Evaluating genotype by environment interaction for growth traits in Limousine cattle

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ABSTRACT

Environmental conditions affect the growth and health of animals, making it crucial to quantify heat stress and the genetic basis of heat tolerance in animal breeding. The main objective of this study was to evaluate heat stress on growth and investigate the genetic background of tolerance to harsh environmental conditions in the Italian Limousine beef cattle. Three growth traits were analysed: average daily gain (**ADG**), weaning weight (**WW**), and yearling weight (**YW**). Data were collected from animals raised between 1991 and 2022 and combined with 14 environmental covariates. Records for ADG, WW, and YW encompassed 108 205, 100 058, and 24 939 individuals, respectively, with 4 617, 4 670, and 2 048 genotyped individuals. Climatic variables were compared for inclusion in a linear mixed model using the Deviance Information Criterion. Multiple-trait models and genomic information incorporated environmental conditions with the largest impact on the studied traits Genotype by environment interaction (**G × E**) was detected in all the studied traits, showing substantial heterogeneity of the variance components across the different environments (**Env**). Heritability for WW remains constant among Env; instead, for ADG and YW decreased under uncomfortable environmental conditions. YW showed the lowest genetic correlation (0.28) between divergent conditions (Env 2 and Env 5,) for ADG and WW correlations dropped below 0.50 among Env. The values of genetic correlations indicate that growth traits are moderately to strongly affected by G × E. Eigenvalue decomposition of the additive genetic (co)variance matrix for ADG, WW, and YW indicated that three components accounted for over 0.80 of the proportion of the variance explained, suggesting different animal performances across Env. Spearman rank correlations showed potential re-ranking of genotyped sires, because ADG, WW, and YW showed correlations between Env below 0.80. The accuracy of single-step genomic EBV was higher compared to EBV for al traits. Overall, the result confirms the existence of G × E for growth traits in the Italian Limousine population. Including G × E in the model allows for more environment-aware predictions, helping breeders understand how different genetic bases respond to varying conditions. Genomic predictions incorporating G × E could accelerate genetic gains and improve response to selection for heat tolerance.

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Implications

In the face of rising global temperatures and climate variability, understanding the genetic and environmental factors affecting animal performance is critical to increase the sustainability of livestock production systems. This study evaluated the effect of heat stress and environmental factors on growth traits, identifying the genetic basis for tolerance to harsh conditions. Our findings show significant variation in growth across environments, underscoring the importance to select animals that cope with climatic conditions. These results can guide breeding programmes to enhance cattle resilience, productivity, and welfare, supporting sustainable beef production in the context of climate change.

Introduction

Heat stress has been reported as a cause of decreased performance in livestock, resulting in significant economic losses and reduced animal health and welfare. Physiology, health, and metabolism could be severely damaged by increased temperatures (Nardone et al., 2010). For example, St.-Pierre et al. (2003) estimated $360 million in annual losses due to heat stress in the US beef sector. One effective strategy to overcome this problem is to select animals that are less sensitive to environmental stress and

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more adapted to harsh conditions (Renaudeau et al., 2012). The genetic control on tolerance to heat stress is attributable to the genotype by environment interaction (G × E) (Tiezzi and Maltecca, 2022). Therefore, genetic evaluation of G × E is constantly increasing in the livestock sector, especially for economically important traits.

Genotype−by−environment interaction implies that different genotypes may respond differently to environmental changes, affecting performance across different environments. Research on cattle and pigs has shown that the genetic component of heat stress is negatively correlated with production performance (Zumbach et al., 2008b; Biffani et al., 2016; Bradford et al., 2016). Additionally, studies have also demonstrated the existence of G × E for reproduction traits, showing a negative association between the genetic component of heat stress and the reproductive performances (Ravagnolo and Misztal, 2002; Bernabucci et al., 2014; Tiezzi et al., 2020).

Quantifying the magnitude of G × E is a significant challenge. Therefore, developing strategies and tools to enhance the efficiency and sustainability of beef production is necessary to understand specific sector problems and the genetic background of sensitivity to environmental variation. One complication in modelling heat stress in beef cattle is that only the weight of animals at particular growth stages is often available. Another complication is compensatory growth, where animals can recover weight lost due to previous stress periods caused by heat stress (Baccari et al., 1983; Mader and Davis, 2004; Santana et al., 2016). One way to address these issues is to assume that heat load accumulates over the animals' lifetime or until a certain weight.

Generally, genetic analyses of heat stress in pigs (Zumbach et al., 2008a,b; Fragomeni et al., 2016) and beef cattle (Bradford et al., 2016; Santana et al., 2016) are based on heat load function for live or carcass weight in growing/finishing animals. In selection, the presence of G × E is explored using multi-trait models (MTs) or reaction norm models (Tiezzi and Maltecca, 2022). In the MT model, a trait measured in multiple environments is considered a different trait in each environment. Consequently, the animal's breeding value on the environmental conditions reflects the heterogeneous impact of the genetic background across different environments. Environmental conditions must be treated as categorical variables so that the MT provides a breeding value estimate for each environment. This approach is called a multi-environment trial, where a set of genotypes or families are raised in several environments (Isik et al., 2017). Proper analyses of multi-environment trial can determine which animals perform better in a specific environment and understand the relationship among environments in terms of G × E patterns. Genetic correlations between environments lower than 0.80 have been proposed in animal breeding as evidence of G × E interactions (Hayes et al., 2016). Moreover, correlations below 0.70, suggest considerable reranking of selection candidates, confirming G × E (Mulder and Bijma, 2007). For this reason, it is recommended to assess separate breeding programmes and consider the effect of the environment on the genetic or genomic model.

In cattle breeding programmes in Italy, routine genetic evaluations do not account for G × E. This justifies a study to identify genetically superior individuals for tolerance to heat stress in the Limousine population, a French beef breed typically used in local or dairy crossbreeding systems or as a pure breed (Bouquet et al., 2011). It is widely raised in the Mediterranean, with a relevant presence in Italy. However, this population is distributed across the entire national territory, predominating in Central and Southern Italy. The diversity of Italian territory led to different farm management and environmental conditions, affecting the animals and exposing them to varying humidity and temperature levels. Consequently, animals' performance can be negatively affected.

Understanding the extent of environmental variability in Italy is crucial. Animals can experience significant heat stress, especially during the summer months. In many regions, cattle may face over 50 days of high temperatures (CNR-ISAC, https://www.isac.cnr.it), leading to heat stress.

This context underscores the importance of considering G × E interactions in breeding programmes, as it could significantly influence animal performance and welfare, guiding breeders towards G × E-aware breeding values. Therefore, the objectives of this study were: (a) to identify the environmental parameter with the most substantial impact on growth; (b) to estimate the impact of heat stress on genetic parameters; (c) to compare pedigree-BLUP and Single-Step genomic BLUP for the genetic evaluations for heat tolerance using a multiple-trait approach. The study was conducted on the Italian Limousine beef cattle population.

Material and methods

Animal data

Data were obtained from a pre-existing database; therefore, Animal Care and Use Committee approval was unnecessary. The National Italian Association of Limousine and Charolais Breeders provided phenotypic, pedigree, and genomic information. Records were collected on animals born between 1991 and 2022 and raised in herds in the national territory. The traits analysed were weaning weight (WW, kg), yearling weight (YW, kg), and average daily gain (ADG, g/d). Firstly, WW was measured considering a range of 170–250 days of age and YW at 290–440 days of age in the Limousine population. For each animal, ADG was calculated as the difference between two weights ranging from 30 days (minimum) to 150 days (maximum).

ADG, WW, and YW records of contemporary groups with less than five individuals were excluded from the dataset for data editing, with groups defined by concatenating the herd and the animal's birth year. Moreover, phenotypic records outside the interval of the mean ±3.5 SD units. After editing, the final database included 108 205, 100 058, and 24 939 animals for ADG, WW, and YW, respectively. For the subsequent analyses, the age of animals was grouped into two classes using the median (118, 205, and 323 days of age for ADG, WW, and YW, respectively). The age of the dam at calving was divided into five classes using the first four quintiles as discriminants to create a balanced number of observations in each class. Dividing the age of animals into two classes using the median reduces variability from individual age differences, which is useful where there is significant variation in age-related growth traits. It is also less sensitive to outliers, producing more robust and reliable results. Moreover, including fixed effects for age classes in our model can help control for age-related variation in weight.

We considered only animals with known sires and dams to analyse all the investigated traits. Finally, general information and descriptive statistics used in this study from the three final datasets were summarised in Table 1. In addition, Fig. 1 illustrates the distribution of animals and herds for ADG, WW, and YW across the 20 Italian regions. Supplementary Table S1 provides the percentage distribution of herds and the number of animals for these growth traits in the seven most representative Italian regions.

Meteorological data and environmental descriptors

Several previous studies have used weather stations; however, data from meteorological stations could be limited for a specific time because the complete information is not always accessible.

Table 1
Descriptive statistics of traits, number of farms, contemporary groups (CG), sires, dams, and effects for cattle under study.

Traits	Descriptive statistics							
	N. of records	N. of animals with records	Mean	SD	N. of Farms	N. of CG	N. of sires	N. of dams
ADG	108 205	108 205	1.04	0.28	829	5 712	3 783	39 014
WW	100 058	100 058	247.9	46.54	838	6 102	4 019	40 548
YW	24 939	24 939	354.5	65.61	550	2 030	2 162	16 090

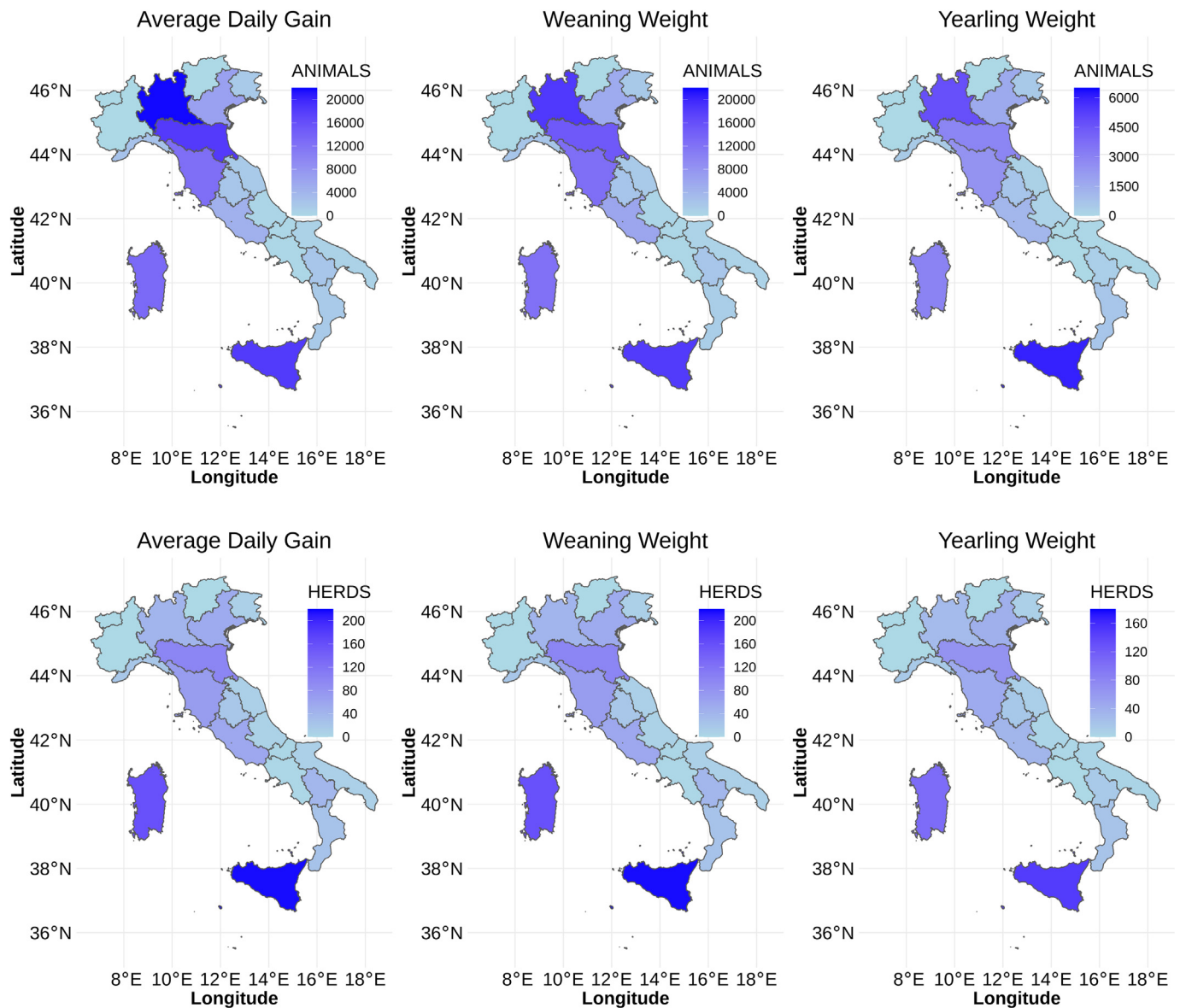Abbreviations: ADG = average daily gain; WW = weaning weight; YW = yearling weight.

Fig. 1. Frequency of cattle and herds across Italian regions for average daily gain (ADG, kg/d), weaning weight (WW, kg), and yearling weight (YW, kg).

The National Aeronautics and Space Administration (NASA/POWER, https://power.larc.nasa.gov) provides a surrogate to the meteorological stations where weather data are obtained from satellite observations (Van Wart et al., 2015). Rockett et al. (2023) compared weather parameters and temperature humidity index (**THI**) values collected from weather stations against NASA/POWER estimates. The study showed that climatic data from the stations were highly correlated (with a Pearson correlation larger than 0.80) with data from NASA POWER; therefore, weather station data could be replaced.

Herds' positions were matched with their corresponding latitude and longitude coordinates to obtain data from NASA POWER. Meteorological data including average daily temperature (**Temp**, °C), relative humidity (**RH**, %), and the dew point (**DP**, °C Td) were downloaded. Subsequently, the average THI (NRC, 1971) was calculated as:

$$\text{THI} = (1.8 \times \text{Temp} + 32) - (0.55 - 0.0055 \times \text{RH})$$
$$\times (1.8 \times \text{Temp} - 26)$$

where Temp is the temperature in degrees Celsius, and RH is the relative humidity, expressed in percentage. Heat stress in animals was further characterised by calculating the heat load, which is the cumulative THI units above a certain threshold (70 or 75) over a specified period (Zumbach et al., 2008a; Santana et al., 2016; Bradford et al., 2016). This was applied to datasets ADG, WW, and YW. The heat load function was defined as follows:

$$\text{heat load } 70 = \max\left(0, \sum \text{THI} - 70\right)$$

$$\text{heat load } 75 = \max\left(0, \sum \text{THI} - 75\right)$$

THI was the accumulated THI for the animals on the days leading up to the weight measurement date or between the two dates for ADG. When THI was below the threshold, the model assumes that heat stress does not impact animal growth, and heat load was assigned a value of 0. Conversely, when the average daily THI exceeds the threshold (either 70 or 75), heat load is assigned a positive value, reflecting the degree of heat stress experienced by the animals.

A range of 30 days before the weight data for WW was chosen based on Bradford et al. (2016). Instead, we reduce YW from 150 to 30 days because Bradford et al. (2016) found that cattle may have recovered to heat stress during the 150 days, resulting in no detectable G × E intersctions. For ADG, a period of 30–150 days was chosen, assuming that in this gap, environmental parameters may negatively affect the growth of animals. Therefore, averaged weather data for the three analysed traits were calculated into these periods. This range was chosen based on the period during which significant weight gain occurs, reflecting the average environmental conditions affecting the cattle. This interval was also selected to assess the impact of heat stress on growth as reported in the literature these time frames are crucial for cattle accumulating stress due to environmental factors. Including this range for ADG was intentional to capture the impact of environmental stressors on cattle growth during these critical periods. Additionally, the mean values at the first and third quartiles were considered because NASA POWER provides daily averages, not hourly values. Using only minimum and maximum would underestimate the effect of extreme conditions on the animals. Finally, 14 variables describing climatic conditions were obtained, as detailed in Supplementary Table S2.

Heat stress analysis model

The 14 environmental variables were categorised into 5 classes (Supplementary Table S2) to define 'environmental conditions' (**Env**). By grouping animals based on these classes, it is possible to evaluate the impact of different levels of environmental stress on growth traits (ADG, WW, and YW). The five classes of the Env were created using the first four quintiles as discriminants, allowing a balanced number of observations per each Env category. For each environmental variable, the 5 classes represent the different levels of environmental stress. Animals were grouped according to the environmental conditions at their respective locations. The five Env were defined as follows: Env 1 (extremely uncomfortable), Env 2 (moderately comfortable), Env 3 (comfortable), Env 4 (moderately uncomfortable), and Env 5 (extremely uncomfortable), respectively. An exception was for RH, where the 5 classes were defined differently: Env 1 (comfortable), Env 2 (moderately com-

fortable), Env 3 (moderately uncomfortable), Env 4 (uncomfortable), and Env (5 extremely uncomfortable), respectively. For heat load, the classes were treated differently: Env 1 (comfortable, with all heat load values equal to 0), and from env 2 until env 5, the classes were divided incrementally based on the heat accumulated by the animals.

Because most of the analysed environmental variables were derived from Temp and DP, Env 1 (extremely cold environment) and Env 5 (extremely hot environment) were both considered "extremely uncomfortable." Although cattle typically do not have problems with cold weather, extreme cold is still classified as uncomfortable due to its potential negative impact. Toghiani et al. (2020) found that cold stress as an environmental stressor could impact overall health and cattle productivity, in particular birth and weaning weight. The classification changes regarding relative humidity, where the lowest values are the most comfortable.

Detection of best environmental covariates

The effect of the environmental conditions on ADG, WW, and YW was assessed using the following linear mixed model (Model 1) to evaluate the response of growth to a specific environment:

$$y_{ijklm} = \mu + \text{env}_i + \text{sex}_j + \text{age}_k + \text{ageD}_l + \text{env}_i * \text{sex}_j + \text{env}_i$$
$$* \text{age}_k + \text{env}_i * \text{ageD}_l + \text{age}_k * \text{ageD}_l + \text{hy}_m + e_{ijklm} \quad (1)$$

where y_{ijklm} was the measurements of ADG, WW, and YW, μ was the intercept of the model; env_i was the fixed effect of the environmental covariates divided into five classes i; sex_j was the fixed effect of the sex; age_k was the fixed effect of the age of the animals, divided into two levels using median (for YW we correct the model using age as a linear covariate); ageD_l was the fixed effect of age dam class (five levels); hy_m was the random effect of the herd year; e_{ijklm} was the residual error. The model also included all the two-way interactions among the fixed effects. These analyses were implemented using the function *lmer* of package 'lme4' (Bates, 2010) of the R software (R Core Team, 2020), using a maximum-likelihood estimator (option REML = FALSE in *lmer*). The models were compared based on the Deviance Information Criterion, with smaller values indicating better model fit.

Pedigree and genotypes

The raw pedigree file included 493 125 animals across more than 10 generations. Therefore, animals were traced back seven generations, including 44 304, 48 231, and 33 478 animals for ADG, WW, and YW, respectively. 269, 265, and 139 animals were genotyped with GeneSeek GGP Bovine 150 K (HD, number of SNPs = 119 854) for ADG, WW, and YW, respectively. 4 348, 4 404, and 1 909 animals were genotyped with GeneSeek GGP Bovine LD v3 (number of SNPs = 28 299) for ADG, WW, and YW, respectively. The two panels shared 14 079 SNPs. Due to the low number of genotyped animals in HD compared to LD, animals genotyped with GeneSeek GGP Bovine 150 K were imputed to GeneSeek GGP Bovine LD starting from the 14 079 SNPs shared. FImpute v.3 (Sargolzaei et al., 2014) was used with default parameters to impute genotypes.

Quality control and data filtering of genotype data were performed with PLINK v1.9 (Chang et al., 2015). Therefore, in the quality control autosomal SNPs and individuals with less than 10% of missing values, minor allele frequency higher than 0.01 and a call rate higher than 90% were retained. Thus, 22 910, 22 903, and 22 921 SNPs for 4 617, 4 670, and 2 048 animals for ADG, WW, and YW, respectively, were included in the successive analyses. Table 2 summarises the number of genotyped animals per cate-

Table 2

Number of genotyped cattle across the three studied traits, considering animals with phenotype, sires, and dams.

Traits	Males with phenotype	Sires	Females with phenotype	Dams	Total
ADG	1 224	551	1 775	1 067	4 617
WW	1 127	675	1 565	1 303	4 670
YW	266	431	449	902	2 048

Abbreviations: ADG = average daily gain; WW = weaning weight; YW = yearling weight; Males with phenotype = are those individuals showing a phenotypic record in the dataset. They may appear as sires or other individuals; Sires = are those individuals not showing a phenotypic record in the dataset, but they appear as sires of individuals with phenotypes; Females with phenotype = are those individuals showing a phenotypic record in the dataset. They may appear as dams or other individuals; Dams = are those individuals not showing a phenotypic record in the dataset, but they appear as dams of individuals with phenotypes.

gory, considering males and females with phenotype, sires, and dams.

Model and analyses for variance components and breeding value estimates

Univariate model. Separate univariate models were used to mimic the national Limousine evaluation for growth traits without including the G × E effect. The models were defined as follows (Model 2):

$$y_{ijklm} = \mu + sex_i + age_j + ageD_k + a_l + cg_m + e_{ijklm} \qquad (2)$$

were y_{ijklm} is the value of ADG, WW, and YW; sex_i is the fixed effect of the sex; age_j is the fixed effect of the age of the animals (continuous covariate or in classes); $ageD_k$, is the fixed effect of age dam class (five levels); a_l is the random additive direct genetic effect of the animal; cg_m is the random effect of the contemporary groups; e_{ijklm} is the random residual error. In matrix notation, the univariate model was represented as follows:

$$y = X\beta + Zu + Wm + e$$

where y is the vector of phenotypic values of ADG, WW, and YW; β is the vector of solutions for fixed effects; u is the vector of solutions for the random genetic effect of the animal; m is vector of solutions for the random effect of contemporary groups; e is the random residual error; and X, Z, W are the incidence matrices associated with fixed, direct genetic, and random genetic effects, respectively. In all the subsequent analyses for WW, the maternal permanent environmental effect was not incorporated in the models. This choice is related to the dam frequency and limited repeated records per dam in the Italian Limousine population. Also, Santana et al. (2016) omitted the permanent maternal environmental effect for one breed because of the limited repeated records per dam.

Multiple traits model including genotype by environment interaction. An MT animal model was used to estimate variance components for growth traits in 5 different Env, selected based on lower Deviance Information Criterion values from Model 1. Utilising the covariance among traits, this model can generate breeding values for all traits of individuals. Consequently, variance–covariance structures can be applied to model G × E interactions. Records were assigned to the corresponding Env class based on the environmental covariate involved (Table 3). Fixed and random effects were the same as in Model 2.

In matrix notation, the following general model was used in five Env analyses:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \\ y_5 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 & 0 & 0 \\ 0 & X_2 & 0 & 0 & 0 \\ 0 & 0 & X_3 & 0 & 0 \\ 0 & 0 & 0 & X_4 & 0 \\ 0 & 0 & 0 & 0 & X_5 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \\ b_5 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & 0 & 0 & 0 \\ 0 & Z_2 & 0 & 0 & 0 \\ 0 & 0 & Z_3 & 0 & 0 \\ 0 & 0 & 0 & Z_4 & 0 \\ 0 & 0 & 0 & 0 & Z_5 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \\ a_5 \end{bmatrix} + \begin{bmatrix} W_1 & 0 & 0 & 0 & 0 \\ 0 & W_2 & 0 & 0 & 0 \\ 0 & 0 & W_3 & 0 & 0 \\ 0 & 0 & 0 & W_4 & 0 \\ 0 & 0 & 0 & 0 & W_5 \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \\ m_3 \\ m_4 \\ m_5 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ e_5 \end{bmatrix}$$

where y_1, y_2, y_3, y_4, and y_5 are trait records for genotypes in Env 1, 2, 3, 4, and 5, respectively, X_1 to X_5 are incidence matrices for fixed

Table 3

Distribution of cattle numbers for average daily gain, weaning weight, and yearling weight across Italy, divided into five different environments.

Traits	Covariate	Interval	Environment	N
ADG	maxRH_CLASS	[40.69–72.44]	Env 1	21 778
	maxRH_CLASS	(72.44–79.12]	Env 2	21 540
	maxRH_CLASS	(79.12–84.92]	Env 3	21 619
	maxRH_CLASS	(84.92–89.94]	Env 4	21 753
	maxRH_CLASS	(89.94–98.70]	Env 5	21 515
WW	T_CLASS	[−11.31–7.41]	Env 1	19 999
	T_CLASS	(7.41–12.35]	Env 2	20 024
	T_CLASS	(12.35–17.45]	Env 3	20 021
	T_CLASS	(17.45–22.72]	Env 4	20 002
	T_CLASS	(22.72–35.66]	Env 5	20 012
YW	DP_CLASS	[−8.65–3.88]	Env 1	4 990
	DP_CLASS	(3.88–7.17]	Env 2	4 985
	DP_CLASS	(7.17–10.25]	Env 3	4 992
	DP_CLASS	(10.25–13.89]	Env 4	4 984
	DP_CLASS	(13.59–23.15]	Env 5	4 988

Abbreviations: ADG = average daily gain; WW = weaning weight; YW = yearling weight; maxRH_CLASS = class of Maximum Relative Humidity; T_CLASS = class of Temperature; DP_CLASS = class of Dew Point.

effect, Z_1 to Z_5 are the matrix of the additive genetic effect, W_1 to W_5 are the incidence matrices of the random effect of contemporary groups. The vectors of the systematic effects are represented by b_1 to b_5, a_1 to a_5 are vectors of additive genetic effect, m_1 to m_5 are vectors of the random effect of contemporary groups, and e_1 to e_5 are vectors of residual error. The assumptions regarding the (co)variance structure of random effects, and additive genetic effect in five Env are:

$$\begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \\ a_5 \end{bmatrix} \sim N \left(0, A \otimes \begin{bmatrix} \sigma_{a1}^2 & \sigma_{a12} & \sigma_{a13} & \sigma_{a14} & \sigma_{a15} \\ \sigma_{a21} & \sigma_{a2}^2 & \sigma_{a23} & \sigma_{a24} & \sigma_{a25} \\ \sigma_{a31} & \sigma_{a32} & \sigma_{a3}^2 & \sigma_{a34} & \sigma_{a35} \\ \sigma_{a41} & \sigma_{a42} & \sigma_{a43} & \sigma_{a4}^2 & \sigma_{a45} \\ \sigma_{a51} & \sigma_{a52} & \sigma_{a53} & \sigma_{a54} & \sigma_{a5}^2 \end{bmatrix} \right)$$

$$\begin{bmatrix} m_1 \\ m_2 \\ m_3 \\ m_4 \\ m_5 \end{bmatrix} \sim N \left(0, I \otimes \begin{bmatrix} \sigma_{m1}^2 & \sigma_{m12} & \sigma_{m13} & \sigma_{m14} & \sigma_{m15} \\ \sigma_{m21} & \sigma_{m2}^2 & \sigma_{m23} & \sigma_{m24} & \sigma_{m25} \\ \sigma_{m31} & \sigma_{m32} & \sigma_{m3}^2 & \sigma_{m34} & \sigma_{m35} \\ \sigma_{m41} & \sigma_{m42} & \sigma_{m43} & \sigma_{m4}^2 & \sigma_{m45} \\ \sigma_{m51} & \sigma_{m52} & \sigma_{m53} & \sigma_{m54} & \sigma_{m5}^2 \end{bmatrix} \right)$$

the random residuals (co)variance structure is:

$$\begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ e_5 \end{bmatrix} \sim N \left(0, I \otimes \begin{bmatrix} \sigma_{e1}^2 & 0 & 0 & 0 & 0 \\ 0 & \sigma_{e2}^2 & 0 & 0 & 0 \\ 0 & 0 & \sigma_{e3}^2 & 0 & 0 \\ 0 & 0 & 0 & \sigma_{e4}^2 & 0 \\ 0 & 0 & 0 & 0 & \sigma_{e5}^2 \end{bmatrix} \right)$$

where A is the matrix of additive genetic relationships among individuals in the pedigree, and I is the identity matrix. The residual covariance between the five Env is set to zero.

Multiple traits genomic-based single-step model including genotype by environment interaction. The SNP information can be included as a genomic relationships matrix among animals to obtain genomic Estimated breeding value (**EBV**). Also, the MT can be extended with the information derived from SNP. The genomic approach combines matrix A (pedigree relationship matrix) with G (relationships matrix from SNP markers). Indeed, genomic EBV was estimated with single-step genomic BLUP (Aguilar et al., 2010), and the H matrix was composed by combining A with G (Legarra et al., 2014):

$$H^{-1} = A^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & G^{-1} - A_{22}^{-1} \end{bmatrix}$$

where A^{-1} is the inverse of the numerator relationship matrix A, and A_{22}^{-1} is the inverse of the A matrix for the genotyped animals and G^{-1} represents the inverse of the SNP genomic relationship matrix, determined with the second method as in VanRaden (2008).

Multiple traits model using permutation. An additional model was assessed to evaluate the effective presence of G × E on the studied traits. MT models using permuted Env assignments (MT with permutations) were implemented, where y is the observation for the YW of the animal assigned randomly in the five Env (permutations). The fixed and random effects were the same in Model 2. Random assignment of the trait of animals in different Env minimises the environmental effect. The MT with permutations model was implemented only for YW, the trait with fewer available records. Ten permutations were carried out, estimating variance components for each.

Bayesian inference, model comparison, and computation

Variance components and genetic parameters were estimated with an animal model through the GIBBS3F90 program, implemented in the BLUPF90 family of programs (Misztal et al., 2014). Therefore, a Gibbs chain of 1 000 000 iterations has been set, plus a burn-in period of 500 000 iterations and a sampling interval of 100 iterations. These constraints ensured model convergence for all traits analysed. Convergence of the parameters was confirmed by visual investigation of trace plots and throughout Geweke's test using the package 'coda' (Plummer et al., 2006) of the R software (R Core Team, 2020).

Heritability (h^2) and herd-year effect (h_i) were defined as follows:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_{hy}^2 + \sigma_e^2}$$

$$h_i = \frac{\sigma_{hy}^2}{\sigma_a^2 + \sigma_{hy}^2 + \sigma_e^2}$$

where σ_a^2 is the estimate of additive genetic variance, σ_{hy}^2 is the estimate of herd-year effect variance, and σ_e^2 is the estimate of residual variance. The posterior mean and 95% empirical confidence intervals of the posterior distribution were used as the estimate and its attached error. Confidence intervals were calculated using the R software package 'TeachingDemos' (Snow, 2020).

The accuracy of EBV and single-step genomic EBV for the trait t taken into consideration of the animal i was estimated as follows:

$$Acc_{it} = \sqrt{1 - \frac{SE_{it}^2}{(1 + F_i)\sigma_{at}^2}}$$

where SE_{it} is the SE of EBV and single-step genomic EBV for animal i in the 5 Env, F_i is the inbreeding coefficient, and finally σ_a^2 is the estimated variance of the animal genetic additive effect (Aguilar et al., 2020). A cross-validation using Linear Regression was performed to evaluate the single-step genomic BLUP and BLUP models (Legarra and Reverter, 2018). The evaluation was conducted by truncating the data to four years prior, using the complete pedigree information. The EBVs and single-step genomic EBVs and their accuracies were obtained by truncating the data to 4 years prior and using the complete pedigree. For the comparison between single-step genomic BLUP and BLUP, bulls with at least five progenies today and zero progeny 4 years ago were selected. The linear regression statistics (bias, slope, and accuracy) were calculated to assess the performance of the models between the whole and truncated datasets. The number of bulls used for the comparison was 619, 704, and 213, for ADG, WW, and YW, respectively.

To compute the genetic correlation between Env, the following equation was used for MT and single-step MT:

$$r_{gen} = \frac{\sigma_{a,xz}}{\sqrt{\sigma_{a,x}^2 \times \sigma_{a,z}^2}}$$

where $\sigma_{a,xz}$ is the genetic covariance between Env x and Env z, and $\sigma_{a,x}^2$ and $\sigma_{a,z}^2$ are the additive genetic variances. Genetic correlations were calculated among all the five Env.

Spearman's rank correlation was estimated between EBV and single-step genomic EBV across the five environmental conditions in the MT and single-step MT models to investigate a possible re-ranking among genotyped sires. Additionally, G × E and possible re-ranking between sires were evaluated by comparing EBV and single-step genomic EBV from univariate analyses without environmental effect and MT analyses. This study also investigated

the impact of G × E interactions on animal growth in the Limousine population using eigenvalue decomposition of the genetic (co)variance matrix (Meyer, 2009). Eigenvalues indicate the amount of variation accounted for by each principal component, with larger eigenvalues indicating that the corresponding principal component captures more substantial variation. In G × E analysis, larger eigenvalues indicate significant patterns of variation across Env. The eigen decomposition of the additive genetic (co)variance matrix from the MT model was used to calculate the effective dimensionality of the genetic variation across the Env. The additive genetic (co)variance matrix summarises the genetic variation within several Env and the (co)variance among Env. To confirm the presence of G × E in growth traits, a comparison was made between the eigenvalue decomposition of additive genetic variance components from the MT and MT with permutations models for YW. The eigen-decomposition was performed using the eigen function of the R software.

Results

Characterisations of climatic conditions and detection of environmental parameters with great impact on growth

Average daily gain was 1.04 kg/d, WW was 247.9 kg, and YW was 354.5 kg. SD values were 0.28, 46.54, and 65.61 for ADG, WW, and YW, respectively. Environmental conditions were categorised into five environmental classes, with maximum RH class (%), average Temp class (°C), and average DP class (°C Td) providing the best model fit for ADG, WW, and YW, respectively. The Deviance Information Criterion values obtained for all the environmental covariates and traits assessed in Model 1 are provided in Supplementary Table S3. The distribution of the number of animals and environmental variables tested for ADG, WW, and YW in the five different Env are shown in Table 3.

Variance components

Estimates of variance components were obtained for all three traits with both MT and single-step MT. Heterogeneity in additive genetic variances (σ_a^2) was observed across different environmental conditions (Table 4). For ADG, σ_a^2 estimates slightly decrease over maxRH levels, indicating lower magnitudes under extreme humidity conditions. The variance estimation for ADG was smaller when the conditions of RH were critical, and greater when the animals were exposed to the lowest RH levels (Table 4). Similar trends were observed for YW, with lower σ_a^2 estimates under stressful environmental conditions. (Table 4). Conversely, WW exhibited higher σ_a^2 estimates at extreme Temp. Detailed variance component estimates for ADG, WW, and YW across five environmental conditions are provided in Supplementary Table S4. Overall, the patterns and trends observed for variance components were consistent between MT and single-step MT analyses.

Heritability and herd-year effect estimates

Table 4 presents heritability estimates for ADG, WW, and YW under different Env using MT and single-step MT models, along with univariate analysis results. These heritabilities were obtained in the five environments through MT models. Only the univariate model, used to mimic the national Limousine evaluation for growth traits, does not include the G × E effect. Heritability generally decreases for ADG and YW when the environmental conditions become less favourable, while remaining relatively stable for WW. Specifically, ADG showed low to moderate heritability across all RH Envs (0.07–0.10), while WW exhibited moderate heritability

Table 4
Herd-year effect, heritability, and additive genetic variance of the three traits for Limousine cattle obtained using single trait, multiple trait, and single-step multiple trait models with environmental covariates having the lowest Deviance Information Criterion values, divided into five different environments. Values within parentheses represent the Highest Posterior Density Interval (HPDI).

Trait	Single Trait BLUP			Single Trait single-step genomic BLUP				Environment MT			single-step MT		
	h_i	h^2	σ_a^2	h_i	h^2	σ_a^2		h_i	h^2	σ_a^2	h_i	h^2	σ_a^2
ADG	0.35 (0.33; 0.36)	0.08 (0.07; 0.08)	0.006 (0.005; 0.006)	0.34 (0.33; 0.35)	0.08 (0.07; 0.08)	0.006 (0.005; 0.006)							
							Env 1	0.47 (0.46; 0.48)	0.10 (0.08; 0.12)	0.008 (0.007; 0.010)	0.47 (0.45; 0.49)	0.10 (0.08; 0.12)	0.008 (0.007; 0.009)
							Env 2	0.47 (0.46; 0.48)	0.08 (0.06; 0.10)	0.006 (0.005; 0.008)	0.47 (0.45; 0.49)	0.08 (0.06; 0.10)	0.006 (0.005; 0.008)
							Env 3	0.47 (0.46; 0.48)	0.09 (0.07; 0.11)	0.007 (0.006; 0.009)	0.47 (0.45; 0.49)	0.09 (0.07; 0.11)	0.007 (0.006; 0.009)
							Env 4	0.46 (0.45; 0.47)	0.09 (0.07; 0.11)	0.007 (0.006; 0.009)	0.46 (0.44; 0.48)	0.10 (0.08; 0.12)	0.008 (0.006; 0.009)
							Env 5	0.44 (0.43; 0.45)	0.07 (0.05; 0.09)	0.005 (0.004; 0.006)	0.44 (0.41; 0.46)	0.08 (0.06; 0.09)	0.006 (0.004; 0.007)
WW	0.45 (0.44; 0.46)	0.12 (0.11; 0.13)	203.15 (189.50; 219.10)	0.43 (0.41; 0.44)	0.12 (0.11; 0.13)	197.86 (183.90; 212.50)							
							Env 1	0.48 (0.47; 0.49)	0.15 (0.13; 0.18)	249.94 (213.40; 282.70)	0.48 (0.46; 0.50)	0.15 (0.13; 0.17)	249.14 (217.90; 282.50)
							Env 2	0.52 (0.52; 0.53)	0.15 (0.13; 0.17)	260.47 (226.40; 294.70)	0.52 (0.50; 0.54)	0.15 (0.13; 0.18)	261.44 (226.70; 300.40)
							Env 3	0.53 (0.52; 0.54)	0.13 (0.11; 0.15)	222.49 (189.70; 255.60)	0.53 (0.51; 0.55)	0.13 (0.10; 0.15)	220.21 (185.10; 259.10)
							Env 4	0.54 (0.53; 0.55)	0.12 (0.10; 0.14)	203.79 (176.40; 244.20)	0.54 (0.52; 0.56)	0.12 (0.10; 0.14)	201.80 (172.10; 237.70)
							Env 5	0.54 (0.53; 0.55)	0.14 (0.12; 0.16)	233.05 (200.60; 265.10)	0.54 (0.52; 0.56)	0.14 (0.11; 0.16)	228.10 (190.20; 258.10)
YW	0.58 (0.56; 0.60)	0.10 (0.08; 0.12)	335.61 (276.50; 388.40)	0.58 (0.56; 0.59)	0.10 (0.08; 0.12)	331.70 (284.70; 389.90)							
							Env 1	0.63 (0.612; 0.64)	0.09 (0.06; 0.11)	273.27 (191.10; 353.00)	0.62 (0.60; 0.65)	0.12 (0.09; 0.15)	362.15 (269.30; 472.90)
							Env 2	0.63 (0.62; 0.64)	0.15 (0.11; 0.19)	492.47 (362.80; 634.00)	0.63 (0.60; 0.66)	0.14 (0.10; 0.18)	453.30 (336.80; 578.30)
							Env 3	0.64 (0.63; 0.65)	0.14 (0.10; 0.17)	457.01 (320.60; 571.20)	0.64 (0.61; 0.67)	0.14 (0.10; 0.17)	469.17 (353.30; 605.20)
							Env 4	0.65 (0.63; 0.66)	0.14 (0.10; 0.19)	514.62 (385.20; 657.40)	0.64 (0.61; 0.67)	0.14 (0.10; 0.19)	509.13 (369.90; 628.40)
							Env 5	0.64 (0.63; 0.65)	0.13 (0.10; 0.16)	421.64 (309.10; 517.70)	0.65 (0.62; 0.68)	0.13 (0.10; 0.16)	423.15 (324.80; 531.60)

Abbreviations: ADG = average daily gain; WW = weaning weight; YW = yearling weight; BLUP = best linear unbiased prediction; MT = multiple trait model; h_i = herd-year effect; h^2 = heritability; σ_a^2 = additive genetic variance.

through Temp Envs (0.12–0.15), and YW showed low to moderate heritability across DP Envs (0.09–0.15). Lastly, univariate models showed heritability estimates of 0.08, 0.12, and 0.10 for ADG, WW, and YW, respectively.

The heritability estimates for ADG showed the highest value in the most comfortable climatic conditions (0.09–0.10) and slightly decreased with increasing RH levels (Table 4). Afterwards, YW heritability decreased in extreme DP Env but remained stable in intermediate conditions. Meanwhile, WW heritability estimates remained constant across Temp Env, with a lower increase at extreme temperatures. The estimates and trends for heritability for ADG, WW, and YW remained consistent between MT and single-step MT analyses.

On the three traits, the herd-year effect (Table 4) was moderately low for ADG, modest for WW, and moderately high for YW in both univariate and MT analyses. Univariate models, on average, had a lower herd-year effect with estimates of 0.35, 0.45, and 0.58 for ADG, WW, and YW, respectively. Including environmental interaction for MT and single-step MT models, the herd-year effect increased, particularly for WW and YW, with the highest values observed in extreme conditions. Average daily gain exhibited a moderate herd-year effect (from 0.47 for Env 1 to 0.44 for Env 5), slightly decreasing over maxRH levels. A relatively higher herd-year effect was found for WW and YW. For WW, the herd-year effect increases over temperatures (0.48 Env 1 – 0.54 Env 5). The highest herd-year effect was detected for YW, with values ranging between 0.62 and 0.65. For all three traits, MT and single-step MT models highlighted the same results.

Genetic correlations between environments and eigenvalue decompositions

The genetic correlations of additive genetic effects across different Env for the three traits are summarised in Fig. 2.

As expected, the genetic correlation decreased gradually across Env (1–5) for WW and YW, with a weaker correlation between more distant Env. These correlations generally decreased as the environmental conditions became more divergent. For ADG, the genetic correlations showed the opposite trend, increasing from Env 1–5. Significant G × E interaction was detected for ADG, WW, and YW in the Limousine population, with a lower genetic correlation of 0.50 between the five Env. The lowest genetic correlation (0.28 ± 0.13) was detected for YW between Env 2 and 5, while the highest (0.89 ± 0.03) was between Env 1 and 3 of DP, suggesting limited G × E effects. Genetic correlations for ADG ranged from 0.36 ± 0.09 to 0.68 ± 0.06 across maxRH Env, indicating a moderate to remarkable G × E effect. Low to moderate interaction for WW was across Temp Env, with genetic correlations from 0.48 ± 0.07 to 0.68 ± 0.05, indicating a moderate G × E effect. For YW genetic correlations between DP Envs ranged from 0.28 ± 0.13 to 0.89 ± 0.03, suggesting a negligible to remarkable G × E effect. Genomic correlations for single-step MT showed similar patterns to those of MT analyses. Fig. 3 highlighted the presence of G × E on the three traits using eigenvalue decomposition of the additive genetic variance matrix. Each trait with two Env had an explained variance higher than 0.80, supporting G × E interactions. Supplementary Figure S1 confirms G × E for YW by comparing eigenvalues from MT models with fiv Env, and 10 random permutations. The permutations revealed substantial differences in the proportion of variance explained with one Env, showing that almost all variance was explained by the additive genetic (co)variance matrix.

Sire re-ranking across environments

The pattern of Spearman's rank correlations between solutions and Env of the models are summarised as a heatmap in Fig. 4. Rank correlations were calculated for genotyped sires using solutions from univariate, MT, and single-step MT models. Some combinations among Env for ADG, WW, and YW showed correlations lower than 0.80, indicating potential re-ranking of sires and G × E interactions among Env. For ADG, rank correlations across Env of
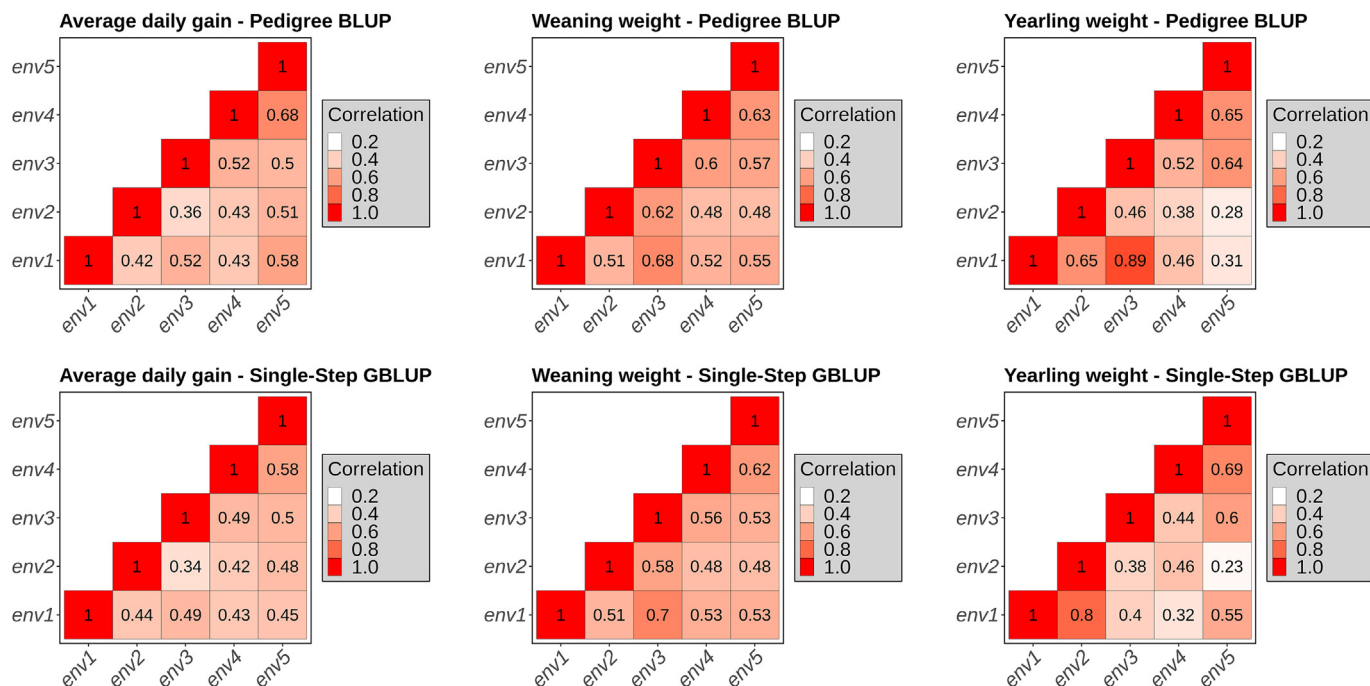

Fig. 2. Genetic correlations between different traits for average daily gain (ADG, kg/d), weaning weight (WW, kg), and yearling weight (YW, kg) for Limousine cattle, using environmental covariates with lower Deviance Information Criterion values for multiple traits and single step multiple traits models, including genotype by environment interaction. Abbreviations: BLUP = best linear unbiased prediction; GBLUP = genomic best linear unbiased prediction.
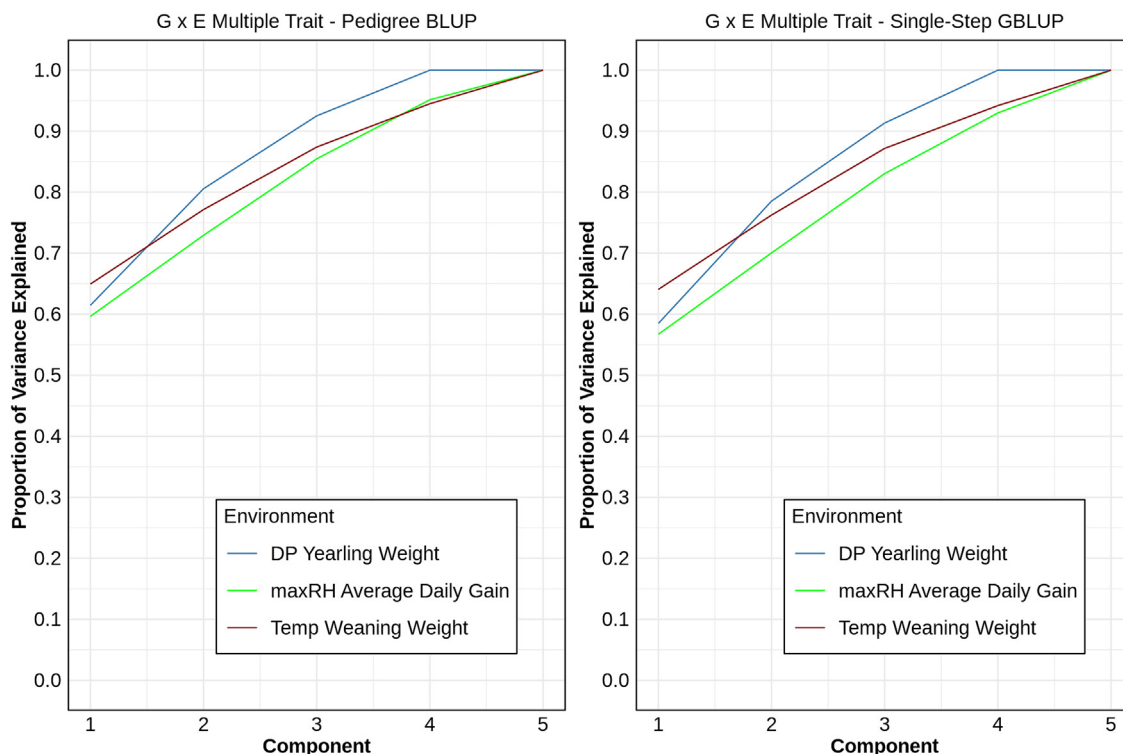
Fig. 3. Eigenvalue decomposition of the (co)variance structure of the additive genetic variance matrix in beef cattle for average daily gain (ADG, kg/d), weaning weight (WW, kg), and yearling weight (YW, kg) using multiple traits and single-step multiple models traits including genotype by environment (G × E) interaction between five different environments. Abbreviations: maxRH = Maximum Relative Humidity; Temp = Temperature; DP = Dew Point; BLUP = best linear unbiased prediction; GBLUP = genomic best linear unbiased prediction.
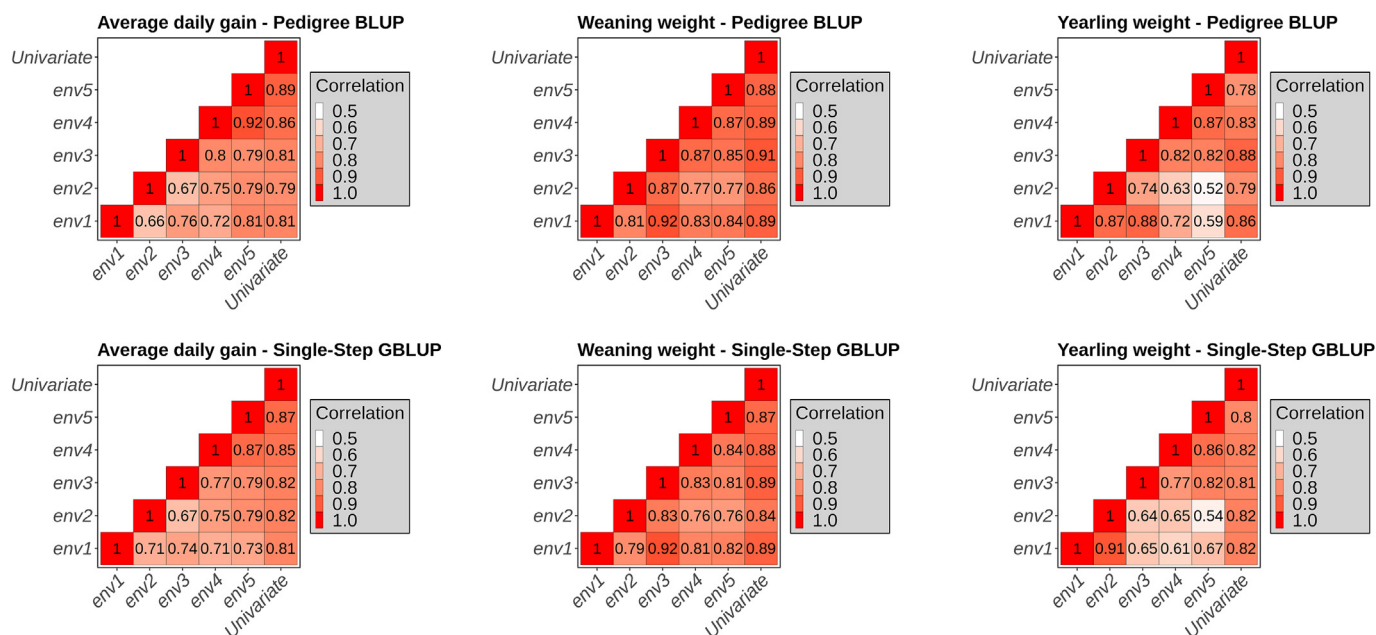
Fig. 4. Heatmap of Spearman rank correlations between solutions for Limousine genotyped sires using univariate and multiple trait models including genotype by environment (G × E) interaction, for average daily gain (ADG, kg/d), weaning weight (WW, kg), and yearling weight (YW, kg). Abbreviations: BLUP = best linear unbiased prediction; GBLUP = genomic best linear unbiased prediction.

maxRH on the MT model indicated moderate to strong re-ranking of sires, with some correlation below 0.70. The highest correlation was 0.92 between Env 4 and Env 5, while the lowest was 0.66 between Env 1 and Env 2. A similar pattern was observed for

ADG in the single-step MT model, with a rank correlation lower than 0.70 between Env 2 and Env 3.

Similar rank correlations between MT and single-step MT models for WW were found across the 5 Temp Env. The highest

Spearman's rank correlation was equal to 0.92 between Env 1 and Env 3, and the lowest was 0.76 between Env 2 and Env 5. This suggests that re-ranking of sires EBV and single-step genomic EBV could occur for WW under extreme Temp conditions. Strong rank correlations existed for YW across the closest DP Env for MT and single-step MT, with values ranging from 0.52 to 0.91. However, reranking could also occur among distant Env, especially under extreme conditions. Daughters of the same sire passing from cold to hot weather have different performances and ranked differently across Env for YW. Overall, the comparison of Spearman's rank correlations was moderate between the univariate and MT models using pedigree and single-step analyses. Re-ranking of proven sires between models could occur for all growth traits, with the lowest correlations equal to 0.80, 0.82, and 0.80 for ADG, WW, and YW, respectively (Fig. 4).

Comparison in accuracy of estimated breeding values and single-step genomic estimated breeding values for genotyped sires

EBV's Accuracy values were estimated for univariate, MT, single-step univariate, and single-step MT models. For ADG, the average accuracy of single-step genomic EBV (0.38) was higher than that of the EBV (0.34) (Fig. 5). Considering WW, the average accuracy of (0.46) increased compared to EBV (0.41) (Fig. 5). Similarly, for YW, the average accuracy values increased with the inclusion of genomic information (0.35 for single-step genomic EBV compared to 0.32 for EBV) (Fig. 5). In univariate analyses, single-step genomic EBV consistently showed higher average accuracies than EBV across all three traits. However, the SD was greater than the difference in accuracy between the single-step and pedigree univariate analyses, making these differences not relevant.
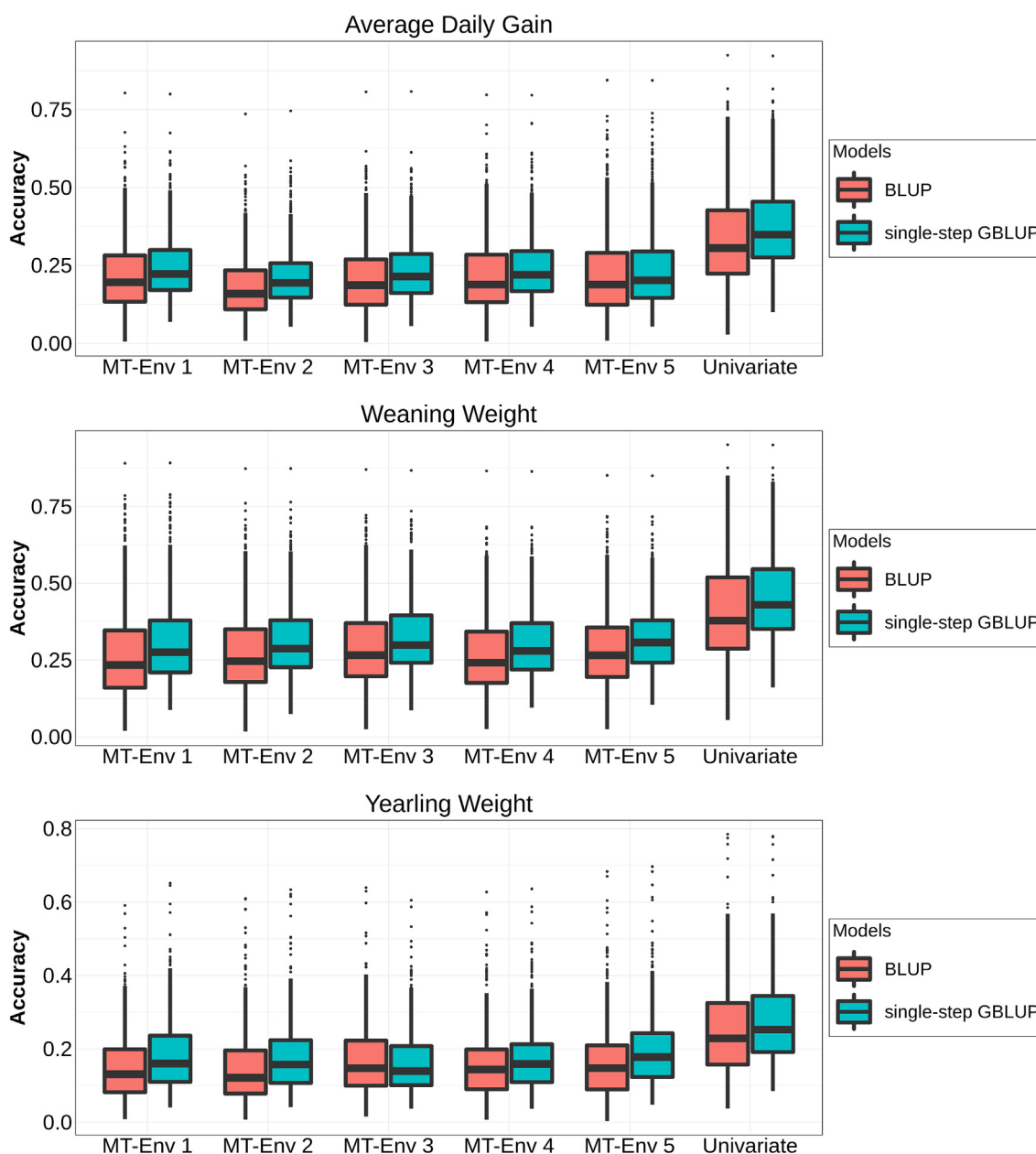

Fig. 5. Comparison of the accuracy of Limousine genotyped sires between univariate models without genotype by environment (G × E) interaction, multiple traits (MT), and single-step multiple traits models for average daily gain (ADG, kg/d), weaning weight (WW, kg), and yearling weight (YW, kg). Abbreviations: BLUP = best linear unbiased prediction; GBLUP = genomic best linear unbiased prediction.

For ADG, WW and YW, in the single-step MT analysis, single-step genomic EBV accuracies of the sires were slightly higher respect EBV accuracies across different Env (Fig. 5). The accuracies increased on average by 0.02–0.04 points across Env. However, the SD exceeded 0.1 in all the Env, indicating that the differences in accuracy between single-step and pedigree models are not relevant. In all cases, including genomic information increased the sires' accuracies, potentially improving the response to selection for specific trait/environment combinations. For instance, in low environments, the accuracy for ADG increased from 0.21 to 0.25 (Env1) when using single-step genomic EBV compared to the univariate model. The accuracy of WW in intermediate environments increased from 0.29 to 0.33 (Env3). Similarly, for YW in extreme environments, the accuracy improved from 0.16 to 0.20 (Env5) with the inclusion of genomic information (Fig. 5) The univariate model without the G × E effect showed larger accuracy compared to MT analyses. Results of linear regression cross-validation are summarised in Supplementary Table S5.

Discussion

Herds and animals included in this study were distributed around all the country, mostly in 7 regions (Lombardy, Sicily, Emilia-Romagna, Sardinia, Tuscany, Veneto, and Lazio), accounting for approximately 83–84% of the herds and 87–88% of the animals. The Limousine breed was introduced in Italy in 1985, and since then, the number of animals and herds has been consistently increasing. Because climate change is expected to modify the production environments in a shorter time (IPCC, 2007), understanding the genetic determination of heat tolerance in beef cattle is crucial. The main challenge in this study was identifying climatic parameters that significantly impact animal growth and quantifying G × E interactions on beef cattle. We explored G × E effects in the Limousine population using an MT model across 5 different environments, considering both pedigree (A), and genomic-pedigree (H) relationship matrices.

Selection of environmental covariates

For beef cattle, compensatory growth occurs after feed restriction or a physiologically stressed period and is generally expected to subsequently befall heat stress events (Mitlöhner et al., 2001). Even though heat stress might temporarily reduce growth, cattle typically experience compensatory gain after heat stress subsides. In the beef sector, heat stress could be confounded by seasonal changes since cattle graze outdoors (Paterson et al., 1995). Moreover, calculating proper heat stress and understanding which environmental covariates have a negative impact on growth is difficult. For these reasons, we included weaning and yearling weights because animals are exposed to a wide range of different climatic conditions during these periods.

Because of the cumulative nature of WW and YW and the type of farm management, heat load functions are mostly used in beef cattle. This approach has also been applied to dairy cattle (Ravagnolo and Misztal, 2000; Aguilar et al., 2009; Carrara et al., 2021) and swine (Zumbach et al., 2008a,b; Fragomeni et al., 2016). Also, THI has been widely used in animal breeding, particularly for dairy cattle (Biffani et al., 2016; Nguyen et al., 2016; Ansari-Mahyari et al., 2019). Some studies have assessed different variables, such as temperature or humidity, to explore their impact on reproductive and productive traits in swine (Tiezzi et al., 2020; Usala et al., 2021; Freitas et al., 2021). For these reasons, one challenge was properly quantifying heat stress in beef cattle and identifying the meteorological parameters that most impact growth. We evaluated 14 Env variables based on Temperature, RH, and

DP to explore the impact of each of the evaluated traits. The most relevant environmental covariate for each trait was selected using the Deviance Information Criterion applied to the baseline model (Model 1). Lower values indicate a better fitting.

The selection of appropriate environmental parameters for assessing heat stress is crucial due to their significant physiological impacts on cattle. Elevated temperatures can cause thermal stress, leading to decreased feed intake, altered metabolism, and reduced growth rates. Chronic exposure to high temperatures can also impair immune function and increase disease susceptibility affecting overall health, reproduction, and productivity. Furthermore, cattle cannot lose heat efficiently through evaporation when RH is high because the air is almost saturated with water vapour. This inefficiency in heat loss occurs because high RH deters evaporative cooling through the skin (Baena et al., 2019). Combined with extreme temperatures, high RH can exacerbate heat stress in cattle, leading to further declines in performance and overall health (Baena et al., 2019). Understanding these physiological implications is essential for developing effective breeding and management strategies to improve cattle heat tolerance. By selecting more resilient animals for heat stress, the negative impacts of climate change on cattle productivity and welfare can be mitigated.

Variance components estimation

Generally, the values were similar between the BLUP and single-step genomic BLUP models, with a comparable pattern for variance components (Table 4). Moderate additive genetic estimates for ADG, WW, and YW suggest that heat stress will affect animal growth. A decrease in σ_a^2 was observed at extreme Env for ADG and YW, respectively, while σ_a^2 was low in most comfortable Env conditions for WW. In extreme environments, genetic variance is often observed to be lower due to stress effects, strong selective pressure, and G × E interaction. Also, fewer animals might perform well, leading to a reduced range of genetic variance. Under these conditions, the ability of individuals to express their genetic potential is diminished, leading to a reduction of genetic variance.

These results indicate the potential for different selection responses for these traits depending on maxRH, Temp, and DP under which the animals are raised. Variance components estimate can be used to evaluate the presence of G × E interactions; a variability suggests that the same genotype may perform differently based on environmental conditions, highlighting the importance of considering G × E interactions in breeding programmes to improve animal performance across diverse Env. Moderate estimates from this study indicate significant genetic variability for traits like ADG, WW, and YW. This variability means selective breeding could be effective, depending on the specific environmental conditions the animals were subjected to.

Change in heritability and herd-year effect across multi-environment analyses

Analyses using BLUP and single-step genomic BLUP showed similar heritability patterns. Across five different Env σ_a^2 varied, resulting in differences in heritability in the Limousine population (Table 4). The heritability estimates suggest varying degrees of genetic control on growth traits under different environmental conditions, particularly in heat tolerance. Heritability estimates for univariate analyses were generally lower than those Bradford et al. (2016) reported for WW and YW in Angus cattle. Cardoso et al. (2011) found similar heritability (0.08–0.23) when including Env effects in a two-step model for post-weaning weight standardised at 345 days in Hereford cattle. Williams et al. (2012) observed changes in heritability of WW (0.26 and 0.28) and post-weaning

weight (0.26 and 0.19) across different altitudes in Angus cattle using a multivariate analysis. Similarly, using a random regression model, Santana et al. (2016) and Bradford et al. (2016) reported higher heritability for WW across the Env gradient. Oliveira et al. (2018) found higher heritability for YW compared to our study.

For ADG in different Env of maxRH, Cardoso and Tempelman (2012) found that the heritability increased in more favourable conditions for postweaning weight gain in Angus cattle, consistent with our finding. Likewise, for YW in Angus cattle, authors noted a reduction in direct heritability as environmental stress increased, using a random regression model (Bradford et al., 2016). Pegolo et al. (2011) observed an increase in the heritability in Nellore cattle in more favourable Env for weight at 450 days. On the contrary, using a reaction norm model, Santana et al. (2013, 2016) reported that WW had higher direct heritability in more favourable conditions in tropical composite cattle, Brangus, and Nellore. The differences in our results compared to other studies may be attributed to several factors. These include variations in the models used for heritability estimation and G × E analysis, the distinct genetic backgrounds and adaptations of the cattle breeds studied, fluctuations in environmental conditions such as climate and management practices, and differences in the structure and quality of the datasets. These disparities underscore the importance of considering breed-specific and environment-specific contexts in genetic studies.

Animals with moderate additive genetic estimates for growth traits may exhibit different physiological responses to environmental stressors. Understanding these responses can help in managing animal welfare more effectively. For instance, animals that maintain better growth rates under heat stress might have different metabolic or hormonal profiles compared to those that do not (Majumdar et al., 2020; Smith et al., 2022). The herd-year effect (Table 4) indicates that management practices moderately impact growth traits. A higher herd-year effect in Env with stressful conditions slows down genetic progress. This moderate herd-effect also contributes to G × E interactions, reflecting varying management practices and environmental conditions across different herds and years. This is the expression of genetic potential and hinders the identification of superior genotypes.

Genetic correlation, eigenvalues, and genotype by environment interactions throughout the environment

Genetic correlations followed a similar pattern when using both MT and single-step MT models (Fig. 2). A genetic correlation below 0.80 indicates evidence of G × E interactions. Genetic correlations did not decrease gradually across the five Env. In this study, the genetic correlation for the three traits reached values below 0.80, confirming the existence of G × E on Limousine growth traits under different environmental conditions. Using a MT approach, Carvalheiro et al., 2019 observed G × E interactions for postweaning weight gain, with a genetic correlation of 0.79 between harsh and favourable Env. Similar findings for WW were reported by Santana et al. (2016) in Brangus and Tropical Composite population, showing lower genetic correlations in extreme environments. Bradford et al. (2016) found genetic correlations below 0.50 for large heat load differences in Angus cattle, indicating that the Env gradient was not the same trait. Conversely, for YW, no significant Env differences were found in the Angus population (Bradford et al., 2016). In swine, Zumbach et al. (2008a,b) reported a genetic correlation of 0.42 for carcass weights between hot and cold months using two-trait analyses, and 0.02 when applying a random regression model for more distant heat load values. Usala et al. (2021) found a genetic correlation of 0.20 for ADG between the 5th and 95th percentiles of RH.

Eigenvalue decomposition of the genetic additive matrix confirmed G × E interactions in the Italian Limousine population (Fig. 3). For maxRH, Temp, and DP, the proportion of variance explained by the first three eigenvalues was 0.86, 0.87, and 0.93 in MT and 0.83, 0.87, and 0.91 in single-step MT for ADG, WW, and YW, respectively. The remaining two eigenvalues accounted for less than 0.20 of the variances explained by the Env. The first eigenvalue absorbed less than 70% of the total variance, and the sum with the second seldom reached 80%. Eigenvalue decomposition on the permuted data (MT with permutations) did not show any G × E (Supplementary Figure S1), supporting the findings from the actual data.

These estimates should interest breeders because the best-performing animals in one Env may not necessarily be the best in another, indicating different adaptability. These results could allow the development of targeted strategies to optimise animal performance and improve breeding and management strategies tailored to different environmental contexts. Thus, ADG, WW, and YW are moderately to largely affected by G × E, indicating that growth in the Limousine population in Italy varies across different Env of maxRH, Temp, and DP showing a potential G × E effect. Furthermore, we observed that the genetic correlations between the Env were often in different directions. This suggests varying relationships between average performance and environmental sensitivity of growth traits. Physiologically, this indicates that animals exhibiting high average performance might not necessarily show high environmental resilience. Different genetic mechanisms may control performance and sensitivity to environmental changes, affecting how traits manifest under varying conditions. Understanding these genetic correlations is crucial to developing breeding strategies that enhance performance and adaptability to diverse Env.

Reranking and identification of heat-tolerant sires

Considering the limited number of genotyped sires, re-ranking using Spearman rank correlation is expected under different Env, particularly when comparing animals in optimal versus extreme conditions. Numerous studies have documented changes in sire re-ranking in dairy cattle (Bernabucci et al., 2014; Carrara et al., 2021) and beef cattle for WW (Bradford et al., 2016). However, Bradford et al., 2016 reported a rank correlation greater than 0.80 for YW, suggesting a low re-ranking of sire across environmental conditions. In swine, a weak rank correlation (0.18–0.54) for carcass traits under high and low Env indicates a higher physiological response to heat stress than beef cattle (Zumbach et al., 2008b).

In our study, many rank correlations for genotypes were below 0.80 between Env of maxRH, Temp, and DP. The findings proved that sire re-ranking across affects genetic gain. Environmental conditions influence an individual's breeding value, with sires excelling in favourable conditions potentially performing poorly and less resilient in extreme conditions. Selective breeding of sire that exhibit strong performance across diverse Env is expected to enhance overall productivity, health, and welfare, thereby increasing the profitability of cattle farms. Physiologically, sires that maintain high ranks in varying environmental conditions demonstrate resilience and adaptability, which are crucial for growth traits under environmental stressors.

Comparison in accuracy of estimated breeding values and single-step genomic estimated breeding values for genotyped sires

Genomic selection has better opportunities to exploit G × E interactions than traditional breeding by achieving high accuracy in unfavourable Env (Mulder, 2016). However, accuracies in

extreme Env tend to be lower, and limited information is available for breeding value in these conditions (Mulder, 2016). Our study compared accuracies between single-step and pedigree-based analysis of genotyped sires across different Env. Results showed a slight improvement in accuracies for single-step MT compared to MT models for ADG, WW, and YW (Fig. 5). Nevertheless, for all three traits, the SD exceeded the differences in accuracies between single-step and pedigree models, indicating non-significant differences. In addition, when univariate pedigree BLUP and single-step genomic BLUP were compared, accuracies increased with the inclusion of the H matrix. Conversely, single-step MT accuracies were lower compared to univariate pedigree BLUP without accounting for G × E. Accuracies using an H matrix were lower, probably because the number of genotyped animals was not large enough and using an MT approach, genotyped animals were distributed among the five Env.

These findings suggest that genomic selection might accelerate genetic gain for heat tolerance. Single-step genomic BLUP improved response to selection across different environments more than pedigree analyses for growth traits. The results imply that as more animals are genotyped, the accuracies of single-step analyses for heat tolerance could further improve. Mulder (2016) highlights that genomic selection enhances resilience compared to traditional breeding schemes. This is emphasised when the reference population is representative of diverse environmental conditions.

Conclusions

These findings provide the basis for the possible genetic or genomic selection development for heat tolerance in the Limousine cattle population. Heritability estimates demonstrate the tolerance to critical environmental conditions under genetic control. This suggests the feasibility of selecting individuals who are particularly tolerant to specific environmental and management conditions through the direct genetic and genomic selection of growth traits. Furthermore, as evidence of G × E interactions, substantial heterogeneity was observed in the variance components for ADG, WW, and YW across different environmental conditions. A possible re-ranking in opposite Env of animals and sires was verified. Indeed, the best-performing genotypes in the less stressful Env may not excel under more challenging conditions. These results underscore that selecting more tolerant animals can optimise the selection programmes, showing that genomic selection could enhance the accuracy of breeding values across diverse Env. Despite these insights, further research is needed to better understand the genetic and genomic background of heat tolerance and the genetic mechanism of adaptability in beef cattle. This aspect could be explored by assessing future analyses by implementing a random regression model. When the number of environmental covariates exceeds one, multidimensional environmental data can be incorporated using Reproducing Kernel Hilbert Spaces regression. Exploring the relationship between genetics and environmental factors can provide relevant insights into heat tolerance ad adaptability in beef cattle breeding programmes.

Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.animal.2024.101344.

Ethics approval

The data used in this study were part of a pre-existing dataset, so ethics approval was not needed.

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

None.

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