2$ corresponded to the phenotypic records considered in each analysis, $\mathbf{X}_1$ and $\mathbf{X}_2$ were the incidence matrices for fixed effects, $\mathbf{W}_1$ and $\mathbf{W}_2$ were the incidence matrices of the random permanent environment, and $\mathbf{Z}_1$ and $\mathbf{Z}_2$ were the matrices of the additive genetic effect. The vectors of the systematic effects were represented by $\mathbf{b}_1$, $\mathbf{b}_2$, whereas $\mathbf{pe}_1$, $\mathbf{pe}_2$ were vectors of the permanent environmental effects, $\mathbf{a}_1$, $\mathbf{a}_2$ were vectors of the additive genetic effect, and $\mathbf{e}_1$, $\mathbf{e}_2$ represented vectors of the residual error terms. In the bivariate model additive genetics, permanent environment, and residual effects were estimated using the following matrix notations:

$$\mathbf{G} = \begin{vmatrix} \sigma_{a1}^2 & \sigma_{a1a2} \\ \sigma_{a1a2} & \sigma_{a2}^2 \end{vmatrix}; \ \mathbf{Pe} = \begin{vmatrix} \sigma_{pe1}^2 & \sigma_{pe1pe2} \\ \sigma_{pe1pe2} & \sigma_{pe2}^2 \end{vmatrix}; \ \mathbf{R} \begin{vmatrix} \sigma_{e1}^2 & \sigma_{e1e2} \\ \sigma_{e1e2} & \sigma_{e2}^2 \end{vmatrix}, \quad [8]$$

where $\mathbf{G}$ was the matrix of additive genetic (co)variances σ_{a1}^2, σ_{a1a2}, σ_{a2}^2 of traits 1 and 2. $\mathbf{Pe}$ was the matrix of permanent environmental (co)variances σ_{pe1}^2, $\sigma_{pe1,pe2}$, σ_{pe2}^2, and $\mathbf{R}$ was the matrix of residual (co)variances σ_{e1}^2, σ_{e1e2}, and σ_{e2}^2 of traits 1 and 2. Note that when different datasets were merged (i.e., milk and fertility traits), residual (co)variance was set to zero because the traits were recorded in different moments.

Reaction Norm Model. A reaction norm model (**RNM**) consisted of the implementation of a single-trait animal model, where, in addition to the animal additive effect $\mathbf{Z}_0\mathbf{a}_0$, the random regression of the environmental gradient estimated in Equation 3 on the additive genetic effect was considered ($\mathbf{Z}_1\mathbf{a}_1$), that was a component representing the GxE quote. Reaction norm models were implemented for all the traits included in the study; therefore, these models can be described as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Wpe} + \mathbf{Z}_0\mathbf{a}_0 + \mathbf{Z}_1\mathbf{a}_1 + \mathbf{e}, \quad [9]$$

where $\mathbf{Z}_0$ and $\mathbf{Z}_1$ were matrices of the 2 additive effects, $\mathbf{Z}_0$ was a matrix that connects $\mathbf{a}_0$ to the phenotype, whereas $\mathbf{Z}_1$ was a matrix related to the environmental gradient $\mathbf{a}_1$ obtained in [3] and used as a covariate. Both effects were distributed as follows:

$$\begin{bmatrix} a_{n0} \\ a_{n1} \end{bmatrix} \sim N\left(0, \mathbf{A} \otimes \begin{bmatrix} \sigma_{a_0}^2 & \sigma_{a_0,a_1} \\ \sigma_{a_0,a_1} & \sigma_{a_1}^2 \end{bmatrix}\right). \quad [10]$$

Residual were considered homogeneous due to the reduced sample size.

Model Computations

The (co)variance components were estimated using the Gibbs sampling algorithm implemented in the blupf90 family software (Aguilar et al., 2018). A total of 500,000 Gibbs samples chains were generated, with an initial burn-in of 100,000, and retaining one of every 100 chains to avoid collinearity. The mean and highest posterior density (HPD) interval of remaining 4,000 chains were reported in the results. A matrix was created by tracing back the maximum number of feasible generations, which corresponds to 9 generations for milk characters and 8 generations for fertility; information regarding the pedigree information is reported in Figure 2.

Model Outcome

Estimated heritability was calculated in the single-trait analysis and RNM as $\mathrm{h}^2 = \dfrac{\sigma_a^2}{\sigma_p^2}$, where σ_p^2 is the total phenotypic variance expressed as $\sigma_p^2 = \sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2$.

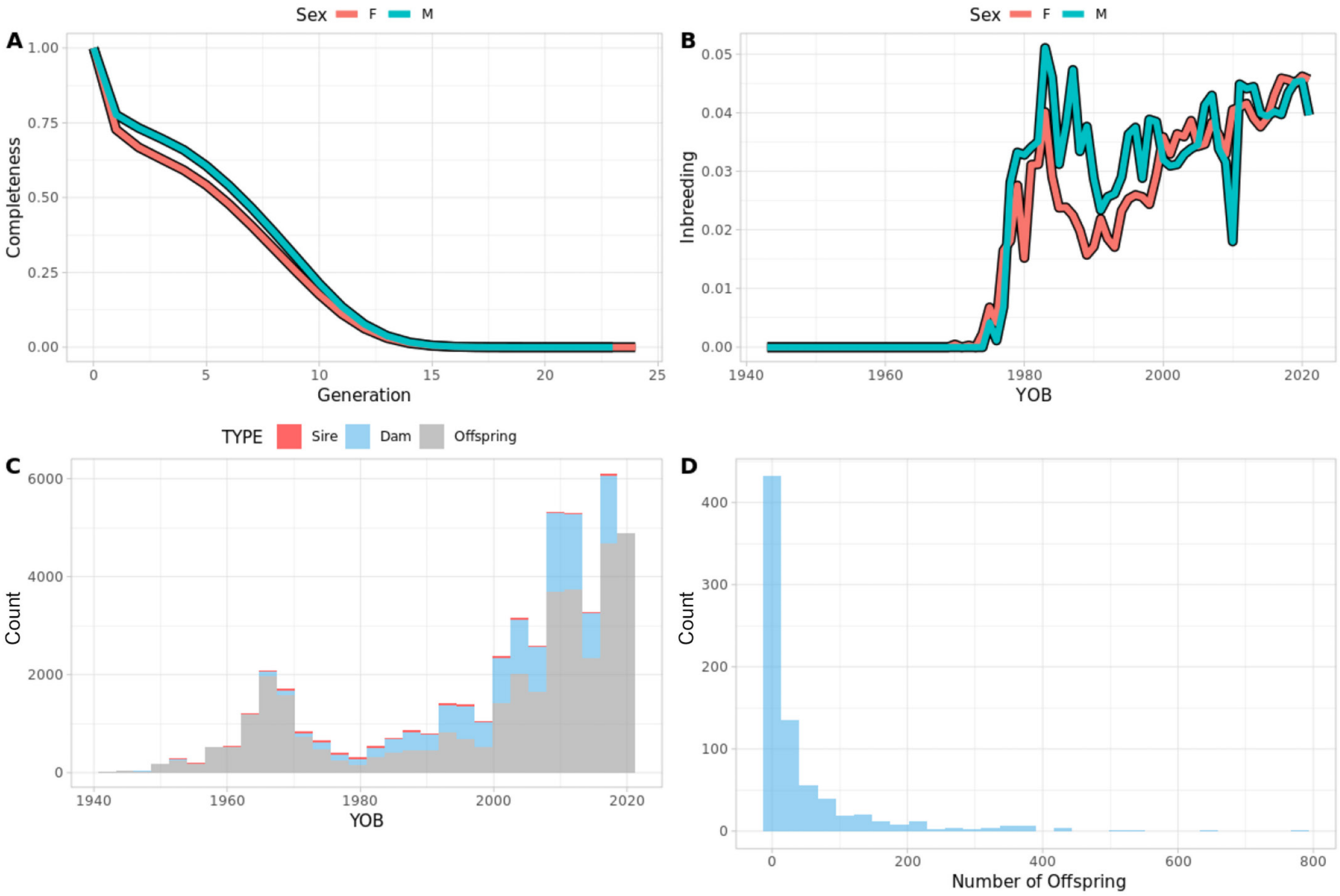


Figure 2. Analysis of the pedigree that encompassed (A) determination of pedigree completeness by generation and sex, (B) examination of inbreeding trends by year of birth (YOB) and sex, (C) characterization of the population, including the number of sires, dams, and offspring per year, and (D) quantification of the number of offspring per sire. M = male; F = female.

The correlation estimates (genetic and phenotypic) were calculated as $r_a = \frac{\operatorname{cov}(x, y)}{\sigma_x \sigma_y}$, where x and y referred to the different traits; cov(x, y) stands for the estimated covariance between the traits; and σ_x and σ_y were the estimated genetic standard deviation of traits.

We also reported the change of heritability (h^2) at the change of the 2 environmental gradients, production levels and THI, with following formula: $\mathbf{EGE'}/\sigma_p^2$, where $\mathbf{E}$ is the standardized vector of environmental variance, and $\mathbf{G}$ is the genetic effect $\mathbf{Z}_0\mathbf{a}_0$ described in Equation 9.

We ran for all traits a Spearman correlation between the bulls' breeding values obtained with and without including the GxE within the model, to investigate a possible reranking. Additionally, reranking using the top 10% and 20% young bulls was also performed (see Supplemental Figure S3, https://doi.org/10.6084/m9.figshare.24619254.v1).

RESULTS AND DISCUSSION

Descriptive Statistics

Table 1 displays the mean, standard deviation, coefficient of variation, as well as minimum and maximum values for 10 phenotypes linked to Reggiana, which include milk production, protein and fat percentage, and fertility parameters. The distribution of these values is shown in Supplemental Figure S2 (https://doi.org/10.6084/m9.figshare.24619254.v1). Before this work, only Gandini et al. (2007) had conducted research on both milk and fertility in Reggiana. Our study found a significant increase in milk production, of an average of 460 kg per lactation, from the 5,360 kg per lactation reported in Gandini et al. (2007) to 5,828 kg per lactation. Protein and fat percentage also showed an increase, with PRT_p increasing from 3.38% to 3.70% ± 0.39 and FAT_p increasing from 3.21% to 3.45% ± 0.86. These improvements might be attributed to the selection program, redefined in 1996, combined with improvements in management conditions. Reggiana had also favorable fertility parameters (Table 1), consistent with values reported for the breed by Pizzi et al. (2003) and Gandini et al. (2007). Reggiana had a CFI interval of 80 ± 42 d, whereas DO and CINT showed values of 108 ± 54 and 391 ± 68 d, respectively, and only 1.30 ± 0.78 AI required for conception. Therefore, it is interesting to note that, compared with more cosmopolitan breeds such as the Holstein, there has not been a reduction in the fertility of Reggiana cattle over the years (Heins et al., 2006).

Regarding daily milk yield, Reggiana had a production of 19.3 kg/d, as shown in Table 1, which is substantially lower than that reported in specialized Italian breeds. For example, on average, Italian Friesians produce 31.3 kg/d, while Italian Browns produce 23.6 kg/d. Reggiana cows also had lower productivity than the dual-purpose Italian Simmental breed (22.0 kg/d; Visentin et al., 2018). However, the scenario changes when comparing the Reggiana milk yield with that of other Italian autochthonous breeds, as Reggiana presented higher daily milk production than breeds such as Alpine Grey (16.3 kg/d; Mancin et al., 2021), Rendena (16.5 kg/d; Guzzo et al., 2019), or Aosta Red Pied breed (13.0 kg/d; Mazza et al., 2016).

The percentage of solid content in Reggiana milk is similar to that of other local and cosmopolitan breeds, such as Rendena and Grigio Alpina (Visentin et al., 2018; Guzzo et al., 2019; Mancin et al., 2021). Previous studies on casein content for these local breeds are lacking, but similar values to other Italian cosmopolitan breeds have been observed, with a casein index of 0.785 (Samorè et al., 2012; Pegolo et al., 2021). However, Reggiana had the highest SCS value compared with the other mentioned local breeds, with a score of 3.22 points versus 2.33 SCS points in Alpine Grey cattle (Mancin et al., 2021). This value indicates that Reggiana is more similar in SCS to cosmopolitan breeds (Italian Friesian and Brown Swiss; Franzoi et al., 2020) than to local breeds.

Regarding fertility traits, Reggiana exhibited significantly lower fertility parameters than specialized breeds such as Italian Holstein and Brown Swiss, indicating better fertility (Toledo-Alvarado et al., 2017; Martinez-Castillero et al., 2020). Reggiana showed fertility parameters similar to Italian Simental and Rendena breeds, with an average DO interval of 108 and 115, respectively (http://bollettino.aia.it, updated on 25 March 2023). On the other hand, Reggiana exhibited slightly higher fertility parameters than other local breeds, such as Alpine Grey, and Aosta Pied Red, with an average DO interval of 92 and 99, respectively (http://bollettino.aia.it, updated on 25 March 2023).

Based on the available information, the Reggiana breed can be placed in an intermediate position among other local breeds. Despite being considered a local breed, Reggiana showed substantially higher dairy aptitude compared with other breeds, although it is still far from Holstein productivity. Additionally, Reggiana demonstrated good fertility parameters, much better than specialized breeds and close to the fertility parameters of local breeds, although it may not be considered one of the best Italian breeds in this regard.

Heritability

Table 2 reports the heritability and variance components analysis. The heritability values for dairy production traits ranged from 0.053 to 0.12, while for milk quality traits, the range was from 0.077 to 0.292, and for fertility traits, it was from 0.018 to 0.026. The heritability values reported here are slightly lower compared with those found in literature, especially for milk production traits (Frigo et al., 2013; Tullo et al., 2014; Guzzo et al., 2019; Mancin et al., 2021).

In terms of milk production, the heritability of MILK_y, and consequently, FAT_y and PRT_y, was substantially lower than that reported in some previous studies (Guzzo et al., 2019; Mancin et al., 2021), with a value of 0.120 [high posterior density distribution: 0.089; 0.151], 0.069 [0.051; 0.089] and 0.097 [0.071; 0.123] for MILK_y, FAT_y, and PRT_y, respectively. However, Costa et al. (2019) found values close to those identified in this study (0.14).

Daily quality traits in the Reggiana breed exhibit higher heritability compared with production traits (Table 2), with PRT_p having the highest heritability value (0.27 [0.24; 0.30]) and CASI having the lowest value (0.11 [0.08; 0.13]). We found that the heritability of PRT_p in Reggiana was similar to the heritability observed in the Rendena breed (Sartori et al., 2022), but it was lower compared with some other Italian breeds such as Friesian, Brown Swiss, and Simmental (Visentin et al., 2018). The heritability of CAS_p was also lower than what has been reported in previous studies e.g., Samorè et al. (2012). On the other hand, the heritability estimates for FAT_p and SCS (0.15 [0.13; 0.17] and 0.07 [0.05; 0.10], respectively) were consistent with those observed in another breed (Samorè et al., 2012, Visentin et al., 2018).

The heritability estimates for fertility traits in the Reggiana breed were relatively low, with values ranging from 0.018 [0.010; 0.023] for N_INS (in liability scale) to 0.026 [0.011; 0.042] for CF. These results were consistent with those found in more specialized breeds in previous studies (González-Recio and Alenda, 2005; Tiezzi et al., 2012; Liu et al., 2017). N_INS had the

Table 1. Descriptive statistics of the 10 phenotypes considered in the study after data editing

Type	Trait[1]	Units	Mean	Min.[2]	Max.[3]	SD	CV	N[4]	Cow[5]	Herd[6]	Pedigree[7]	Sire[8]	Dams[9]
Milk production	MILK_y	kg/d	19.110	0.200	90.000	7.185	0.376	115,432	6,921	183	9,400	527	5,194 (3,855)
	FAT_y	kg/d	0.660	0.008	5.359	0.283	0.429	115,432	6,921	183	9,400	527	5,194 (3,855)
	PRT_y	kg/d	0.637	0.006	3.456	0.217	0.341	115,432	6,921	183	9,400	527	5,194 (3,855)
	CAS_y	kg/d	0.501	0.003	2.138	0.025	0.0494	61,989	5,780	134	8,932	527	5,201 (3,678)
Milk quality	FAT_p	%	3.701	0.053	16.930	0.862	0.233	115,432	6,921	183	9,400	527	5,194 (3,855)
	PRT_p	%	3.450	0.160	10.650	0.386	0.112	115,432	6,921	183	9,400	527	5,194 (3,855)
	CAS_p	%	2.797	0.270	5.910	0.308	0.11	61,989	5,780	134	8,932	527	5,201 (3,678)
	CAS_I	%	0.784	69.59	0.897	0.016	0.02	61,989	5,780	134	8,932	527	5,201 (3,678)
	SCS	Log(count)	3.227	−3.644	10.893	1.836	0.569	115,397	6,921	183	9,400	527	5,194 (3,855)
Fertility	DO	Days	108.930	3	299	54.797	0.625	17,350	6,941	215	8,002	418	4,781 (4,060)
	CINT	Days	391.410	279	594	68.081	0.140	13,826	5,788	201	6,661	400	4,093 (3,327)
	CFI	Days	80.580	3	199	42.305	0.525	17,350	6,941	215	6,661	400	4,093 (3,327)
	N_INS	Number	1.330	1	5	0.775	0.583	22,535	8,007	234	5,750	388	3,628 (2,855)

[1] Categorical traits: milk yields (MILK_y), fat yields (FAT_y), protein yields (PRT_y), casein yields (CAS_y), percentage of fat (FAT_p), percentage of protein (PRT_p), percentage of casein (CAS_p), casein index (CAS_I), days open (DO), calving interval (CINT), calving-to-first-insemination interval (CFI), and number of inseminations (N_INS).

[2] Min: minimum value.

[3] Max: maximum value.

[4] N: number of phenotypes.

[5] Number of animals with phenotypic records.

[6] Number of herds in the dataset.

[7] Pedigree: number of animals traced back in the pedigree.

[8] Sire: number of sires in the pedigree.

[9] Dam: number of dams in the pedigree; the number of dams with phenotypic records is inside the parentheses.

Table 2. Variance components estimated using single trait models; the numbers within parentheses are the extremes of the high posterior density distribution interval[1]

Trait[2]	Va	Vpe	Vres	h^2
MILK_y	2.995	8.205	13.692	0.120
	(2.170; 3.785)	(7.520; 8.822)	(13.590; 13.830)	(0.089; 0.151)
FAT_y	0.376^3	1.080^3	3.950^3	0.069
	(0.2721; 0.4823)	(0.986; 1.170)	(3.918; 3.986)	(0.051; 0.089)
PRT_y	0.2571^3	0.837^3	1.5673^3	0.097
	(0.1863; 0.3300)	(0.7748; 0.9016)	(1.5540; 1.581)	(0.071; 0.123)
CAS_y	9.273	59.705	106.4	0.053
	(5.308; 15.060)	(54.984; 64.217)	(105.1; 107.7)	(0.030; 0.084)
FAT_p	0.0902	0.044	0.4664	0.150
	(0.0776; 0.1033)	(0.0366; 0.0532)	(0.4624; 0.4704)	(0.130; 0.170)
PRT_p	0.024	0.014	0.051	0.273
	(0.0213; 0.0277)	(0.0117; 0.0158)	(0.0506; 0.0515)	(0.242; 0.305)
CAS_p	0.016	0.009	0.029	0.292
	(0.013; 0.018)	(0.007; 0.010)	(0.028; 0.029)	(0.253; 0.333)
CAS_I	0.182	0.275	1.274	0.106
	(0.141; 0.234)	(0.240; 0.314)	(1.259; 1.291)	(0.080; 0.133)
SCS	0.213	0.774	1.787	0.077
	(0.1506; 0.2837)	(0.7147; 0.8320)	(1.7680; 1.7990)	(0.054; 0.100)
DO	57.355	173.99	2,742	0.0196
	(22.710; 97.470)	(117.5; 236.3)	(2,668; 2,818)	(0.008; 0.033)
CINT	55.176	169.380	2,570	0.0197
	(14.790; 99.780)	(102.0; 231.3)	(2,489; 2,650)	(0.06; 0.0356)
CFI	29.383	57.395	1,037.2	0.0261
	(11.880; 46.610)	(35.400; 82.810)	(1,010; 1,067)	(0.011; 0.042)
N_INS[4]	0.020	0.047	1.033	0.0181
	(0.010; 0.036)	(0.017; 0.066)	(0.987; 1.233)	(0.010; 0.0233)

[1] Additive genetic variance (Va), permanent environment variance (Vpe), residual variances (Vres).

[2] Traits: milk yields (MILK_y), fat yields (FAT_y), protein yields (PRT_y), casein yields (CAS_y), percentage of fat (FAT_p), percentage of protein (PRT_p), percentage of casein (CAS_p), casein index (CAS_I), days open (DO), calving interval (CINT), calving-to-first-insemination interval (CFI), and number of inseminations (N_INS).

[3] Variance multiplied by 10^3.

[4] Expressed as liability.

lowest heritability estimate, while CFI had the highest, similar to the findings of Zhang et al. (2019). However, the heritability estimates for these traits were lower than in Ismael et al. (2016).

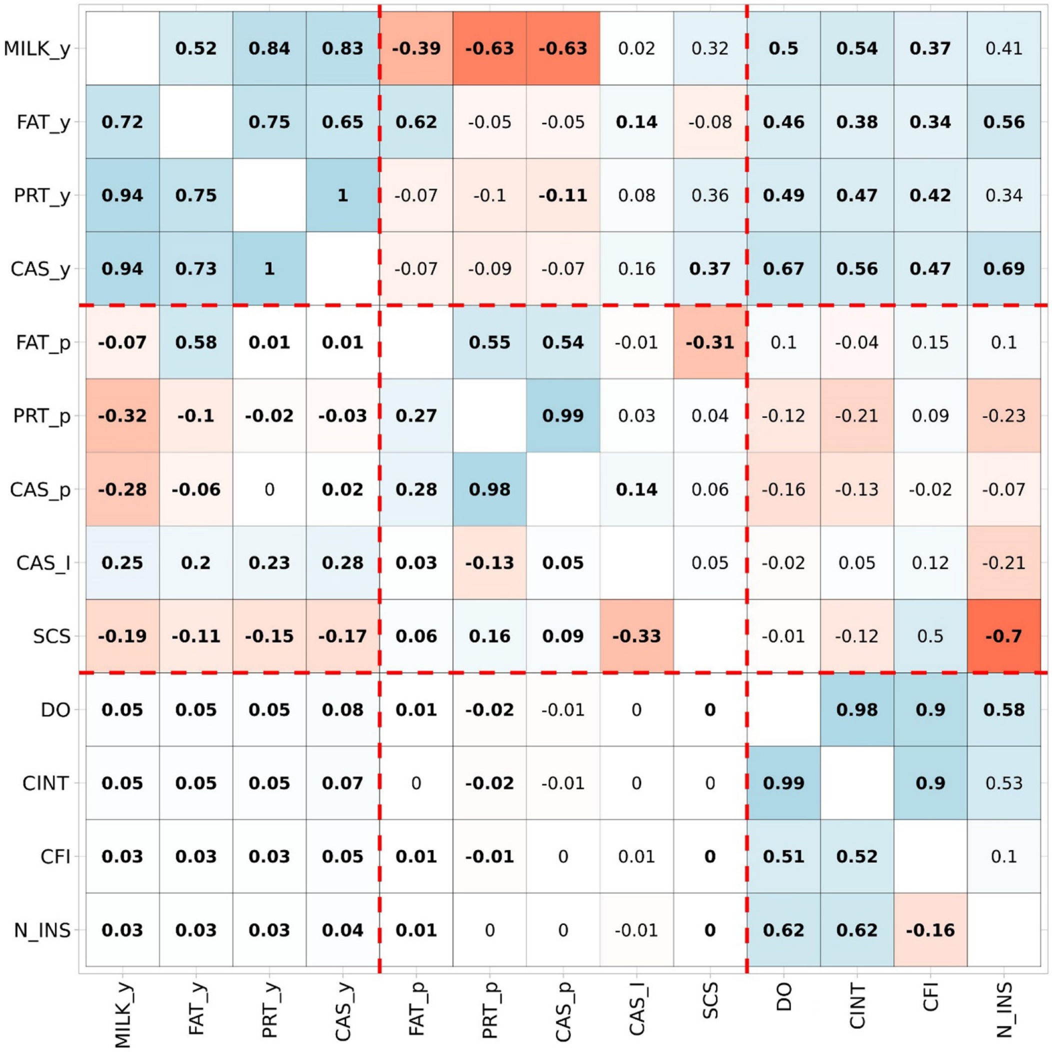
The lower heritability observed in Reggiana cattle may be attributed to various factors, such as the reduced genetic variability of the population resulting from a bottleneck in the 1980, which was followed by a gradual recovery that began in the 1990s. During this time, a small and closely related nucleus of animals reconstructed the population, leading to a significant increase in the level of inbreeding that has since stabilized over the years. Other, nonexclusive reasons for the lower heritability seen in Reggiana might be the generally low number of progenies per each sire, as the largest number of sires have only one or very few offspring, and possible errors in pedigree data collection or incomplete pedigree information (Mantovani and Fontanesi, personal communication). Indeed, as shown in Figure 2, recent generations (1–3) have a high degree of completeness approaching 100%, whereas substantial incompleteness is observed moving back 5 generations (nearly 60%). The last point is highlighted also by the comparisons of inbreeding estimates based on pedigree data to those based on genomic data, which have shown poor correlation (Schiavo et al., 2022).

Genetic Correlations

In this study, we examined the genetic and phenotypic correlations among various traits in dairy cattle. Figure 3 shows the estimated correlations, with those having a 95% posterior density interval that did not include zero considered significant. The genetic correlations were grouped into 3 categories: productive traits, milk quality traits, and fertility traits.

We found that milk production traits showed negative genetic correlations with fertility traits, averaging 0.47 across all traits. In contrast, they had a slightly negative or almost null correlation with milk quality traits. Fertility and milk quality traits were found to have no significant genetic correlation.

We found high genetic correlations among the milk production traits themselves. For instance, PRT_y and CAS_y was highly correlated with MILK_y (0.84), whereas FAT_y had a lower correlation with MILK_y



	MILK_y	FAT_y	PRT_y	CAS_y	FAT_p	PRT_p	CAS_p	CAS_I	SCS	DO	CINT	CFI	N_INS
MILK_y		**0.52**	**0.84**	**0.83**	**-0.39**	**-0.63**	**-0.63**	0.02	0.32	**0.5**	**0.54**	**0.37**	0.41
FAT_y	**0.72**		**0.75**	**0.65**	**0.62**	-0.05	-0.05	**0.14**	-0.08	**0.46**	**0.38**	**0.34**	**0.56**
PRT_y	**0.94**	**0.75**		**1**	-0.07	-0.1	**-0.11**	0.08	0.36	**0.49**	**0.47**	**0.42**	0.34
CAS_y	**0.94**	**0.73**	**1**		-0.07	-0.09	-0.07	0.16	**0.37**	**0.67**	**0.56**	**0.47**	**0.69**
FAT_p	**-0.07**	**0.58**	**0.01**	**0.01**		**0.55**	**0.54**	-0.01	**-0.31**	0.1	-0.04	0.15	0.1
PRT_p	**-0.32**	**-0.1**	**-0.02**	**-0.03**	**0.27**		**0.99**	0.03	0.04	-0.12	-0.21	0.09	-0.23
CAS_p	**-0.28**	**-0.06**	0	**0.02**	**0.28**	**0.98**		**0.14**	0.06	-0.16	-0.13	-0.02	-0.07
CAS_I	**0.25**	**0.2**	**0.23**	**0.28**	**0.03**	**-0.13**	**0.05**		0.05	-0.02	0.05	0.12	-0.21
SCS	**-0.19**	**-0.11**	**-0.15**	**-0.17**	**0.06**	**0.16**	**0.09**	**-0.33**		-0.01	-0.12	0.5	**-0.7**
DO	**0.05**	**0.05**	**0.05**	**0.08**	**0.01**	**-0.02**	-0.01	0	**0**		**0.98**	**0.9**	**0.58**
CINT	**0.05**	**0.05**	**0.05**	**0.07**	0	**-0.02**	-0.01	0	0	**0.99**		**0.9**	0.53
CFI	**0.03**	**0.03**	**0.03**	**0.05**	**0.01**	**-0.01**	0	0.01	**0**	**0.51**	**0.52**		0.1
N_INS	**0.03**	**0.03**	**0.03**	**0.04**	**0.01**	0	0	-0.01	**0**	**0.62**	**0.62**	**-0.16**	

Figure 3. Correlation plots where genetic correlations are shown on the upper diagonal and phenotypic correlations on the lower diagonal. Significant correlations (those with zero falling outside the confidence interval) are denoted in bold. Traits within the same category (such as milk yield, milk quality, and fertility) are highlighted in bold. Milk yields (MILK_y), fat yields (FAT_y), protein yields (PRT_y), casein yields (CAS_y), percentage of fat (FAT_p), percentage of protein (PRT_p), percentage of casein (CAS_p), casein index (CAS_I), days open (DO), calving interval (CINT), calving-to-first-insemination interval (CFI), and number of inseminations (N_INS), expressed on a liability scale.

(0.52). Furthermore, the genetic correlations between PRT_y and CAS_y with FAT_y were 0.75 and 0.65, respectively. These findings are consistent with previous studies on both local and specialized breeds, which have also reported high correlations among these milk traits. Interestingly, we also observed a strong genetic correlation ($r = 1$) between CAS_y and PRT_y, which was reflected in the correlation between PRT_p and CAS_p ($r = 0.99$).

Focusing on milk quality traits instead, we observe that FAT_p had positive correlation ($r = 0.55$) with PRT_p, and consequently with CAS_p, ($r = 0.54$). The trait CAS_I showed null correlation with all milk quality traits, except with CAS_p, with which it showed a weak but significant correlation of 0.14. This was expected, as CAS_I is the ratio of CAS_p and PRT_p. Interestingly, SCS showed only negative correlations with FAT_p.

From the point of view of selection plans it is interesting to note the antagonistic correlations of FAT_p and PRT_p with milk yield ($r = -0.39$, -0.63, respectively) also supported by a large literature (de Jager and Kennedy, 1987; van Binsbergen et al., 2012). We found also negligible correlation between CAS_I and MILK_y. We also found that SCS had a beneficial correlation with fat and protein percentages; therefore, a selection focused on increasing the percentage of solid content, as mentioned before, could also be beneficial for udder health. On the other hand, SCS had a significant positive genetic correlation with MILK_y, which means that an increase in milk productivity leads to the detriment of udder condition due to the increased somatic cells concentration in milk (Kheirabadi and Razmkabir, 2016).

All fertility traits showed high genetic correlations with each other, with DO and CINT being strong genetically related ($r = 0.984$) as they only differed in gestation length. These traits were also highly genetically correlated with CFI ($r = 0.89$). On the other hand, N_INS had a lower overall correlation with these traits, an average correlation of 0.50 with DO and CINT, and no significant correlation with CFI. Again, this pattern of genetic correlations has been observed in previous studies (González-Recio and Alenda, 2005; Tiezzi et al., 2012). The study also found a higher negative correlation between SCS and N_INS ($r = -0.7$). This negative correlation between dairy production and fertility is attributed to the fact that cows with higher productivity experience a state of negative energy balance, resulting in a reduction in energy allocation toward reproductive processes.

The results relative to negative genetic correlations are crucial, as they can be used to inform the fine-tuning of breeding programs in the Reggiana breed, specifically in regard to maintaining the cheesemaking properties required for producing Parmigiano Reggiano cheese. This involves adjusting the milk yield index for fat, protein, and casein content while also considering the genetic correlations between these traits (Guinee et al., 2007). Estimating these correlations is the first, key step in assigning appropriate economic weights to each phenotype for inclusion in the selection index.

Functional traits such as SCS can be easily improved through indirect selection aimed at maintaining the cheesemaking quality of milk, for example, through selection for FAT_p. However, the same cannot be applied to traits such as fertility due to their low heritability and strong antagonistic correlation with milk, making fertility selection a challenging task (Lucy, 2019).

Genotype by Environment

Motivations of the 2 Environmental Gradients. As previously mentioned, GxE refers to the response of the genotype to changes in environmental descriptors. Specifically, in our cases, reaction norm models describe the linear response of the genotype to the 2 continuous environmental gradients (Falconer 1990), environment productivity, and THI.

Regarding environmental productivity, we were interested in investigating whether more productive environments had a negative or positive effect on the genetic response for traits. In fact, productive environments might negatively affect traits, as they drive cows to higher energy output with various negative effects on metabolism (Martinez-Castillero et al., 2020). On the other hand, higher productivity environments might have the opposite effect and be beneficial, as they might represent better welfare and technical inputs for the breed. We defined positive or negative influence traits based on the sign of the correlations: more than on productive traits, the main interest is to see how the GxE interaction can affect reproductive traits and milk quality. Figure 4A shows the distribution of environmental productivity, and there is a difference of nearly 12 standard deviations between the most productive and the least productive environment, corresponding almost to 14 kg of milk, which is very high for a breed such as Reggiana.

A high of THI is widely recognized to have a negative effect not only on production traits but also on reproductive traits (Liu et al., 2017). Quantifying the percentage of variation captured by GxE in a breed such as the Reggiana is essential to assess whether Reggiana, like other local breeds, might be able to cope with different environmental conditions. Furthermore, the consideration of THI in the genetic evaluation plans has practical implications for the Reggiana breed, as it provides the tools for selecting animals more resistant to higher levels of THI and less biased EBV (Mulder, 2016). This is essential for the Reggiana breed, which is bred in a restricted area, Reggio Emilia, which suffers from a large discrepancy between summer and winter temperatures (Figure 4B), which has been exacerbated in recent years due to climate change.

GxE Variance Components. The intercept $\sigma^2_{a_1}$ of the reaction norm represents the total genetic variance at the mean values of the 2 environmental descriptors, while the slope $\sigma^2_{a_1}$ quantifies the variation of this variance per standardized unit of the descriptors of the 2 environmental gradients. However, a higher slope does not necessarily indicate greater EBV recombination. A significant reranking of the animals requires also that a good proportion of the variance is expressed by the covariance between the 2. In fact, higher slopes and zeroes $\sigma^2_{a_1}$ imply that each animal's EBV increases or decrease with the same magnitude as the environmental gradients increase (Falconer, 1990; Strand and Weisner, 2004). Strong positive correlations imply that animals with above-average EBV will be more favored as the environmental gradient increases, while animals with below-average genetic value will be less favored. Conversely, negative correlations between gradient and intercept mean that animals with higher EBV will tend to be disadvantaged as the environmental gradient increases.

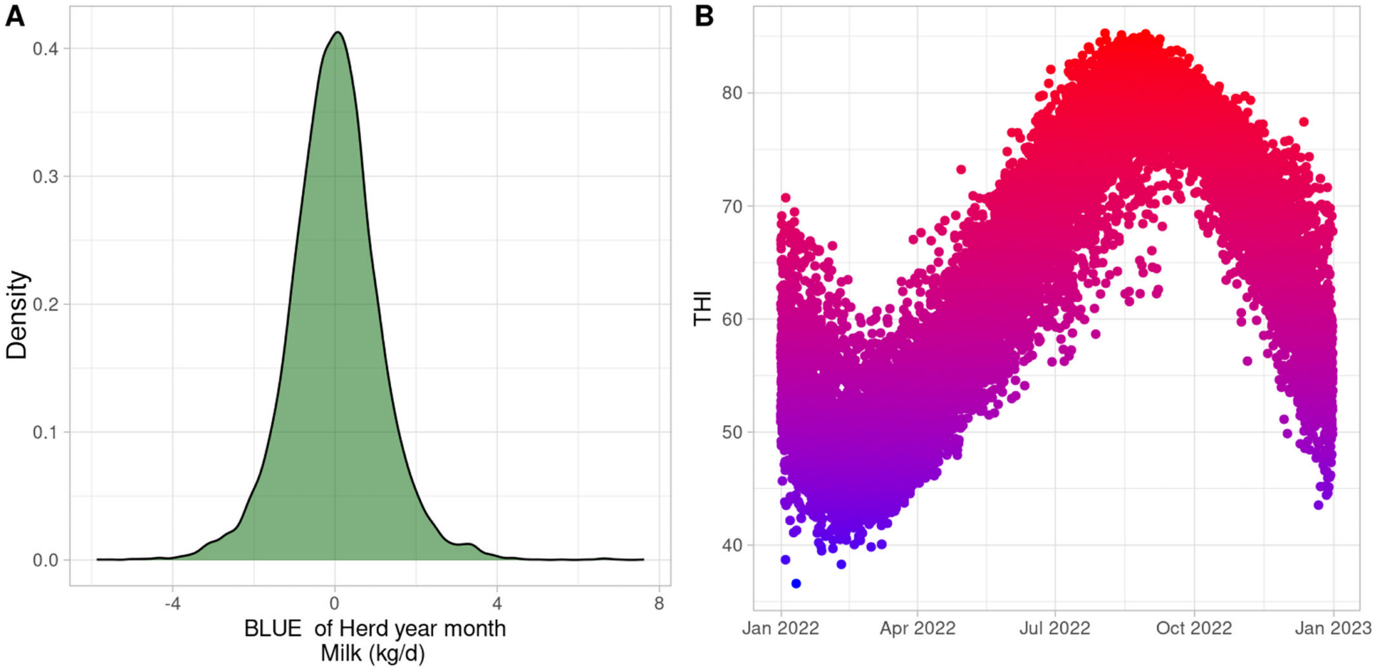


Figure 4. Figure depicting the 2 environmental gradient descriptors: (A) the best linear unbiased estimator (BLUE) solutions of the herd-year-month effect and (B) the temperature-humidity index (THI) over the course of a year.

Slope

Productivity Traits. The slope of the reaction norm is interpreted as environmental sensitivity, which determines how much the additive variation of the traits is influenced by the environmental gradient. The dairy production traits (e.g., MILK_y) were greatly influenced by the 2 environmental descriptors, as shown in Figure 5. For the productivity environmental gradient (as shown in Figure 4) the slope accounts for approximately 3% of the total phenotype variance across all production traits. These results are consistent with those of previous studies by Schmid et al. (2021) and Sartori et al. (2022), which identified similar values.

Similar trends were observed when THI was used as an environmental gradient, with a slope accounting from 3.5% in CAS_Y to 2% in FAT_Y of the total phenotypic variance, that corresponds to the 7% and 3% of total genetic variance, respectively.

The studies of Cheruiyot et al. (2020) and Landi et al. (2023) found higher slope values for milk production traits compared with other traits, although the latter study considered THI as a nonlinear variation. One possible explanation for the higher GxE identified in milk production traits could be that they are not closely related to fitness (i.e., traits linked to survival or reproduction of animals). This means that animals can regulate and be more flexible in adapting and expressing these phenotypes compared with traits such as fertility (Mousseau and Roff, 1987).

Milk Quality Traits. When THI was used as an environmental gradient, FAT_p, PRT_p, and CAS_p presented slope values ranging from 2% to 3%. However, the slope was close to zero when productivity was used as an environmental gradient. Previous studies by Schmid et al. (2021) and Sartori et al. (2022) similarly found no GxE interaction when environmental productivity was considered. In general, similar results were also found in Tiezzi et al. (2017), where no GxE interaction was observed when environmental productivity was considered, while substantial GxE was identified for percentage of solid content when a climate descriptor was used.

In contrast, milk quality traits such as SCS and CAS_I exhibited a substantial slope for both gradients. Specifically, the slope values were, respectively, 2.5% and 2% of total phenotypic variance for the productive gradient, and, respectively, 3% and 1% of total phenotypic variance for THI.

Fertility Traits. For reproductive traits, much less phenotypic variance was absorbed by the slope, with a value lower than 0.5% for all traits when productivity was used as the environmental covariate (with higher values for CFI and lower values for CINT). Despite the low values, it represents a good proportion of the total genetic variance of these traits, as total genetic variance was 2%.

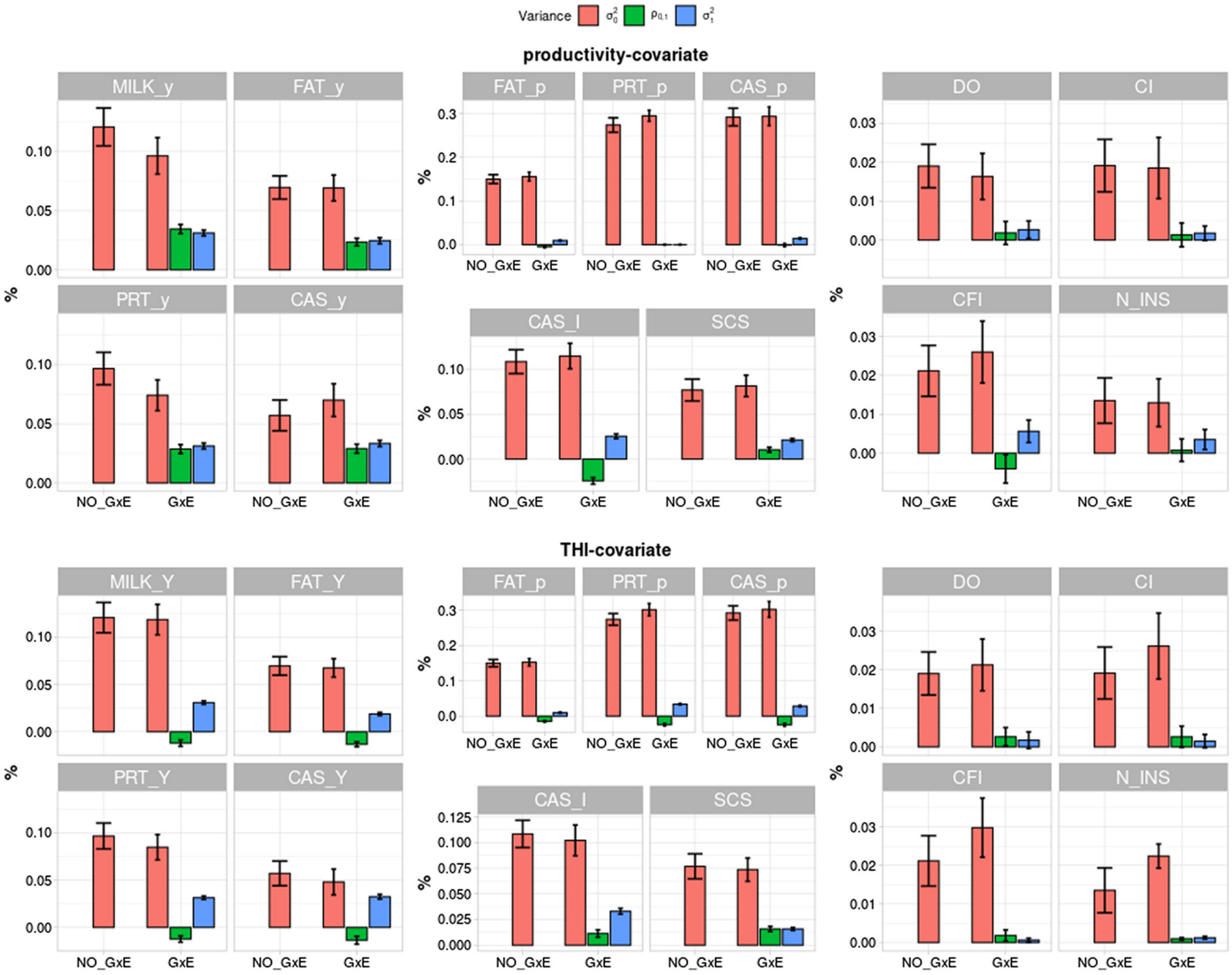


Figure 5. Bar plots describing the ratio between intercept $\left(\sigma_0^2\right)$, covariance between slope and intercept $\left(\rho_{0,1}\right)$, and slope $\left(\sigma_1^2\right)$, and phenotypic variance. Traditional models (NO_GxE) and reaction norm models (GxE) were compared. The standard deviation of estimation is also reported as a black bar. We divided the plot based on the 2 environments descriptor. Milk yields (MILK_y), fat yields (FAT_y), protein yields (PRT_y), casein yields (CAS_y), percentage of fat (FAT_p), percentage of protein (PRT_p), percentage of casein (CAS_p), casein index (CAS_I), days open (DO), calving interval (CINT), calving-to-first-insemination interval (CFI), and number of inseminations (N_INS), expressed on a liability scale.

The values identified in this study were significantly lower than those identified in Zhang et al. (2019) and similar to those reported by Schmid et al. (2021). This can be attributed to the use of different models, as Zhang et al. (2019) used heterogeneous residual variances. However, the situation changed when THI was used as the environmental covariate, as we identified almost no slope values for fertility traits. Smaller values close to zero were also identified in the study of Shi et al. (2021), although they used different indicators of fertility compared with ours. Almost null slope on THI might be attributable to the fact that Reggiana is effectively able to cope with different climate conditions as reported in another local breed (Mancin et al., 2022) or it might be attributable to the lower number of fertility phenotype that combined with the generally low heritability values of the traits might fall to identify a reliable estimation of slope (Misztal and Legarra, 2017).

Correlation

As mentioned before, it is also of interest to observe the direction of GxE interaction (i.e., whether the increase of the environmental gradient has a positive or negative effect on the genetic expression of the traits). This is represented by the sign of the covariance; in the following section, we discuss the correlation between the 2 components, reported in Table 3, as it represents the proportion of $\sigma^2_{a_0}$ effect on $\sigma^2_{a_1}$ (Waters et al., 2023).

Productivity Traits. Greater positive correlations were observed for milk production traits and environmental productivity (ranging from 0.578 for fat to 0.635 for milk yield). This means that more productive animals, from a genetic point of view, are capable of fully expressing their genetic ability for milk production in more productive environments. In contrast, the same animals were penalized when the THI increased (correlation ranged from r = −0.28 and for PRT_y and to −0.37 FAT_y). The negative impact of high THI for milk production traits was consistent in the literature (Bohlouli et al., 2014; Tiezzi et al., 2017).

Milk Quality Traits. In accordance with previous studies (Sartori et al., 2022), we found no significant correlations between the percentage of solid content and milk productivity, indicating that variations in milk productivity did not influence the genetic expression of solid content in milk.

However, in contradiction to what was reported at the phenotypic level (Bernabucci et al., 2001; Zendri et al., 2016), we observed a noteworthy negative correlation (r = −0.452) between CAS_I and environmental productivity. This unexpected finding suggests that low CAS_I may not necessarily be associated with reduced concentrate intake in cows' diet in less productive environments (Zendri et al., 2016). Instead, the negative values of CAS_I, as observed in a study on milk protein fractions (Pegolo et al., 2021), could be attributed to an increase in serum proteins associated with the presence of subclinical or clinical mastitis, which is supported by the undesirable correlation we found between SCS and environmental productivity (r = 0.25). In fact, the positive correlation between higher productivity levels and SCS indicates that more productive environments may pose a higher risk of elevated SCS due to increased stress and shorter dry periods for cows (Stocco et al., 2023).

On the contrary, when THI was considered as environmental gradient, we observed negative correlations between the percentage of solid content and milk production traits, specifically fat (r = −0.38) and PRT_p (r = −0.24). This aligns with the findings suggesting that heat stress may induce a condition resembling ruminal acidosis, subsequently reducing milk fat percentage (Bauman et al., 2011). Moreover, we found that increased temperature had an unfavorable effect on SCS expression (r = 0.469), consistent with the well-known association between warmer environments, increased stress, and a higher incidence of mastitis, both clinical and subclinical as reported by Mulim et al. (2021). The positive correlation observed between CAS_I and THI (r = 0.018) requires further investigation, as no study has specifically examined the effect of THI on CAS_I. Future research is warranted to gain clearer insights into this relationship.

Fertility Traits. Although analyzing the relationship between the environmental production gradient and reproductive traits, we did not observe any clear patterns. However, we did find suggestive values for CFI, with a value of −0.373 and an HPD range of (−0.798 to 0.178). This indicates that more favorable environments may have a positive effect on fertility traits, although the wider range of the HPD interval suggests some uncertainty. That means that higher productivity in breeding is associated with a more favorable environment, characterized by greater technological inputs that allow animals to express their genetic potential more effectively both for production and reproduction traits. However, it is important to note that the large confidence intervals in our study weaken the support for this hypothesis, indicating the need for further investigation. Nevertheless, our findings are consistent with the study conducted by Toledo-Alvarado et al. (2017), who explained a similar apparent contradiction.

When considering THI, our results reveal a notable shift in the correlation patterns. Although not significant in most cases, the correlations range from 0.566 to 0.168, indicating an unfavorable relationship between THI and the studied traits. Among the traits, N_INS is the only one where a significant positive correlation was observed (r = 0.18). This finding aligns with the biological sense that a positive relationship exists between fertility and robustness. More specifically, animals with higher fertility tend to exhibit greater robustness, enabling them to adapt and perform well in diverse environments. In contrast, less fertile cows tend to be more sensitive and experience reduced fertility in environments characterized by higher THI, which suggests their lower ability to cope with thermal stress. Although the lack of statistical significance in most cases calls for caution, these results provide valuable insights into the relationship between fertility and the influence of THI on cow performance.

Heritability Trends

Figure 6 illustrates the variation in heritability across 2 environmental gradients.

Environmental Productivity Covariate. When examining productivity as an environmental gradient, we observe a distinct "U" shape in relation to milk pro-

Table 3. Variance components estimated under random regression models; the numbers within parentheses are the extremes of the high posterior density distribution interval[1]

Trait[2]	ga	cov	ga1	pe	res	corr	ENVG
MILK_y	2.607 (1.946; 3.408)	0.94 (0.757; 1.123)	0.851 (0.74; 0.962)	8.487 (7.862; 9.151)	14.4 (14.24; 14.55)	0.635* (0.513; 0.75)*	Production
FAT_y[3]	0.409 (0.307; 0.531)	0.140 (0.109; 0.174)	0.146 (0.1212; 0.1732)	1.08 (0.9858; 1.179)	4.194 (4.15; 4.237)	0.577* (0.440; 0.691)*	Production
PRT_y[3]	0.2124 (0.1563; 0.2841)	0.083 (0.065; 0.1026)	0.0907 (0.078; 0.107)	0.8762 (0.811; 0.93)	1.6355 (1.618; 1.652)	0.604* (0.475; 0.721)*	Production
CAS_y	0.001 (0.001; 0.002)	0.001 (0.000; 0.001)	0.001 (0.001; 0.001)	0.006 (0.005; 0.006)	0.01 (0.01; 0.01)	0.609* (0.471; 0.744)*	Production
FAT_P	0.0926 (0.089; 0.150)	0 (0.000; 0.000)	0.00 (0.002; 0.006	0.0408 (0.0350; 0.0459)	0.4592 (0.4557; 0.4618)	−0.124* (−0.215; −0.0317)*	Production
PRT_P	0.116 (0.064; 0.178)	0 (0.000; 0.000)	0 (0.000; 0.000)	0.069 (0.042; 0.102)	0.542 (0.523; 0.556)	−0.004 (−0.0545; 0.0022)	Production
CAS_P	0.016 (0.014; 0.018)	0 (0.000; 0.000)	0.001 (0.001; 0.001)	0.009 (0.008; 0.01)	0.029 (0.028; 0.029)	−0.016 (−0.1; 0.08)	Production
CAS_I	0.019 (0.016; 0.023)	−0.004 (−0.005; −0.003)	0.004 (0.004; 0.005)	0.026 (0.024; 0.03)	0.125 (0.123; 0.126)	-0.451* (−0.553; −0.345)*	Production
SCS	0.226 (0.172; 0.286)	0.029 (0.016; 0.042)	0.059 (0.051; 0.067)	0.744 (0.696; 0.795)	1.724 (1.711; 1.738)	0.251* (0.139; 0.364)*	Production
DO	47.425 (22.19; 80.341)	6.021 (−8.593; 19.951)	6.027 (0.923; 21.22)	184.4 (136.8; 232.1)	2,741 (2,677; 2,805)	0.403 (−0.707; 0.862)	Production
CINT	50.11 (19.119; 91.341)	3.558 (−10.64; 18.151)	2.988 (0.525; 15.45)	173.2 (122.4; 225.905)	2,570 (2,504; 2,638)	0.386 (−0.694; 0.848)	Production
CFI	28.295 (15.829; 44.95)	−4.42 (−11.25; 2.102)	5.922 (1.589; 12.19)	59.765 (39.529; 78.811)	1,031 (1,007; 1,056)	−0.373 (−0.798; 0.178)	Production
N_INS[4]	0.02 (0.007; 0.037)	0.001 (−0.006; 0.009)	0.005 (0.001; 0.013)	0.055 (0.032; 0.08)	1.498 (1.148; 2.146)	0.165 (−0.718; 0.905)	Production
MILK_y	3.027 (2.384; 3.816)	−0.520 (−0.851; −0.354)	0.791 (0.721; 0.866)	8.152 (7.534; 8.708)	13.83 (13.73; 13.94)	-0.323* (−0.586; −0.275)*	THI
FAT_y[3]	0.375 (0.288; 0.470)	−0.073 (−0.0962; −0.0502)	0.010 (0.009; 0.011)	1.097 (1.017; 1.175)	4.046 (4.014 4.097)	−0.371* (−0.482; −0.262)*	THI
PRT_y[3]	0.227 (0.172; 0.295)	−0.033 (−0.407; −0.018)	0.085 (0.077; 0.093)	0.8519 (0.795; 0.905)	1.581 (1.562; 1.595)	−0.238* (−0.346; −0.137)*	THI
CAS_y	0.085 (0.056; 0.135)	0.003 (0.001; 0.003)	0.006 (0.005; 0.007)	0.062 (0.057; 0.066)	1.04 (1.03; 1.05)	−0.349 (−0.521; −0.177)	THI
FAT_P	0.093 (0.082; 0.104)	−0.009 (−0.011; −0.007)	0.006 (0.005; 0.007)	0.043 (0.037; 0.051)	0.472 (0.47; 0.477)	−0.38* (−0.466; −0.291)*	THI
PRT_P	0.026 (0.024; 0.03)	−0.002 (−0.003; −0.002)	0.003 (0.003; 0.003)	0.012 (0.011; 0.014)	0.048 (0.048; 0.049)	−0.24* (−0.292; −0.189)*	THI
CAS_P	0.016 (0.014; 0.019)	−0.001 (−0.002; −0.001)	0.002 (0.001; 0.002)	0.009 (0.007; 0.01)	0.029 (0.028; 0.029)	−0.264* (−0.338; −0.195)*	THI
CAS_I	0.018 (0.014; 0.023)	0.003 (0.001; 0.003)	0.006 (0.005; 0.007)	0.028 (0.025; 0.032)	1.250 (1.240; 1.270)	0.018* (0.014; 0.023)*	THI
SCS	0.018 (0.014; 0.024)	0.004 (0.003; 0.005)	0.004 (0.003; 0.005)	0.067 (0.062; 0.071)	0.159 (0.157; 0.16)	0.469* (0.347; 0.585)*	THI
DO	61.59 (34.56; 100.2)	6.622 (−1.426; 21.11)	2.979 (0.272; 17.701)	162.6 (112.6; 214.705)	2,754.5 (2,686; 2,824)	0.566 (−0.14; 0.874)	THI
CINT	70.995 (38.209; 116.605)	6.168 (−3.315; 22.152)	2.254 (0.349; 13.71)	137 (85.42; 193.9)	2,587 (2,514; 2,660)	0.605 (−0.263; 0.902)	THI
CFI	32.32 (20.51; 48.4)	1.879 (−0.277; 4.975)	0.54 (0.154; 1.787)	41.13 (23; 59.921)	1,033 (1,007.95; 1,058)	0.503 (−0.068; 0.81)	THI

Continued

duction and quality traits. Specifically, milk production traits demonstrate a skewed "U" shape pattern, with values decreasing of heritability from 0.30 to 0.05 across the environmental gradient, ranging from the lowest (−4) to average production (zero). Subsequently, there is a significant increase from 0 to 0.6 as the environmental gradient ranges from 0 to 4 standardized units. This indicates that in highly productive environmental conditions, animals tend to have higher heritability compared with the average production values (0). We also observed that environments that are less favorable than average (negative values), there is also slight increase in h^2, albeit less pronounced. Interestingly, Shariati et al. (2007) reported a more pronounced and linear trend when an unknown covariate was used, which is in contrast with our findings. However, our results align with those of Kolmodin et al. (2004), providing consistency and support to our observed patterns.

For CAS_I, the heritability values indicate that animals with higher EBVs were identified in lower productive environments. Specifically, the heritability decreased from 0.5 to 0.05 when the standardized environment gradient ranged from −4 to 1. However, a slight increase to 0.25 was observed as the environmental gradient increased. In contrast, for SCS, the heritability increased significantly as the environmental gradient moved from −2 to 4 on the x-axis.

Regarding fertility traits, the heritability exhibited minimal changes. The CFI interval was the only trait that showed a significant decline in heritability. This implies that the genetic control of fertility traits was relatively stable across different productive environments, except for CFI, which displayed a notable decrease.

THI Covariate. When THI was considered, milk production traits showed an almost linear decrease until 90 THI, followed by a small increase. Specifically, Figure 4 shows a decline from nearly 0.4 to 0.05, followed by a slight increase to an average of 0.22 when THI reached 100. This is consistent with the findings of Landi et al. (2023), Carabaño et al. (2014), and Brügemann et al. (2011), who conducted studies in productive cows such as Holstein or Brown Swiss. However, these studies observed higher heritability values under extreme THI conditions. Nevertheless, the shape of heritability depends on various factors, including the number of heterogeneous residuals used in the aforementioned studies and the type of THI regression (linear or nonlinear). In our study, we detected a trend of higher h^2 at lower THI values. We observed an almost linear decline for the percentage of solid content and an increase for SCS, especially when THI surpassed 80. As in Landi et al. (2023), fertility traits showed less variation among traits; however, in our case we observed a small, almost linear increase in heritability values.

Table 3 (Continued). Variance components estimated under random regression models; the numbers within parentheses are the extremes of the high posterior density distribution interval[1]

Trait[2]	ga	cov	ga1	pe	res	corr	ENVG
N_INS[4]	0.0626 (0.531; 0.77)	0.002 (0.014; 0.042)	0.0034 (0.023; 0.049)	0.003 (0; 0.012)	2.106 (1.515; 3.188)	0.189* (0.09; 0.289)*	THI

[1] Additive variance intercept (ga0), covariance between intercept and slope (covga01) slope (ga1), permanent environment (pe), residual (res), correlation between ga0 and ga1 (corr), environmental covariate (ENVG).

[2] Traits: milk yields (MILK_y), fat yields (FAT_y), protein yields (PRT_y), casein yields (CAS_y), percentage of fat (FAT_p), percentage of protein (PRT_p), percentage of casein (CAS_p), casein index (CAS_I), days open (DO), calving interval (CINT), calving-to-first-insemination interval (CFI), and number of inseminations (N_INS).

[3] Variance multiply by 10^3.

[4] Expressed on a liability scale.

*Value of 0 is outside the high posterior density distribution.

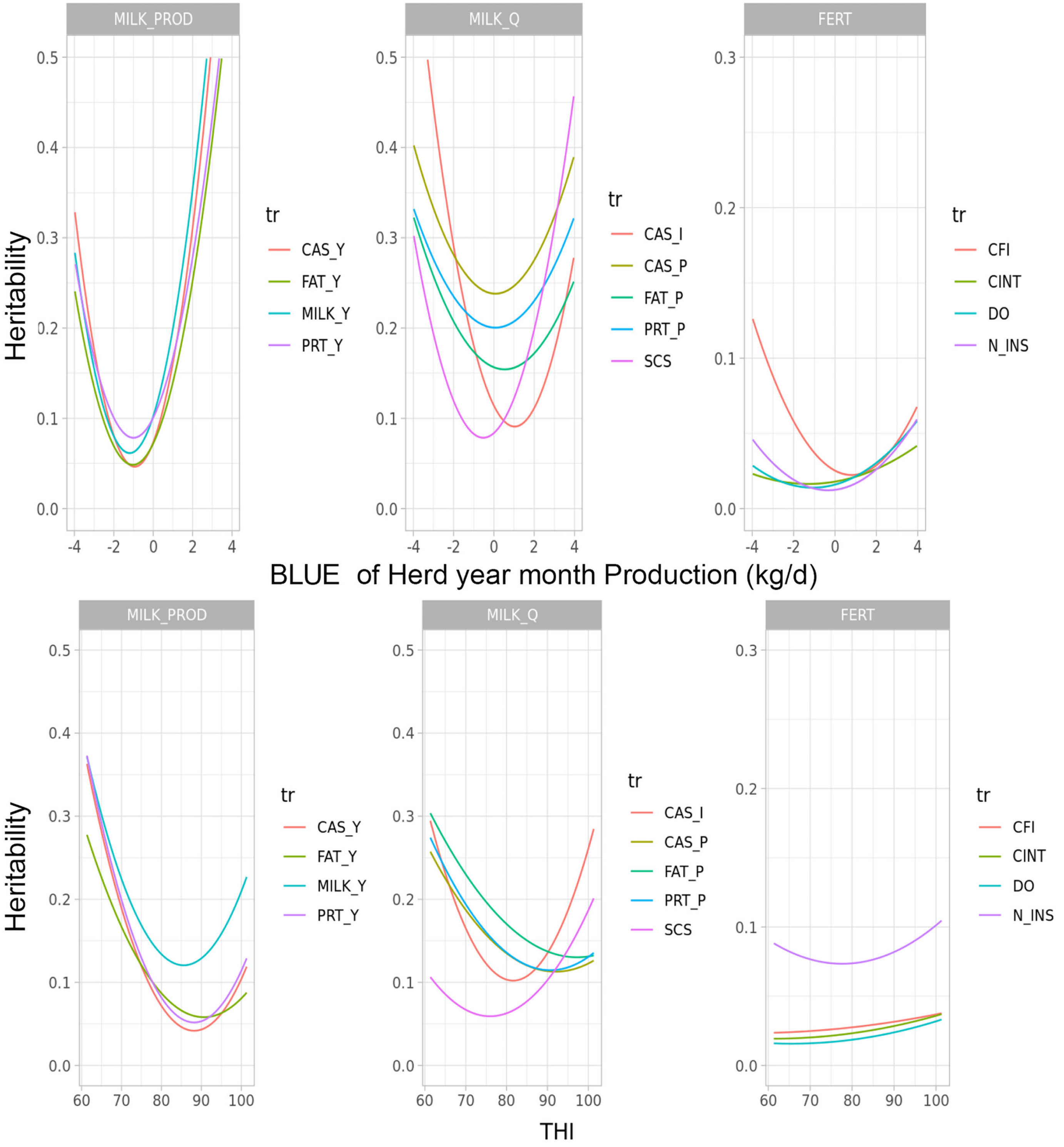


Figure 6. Heritability of trends based on different environmental gradient (herd-year-month production) and temperature-humidity index (THI). Milk yields (MILK_y), fat yields (FAT_y), protein yields (PRT_y), casein yields (CAS_y), percentage of fat (FAT_p), percentage of protein (PRT_p), percentage of casein (CAS_p), casein index (CAS_I), days open (DO), calving interval (CINT), calving-to-first-insemination interval (CFI), and number of inseminations (N_INS), expressed on a liability scale. BLUE = best linear unbiased estimator; tr=traits; MILK PROD= milk production traits; MILK Q = milk quality traits; FERT = fertility traits.

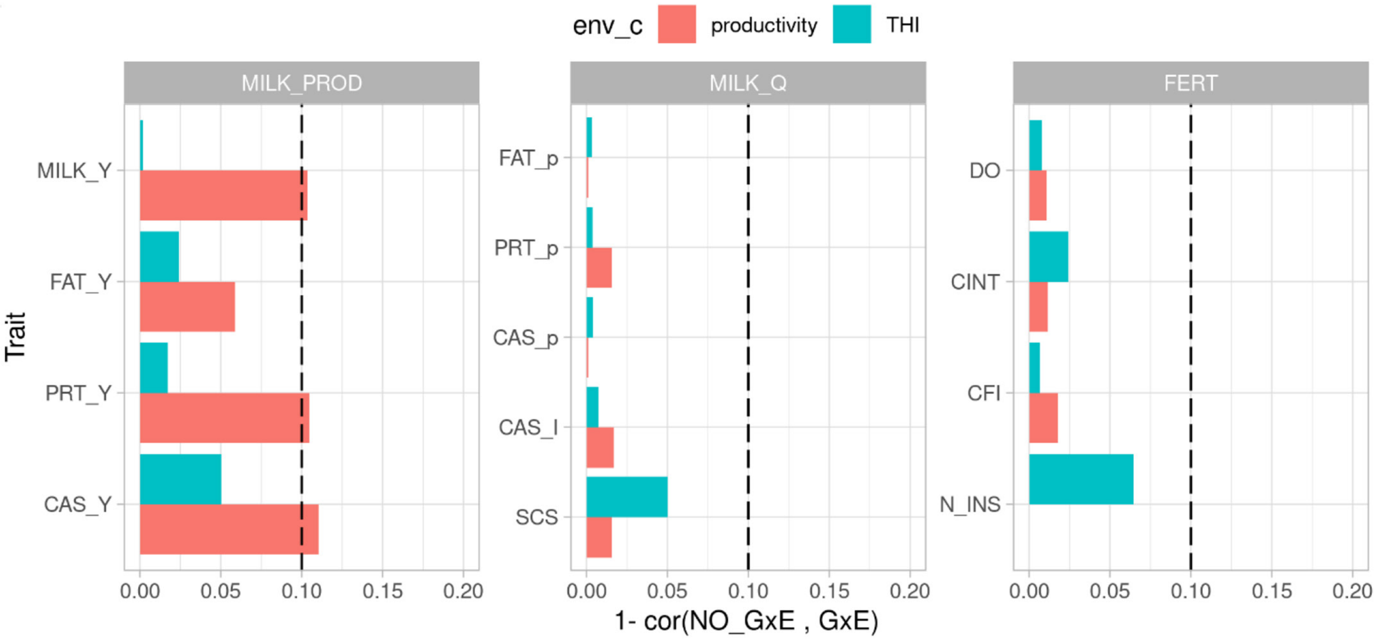


Figure 7. Reranking of bulls obtained using the traditional model (NO_GxE) and reaction norm models. The bar plot represents 1 − the Spearman correlation (cor) between the bulls evaluated with the 2 models. Vertical lines at 0.10 indicate that bars lower than this value represent a reranking higher than 0.90. Milk yields (MILK_y), fat yields (FAT_y), protein yields (PRT_y), casein yields (CAS_y), percentage of fat (FAT_p), percentage of protein (PRT_p), percentage of casein (CAS_p), casein index (CAS_I), days open (DO), calving interval (CINT), calving-to-first-insemination interval (CFI), and number of inseminations (N_INS). GxE = genotype by environment included in the model; env_c = environmental covariate; THI = temperature-humidity index; MILK PROD = milk production traits; MILK Q = milk quality traits; FERT = fertility traits.

Bull Reranking. The Spearman correlation of bulls' breeding values (reranking) obtained with and without GxE interaction is a common criterion to establish the need to use RNM in common evaluation practice. Bull reranking is shown in Figure 7; for a matter of clarity, only young bulls (born after 2010) were considered. Figure 7 reported the 1 − correlation values, that was made to visual appraise the impact of GxE as high quote of GxE imply the reranking of the animals. No substantial reranking has been observed for all milk traits. The highest reranking values were for MILK_y and PRT_y and PRT_p, with correlation values of 0.90, when herd-year-months milk production was considered as environmental covariate. When THI was considered, correlation was on average 0.95 for all traits. The SCS showed an intermediate value of 0.96. No substantial reranking was observed for the other traits except for SCS and N_INS when THI was the environmental covariate. Other studies investigated the effect of RNM models on bull reranking, using a variety of environmental descriptors; nonetheless, the majority did not find any significant bull reranking for productive and reproductive traits (Craig et al., 2018). Even so, few examples of bull reranking for fertility traits were observed (Ismael et al., 2016), although they used bivariate models (e.g., class of environmental gradient) and not RNM. Smaller correlation values, and therefore higher recombination events were observed when reranking was restricted to the top 10% and 20% young bulls (Supplemental Figure S10, https://doi.org/10.6084/m9.figshare.24619254.v1); this was more evident for milk traits when each gradient was considered.

Quantifying the percentage of variation captured by GxE interaction in a breed such as Reggiana can help assess whether it can cope with different environmental conditions. Our results show that high levels of THI have an unfavorable effect on the genetic expression of all phenotypes except reproduction. Environmental productivity has a positive effect on production traits but, negligible for dairy quality and reproductive traits. However, it negatively influences SCC and casein index. Considering both gradients in genetic evaluation plans has practical implications for the Reggiana breed; despite the minimal reranking of bulls, the addition of GxE provided a less biased estimation of EBVs when milk production traits were considered, which indicates that it might be a tool for the selection of animals more resistant to higher levels of THI. These results are fundamental for a breed such as Reggiana, where milk is used for processing into PDO cheese and should be considered in future selection plans.

CONCLUSIONS

This study's primary aim was to craft a sustainable selection blueprint for the Reggiana breed, with a focus on enhancing milk quality while preserving the breed's health and cheese-making characteristics. It uncovered an unfavorable genetic correlation among milk yield, fertility, and dairy quality traits, highlighting the necessity for revamped selection strategies. Additionally, the study underscored significant environmental influences on milk production traits, contrasting sharply with the minimal impact of environmental factors on fertility and quality traits. Moreover, traits such as SCS and casein index displayed modest environmental effects, signaling the importance of considering GxE interactions, especially for productive traits, in future selection plans. Finally, recognizing the environmental adaptability of native breeds, particularly through GxE interactions, emerges as crucial in contemporary agricultural practices. This understanding is pivotal for ensuring resilience in diverse and evolving environmental conditions, further emphasizing the need for nuanced selection approaches that encompass environmental interactions.

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ORCIDS

E. Mancin https://orcid.org/0000-0002-4130-4639
G. Gomez Proto https://orcid.org/0000-0003-4503-7088
B. Tuliozi https://orcid.org/0000-0001-5656-4858
G. Schiavo https://orcid.org/0000-0002-3497-1337
S. Bovo https://orcid.org/0000-0002-5712-8211
L. Fontanesi https://orcid.org/0000-0001-7050-3760
C. Sartori https://orcid.org/0000-0002-2091-2280
R. Mantovani https://orcid.org/0000-0002-1919-0559