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Exploring the impact of heat stress on feed efficiency in tropical beef cattle using genomic reaction norm models

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ABSTRACT

Global climate change poses significant challenges to livestock production, particularly in tropical regions where cattle frequently experience heat stress (**HS**). HS negatively impacts feed efficiency by reducing feed intake, altering metabolic processes, and increasing energy requirements, leading to decreased animal performance. Understanding how cattle respond to environmental stressors is essential for improving efficiency by breeding programs. In this context, we investigated genotype-by-environment interaction (**G** × **E**) for dry matter intake (**DMI**) and residual feed intake (**RFI**) in Nellore cattle using bi-trait genomic reaction norm models and considering the temperature-humidity index (**THI**) as the environmental descriptor. Data from 22 838 animals collected between 2011 and 2023 across 21 Brazilian farms were analyzed. Meteorological data were obtained via NASA POWER, and THI values were calculated based on the average temperatures and relative humidity recorded during feed efficiency trials. Genomic data were available for 18 567 animals, and the genetic parameters were estimated using the single-step genomic best linear unbiased prediction approach. The genetic expression of feed efficiency traits was found to be influenced by climatic conditions, with heritability estimates for DMI (ranging from 0.22 to 0.39) and RFI (ranging from 0.08 to 0.28) varying across the THI gradient. Additionally, a reduction in additive genetic variance for both traits was observed under intense heat stress conditions, suggesting the important role of environmental factors on phenotypic variability of feed efficiency traits in Nellore cattle. The presence of G × E was more pronounced when THI exceeded 76, as genetic correlations for the same trait across different environmental gradients dropped below 0.80, leading to substantial sire reranking. Moreover, the genetic relationship between DMI and RFI also varied along the THI, with genetic correlations ranging from 0.64 to 0.72, highlighting alterations in the genetic expression of feed efficiency traits under different heat stress levels. These findings emphasize the need to consider genetic plasticity when selecting animals for improved feed efficiency in tropical regions. Overall, this study provides valuable insights for breeding programs aimed at improving beef cattle resilience to heat stress, ensuring sustainable production in the face of climate change.

Implications

Climate change threatens livestock systems in tropical regions by increasing heat load and reducing animal performance. This study demonstrates that feed intake and metabolic efficiency in beef cattle are genetically influenced by environmental temperature and humidity. Genetic rankings varied across heat conditions, especially under severe stress, revealing substantial genotype-by-environment interaction. These findings support the implementation of climate-responsive breeding programs that consider genetic sensitivity to temperature to improve the selection of animals that are more robust to thermal stress, contributing to sustainable beef production under future climate scenarios.

Introduction

Global climate change significantly impacts livestock production, particularly in tropical environments (Bernabucci, 2019). In these regions, where cattle often face thermal stress, the relationship between feed efficiency traits and heat tolerance has become increasingly relevant (West, 2003; Lacetera, 2019). Thermal stress decreases feed intake, growth, reproduction, and overall productiv-

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ity, leading to significant economic losses in livestock production systems (West, 2003; Marai et al., 2007). The temperature-humidity index (**THI**) is a widely used metric for quantifying heat conditions and estimating the severity of heat stress based on environmental temperature and relative humidity (Marai et al., 2001; Cheruiyot et al., 2020). High THI values increase thermoregulatory demands, such as elevated respiration rates and water intake, while reducing feed intake and, consequently, production efficiency (West, 2003; Marai et al., 2007). Genetic variability plays a critical role in individual responses to heat stress, with more heat–tolerant animals displaying wider thermoneutral zones and smaller declines in performance under heat stress conditions (Carabaño et al., 2017). Identifying these animals is essential for breeding programs aimed at improving heat tolerance.

Reaction norm models using THI as a continuous variable to estimate individual production responses to increasing heat loads has been proposed a few decades ago (Ravagnolo and Misztal, 2000). These models identify thermoneutral zones, where THI levels minimally affect animal performance, followed by linear declines in productivity as heat stress intensifies (Ravagnolo and Misztal, 2000). More heat–tolerant animals exhibit wider thermoneutral zones (quantified by maintenance of performance) and smaller slopes of performance decline (Cheruiyot et al., 2022; Oloo et al., 2024). Reaction norm models have been widely applied to assess genotype-by-environment interaction (**G × E**) for various traits in beef cattle (Pégolo et al., 2009; Santana et al., 2014; Mota et al., 2020a, b; Santos et al., 2020). However, most studies on feed efficiency traits, such as DM intake and residual feed intake (**RFI**), have focused on genetic parameters and genomic regions without considering G × E (Grigoletto et al., 2017; Polizel et al., 2018; Mota et al., 2022; Kava et al., 2023; Valente et al., 2024). Given the economic importance of feed efficiency in beef cattle production, there is a need to assess the impact of G × E on these traits, and, if substantial, it should be accounted for in breeding programs.

We have previously assessed G × E for DM intake and RFI in Nellore cattle using bivariate reaction norm model (Silva Neto et al., 2023). The environmental gradient (**EG**) was defined based on the best linear unbiased estimation solutions of the contemporary groups for average daily gain, which captures differences in nutritional, environmental, and management practices during the feed efficiency trials. We identified significant G × E, particularly under extreme environmental conditions (low and high EG values). However, G × E based on best linear unbiased estimation solutions of contemporary groups captures all different types of stressors, including diet composition, management, and climatic variables. Therefore, there is a need for evaluating G × E due to heat stress conditions for feed efficiency traits in beef cattle raised in tropical regions such as Nellore cattle in Brazil (Silva Neto et al., 2024).

Understanding these interactions across diverse climatic conditions is essential for developing effective Nellore cattle breeding programs tailored to the selection of more resilient individuals (Rodrigues et al., 2024). Therefore, the primary objectives of this study were: (i) to estimate genetic parameters, including heritabilities and genetic correlations, for DM intake and RFI using a bi-trait genomic reaction norm model, considering the THI (based on different equations) as the environmental gradient descriptor; (ii) to assess the presence of G × E for DM intake and RFI across different climatic conditions; and (iii) to evaluate the genetic relationship between DM intake and RFI under varying climatic conditions. The results of this study are expected to form the foundation for selecting more heat–tolerant and feed–efficient animals under variable or extreme environmental conditions, such as those characterized by thermal stress.

Material and methods

Field data and phenotypic information

Individual feed intake was measured on 22 838 Nellore animals (16 233 males and 6 605 females) from 2011 to 2023. The datasets were provided by the National Association of Breeders and Researchers (ANCP, Ribeirão Preto, SP, Brazil; https://www.ancp.org.br). Animals were recorded during 296 feeding trials performed in 21 farms located across different Brazilian regions. The dataset used included phenotypic information for DM intake and RFI, following the procedures for measuring individual feed intake in beef cattle described by Mendes et al. (2020). The feeding trials were performed in group pens with animals grouped by sex and age. Feed intake was automatically recorded using the GrowSafe (https://www.vytelle.com) and Intergado (https://www.intergado.com) feeding systems. Each performance trial was conducted using a single feeding system brand, ensuring that all animals within the same group were evaluated under the same recording conditions. Detailed information on diet composition, management, and the description of the evaluated traits is provided in Silva Neto et al. (2023). Descriptive statistics for the studied traits are presented in Table 1.

The herds involved are highly connected at the genetic level due to the use of common sires through artificial insemination, with at least five genetic links across the feeding trials, which were evaluated using the across-herd mean connectedness package (Roso and Schenkel, 2006). The animals were raised on pasture-based systems, with a predominance of the *Urochloa brizantha cv* forage. The commercial herds adopted different nutritional practices with some farms providing protein and mineral supplementation, especially during the dry season, while others provided only urea supplementation (Silva Neto et al., 2023).

Table 1
Descriptive statistics for DM intake (DMI), residual feed intake (RFI), and temperature and humidity index (THI) during feeding trials in Nellore cattle.

Variable	RFI (kg/day)	DMI (kg/day)	THI
Number of records	22 838	22 838	239
Average	0.000	8.530	74.37
SD	0.842	2.151	3.52
Minimum	−7.109	2.519	66.86
Maximum	6.940	20.658	81.66
Feeding trials information			
Number of trials with only males	209		
Number of trials with only females	87		
Animals in the pedigree	46 383		
Sires	2 816		
Dams	21 749		
Sires with progeny records	817		
Dams with progeny records	10 339		
Number of contemporary groups	742		
Distribution of trials by seasons			
Summer	19		
Fall	34		
Winter	45		
Spring	48		
*Summer and Fall	28		
*Fall and Winter	49		
*Winter and Spring	53		
*Spring and Summer	20		

Trials were distributed across seasons as follows: 15.02% in Summer, 24.89% in Fall, 32.96% in Winter, and 27.13% in Spring. Some trials spanned two consecutive seasons, as marked with an asterisk (*) in the table.

Genomic data

A total of 18 567 animals born between 2014 and 2022 were genotyped with a single nucleotide polymorphism panel containing 65 414 markers (Clarifide® Nelore 3.0). The genotypes were imputed to a high-density (**HD**) single nucleotide polymorphism panel considering the Illumina BovineHD BeadChip (Illumina Inc., San Diego, CA, USA), containing 735 964 autosomal markers using the Fimpute 3.0 software (Sargolzaei et al., 2014). Before imputation of the 18 567 animals' genomic data, we removed monomorphic markers, markers with duplicated coordinates, located on non-autosomal chromosomes, and with GenCall score lower than 0.60 (Mota et al., 2024). The reference population for genotype imputation consisted of 963 representative sires of the main Nellore lineages (i.e., Karvadi, Golias, Godhavari, Taj Mahal, Akasamu, and Nagpur). These reference sires were born between 1995 and 2015 and genotyped with the Illumina BovineHD BeadChip (Illumina Inc., San Diego, CA, USA). The genomic quality control was performed using the QCF90 software (Misztal et al., 2014). After genotype imputation, we removed samples and single nucleotide polymorphisms with a call rate lower than 0.90, markers with Mendelian conflicts higher than 1%, extreme deviations (*P*-value $\leq 10^{-8}$) from Hardy-Weinberg equilibrium, minor allele frequency lower than 0.05, and those located in non-autosomal chromosomes. After quality control, 18 567 genotyped animals and 452 283 single nucleotide polymorphisms were retained for further analyses.

Weather data

Meteorological data corresponding to the days when the evaluated traits were recorded (2011–2023) were retrieved from NASA POWER (https://power.larc.nasa.gov/) based on each herd's geographical coordinates. The addresses for each herd were converted to latitude and longitude coordinates using Google Maps Geocoding (https://developers.google.com/maps/documentation/geocoding). NASA POWER weather data are freely available and can be accessed through its data access viewer or by integrating a POWER API URL into a scripting application.

To calculate the THI, four different approaches were tested:

I. Using temperature (**T**) and relative humidity (**RH**) data from three specific hours of the day (0900, 1500, and 2100 h), we calculated the average T and RH for each period (feed efficiency trials) and then computed THI.
II. Using T and RH data from all available hours of the day (24 h), we calculated the average T and RH per period, and then computed THI.
III. We calculated THI for each hour of the day and then averaged the hourly THI values to obtain the period THI.
IV. We calculated THI directly for the three selected hours of the day and averaged these values to obtain the period THI.

The Pearson correlation coefficients for THI values derived from these four approaches using the (NRC, 1971) equation were all close to 1.0 (see Supplementary Table S1), indicating strong agreement across methods. Thus, any of these approaches can be used without significant differences in THI outcomes. Here, we used the "I" approach to compute the THI. In addition, seven equations for calculating THI were evaluated:

1. $THI = [(1.8xT_{db} + 32)] - (0.55 - (0.0055xRH)x(1.8xT_{db} - 26))]$ (NRC, 1971);
2. $THI = (T_{db} + T_{wb})x0.72 + 40.6$ (NRC, 1971);
3. $THI = (0.55\,xT_{db} + 0.2\,xT_{dp})x1.8 + 32 + 17.5$ (NRC, 1971);
4. $THI = [0.4x(T_{db} + T_{wb})]x1.8 + 32 + 15$ (Thom, 1959);
5. $THI = (0.35\,xT_{db} + 0.65\,xT_{dp})\,x\,1.8 + 32$ (Bianca, 1962);
6. $THI = T_{db} + (0.36\,xT_{dp}) + 41.2$ (Yousef, 1985); and,
7. $THI = (0.8xT_{db}) + [(RH/100)\,x\,(T_{db} - 14.4)] + 46.4$ (Mader et al., 2006).

where, T_{db} is the dry bulb temperature; T_{wb} is the wet bulb temperature, and T_{dp} is the dew point temperature. The temperature unit used was Celsius degrees.

Pearson correlation coefficients between THI values derived from these equations ranged from 0.992 to 0.999 (see Supplementary Table S2), confirming high consistency across methods. Similar findings were reported for these same models by Dikmen and Hansen (2009). The descriptive statistics for each tested model are presented in the Supplementary Table S3. The first equation (NRC, 1971) was selected for this study due to its frequent application in similar studies (Bohmanova et al., 2008; Santana et al., 2015; Menéndez-Buxadera et al., 2020) and no substantial difference as compared to the other ones.

The impact of heat stress on Nellore cattle was assessed considering a THI of 76 as the threshold for the onset of thermal stress in beef cattle. This value was defined based on literature. For instance, a decline in conception rates in Nellore cattle was observed when THI reached 75.7 (Cordeiro et al., 2020), as well as changes in feed intake, physiological parameters, and behavior in Nellore cattle exposed to a THI of approximately 76 (Valente et al., 2015). Furthermore, research on epigenetic patterns reported that THI values exceeding 75 already represented a moderate level of stress for the Nellore breed (Del Corvo et al., 2021). Therefore, a THI of 76 was used as a reference threshold for identifying the beginning of physiological and productive responses to heat exposure in Nellore cattle.

Statistical modelling

To estimate the genetic parameters for DM intake and RFI across the EG levels (THI), a single–step bi-trait genomic reaction norm model (**ssBRN**) was used. In this approach, the EG was modeled as a continuous covariate, and each trait was modeled as the same trait expressed across distinct points of the THI levels. This model can be described as follows:

$$y_{ij} = Xb + \omega_f \Phi_f(EG_j) + \alpha_{fi} \Phi_f(EG_j) + e_{ij}$$

where y_{ij} is the vector of phenotypic information for DM intake and RFI of the animal i recorded at the level j of EG, b is the systematic effect of contemporary groups, which was defined by concatenating the effects of farm, year and season of the feeding trial, and sex (males and females were evaluated in separate groups), and the linear covariate of the age of the animal at the beginning of the feed efficiency trials, X is the incidence matrix, ω_f are the f-th fixed regression coefficients for intercept (f = 0) and slope (f = 1) on $\Phi_f(EG_j)$; $\Phi_f(EG_j)$ are the f-th Legendre orthogonal polynomials corresponding to EG level j (EG_j), α_{fi} are the random regression coefficients for additive genetic effects of the intercept (f = 0) and slope (f = 1) corresponding to animal i on EG level j, and e_{ij} is a random residual term.

The additive and residual genetic effects were considered normally distributed: $\alpha = \{\alpha\} \approx N(0, H \otimes K_a)$ and $e = \{e\} \approx N(0, I \otimes K_e)$, where K_a and K_e are the covariance-variance matrices for the additive genetic and residual effects, respectively, for the reaction norm coefficients (intercept and slope); I is an identity matrix, $\otimes$ is the Kronecker product, and H is a matrix combining pedigree and genomic relationships. The H^{-1} was calculated as (Aguilar et al., 2010):

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

where A^{-1} is the inverse of the pedigree-based relationship matrix, A_{22}^{-1} represents the inverse of the relationship matrix based on pedigree for the genotyped animals, and G^{-1} is the inverse of the genomic relationship matrix obtained according to the first method proposed by VanRaden (2008).

The ssBRN was evaluated considering the residual variances as homogeneous or heterogeneous across EG levels. For heterogeneous residual variances, the different classes of residual variance were determined using the K-means clustering approach (Hartigan and Wong, 1979) and the best model with different classes of residual variance was chosen based on the Deviance Information Criterion (**DIC**) (Spiegelhalter et al., 2002). For this, we considered 25, 20, 15, 13, 11, nine, seven, and five classes of residual variance. THI was incorporated as an environmental variable using the first-order Legendre orthogonal polynomial coefficients. In addition, a quadratic Legendre orthogonal polynomial of second order was tested for the best linear model according to DIC values.

The genetic variance ($\widehat{\sigma}^2_{aEG_i}$) and heritability ($\widehat{h}^2_{EG_i}$) estimates for these traits across the EG level were calculated based on the following equations: $\widehat{\sigma}^2_{aEG_i} = \Phi_f K_a \Phi_{f'}$, where K_a is the matrix for the additive genetic effects, as defined above, and Φ_f is the vector of Legendre orthogonal polynomial estimate (intercept and slope) corresponding to each EG level. The heritability ($\widehat{h}^2_{EG_i}$) for each EG level was calculated as: $\widehat{h}^2_{EG_i} = \frac{\widehat{\sigma}^2_{aEG_i}}{\widehat{\sigma}^2_{aEG_i} + \widehat{\sigma}^2_{eEG_i}}$, in which $\widehat{\sigma}^2_{aEG_i}$ and $\widehat{\sigma}^2_{eEG_i}$ are the additive genetic and residual variances, respectively, in the environment *i*. The genetic correlation across EG levels ($r_{EGi,EGi'}$) was determined as: $r_{EGi,EGi'} = \sigma_{EGi,EGi'} / \sqrt{\widehat{\sigma}^2_{aEG_i} * \widehat{\sigma}^2_{aEG_{i'}}}$, where $\sigma_{EGi,EGi'}$ represents the covariance between EG level *i* and EG level *i'*, estimated the same way as the genetic variance in each EG level.

Posterior distribution samples of the (co)variance components were obtained through Bayesian inference using the Gibbs sampling algorithm, implemented in the GIBBSF90 software (Misztal et al., 2014). The Bayesian analyses consisted of a single chain of 500 000 cycles, a burn-in of 50 000 iterations, and values saved at every ten cycles. The convergence was evaluated through visual inspection using the Bayesian Output Analysis (BOA) (Smith, 2007) and Geweke test (Geweke, 1992).

Genomic estimated breeding values

The genomic estimated breeding values associated with each level of EG were obtained as:

$$\widehat{g}_{iEG_j} = \alpha_i \Phi_{f'}$$

where α_i is the estimated additive genetic coefficient for the intercept and slope of animal *i* and $\Phi_{f'}$ is the transposed vector of estimates of Legendre orthogonal polynomials for level *j* of EG.

Environmental sensitivity

The genetic variabilities observed for the slope of reaction norm model offer the possibility to use the random slope to identify animals that are more robust to environmental changes (De Jong and Bijma, 2002; Mota et al., 2020a, b). For this purpose, a plasticity scale was based on the absolute individual value of the slope (f_1) and SD of the population slope (σ_{f1}). The animals were classified as environmentally robust ($|f_1| < \sigma_{f1}$), environmentally plastic ($\sigma_{f1} < |f_1| < 2\sigma_{f1}$), and extremely environmentally plastic ($|f_1| > 2\sigma_{f1}$).

Results and Discussion

Characterization of the environmental gradient

Fig. 1 displays the annual mean variation in THI during the feed efficiency trials conducted between 2011 and 2023. The results indicate a gradual increase in the average THI values over the years, particularly from 2018 onwards (THI > 71), suggesting that climatic conditions during the feed efficiency trial periods became progressively warmer and/or more humid. The distribution of THI across seasons of the year exhibited a clear seasonal variation, with the highest values observed in Spring and Summer, followed by Fall. Winter, in contrast, displayed the lowest THI values. These patterns reflect typical seasonal variation, where Summer is characterized by warmer and more humid conditions, while Winter is milder and drier. Additionally, the higher values observed in Spring compared to Summer are due to the imbalance in the number of observations by season, with more feed efficiency trials conducted in Spring (27.13%) than in Summer (15.02%) (Table 1). This results in a higher absolute number of THI measurements in Spring, which could potentially influence the mean and distribution of THI values due to the greater representation of this season in the data.

Fig. 2 illustrates the relative frequency of observations with THI values equal to or exceeding 76, a threshold indicating the onset of thermal stress conditions for the Nellore cattle breed (Valente et al., 2015; Cordeiro et al., 2020; Del Corvo et al., 2021), during feed efficiency trials. Between 2011 and 2017, the frequency of THI ≥ 76 remained below 34% across all seasons, with a higher incidence during the Summer (from 10.3 to 31.4%) and Spring (from 14.8 to 33.7%) seasons. However, in years such as 2018, 2019, 2020, and 2023, an increase in the proportion of thermal stress conditions (THI ≥ 76) was observed across all seasons, with growing contributions from the warmer seasons, such as Summer (29.2 to 50.8%) and Spring (26.8 to 63.0%). The higher percentage of THI ≥ 76 observed in Spring compared to Summer may be linked to the greater concentration of feed efficiency trials conducted during periods of increased susceptibility to thermal stress in this season. Furthermore, the trial location could distort the results if more trials were conducted in regions with a higher predisposition to thermal stress during spring. Additionally, variations in the years may have involved different farms or experimental facilities, which could impact the distribution of the data.

The results highlight the impact of seasonal weather conditions on the thermal comfort of animals during feed efficiency trials. The increased occurrence of THI conditions ≥ 76 in recent years underscores the importance of management strategies and genetic selection for improved heat tolerance. Strategies such as adjusting management practices, implementing cooling technologies, and selecting more climatic–resilient animals are essential to mitigate the adverse effects of increased heat stress conditions on animal productivity and welfare. These strategies are particularly relevant in the context of climate change, where the rising frequency and intensity of adverse conditions may compromise the sustainability of livestock production (Henry et al., 2018).

Phenotypic means of residual feed intake and DM intake across temperature-humidity index levels

Table 2 presents the descriptive statistics for DM intake and RFI in Nellore cattle. Means and SDs are reported for each corresponding THI level. Regarding feed efficiency, as measured by RFI, it is observed that values are predominantly negative at lower THI

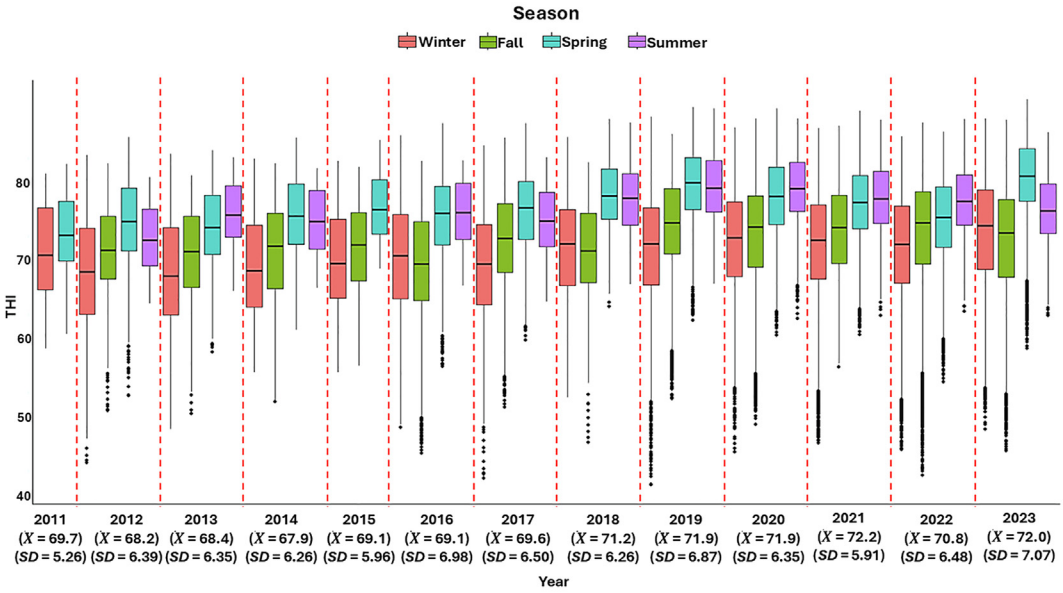

Fig. 1. Distribution of the temperature-humidity index (THI) across seasons (Winter, Fall, Spring, Summer) from 2011 to 2023 during feeding trials recording in Nellore cattle. Boxplots represent seasonal THI variation per year. Annual mean (*X*) and SD are shown below each year. Red dashed lines separate recording years.

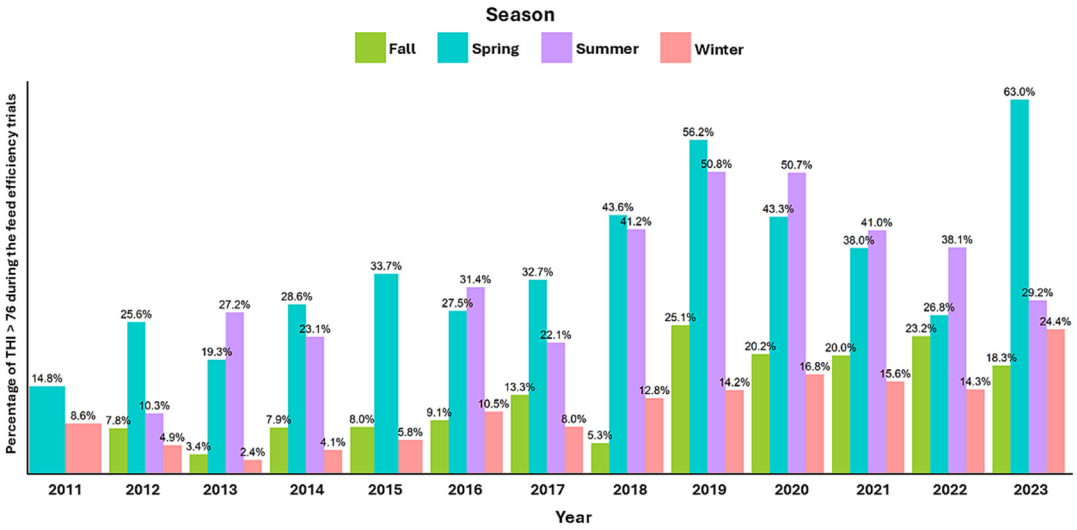

Fig. 2. Proportion of days with temperature-humidity index (THI) ≥76 during feed efficiency trials from 2011 to 2023 in Nellore cattle. Bars are grouped by season (Winter, Fall, Spring, Summer) illustrating seasonal and annual exposure to heat stress.

levels (67–69), suggesting that cattle are more efficient in feed conversion under more thermoneutral conditions, consuming less feed than expected based on their production level. In physiological terms, this increase in feed efficiency may be related to a greater ability to maintain homeothermy and a more efficient use of metabolic energy, without the losses associated with thermal stress (Shephard and Maloney, 2023). Therefore, negative RFI may reflect a state of lower metabolic overload, where cattle are able to make better use of their feed for performance.

As THI increases, particularly beyond 73, the mean RFI approached zero or became positive (Table 2), indicating a reduction in feed efficiency. This shift may be attributed to increased heat stress, which compromises the efficient utilization of nutrients by the animals. Elevated temperatures disrupt thermal balance mechanisms, negatively affecting health, welfare, growth, and production (Bernabucci, 2019; Chevin and Hoffmann, 2017; Osei-Amponsah et al., 2019), ultimately impacting productivity and economic outcomes (West, 2003).

In terms of DM intake, the feed intake reduced as the THI becomes more stressful, with the average values ranging from 9.75 kg/day (for THI 69) to 6.93 kg/day (for THI 81), with intermediate variations between 7.55 kg/day and 9.61 kg/day under more moderate THI conditions (Table 2). Feed intake tends to be lower under extreme heat stress conditions, such as at THI 81, possibly due to a reduction in appetite or motivation to consume feed under high temperature and humidity (Henry et al., 2018). In this case, environmental temperatures often approach or exceed the animal's body temperature, with mean radiant temperatures surpassing air temperatures, thereby limiting heat dissipation through convection and radiation (Lacetera, 2019). High humidity further diminishes the efficiency of evaporative heat loss mechanisms (Berman, 2011), preventing animals from dissipating excess heat

Table 2
Number of records (N) and descriptive statistics for DM intake (DMI) and residual feed intake (RFI) by temperature and humidity index (THI) in Nellore cattle.

THI	N	RFI (kg DM/day) Mean ± SD	DMI (kg DM/day)
67	1 036	−0.23 ± 1.42	8.11 ± 1.89
68	1 335	−0.05 ± 0.68	8.36 ± 2.01
69	1 028	−0.01 ± 0.78	9.75 ± 2.42
70	1 182	0.39 ± 1.52	9.44 ± 2.84
71	1 321	−0.13 ± 0.82	8.75 ± 1.97
72	1 418	0.00 ± 0.74	8.32 ± 1.72
73	2 695	0.04 ± 0.85	8.92 ± 1.72
74	1 964	−0.02 ± 0.82	8.07 ± 1.95
75	3 233	0.01 ± 0.65	8.67 ± 2.57
76	1 167	0.00 ± 0.61	9.61 ± 1.47
77	2 657	0.00 ± 0.59	7.55 ± 1.47
78	1 362	0.00 ± 0.77	9.07 ± 2.96
79	1 701	0.00 ± 0.85	7.97 ± 1.60
80	511	0.00 ± 0.53	7.90 ± 1.21
81	228	0.00 ± 0.56	6.93 ± 1.02

and maintaining homeothermy, directly reflecting a decrease in feed intake to avoid the heat generated by the feed's metabolic energy (Lees et al., 2019).

At moderate to mildly high THI levels (69–76), DM intake appeared to stabilize, averaging between 8.07 and 9.75 kg/day (Table 2). Although these descriptive values suggest that cattle may maintain a relatively consistent intake under such conditions, it is important to note that no formal statistical tests were conducted in this analysis. Therefore, these observations should be interpreted as indicative trends rather than statistically validated effects. However, in support of this interpretation, the literature reports that feed intake and feeding behavior in crossbred cattle have been strongly influenced by thermal conditions and access to shade (Brown-Brandl et al., 2005), highlighting compensatory strategies employed by cattle to cope with heat stress. Brown-Brandl et al. (2005) reported that in intermediate climatic categories (THI 74–THI 78), cattle adjusted meal frequency and size, maintaining a relatively stable daily feed intake, as observed in this study. Furthermore, under severe climatic conditions, these strategies were insufficient to overcome the adverse effects of extreme heat, resulting in significant reductions in feed intake, meal frequency, and total feeding duration (Brown-Brandl et al., 2005).

In dairy cattle, the negative impact of heat stress on feed efficiency is well documented. For instance, Chen et al. (2024) conducted a meta-analysis of 31 studies and found that each unit increase in THI led to a 4.13% reduction in DM intake and a 3.25% decrease in energy-corrected milk (**ECM**) yield, particularly in mid-lactation cows. Interestingly, despite the decline in feed intake, feed efficiency (kg ECM/kg DM intake) remained relatively stable, suggesting that metabolic adjustments may partially compensate for reduced nutrient intake. Similarly, Gorniak et al. (2014) investigated the effects of mild heat stress (THI > 60) on mid-lactation Holstein cows in a temperate climate, finding that even moderate increases in THI led to significant reductions in DM intake, affecting dairy cattle productive performance by impairing nutrient utilization efficiency. Moreover, Chang-Fung-Martel et al. (2021) conducted a global meta-analysis to assess the relationship between THI and DM intake across cattle breeds and management systems. The authors reported a strong negative correlation (−0.82) between THI and DM intake, with an estimated reduction of 0.45 kg/day in DM intake for each unit increase in THI. These results provide robust evidence that reductions in feed intake under heat stress conditions are a widespread phenomenon, necessitating targeted interventions to minimize production losses. Furthermore, prolonged heat exposure (32 °C) has been reported to influence energy utilization in Large White pigs diver-gently selected for RFI (Renaudeau et al., 2013). The authors found that metabolizable energy intake decreased by 38% and heat production by 20% under heat stress conditions, independent of genetic differences in feed efficiency.

These findings have significant implications for the management of animals in tropical environments, where heat stress can impact both feed intake and feed conversion efficiency. Management strategies, such as providing shade, fresh water, and other measures to mitigate heat stress, are crucial for optimizing the animals' feeding performance during periods of high temperature and humidity.

Comparison of reaction norm models

Table 3 presents a comparative analysis of reaction norm model for DM intake and RFI in Nellore cattle based on DIC values. This criterion assesses model fit while penalizing model complexity, with lower values indicating superior model performance (Spiegelhalter et al., 2002; Berg et al., 2004; Celeux et al., 2006). Additionally, Table 3 provides information on the number of estimated parameters and rankings of the models based on their DIC values.

The linear model incorporating five classes of residual variance (Lin_het_5) demonstrated optimal performance, exhibiting the lowest DIC value (−871 322.55) and the highest rank (Table 3). This model provides an effective balance between goodness of fit and model simplicity with 25 parameters, thereby ensuring a more parsimonious representation of the data while maintaining an adequate fit. In contrast, the linear model with homogeneous residual variance (Lin_hom) ranked sixth, with a DIC of −186 813.35 and number of estimated parameters = 13. Although relatively simple and easy to interpret, the assumption of homogeneous residual variance across all environmental conditions failed to reflect the heterogeneous nature of variability inherent in the dataset. This structural limitation reduced the model's ability to accurately represent the intrinsic differences within the data, leading to a less precise fit of the data. Conversely, models that incorporate heterogeneous residual variances are better suited for capturing the complexity of data from Nellore cattle evaluated under diverse environmental and management conditions (Carvalheiro et al., 2019; Mota et al., 2020a, b; Carvalho Filho et al., 2022).

The quadratic model with five residual variance classes (Qua_het_5) demonstrated the poorest overall performance with a DIC of −4 071.03 (Table 3). This outcome suggests that the quadratic functional form is less effective in modeling reaction norms for DM intake and RFI in Nellore cattle. This can be attributed to the negative linear expected phenotypic patterns for feed efficiency traits, such as DM intake and RFI, in cattle under thermal stress conditions (Lees et al., 2019). The quadratic model assumes non −linear curvatures, which, in this context, may lead to overestimation or underestimation of responses, deviating from the biological and statistical reality of the data.

The results indicate that models incorporating a greater number of residual variance classes, such as Lin_het_15 and Lin_het_25, generally exhibited improved performance, ranking second and third, respectively. However, increased model complexity does not always result in substantial improvements, as evidenced by the performance of models Lin_het_20 and Lin_het_9, which ranked eighth and ninth, respectively. To select the optimal model, Meyer (2005) recommended balancing the number of residual variance classes with the amount of available data, particularly when the number of records is unevenly distributed across EG levels. Conversely, more parsimonious models, such as Lin_het_5, demonstrated greater efficiency by striking a balance between model fit and simplicity.

Table 3
Comparison of the reaction norm models according to the deviance information criterion (DIC) for DM intake (DMI) and residual feed intake (RFI) in Nellore cattle.

Model	PO	CRV	DIC	NP	Rank
Lin_hom	1	1	−186 813.35	13	6
Lin_het_25	1	25	−424 824.88	85	3
Lin_het_20	1	20	−40 009.12	70	8
Lin_het_15	1	15	−560 332.90	55	2
Lin_het_13	1	13	−251 469.08	49	5
Lin_het_11	1	11	−378 719.06	43	4
Lin_het_9	1	9	−10 693.63	37	9
Lin_het_7	1	7	−41 440.74	31	7
Lin_het_5	1	5	−871 322.55	25	1
Qua_het_5	2	5	−4 071.03	36	10

The best-fitting model is Lin_het_5; PO: Legendre orthogonal polynomial order; CRV: Number of classes of residual variance; NP: number of estimated parameters; Lin_hom: linear model with homogeneous residual variance; Lin_het_25: linear model with twenty-two classes of residual variance; Lin_het_20: linear model with twenty classes of residual variance; Lin_het_15: linear model with fifteen classes of residual variance; Lin_het_13: linear model with thirteen classes of residual variance; Lin_het_11: linear model with eleven classes of residual variance; Lin_het_9: linear model with nine classes of residual variance; Lin_het_7: linear model with seven classes of residual variance; Lin_het_5: linear model with five classes of residual variance; Qua_het_5: quadratic model with five classes of residual variance; Rank: models ranking based on DIC values.

Silva Neto et al. (2023) assessed G × E for DM intake and RFI in Nellore cattle using best linear unbiased estimation solutions of the contemporary groups for average daily gain. According to the Bayesian Information Criterion, the authors concluded that a linear model considering heterogeneous residual variances with six classes was the most appropriate model to fit the residual structure of DM intake and RFI. The quadratic model and the homogeneous residual variance model did not improve data fit, consistent with the findings of this study. It is important to note that the choice of the best-fitting model is strongly influenced by the data structure across the environmental gradient and by how the trait-specific variance components behave along this gradient. For instance, traits influenced by stage of growth, such as average daily gain, or by environmental adaptation, such as DM intake and RFI, may exhibit linear patterns along certain gradients, which may justify the use of linear reaction norm models in such scenarios. These results underscore the importance of incorporating heterogeneous residual variance when modeling reaction norms, particularly in datasets with feeding trials conducted across multiple and diverse environments, such as in Brazil. This approach ensures a more accurate representation of G × E by accounting for the intrinsic heterogeneity of the feed efficiency trials included in this study. Future studies should explore alternative residual variance structures to refine model selection and enhance the accuracy of genetic evaluations.

(Co)Variance components

Table 4 presents the posterior means of variance component estimates and posterior SD (values in parentheses) for the parameters of the reaction norm model selected as the best-fitting model (Lin_het_5, i.e., linear reaction norm model with five heterogeneous residual classes) using genomic and pedigree information for feed efficiency traits in Nellore cattle. The slope/intercept ratio was low, with values of 0.205 for RFI and 0.102 for DM intake, indicating a lower slope estimate and suggesting that Nellore cattle exhibit lower sensitivity to thermal stress for feed efficiency traits (Table 4). Animals with higher average values tend to respond more when environmental conditions become less challenging. Thus, increasing the slope/intercept ratio leads to a greater effect on animal sensitivity, as a high slope variation was observed, indicating a higher degree of G × E (Kolmodin and Bijma, 2004). Despite the low estimates for both traits, the values were different from zero, suggesting non-null environmental sensitivity and, therefore, some degree of G × E, with a greater intensity for RFI compared to DM intake (Table 4). This finding is consistent with the nature of these traits, as DM intake represents the feeding intake, while RFI represents an indicator of metabolic efficiency and may be more susceptible to physiological variations induced by heat stress. The non-zero slope/intercept ratio at the population level provides complementary evidence that animals differ in their genetic sensitivity to the EG, supporting the notion that genotypes do not respond uniformly across environments.

Table 4
Posterior means of variance component estimates (posterior SD) for the genomic reaction norm model parameters for residual feed intake (RFI) and DM intake (DMI) in Nellore cattle.

Variance component	RFI	DMI
Intercept (σ^2_a)	0.124 (0.010)	0.467 (0.025)
Slope (σ^2_b)	0.025 (0.008)	0.048 (0.011)
Covariance (σ_{ab})	−0.029 (0.008)	−0.032 (0.014)
Slope/intercept ratio	0.205 (0.071)	0.102 (0.026)
Correlation (r_{ab})	−0.514 (0.114)	−0.212 (0.094)
Covariance intercept RFI × DMI (σ_{a1a2})	0.159 (0.014)	
Covariance slope RFI × DMI (σ_{b1b2})	0.029 (0.008)	
Covariance intercept RFI × Slope DMI (σ_{a1b2})	−0.021 (0.009)	
Covariance intercept DMI × Slope RFI (σ_{a2b1})	−0.037 (0.011)	
Residual class 1 (σ^2_{e1})	0.392 (0.015)	0.570 (0.023)
Residual class 2 (σ^2_{e2})	0.608 (0.017)	0.857 (0.026)
Residual class 3(σ^2_{e3})	0.557 (0.012)	0.837 (0.019)
Residual class 4 (σ^2_{e4})	0.382 (0.008)	0.618 (0.014)
Residual class 5 (σ^2_{e5})	0.499 (0.011)	0.792 (0.019)
Average heritability (h^2)	0.130 (0.051)	0.257 (0.048)
Average genetic correlations RFI × DMI (r_g)	0.667 (0.024)	
Average phenotypic correlations RFI × DMI (r_p)	0.708 (0.023)	

The genetic correlation between intercept and slope (Table 4) was negative for both traits (−0.514 for RFI and −0.212 for DM intake), suggesting that animals with a higher intercept (better average performance) tend to be less sensitive to environmental variations (THI). Regarding residual variances, the values for RFI ranged from 0.382 (class 4) to 0.608 (class 2), while for DM intake, the values were higher, ranging from 0.570 (class 1) to 0.857 (class 2).

Heritability, phenotypic, and additive genetic variance estimates

The heritability estimates obtained for RFI and DM intake across the EG values ranged from 0.08 to 0.28 and from 0.22 to 0.39, respectively (Fig. 3). The heritability of DM intake was higher under lower THI conditions, progressively decreasing as THI increased. This pattern suggests that additive genetic effects play a more pronounced role in determining DM intake under less

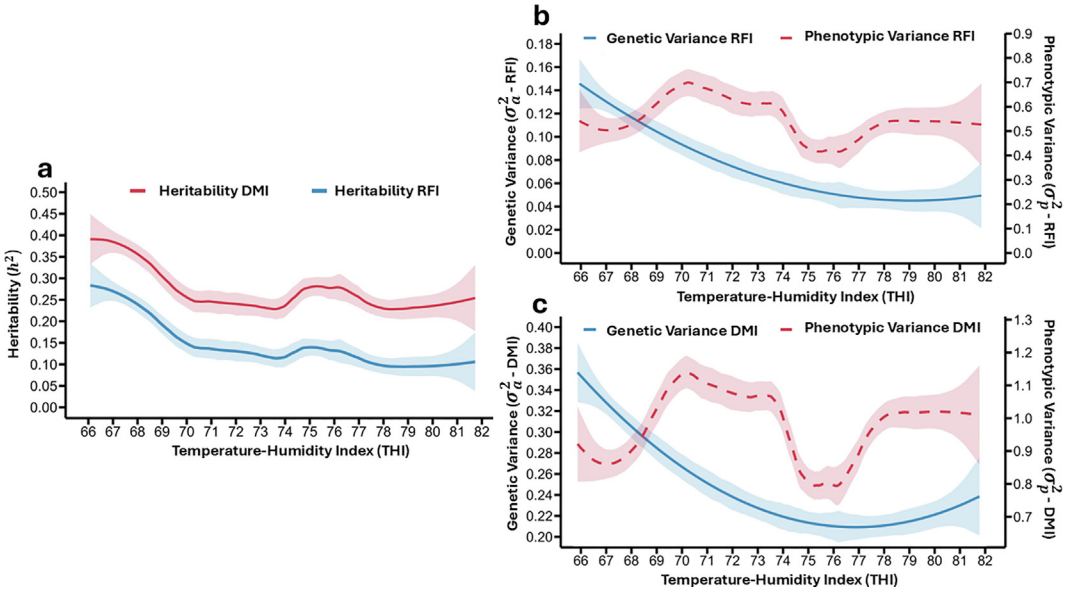

Fig. 3. Estimates of heritability (h^2) (a), additive genetic variance (σ^2_a), and phenotypic variance (σ^2_p) for residual feed intake (RFI) (b) and DM intake (DMI) (c) in Nellore cattle across environmental gradients (THI). Shaded areas around the lines represent the posterior standard deviation (PSD), considering a 95% confidence interval.

stressful environmental conditions. For RFI, heritability estimates were consistently lower than those for DM intake across all THI levels but followed a similar trend, with the lowest heritability values observed under high THI conditions (Fig. 3). This indicates a greater environmental influence on the trait under more challenging environments. As a reference, heritability estimates from the traditional model without accounting for G × E were 0.11 for RFI and 0.24 for DM intake (Table S4), which fall within the range observed in the G × E model (reaction norm model). However, heritability estimates were generally higher when G × E was modeled. Compared to the average heritability estimates obtained from the reaction norm model (Table 4), the values from the traditional model were similar for both traits. These results indicate that the estimates obtained from the traditional model represent average values that may mask the underlying genetic variability expressed under different environmental conditions. For RFI, the traditional estimate was similar to those obtained at THI levels 72 to 74 and 76, higher than estimates under more severe heat stress (THI 77 to 81), and lower than those observed under more favorable conditions (THI 66–71 and 75). In the case of DM intake, the pattern was similar, although less pronounced. The traditional estimate was close to those obtained at a broader range of THI levels (71–74 and 77–81), but lower than the estimates at THI 66–70, 75, and 76. This suggests that, even for highly correlated traits, the magnitude and pattern of G × E effects can differ.

Silva Neto et al. (2023) reported higher heritability estimates for RFI and DM intake in Nellore cattle along the EG, ranging from 0.07 to 0.41 and 0.26–0.54, respectively. The authors used best linear unbiased estimation solutions of the contemporary groups for average daily gain. For both traits, heritability initially decreased from lower EG levels (lower environmental quality) to intermediate levels, then increased at higher EG levels (higher environmental quality). This pattern contrasts with the present study, where the lowest heritability estimates were observed under more challenging environments (high THI values). The difference in heritability estimates between the two studies can be attributed to various factors, including the definition of the EG. In the present study, THI directly reflects heat stress conditions (temperature and humidity), whereas the EG based on best linear unbiased estimation solutions of average daily gain captures a broader range of environmental factors, such as feed availability and quality, management practices, and farm health conditions. Furthermore, differences between the populations studied, such as sample size, may also contribute to variability and subsequent differences in the heritability estimates.

The additive genetic variance for DM intake (0.22–0.36) and RFI (0.04–0.15) across the THI gradient is presented in Fig. 3. For DM intake, higher values were observed under lower THI conditions, progressively decreasing as THI increased. This pattern suggests that the genetic potential for this trait is more efficiently expressed in less stressful environments. A similar trend was observed for the additive genetic variance of RFI, although with less variation across the THI levels.

The phenotypic variance estimates for both traits showed an increasing trend with rising THI (Fig. 3). However, a notable decline was observed at THI levels 75 and 76, particularly for DM intake. This temporary drop in phenotypic variance is supported by the residual variance estimates from the reaction norm model (Table 4), where the lowest posterior values for both DM intake and RFI were observed in class 4, which corresponds to this THI range. The reduction in the residual component at this point decreases the total phenotypic variance without a proportional change in genetic variance, indicating a period of lower environmental heterogeneity or more uniform animal responses under those heat stress conditions. In general, for DM intake (0.84–1.15), the increase observed was accompanied by a disproportionately smaller additive genetic variance, which did not rise at the same rate, reflecting a greater environmental influence as THI increased. For RFI (0.43–0.71), the increase in phenotypic variance was predominantly associated with greater environmental variance, thereby diluting the relative contribution of additive genetic effects. These findings emphasize the critical role of environmental factors in shaping the observed phenotypes, particularly under thermal stress conditions.

Comparatively, Silva Neto et al. (2023) reported additive genetic variance estimates for DM intake progressively increasing in more favorable environmental conditions (0.26–0.75), suggesting that better environments amplify genetic differences among animals. However, for RFI, the values remained relatively stable (0.07–0.11) across EG levels. Similarly, the phenotypic variance for both

traits increased with EG (0.27–1.08 for RFI and 0.55–1.71 for DM intake), driven primarily by greater environmental variance. This effect was more pronounced for RFI, where heritability decreased as EG increased, indicating that variance heterogeneity had a greater impact on this trait than on DM intake.

In conclusion, these findings highlight the dynamic nature of heritability and variance estimates for DM intake and RFI across environmental gradients. The observed patterns reinforce the need for selection strategies that account for G × E, particularly in tropical production systems where environmental stressors, such as THI, play a significant role in modulating phenotypic expression and genetic potential of animals.

Genetic correlation estimates across temperature-humidity index levels

The genetic correlation estimates for the evaluated traits across THI levels ranged from 0.29 to 0.99 for RFI and from 0.55 to 0.99 for DM intake, with mean (±SD) values of 0.83 ± 0.18 and 0.90 ± 0.11, respectively, indicating the presence of G × E (Fig. 4). When EG levels were more similar, the genetic correlations were above 0.80, suggesting that a more similar set of genes is regulating performance in similar environments. However, as the environments became more divergent, the correlations dropped below 0.80, indicating more different genetic control and reflecting a higher genetic plasticity in response to environmental changes. The progressive decrease in genetic correlations below 0.80 was observed from THI 76 for both traits, suggesting significant G × E effects as environmental differences became more pronounced with increasing thermal stress. Similarly, Silva Neto et al. (2023) also observed G × E for these same traits in Nellore cattle, using best linear unbiased estimation solutions for average daily gain as EG. The genetic correlation for RFI across different EG levels ranged from 0.22 to 0.99, with an average (± SD) of 0.81 ± 0.21, while for DM intake, the correlation ranged from 0.26 to 0.99, with an average (± SD) of 0.83 ± 0.19, showing a broader range compared to the present study, mainly for DM intake. High genetic correlations were observed when the EG levels were more similar, indicating consistent genetic performance under similar conditions, which mirrors the findings in our study. However, as environmental conditions became more divergent, the genetic correlation decreased below 0.80, suggesting the presence of significant G × E. This decrease in genetic correlation implies that performance for feed efficiency and feed intake may vary across environments, potentially leading to a reranking of breeding animals by the variations in their estimated breeding values. This further emphasizes the need to account for environmental variations in breeding programs to ensure consistent genetic progress, especially when dealing with different levels of thermal stress in the production systems.

Genetic and phenotypic correlations between feed intake and efficiency trait

Estimated genetic and phenotypic correlations between RFI and DM intake across the THI levels were consistently positive, ranging from 0.64 to 0.72 and 0.70 to 0.73, respectively (Fig. 5). Compared to the traditional model, these estimates fell within the range observed in the reaction norm model models and were also similar to their average values (Table 4), with approximately 0.65 (genetic) and 0.72 (phenotypic) (Table S4), reinforcing that traditional models represent average estimates across environmental conditions. The phenotypic correlation between RFI and DM intake exhibited greater stability across the entire THI gradient. Although slight variations were observed at moderate THI levels, the curve pattern suggests that non-genetic factors, such as management practices or specific environmental conditions, may play a crucial role in maintaining this relationship. Conversely, looking at the pattern of genetic correlations, a gradual decline was observed along increasing THI levels. The correlations remained relatively stable under thermoneutral conditions (THI < 76), but progressively decreased as heat stress intensified, suggesting that environmental heat load may influence the genetic regulation of feed efficiency traits. These reductions in genetic correlations indicate changes in genetic responses in more stressful environments, potentially driven by adaptive mechanisms or physiological trade-offs.

The stability of phenotypic correlations across the THI gradient indicates that, even under heat stress conditions, animals maintain a consistent relationship between DM intake and RFI. In contrast, the reduction in genetic correlations in high THI environments underscores the relevance of G × E in selection decisions. Therefore, incorporating environmental gradients into breeding programs is essential to more effectively capture G × E variation. Furthermore, a multivariate approach may be beneficial in identifying traits that are more stable and those requiring greater attention under extreme environmental conditions.

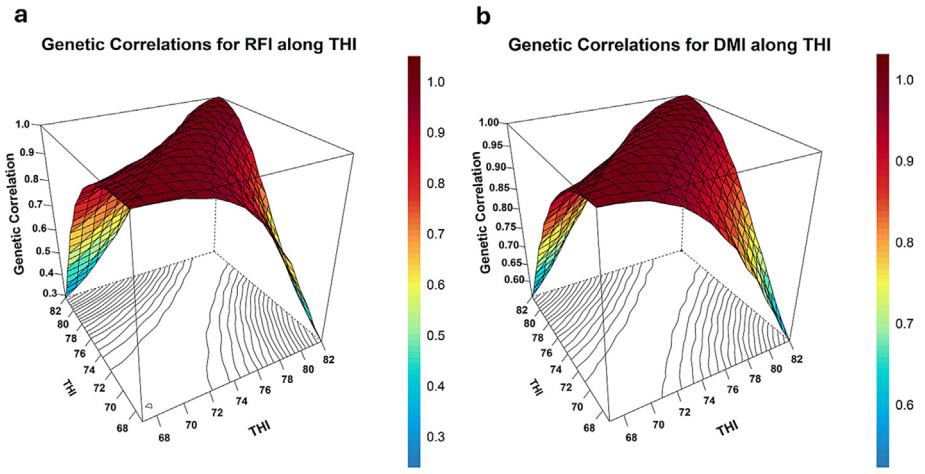

Fig. 4. 3D surface plots of genetic correlation estimates for residual feed intake (RFI) (a) and DM intake (DMI) (b) across environmental gradients (THI – temperature humidity index) in Nellore cattle. Horizontal axes represent specific THI levels in pairwise comparisons, while the vertical axis shows the genetic correlation between those levels for the same trait. The surface illustrates variation in genetic correlations along the environmental gradient. The color scale indicates the magnitude of the correlations, ranging from low (blue) to high (red).

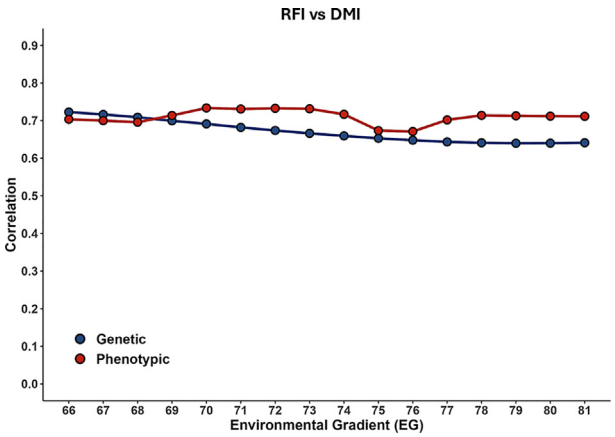

Fig. 5. Genetic and phenotypic correlation estimates between residual feed intake (RFI) and DM intake (DMI) in Nellore cattle across environmental gradients (THI).

Reaction norms for genomic estimated breeding values

The reaction norms for the top 50 sires with the largest number of progeny (average of 285.78, ranging from 111 to 1 171 offspring) for RFI and DM intake showed reranking among these sires (Fig. 6). The effect of G × E on the sensitivity of animals across EG levels, especially between extreme THI levels, was expected due to a genetic correlation lower than 0.80 (Fig. 4). The average genomic estimated breeding values for RFI and DM intake were, respectively, 0.014 kg/DM per day and 0.548 kg/DM per day for the lowest EG level (THI = 67), – 0.001 kg/DM per day and 0.532 kg/DM per day for the intermediate EG level (THI = 74), and –0.015 kg/DM per day and 0.516 kg/DM per day for the highest EG level (THI = 81). These values are part of internal results not shown in tables or figures.

The reaction norm pattern highlights the significance of the G × E interaction. Genotypes with high plasticity, characterized by greater sensitivity to environmental changes, are associated with steeper slopes, whereas more robust genotypes exhibit flatter slopes. Based on the slope (f_1) solutions, 18.0 and 20.0% of the top 50 sires were classified as highly plastic to environmental changes, 38.0 and 26% as plastic, and 44.0 and 54.0% as more robust to environmental changes for RFI and DM intake, respectively (Table 5). When considering sire classifications for both traits simultaneously, 14.0% were classified as highly plastic, 14.0% as plastic, 34.0% as more robust, and 38.0% fell into different categories, meaning they were not consistently categorized for both traits. The desirability of each category depends on the production system and environmental challenges, particularly in the context of heat stress. In environments with frequent thermal stress, high plasticity may not be advantageous, as animals that drastically

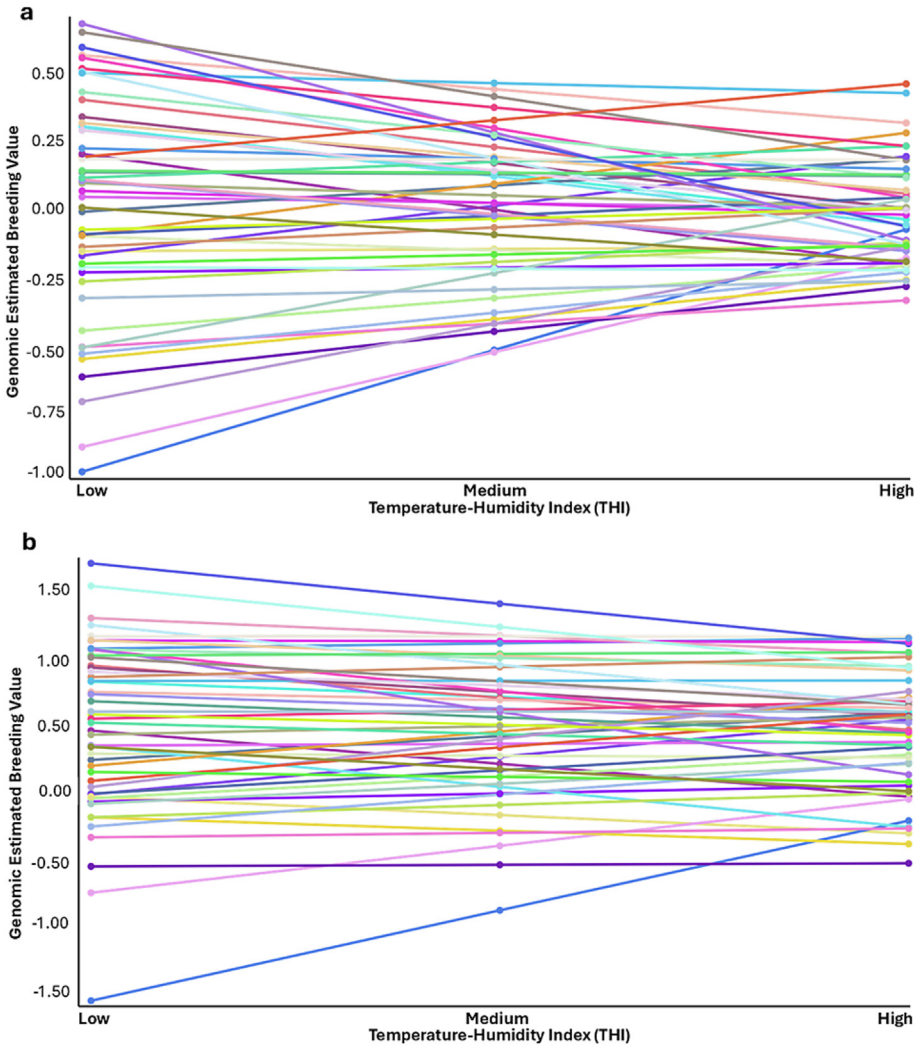

Fig. 6. Reaction norms for the 50 Nellore sires with the highest number of progenies for residual feed intake (RFI) (a) and DM intake (DMI) (b). Each line represents a sire, with colors consistently assigned so that the same sire is represented by the same color across both traits.

Table 5
Proportion of animals by plasticity category for residual feed intake (RFI) and DM intake (DMI) in Nellore cattle: all individuals and top sires.

Classification	All individuals			Top sires		
	RFI	DMI	Both traits[1]	RFI	DMI	Both traits[1]
Robust	72.6%	73.7%	65.2%	44.0%	54.0%	34.0%
Plastic	21.2%	19.8%	10.6%	38.0%	26.0%	14.0%
High plasticity	6.2%	6.5%	3.9%	18.0%	20.0%	14.0%
Number of animals (%)	46 386 (100%)	36 970 (79.7%)[1]		50 (100%)		31 (62.0%)[1]

f_1 : absolute individual value of the slope; σ_{f1}: SD of the population slope; Robust: $|f_1| < \sigma_{f1}$; Plastic: $\sigma_{f1} < |f_1| < 2\sigma_{f1}$; Extreme plasticity: $|f_1| > 2\sigma_{f1}$.
[1] 20.3 and 38.0% of the population and sires, respectively, fell into different categories for RFI and DMI, meaning they were not consistently classified across both traits and, therefore, were not included in the "Both traits" category.

change their performance in response to environmental fluctuations could show unstable productivity under heat stress. On the other hand, in systems with stable or only moderately variable environmental conditions, high plasticity may represent an adaptive advantage by allowing animals to maximize the expression of their genetic potential whenever conditions are favorable. Additionally, a moderate degree of plasticity might be advantageous even in changing environments, as it could allow for a certain degree of adaptability without the metabolic cost of maintaining strict homeostasis. Therefore, the optimal genotype depends on the specific environmental context, as initially mentioned.

At the population level, 6.2 and 6.5% of animals were classified as highly plastic to environmental changes, 21.2 and 19.8% as plastic, and 72.6 and 73.7% as more robust to environmental changes for RFI and DM intake, respectively (Table 5). For both traits simultaneously, 3.9% were classified as highly plastic, 10.6% as plastic, 65.2% as more robust, and 20.3% fell into different categories, meaning they were not consistently classified for both traits.

The predominance of animals classified as robust reflects the inherent ability of Nellore cattle to maintain stable metabolic function despite environmental fluctuations. The breed's short, light-colored hair facilitates heat dissipation, while its well-developed sweat glands and loose skin enhance evaporative cooling, enabling animals to regulate body temperature more efficiently under high temperatures and elevated THI (Nonato et al., 2023). Beyond thermoregulation, Nellore cattle exhibit additional traits that contribute to their robustness and reduced plasticity. The relatively low proportion of highly plastic individuals (6.2% for RFI and 6.5% for DM intake) suggests that most Nellore cattle do not rely on drastic physiological adjustments in response to environmental changes but instead maintain performance through adaptive mechanisms. While this lower plasticity may limit the breed's ability to capitalize on high-input systems to the same extent as more plastic breeds, it provides a crucial advantage in tropical climates where resilience to environmental challenges is essential toward more sustainable production (Rodrigues et al., 2024).

Spearman correlation and selection coincidence

The top 50 sires were ranked based on their genomic estimated breeding values for both traits, and 30% (15 sires) were selected to assess Spearman correlations and selection coincidence, defined as the proportion of sires that were simultaneously selected across different EG. Each of these top 15 sires had at least five progeny distributed across a minimum of five EG levels (i.e., THI 66, 71, 74, 77, and 81), with an average of 108 progeny per sire (ranging from 25 to 359). The rank, genomic estimated breeding values, and number of progeny for each sire by trait are presented in Supplementary Tables S5 and S6.

The Spearman correlations and selection coincidence percentages for RFI and DM intake among the top 15 sires are presented in Fig. 7. The ranking correlation analyses indicate that the performance of sires for RFI is highly sensitive to environmental variations, with correlations across environmental gradients ranging from 0.55 to 0.99 (Fig. 7a). The lowest estimates were observed between the extreme THI levels (66 and 81), suggesting that the ranking of sires for RFI is more prone to changes under extreme environmental conditions, such as higher or lower temperatures and humidity.

In contrast, the ranking correlations for DM intake showed greater consistency, remaining above 0.76 in all comparisons (Fig. 7c). This result suggests that DM intake is less influenced by environmental changes than RFI, reflecting lower variability in the ranking of sires under different environmental conditions. However, considering the trend of decreasing Spearman correlation values as the environments become more divergent, it suggests that extreme thermal stress conditions may still influence the ranking of sires.

The selection coincidence analyses revealed a pattern similar to that observed in the ranking correlations. For both traits, the selection coincidence percentages ranged from 66.67 to 93.33% (Fig. 7b), with lower values observed between the extreme THI levels (e.g., 66.67% between levels 66 and 81). This reinforces that selection under extreme environmental conditions can lead to substantial differences in sire performance, suggesting that the effectiveness of RFI and DM intake selection may be reduced under such conditions. Considering the magnitude of the values obtained between THI levels 66–77 compared with the extreme environment (THI 81), the results suggest that selection for RFI is more affected by environmental variation than DM intake, which generally showed higher coincidence values. This is consistent with the ranking correlations, which indicate greater relative stability of DM intake across environmental conditions.

In addition to comparisons across gradients, the Spearman correlations between the traditional model without G × E and each EG from the reaction norm model model are reported in Supplementary Table S7. For RFI, Spearman correlations ranged from 0.78 (THI 81) to 0.99 (THI 74), and for DM intake, from 0.91 (THI 81) to 1.00 (THI 74), highlighting a close alignment between the traditional model and intermediate environmental conditions. Similarly, the selection coincidence percentages between the traditional model and each EG ranged from 73.33 to 93.33% for RFI and from 80.00 to 100% for DM intake, with the lowest values again observed in comparisons involving the most extreme environmental gradient (THI 81). This pattern consistently reinforces the results previously discussed in this study, indicating that the traditional model captures an overall average performance across environments.

Overall, these results indicate that RFI is more sensitive to environmental conditions than DM intake, as evidenced by the lower correlations and lower selection coincidence observed at the extreme THI levels. This suggests that sire performance for RFI may be significantly altered by environmental variations, particularly under more extreme conditions. The greater stability of DM intake to environmental changes makes it a less variable metric for sire performance. On the other hand, the instability of RFI

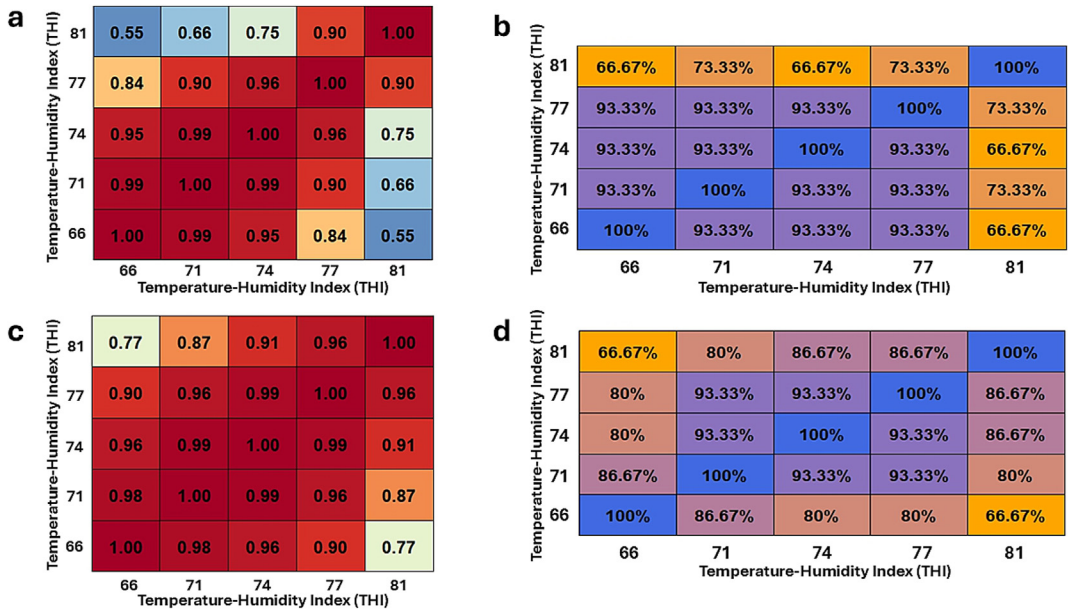

Fig. 7. Spearman's rank correlations for residual feed intake (RFI) (a) and DM intake (DMI) (c), and selection coincidence for RFI (b) and DMI (d), among the top 15 Nellore sires with at least five progenies in each of the five temperature-humidity index (THI) levels.

highlights the need to consider G × E in selection programs, to minimize the reranking of sires across different environmental conditions and thereby enhance selection efficacy. Incorporating models that account for these interactions can improve the accuracy of selection and ensure that the most suitable sires (or other breeding animals) are chosen for varying environmental conditions, such as THI.

Future research directions

In the present study, we used the phenotypic averages for each test period to assess the impact of heat stress on feed efficiency traits. While this approach facilitates the modeling of G × E and captures general trends, it may mask daily or even hourly variations in the effects of heat stress on DM intake and RFI. Heat stress is a dynamic phenomenon, with substantial fluctuations throughout the day due to variations in ambient temperature, relative humidity, and solar radiation. Previous studies indicate that THI at specific times of the day can have distinct effects on metabolism and feeding behavior in cattle. For instance, animals tend to reduce feed intake during periods of higher temperatures and compensate for this reduction during cooler periods (Brown-Brandl et al., 2005). However, given the use of THI averages and phenotypic means for each feeding trial period, it was not possible to capture short-term variations and their direct implications on feed efficiency.

Future studies should use longitudinal data, allowing for a more precise assessment of how THI fluctuations affect DM intake and RFI over time. Such an approach would enable the: (i) identification of critical periods of the day during which heat stress has the greatest impact on feed intake; (ii) evaluation of individual adaptation patterns to heat stress, determining whether certain animals adjust their feeding behavior throughout the day to mitigate heat stress effects; and (iii) direct modeling of phenotypic responses based on daily THI variations, rather than relying solely on period-averaged values. Incorporating continuous records of feed intake and associated environmental variables could significantly enhance G × E modeling accuracy, providing more precise insights for selecting animals with greater resilience to heat stress. Future studies could greatly benefit from this approach to further elucidate the mechanisms that influence feed efficiency in tropical production systems and to support the development of more robust breeding programs in the face of climate change.

Conclusions

This study demonstrated the influence of heat stress on feed efficiency traits in Nellore cattle using genomic reaction norm models. Heritability estimates varied along the environmental gradient (THI), indicating that the genetic expression of these traits is sensitive to climatic variations. The detection of G × E was more evident at higher THI values, particularly above 76, where genetic correlations for the same trait across different environments dropped below 0.80 and sire reranking became more pronounced. However, progressive changes in genetic parameters were also observed across the full range of THI values, reinforcing the continuous nature of environmental influence. Additionally, the relationship between DM intake and RFI was not constant along the environmental gradient, showing substantial genetic instability under extreme heat conditions, reinforcing the need to consider genetic plasticity when selecting beef cattle for improved feed efficiency in tropical regions.

Supplementary material

Supplementary Material for this article (https://doi.org/10.1016/j.animal.2025.101612) can be found at the foot of the online page, in the Appendix section.

Ethics approval

The collection of the phenotypes was restricted to routine on-farm procedures that did not cause any inconvenience or stress to the animals. Therefore, no specific ethical approval was required. In accordance with national legislation and institutional guidelines, ethical review was not necessary for this study, as all data were obtained from an existing database and no additional animal procedures were conducted.

Data and model availability statement

The data analyzed in this study were obtained from the National Association of Breeders and Researchers (ANCP). The phenotypic and genotypic information was provided to the authors for academic research purposes only. The following restrictions apply: the dataset is not publicly available, and its use requires formal authorization. Requests to access these datasets should be directed to Dr. João Carlos G. Giffoni Filho, President of ANCP (email: presidencia@ancp.org.br).

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

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

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Declaration of interest

The authors declare that they have no conflicts of interest.

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