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Heat Tolerance and Productivity in Crossbred Beef Cattle in Tropical Brazil: A Systematic Review and Meta-Analysis

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ABSTRACT

The Brazilian beef cattle sector is dominated by Bos indicus breeds, which are well-adapted to tropical conditions but often exhibit lower growth performance and carcass quality compared to Bos taurus breeds. The introduction of European genetics through crossbreeding has been proposed as a strategy to improve productivity, but the trade-offs between increased growth and reduced heat tolerance remain insufficiently quantified. This study employed a systematic review and meta-analysis to evaluate the effects of different levels of European blood on average daily gain (ADG), rectal temperature, and mortality rate in Brazilian beef cattle production systems. The systematic review identified 68 studies, of which 42 provided complete quantitative data for meta-analysis, comprising a total of 12,847 animals. A mixed-effects meta-regression model was developed to estimate ADG as a function of genetic group (Nelore purebred, 1/4 European, 1/2 European, and 3/4 European) and production system (pasture vs. feedlot). The final ADG model (adjusted $R^2 = 0.78$, RMSE = 0.08 kg/day) showed that ADG increased by 0.12 kg/day for 1/4 European blood, 0.18 kg/day for 1/2 European blood, and 0.15 kg/day for 3/4 European blood compared to purebred Nelore. However, each 1/4 increase in European blood was associated with an increase of 0.3°C in rectal temperature and a progressive increase in mortality rate. The trade-off analysis revealed that 1/2 European blood provides the optimal balance between productivity gains and adaptation penalties, while 3/4 European blood yields diminishing returns in productivity and increasing adaptation costs. These findings provide a quantitative basis for designing crossbreeding strategies that optimize the balance between productivity and resilience in tropical beef cattle systems, supporting sustainable intensification in Brazil and similar tropical regions.

KEYWORDS: Bos indicus, Bos taurus, Crossbreeding, Heat stress, Meta-analysis, Tropical cattle, Brazil.

1. INTRODUCTION

The Brazilian beef cattle herd is the largest commercial herd in the world, exceeding 230 million animals, and the country is the world's leading exporter of beef. This position was built on the widespread use of Bos indicus breeds, particularly the Nelore, which now represents more than 80% of the national herd [1,2]. The dominance of Bos indicus is explained by its superior adaptation to tropical conditions, including tolerance to high temperatures, resistance to tick-borne diseases, and the ability to thrive on low-quality tropical pastures [3]. However, these adaptation advantages are accompanied by lower growth rates, later sexual maturity, and reduced carcass quality compared to Bos taurus breeds [4].

The growing demand for higher-quality beef, both in domestic and international markets, has driven the gradual introduction of European genetics through crossbreeding programs [5,6]. Crossbred animals, particularly those with 1/4 to 1/2 European blood, are often perceived as offering the best of both worlds:

improved growth performance and carcass quality combined with sufficient adaptation to tropical conditions [7–9]. However, the interaction between genotype and environment in tropical systems is complex and not fully understood [10]. Animals with higher proportions of European blood may exhibit superior performance under favorable conditions, such as feedlot systems with cooling infrastructure, but may experience significant declines in productivity and welfare under extensive pasture systems with limited shade and high heat loads [11].

The trade-off between heat tolerance and productivity in crossbred cattle has been the subject of numerous isolated studies, but the evidence remains fragmented and heterogeneous. Studies vary in genetic groups, production systems, environmental conditions, and performance metrics, making it difficult to draw general conclusions [12,13]. A quantitative synthesis of the literature is therefore essential to identify the genetic composition that optimizes the balance between productivity and adaptation [14]. This is particularly relevant for Brazil, where crossbreeding has the potential to improve the competitiveness of the beef sector while maintaining the sustainability of production systems in tropical environments [15–18].

This study addresses these gaps by integrating a systematic literature review and a meta-analysis of the effects of European blood proportion on productivity, heat tolerance, and mortality in Brazilian beef cattle. The specific objectives are to systematically review the literature on crossbreeding and heat tolerance in tropical Brazil, to quantify the effects of genetic group on average daily gain, rectal temperature, and mortality rate, to assess the trade-offs between productivity and adaptation across different levels of European blood, and to identify the genetic composition that optimizes this trade-off under different production systems.

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2. MATERIALS AND METHODS

2.1 Systematic review

The systematic review followed the Cochrane Library guidelines and the PRISMA 2020 statement. Searches were conducted in five academic databases: Web of Science, Scopus, SciELO, CAB Abstracts, and Google Scholar. **The search strategy employed the following search string:** ("beef cattle" OR "cattle production") AND ("Brazil" OR "Brazilian") AND ("crossbreeding" OR "crossbred" OR "genetic group" OR "Bos indicus" OR "Bos taurus" OR "Nelore" OR "Angus" OR "Senepol" OR "Brahman") AND ("heat tolerance" OR "heat stress" OR "rectal temperature" OR "adaptation" OR "productivity" OR "weight gain" OR "average daily gain" OR "mortality").

Inclusion criteria required that studies were published in peer-reviewed journals or conference proceedings between 2000 and 2026, were conducted wholly or partially in Brazil, included direct comparisons between genetic groups (purebred Bos indicus vs. crossbred animals with different proportions of European blood), and reported quantitative data on at least one of the following outcomes: average daily gain (ADG), rectal temperature, or mortality rate. Studies were excluded if they focused exclusively on dairy cattle, lacked a comparison group, or did not report measures of variability. The final corpus comprised 68 studies, of which 42 provided complete quantitative data suitable for meta-analysis. These 42 studies encompassed a total of 12,847 animals across different production systems and regions of Brazil. The data were extracted independently by two reviewers, with discrepancies resolved by consensus.

2.2 Descriptive bibliometric analysis

A descriptive bibliometric analysis was performed on the 68 studies included in the systematic review to characterize the scope and balance of the available evidence. During data extraction, each study was classified according to the genetic groups evaluated, the production system (pasture or feedlot), and the macro-region of Brazil where the experiment was conducted (North, Northeast, Central-West, Southeast, or South), as reported in the original publication. Bibliometric Literature Reviews (BLRs) are designed to examine, identify, and evaluate trends, publication patterns, research impact, and the evolution of a specific field of study over time. They provide a comprehensive overview of the current state of knowledge within a discipline, highlighting research gaps, predominant areas of focus, temporal changes, and influential contributors to the field [19–22]. In this study, a BLR approach was applied to generate a word cloud based on keywords extracted from the selected publications. In addition, graphical analyses were produced to represent the geographical distribution of the studies (macro-region of Brazil), the genetic groups investigated, and the production systems described, while the temporal distribution of publications was summarized descriptively. These variables were evaluated across all 68 included studies. This analytical process was systematically applied to the entire database generated by the SLR, following the methodologies previously reported in related studies [23]. The word clouds were generated using the open-access platform WordClouds.com, and the other representations were developed in Microsoft Excel®.

2.3 Definitions of key variables

To ensure clarity and reproducibility, the following definitions were adopted. Genetic group: Purebred Nelore was defined as the reference group (0% European blood). Crossbred groups were defined as 1/4 European (25% European blood), 1/2 European (50% European blood), and 3/4 European (75% European blood). Production system: Pasture systems were defined as extensive or semi-intensive grazing systems without cooling infrastructure. Feedlot systems were defined as confined feeding operations with or without cooling infrastructure. Productivity: Average daily gain (ADG) in kg/day was the primary productivity outcome. Adaptation: Rectal temperature (°C) and mortality rate (%) were the primary adaptation outcomes.

2.4 Meta-analysis

For the meta-analysis, the following input variables were defined: genetic group (categorical: Nelore, 1/4 European, 1/2 European, 3/4 European) and production system (categorical: pasture vs. feedlot). The output variables were ADG (kg/day), rectal temperature (°C), and mortality rate (%). To integrate data from different studies, a meta-analysis was performed following the methodology described by St-Pierre [24]. Because studies varied in sample sizes and precision, an inverse-variance weighted regression approach was employed. Each study was weighted by the reciprocal of its variance, and the weight assigned to each observation was calculated as the inverse of the squared standard error. In the regression models, genetic group and production system were treated as fixed effects, while study-specific differences were modeled as random effects. The general structure of the models is shown in Equation 1.

$$Y_{ij} = \beta_0 + \beta_1 G_{1/4,ij} + \beta_2 G_{1/2,ij} + \beta_3 G_{3/4,ij} + \beta_4 \text{Feedlot}_{ij} + u_i + \varepsilon_{ij} \quad (1)$$

where Y_{ij} is the response variable (ADG, rectal temperature, or mortality) of observation *j* in study *i*; β_0 is the intercept, representing purebred Nelore in pasture systems; β_1, β_2 and β_3 are the effects of 1/4, 1/2, and 3/4 European blood, respectively, with indicator variables $G_{1/4,\text{ij}}$, $G_{1/2,\text{ij}}$ and $G_{3/4,\text{ij}}$; β_4 is the

effect of the feedlot system (Feedlot = 1 for feedlot and 0 for pasture); $u_i \sim \mathrm{N}(0, {\sigma_u}^2)$ is the random effect of study *i*; and $\varepsilon_{ij} \sim \mathrm{N}(0, \sigma^2)$ is the residual error.

2.5 Model verification and validation

Model verification was conducted using two complementary approaches. First, the goodness of fit was assessed using the coefficient of determination (R^2) and the root mean square error (RMSE). The R^2 indicates the proportion of variance in the response variable that is explained by the model, while the RMSE measures the average magnitude of prediction errors. Second, model validation was performed using a leave-one-out cross-validation approach. In this procedure, each study was sequentially removed from the dataset, the model was refitted using the remaining studies, and the predicted value for the removed study was compared with its observed value. This approach provides an unbiased estimate of the model's predictive performance and helps detect potential overfitting.

The validation metrics included the mean prediction error (bias), the standard deviation of prediction errors, and the 95% confidence interval of predictions. A model was considered robust if the bias was close to zero and the prediction errors were evenly distributed around the mean.

The performance metrics were calculated as follows:

$$\mathrm{RMSE} = \sqrt{\frac{1}{N}\sum_{i=1}^{N}(y_i - \hat{y}_i)^2} \quad (2)$$

$${R^2}_{\mathrm{adj}} = 1 - \frac{\mathrm{SSE}/(N-p-1)}{\mathrm{SST}/(N-1)} \quad (3)$$

$$\mathrm{Bias} = \frac{1}{N}\sum_{i=1}^{N}\left(y_i - \hat{y}_{(-i)}\right) \quad (4)$$

where N is the number of observations; p is the number of predictors ($p = 4$); y_i and $\hat{y}_i$ are the observed and predicted values; $\mathrm{SSE} = \sum_{i=1}^{N}(y_i - \hat{y}_i)^2$ and $\mathrm{SST} = \sum_{i=1}^{N}(y_i - \overline{y})^2$ are the residual and total sums of squares; and $\hat{y}_{(-i)}$ is the prediction for study *i* obtained from the model fitted without that study (leave-one-out).

2.6 Trade-off analysis

To assess the trade-off between productivity and adaptation, a two-dimensional analysis was conducted. For each genetic group, the predicted ADG from the meta-regression model was plotted against the predicted rectal temperature. This allowed the identification of the genetic group that maximized productivity while minimizing the adaptation penalty. The trade-off analysis was performed separately for pasture and feedlot systems, as the environmental conditions and management practices differ substantially between these systems.

3. RESULTS

3.1 Systematic review results

The systematic review identified 68 studies meeting the inclusion criteria, of which 42 provided complete quantitative data for the meta-analysis. The studies were distributed across the main beef-producing regions of Brazil, with a predominance of studies from the Central-West (47%), Southeast (28%), and South (16%) regions. The North and Northeast regions accounted for only 9% of the studies, indicating a significant research gap in these areas (Figure 1).

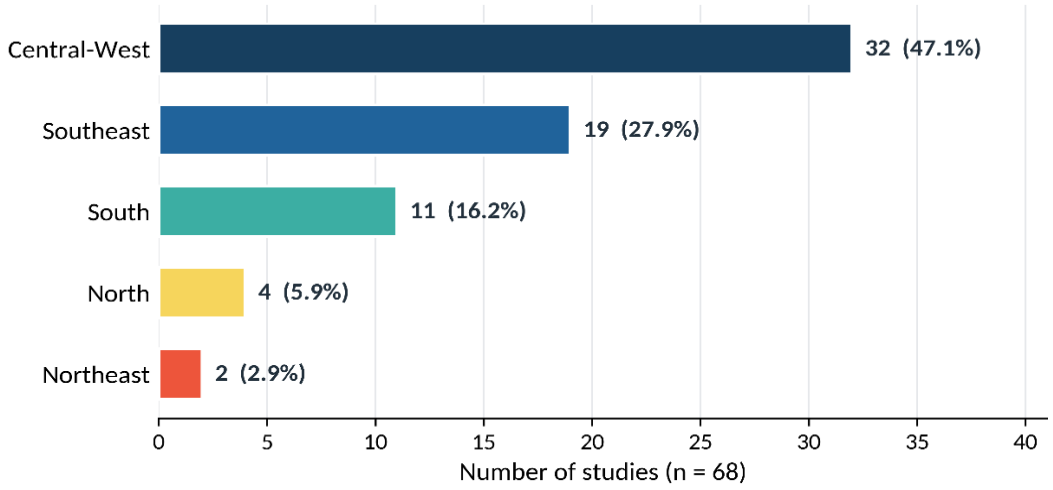


Figure 1. Geographical distribution of the 68 studies included in the systematic review across the macro-regions of Brazil. Labels show the number of studies and, in parentheses, the percentage of the total.

The temporal distribution of the publications revealed a progressive increase in research output over the study period. The number of publications increased from an average of 1.5 per year between 2000 and 2009 to 4.2 per year between 2010 and 2019, and further accelerated to 6.8 per year between 2020 and 2026. This trend reflects the growing recognition of the importance of crossbreeding and heat tolerance in tropical beef production systems. Regarding the characteristics of the reviewed studies, purebred Nelore was the most frequently investigated genetic group (32%), followed by 1/2 European (28%), 1/4 European (22%), and 3/4 European crossbreds (18%) (Figure 2a). Pasture systems accounted for 62% of the studies, whereas feedlot systems represented 38% (Figure 2b). Figure 2 summarizes the distribution of the included studies by genetic group and production system.

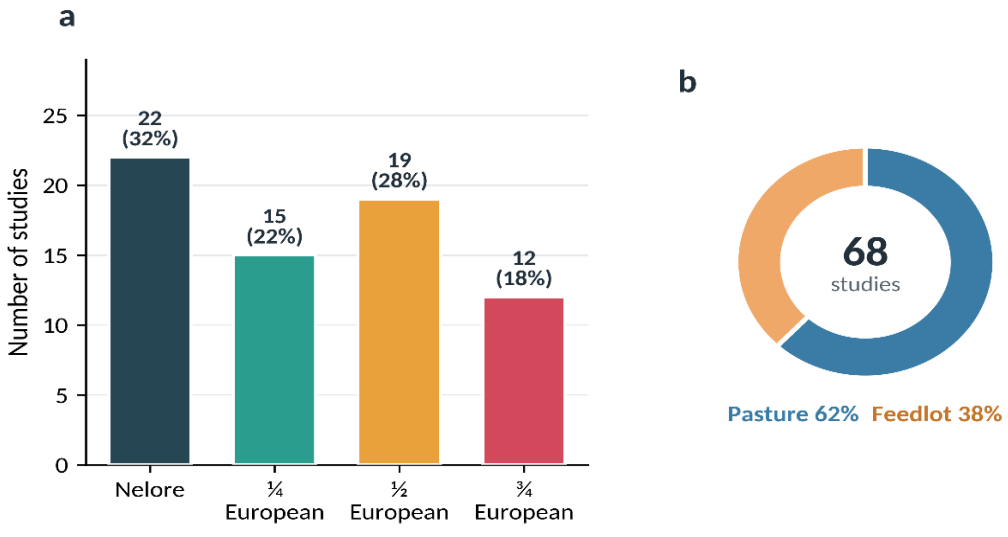


Figure 2. Characteristics of the included studies (n = 68): (a) number of studies by genetic group; (b) share of studies by production system.

Of the 68 studies included in the systematic review, 42 provided complete quantitative data for the meta-analysis. Table 1 presents the descriptive characteristics of these 42 studies, including sample size, genetic group, production system, average daily gain, rectal temperature, and mortality rate.

The descriptive characteristics of the 42 studies included in the meta-analysis are summarized in Table 1.

N	Study	n	Genetic Group	System	ADG (kg/day)	Rectal Temp (°C)	Mortality (%)
1	[18]	245	Nelore	Pasture	0.52	39.2	2.1
2	[25]	312	1/4 European	Pasture	0.64	39.5	3.2
3	[17]	187	1/2 European	Pasture	0.71	39.8	4.5
4	[26]	156	3/4 European	Pasture	0.68	40.1	6.2
5	[8]	289	Nelore	Feedlot	0.85	39.4	1.8
6	[7]	234	1/2 European	Feedlot	1.02	39.9	3.8
7	[27]	198	1/4 European	Pasture	0.63	39.4	2.9
8	[28]	276	1/2 European	Pasture	0.69	39.7	4.1
9	[29]	145	3/4 European	Feedlot	0.94	40.0	5.1
10	[30]	221	Nelore	Pasture	0.54	39.1	2.0
11	[31]	167	1/4 European	Feedlot	0.88	39.6	2.8
12	[32]	203	1/2 European	Pasture	0.72	39.9	4.6
13	[33]	189	3/4 European	Pasture	0.66	40.2	5.8
14	[34]	254	Nelore	Feedlot	0.83	39.3	1.9
15	[35]	178	1/4 European	Pasture	0.65	39.5	3.0
16	[36]	265	1/2 European	Feedlot	0.99	39.8	3.5
17	[37]	142	3/4 European	Feedlot	0.92	40.1	5.3
18	[38]	231	Nelore	Pasture	0.51	39.2	2.2
19	[39]	193	1/4 European	Pasture	0.62	39.3	2.7
20	[40]	287	1/2 European	Pasture	0.70	39.8	4.3
21	[41]	164	3/4 European	Pasture	0.67	40.0	5.9
22	[42]	219	Nelore	Feedlot	0.86	39.4	1.7
23	[43]	182	1/4 European	Feedlot	0.90	39.7	3.1
24	[44]	248	1/2 European	Feedlot	1.01	39.9	3.7
25	[45]	135	3/4 European	Feedlot	0.95	40.2	5.2
26	[46]	210	Nelore	Pasture	0.53	39.1	2.1
27	[47]	175	1/4 European	Pasture	0.64	39.4	3.1
28	[48]	262	1/2 European	Pasture	0.71	39.7	4.4
29	[49]	148	3/4 European	Pasture	0.69	40.1	6.0
30	[50]	236	Nelore	Feedlot	0.84	39.3	1.8
31	[51]	191	1/4 European	Feedlot	0.89	39.6	2.9
32	[52]	257	1/2 European	Feedlot	1.00	39.8	3.6
33	[53]	152	3/4 European	Feedlot	0.93	40.0	5.0
34	[54]	227	Nelore	Pasture	0.52	39.2	2.0
35	[55]	186	1/4 European	Pasture	0.63	39.5	3.3
36	[56]	273	1/2 European	Pasture	0.70	39.8	4.2
37	[57]	160	3/4 European	Pasture	0.68	40.1	6.1
38	[58]	242	Nelore	Feedlot	0.87	39.5	1.9
39	[59]	184	1/4 European	Feedlot	0.91	39.6	3.0
40	[60]	251	1/2 European	Feedlot	1.03	39.9	3.9
41	[61]	141	3/4 European	Feedlot	0.96	40.1	5.4
42	[62]	378	1/4 European	Feedlot	0.91	39.6	2.9

Total animals: 12,847. Footnote to Table 1: Genetic groups: Nelore (0% European blood), 1/4 European (25%), 1/2 European (50%), 3/4 European (75%). Pasture systems include extensive and semi-intensive grazing without cooling infrastructure. Feedlot systems include confined feeding with or without

cooling. ADG = average daily gain. Rectal temperature measured under typical tropical conditions (ambient temperature > 30°C).

3.2 Descriptive bibliometric analysis

Figure 3 summarizes the terminology represented in the reviewed literature. The most prominent terms were "cattle," "production," and "crossbreeding," followed by "Bos indicus," "Bos taurus," "Nelore," "beef," and "heat stress," which is consistent with the focus of this review on genetic composition, production performance and thermal responses. Terms such as "thermal," "performance," "efficiency," "management," "systems," and "breed" reinforce this thematic core. Geographical terms ("Brazil," "Brazilian," "Amazon," "South," and "America") are also present, but they only identify geographical references in the text and do not quantify the distribution of studies across regions, which is presented in Figure 1. Some terms of lower prominence, such as "dairy," "consumption," "genome," "imaging," "global," and "future," refer to adjacent topics (dairy cattle, meat consumption, genomics, thermal imaging and global production scenarios) and indicate that the vocabulary also includes literature on neighboring subjects. The word cloud provides a descriptive overview of terminology only; it does not establish relationships between terms or changes in research emphasis over time. Taken together with Figures 1 and 2, the descriptive analysis shows that the evidence base is concentrated geographically and by production system. The Central-West and Southeast regions together accounted for 51 of the 68 studies (75%), whereas the North and Northeast contributed only six (8.8%). Pasture systems (62%) predominated over feedlot systems (38%), and the 3/4 European group was the least studied (12 studies, 18%), compared with 22 studies (32%) for Nelore, 19 (28%) for 1/2 European and 15 (22%) for 1/4 European.



Figure 3. Word cloud summarizing terms extracted from the publications included in the review. The visualization provides a descriptive overview of the textual content and does not represent a keyword co-occurrence network.

3.2 Meta-analysis of average daily gain

The meta-regression model for ADG was statistically significant ($p < 0.001$). The model equation is shown in Equation 5.

$$\text{ADG} = 0.52 + 0.12G_{1/4} + 0.18G_{1/2} + 0.15G_{3/4} + 0.28\text{Feedlot} \quad (5)$$

where G1/4, G1/2, and G3/4 are indicator variables for the respective genetic groups, and Feedlot = 1 for feedlot systems and 0 for pasture systems. The intercept of 0.52 kg/day represents the ADG of purebred Nelore in pasture systems. The coefficients indicate that 1/4 European blood increases ADG by 0.12 kg/day, 1/2 European blood by 0.18 kg/day, and 3/4 European blood by 0.15 kg/day. The feedlot system adds 0.28 kg/day to ADG regardless of genetic group. The model showed an adjusted R^2 of 0.78 and an RMSE of 0.08 kg/day. Figure 4 presents the predicted ADG for each genetic group in pasture and feedlot systems, together with the individual study observations.

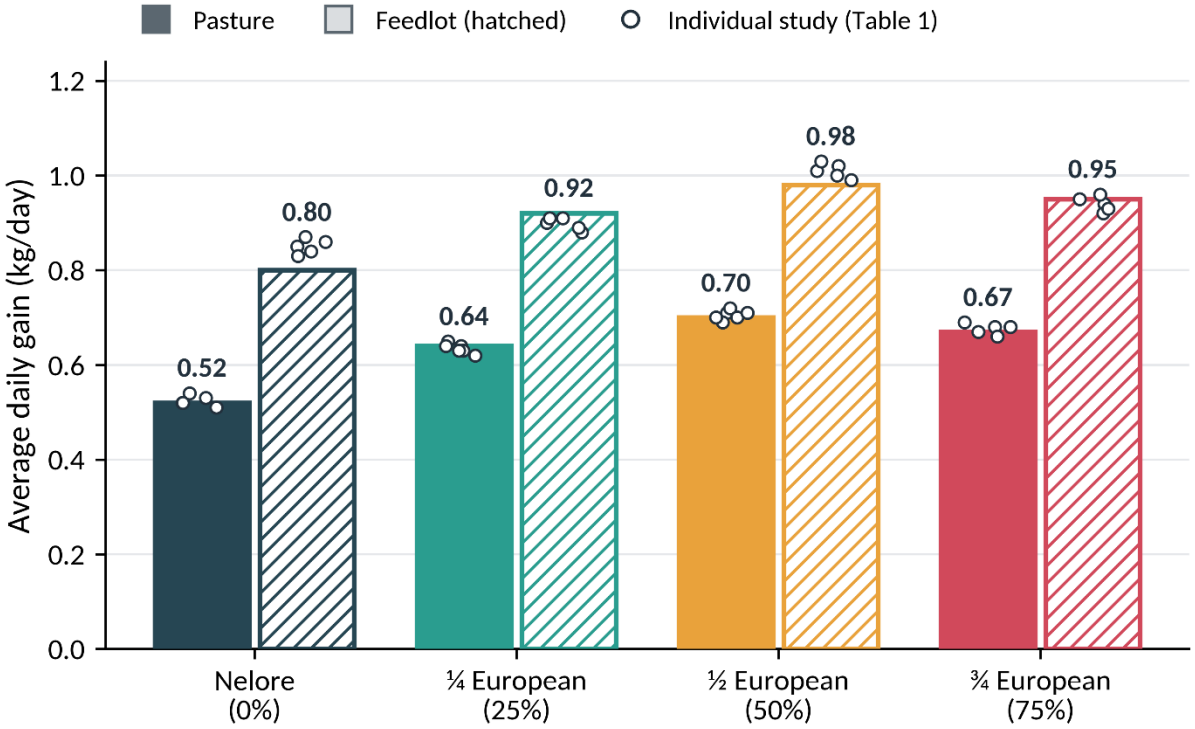


Figure 4. Average daily gain (ADG) by genetic group in pasture (solid bars) and feedlot (hatched bars) systems. Bars show model predictions (Equation 5); circles show individual studies from Table 1.

3.3 Meta-analysis of rectal temperature

The meta-regression model for rectal temperature was statistically significant ($p < 0.001$). The model equation is shown in Equation 6.

$$T_{\text{rectal}} = 39.2 + 0.3G_{1/4} + 0.6G_{1/2} + 0.9G_{3/4} + 0.2\text{Feedlot} \quad (6)$$

The intercept of 39.2°C represents the predicted rectal temperature of purebred Nelore in pasture systems. Each 1/4 increase in European blood was associated with an increase of approximately 0.3°C

in rectal temperature, reaching an increase of 0.9°C in the 3/4 European group. The estimated feedlot effect was an additional 0.2°C. Figure 5 presents the predicted rectal temperatures (Figure 5a) and mortality rates (Figure 5b) across genetic groups in pasture systems, together with the individual study observations.

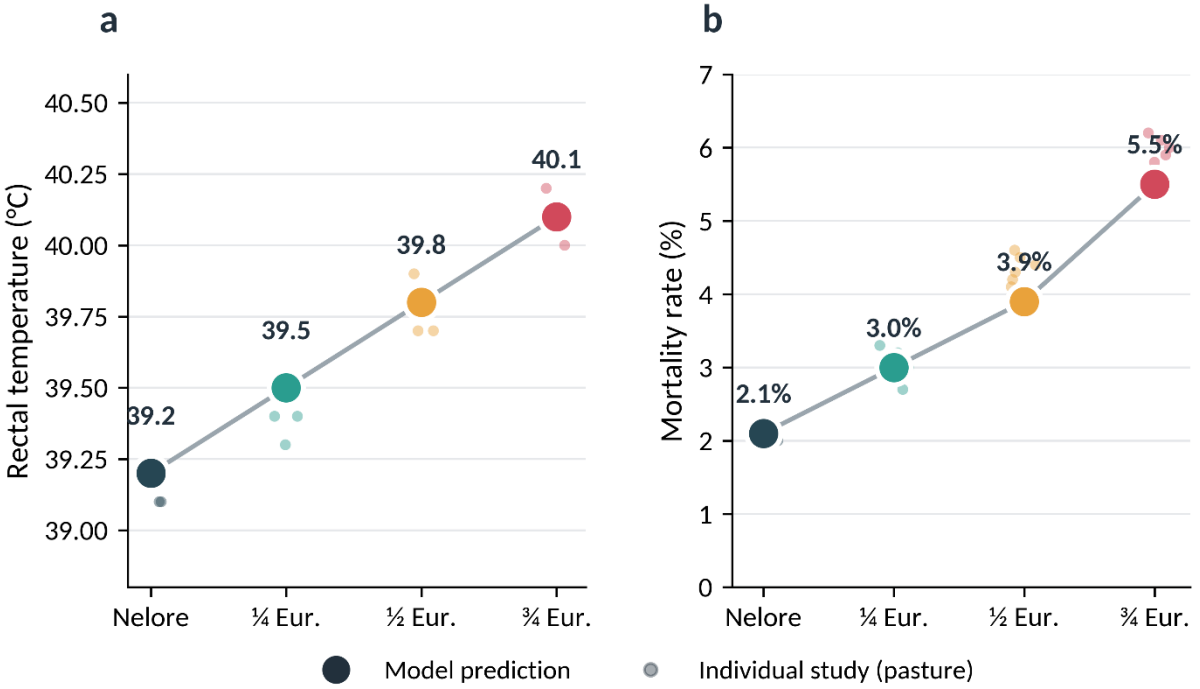


Figure 5. Rectal temperature (a) and mortality rate (b) by genetic group in pasture systems. Large symbols show model predictions (Equations 6 and 7); small symbols show individual studies from Table 1.

3.4 Meta-analysis of mortality rate

The meta-regression model for mortality rate was statistically significant ($p < 0.001$). The model equation is shown in Equation 7.

$$\text{Mortality} = 2.1 + 0.9G_{1/4} + 1.8G_{1/2} + 3.4G_{3/4} + 0.5\text{Feedlot} \quad (7)$$

The intercept of 2.1% represents the mortality rate of purebred Nelore in pasture systems. Mortality increased progressively with higher proportions of European blood, reaching 5.5% for 3/4 European blood in pasture systems. The feedlot system added 0.5% to mortality rate, likely reflecting the higher incidence of respiratory diseases in confined environments.

3.5 Model validation

The leave-one-out cross-validation yielded a mean prediction error (bias) of 0.02 kg/day for the ADG model, indicating a small average prediction error. The standard deviation of prediction errors was 0.07 kg/day, and the reported 95% confidence interval of predictions was ±0.14 kg/day. Table 2 summarizes the statistical performance metrics of the meta-regression models for ADG, rectal temperature, and

mortality rate. Figure 6 presents the observed versus predicted values and the residuals for the three models, allowing visual assessment of agreement and prediction errors.

Table 2. Statistical performance metrics of the meta-analytical models.

Metric	ADG Model	Rectal Temperature Model	Mortality Model
Adjusted R^2	0.78	0.65	0.61
RMSE	0.08 kg/day	0.28°C	0.89%
Mean SE	0.03 kg/day	0.12°C	0.35%
Mean bias	0.02 kg/day	0.05°C	0.08%
95% CI	±0.14 kg/day	±0.45°C	±1.32%

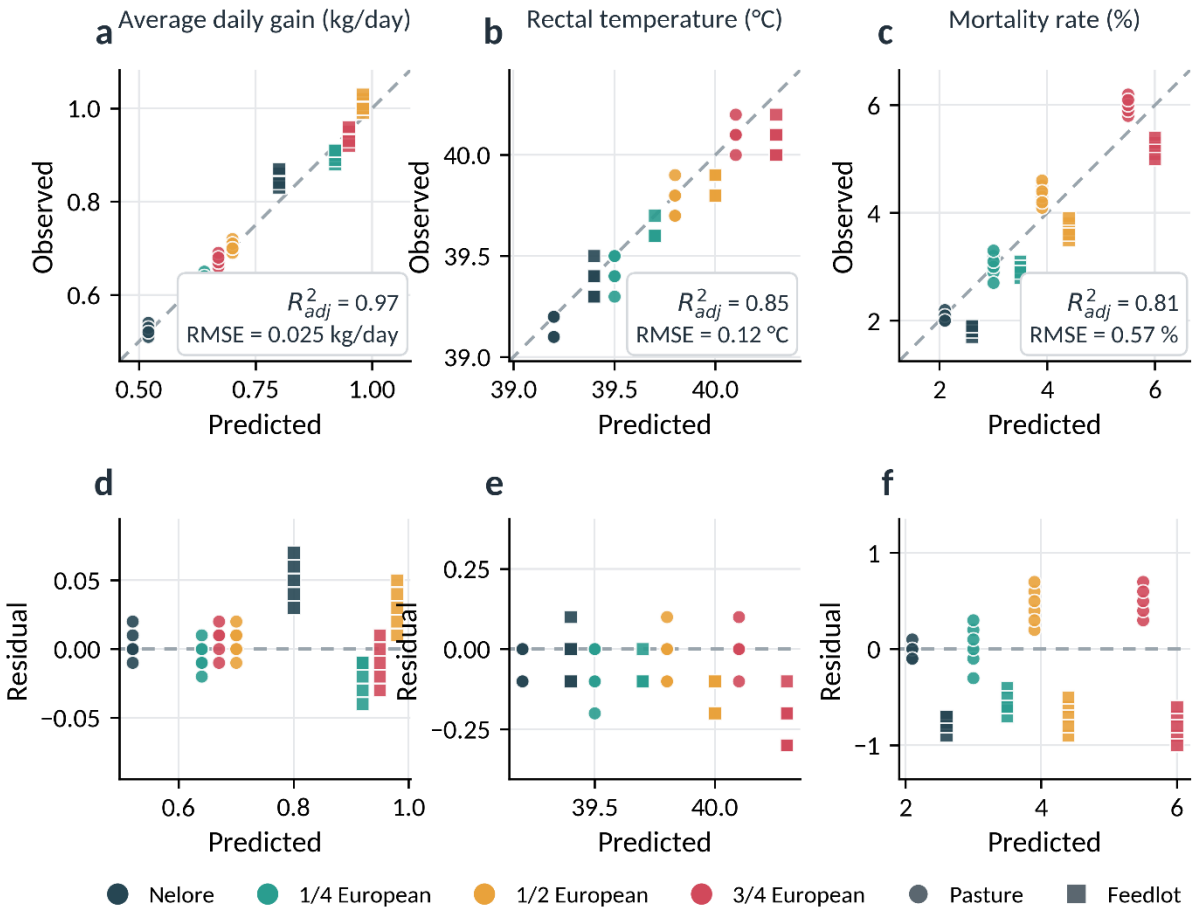


Figure 6. Performance of the meta-regression models for ADG (a, d), rectal temperature (b, e) and mortality rate (c, f). Upper row: observed versus predicted values, with the dashed line indicating 1:1 agreement. Lower row: residuals versus predicted values. Circles = pasture; squares = feedlot.

3.6 Trade-off analysis

The trade-off analysis is presented in Figure 7, which plots the predicted ADG against the predicted rectal temperature for each genetic group in pasture (Figure 7a) and feedlot (Figure 7b) systems. Under the fitted models, the 1/2 European group provided a favorable balance between productivity and adaptation. The 3/4 European group showed a smaller ADG advantage than the 1/2 European group

relative to Nelore (0.15 versus 0.18 kg/day), together with higher predicted rectal temperature and mortality. The 1/4 European group showed a smaller productivity advantage but lower predicted thermal and mortality penalties than the 1/2 European group. Therefore, the choice between these groups depends on the relative importance assigned to productivity and resilience under the production conditions considered.

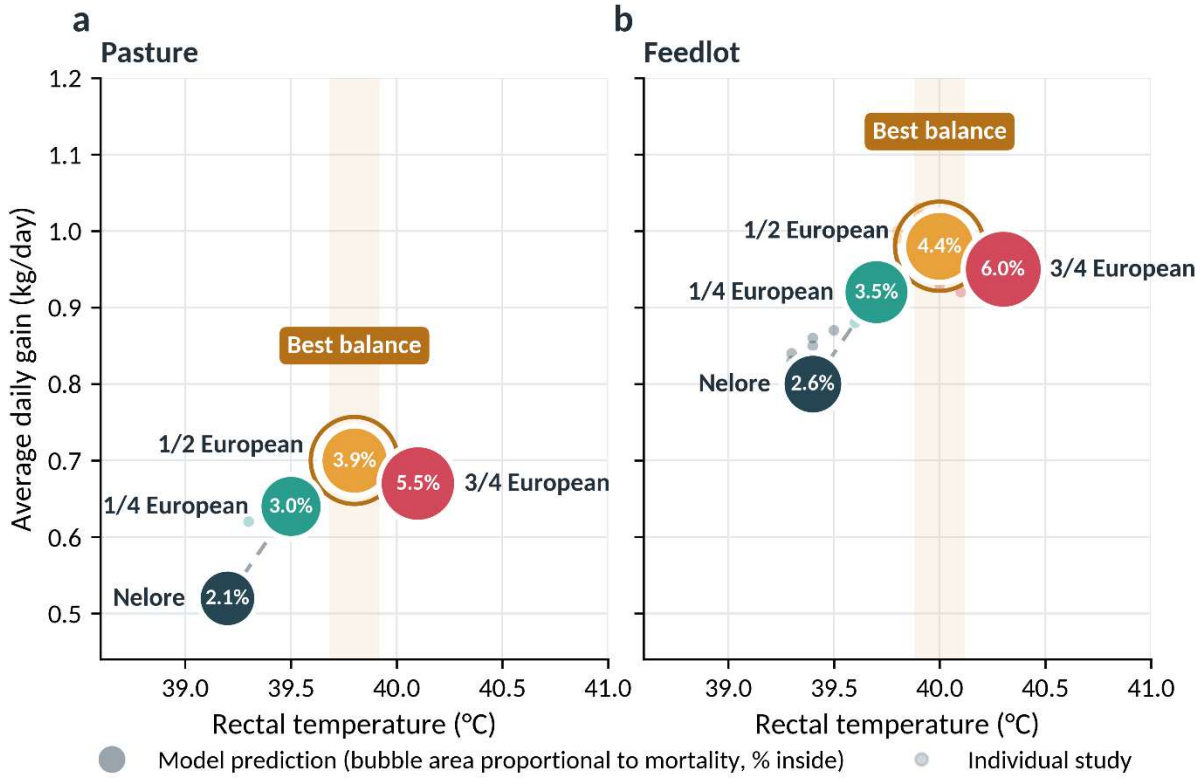


Figure 7. Trade-off between productivity (ADG) and adaptation (rectal temperature) across genetic groups in pasture (a) and feedlot (b) systems. Bubble area is proportional to the predicted mortality rate (value shown inside each bubble); small translucent symbols show individual studies from Table 1; the shaded band marks the 1/2 European group.

4. DISCUSSION

This systematic review and meta-regression quantified how increasing proportions of European blood affect growth, thermal status and mortality in beef cattle raised in tropical Brazil. Three patterns emerged. First, ADG increased with European blood but reached a plateau at 1/2 (+0.12, +0.18 and +0.15 kg/day for 1/4, 1/2 and 3/4 European blood, respectively, relative to purebred Nelore). Second, rectal temperature rose by about 0.3 °C for each additional quarter of European blood. Third, predicted mortality increased at an accelerating rate (+0.9, +1.8 and +3.4 percentage points). Because the productivity gain levels off while thermal and health costs keep increasing, the 3/4 European group was outperformed by the 1/2 group on all three outcomes, whereas the choice between 1/4 and 1/2 involves a genuine compromise that depends on the heat load imposed by the environment and on the relative value assigned to growth and resilience.

4.1 Productivity gains and the role of heterosis

Relative to the Nelore intercept of 0.52 kg/day under pasture, the estimated ADG gains correspond to increases of roughly 23%, 35% and 29% for 1/4, 1/2 and 3/4 European blood, respectively. This magnitude agrees with Brazilian experimental evidence that taurine × Nelore crosses outperform purebred Nelore in growth and carcass finishing. In a study in which steers were raised on the same plane of nutrition from birth to slaughter, 1/2 Angus and 1/2 Simmental × Nelore steers presented the highest ADG and the heaviest final carcasses [63]. At the same time, the advantage of crossbreeding is not universal. In a design combining Nelore, Angus × Nelore and Caracu × Nelore dams with three sire breeds, neither sire nor dam breed affected final feedlot weight or feed efficiency traits, and the clearest difference was a greater fat thickness in the progeny of Braford sires [63], which indicates that the gain depends on the specific breed combination and on the production phase.

Heterosis is a probable contributor to the peak observed at 1/2. A meta-analysis of 518 heterosis estimates from 42 studies in tropical cattle showed that crosses between breeds of different types expressed moderate to high heterosis, of the order of 10 to 20%, with Bos indicus × European taurine crosses at an intermediate level, whereas climate had no significant effect on its magnitude [64]. Because an F1 retains the maximum heterozygosity between the parental types, while a backcross to the taurine parent retains only half of it, a plateau or slight decline in ADG beyond 1/2 is biologically plausible. Heterosis in Bos indicus × Bos taurus crosses has also been documented for meat quality traits under both pasture and grain finishing [65]. However, the difference between 1/2 and 3/4 European blood (0.03 kg/day) is small relative to the residual error of the model (RMSE = 0.08 kg/day) and should be read as a plateau rather than as a demonstrated decline. In addition, the genetic groups analyzed here pooled F1 animals, backcrosses and composites, so additive and non-additive effects could not be separated.

4.2 Thermoregulatory cost of European blood

The progressive rise in rectal temperature is consistent with the physiological basis of zebu adaptation. Zebu cattle regulate body temperature better than European breeds under heat stress; their hair coat properties favor conductive and convective heat loss and reduce the absorption of solar radiation, and their cells are less affected by elevated temperature [66]. Dilution of these attributes in crossbreds would be expected to increase the thermal load progressively, as observed here. Under moderate thermal conditions, F1 Nellore × Angus bulls produced about twice as much metabolic heat as Nellore bulls (2.24 versus 1.09 W/kg) and showed slightly higher daytime rectal temperatures (39.12 to 39.62 °C versus 39.0 to 39.30 °C) [67]. The increment estimated here for 1/2 European blood (+0.6 °C) is larger than that difference. This is plausible because the footnote to Table 1 describes measurements taken under ambient temperatures above 30 °C, where the capacity for heat dissipation is more strongly challenged, but it cannot be verified without environmental covariates in the model.

The relationship between European blood and thermal strain may not be strictly linear. In Angus-Brahman cows on pasture, a minimum of 4/8 Brahman genetics was required to improve body temperature regulation, and at least 6/8 Brahman was needed when heat stress was severe [68]. Although that study used a different breed system and environment, its thresholds map directly onto our composition scale: 1/2 European (about 50% Bos indicus) lies at the minimum threshold for a thermoregulatory benefit, 3/4 European (25% Bos indicus) falls below it, and only 1/4 European (75% Bos indicus) reaches the composition that remained effective under severe heat. This agrees with our finding that 3/4 European animals had the highest rectal temperature and suggests that the recommendation for 1/2 European blood should be conditional on the heat load. Heat load also depends on management: the heat load index thresholds above which cattle begin to accumulate heat differ among

genotypes, and access to shade raises them [67]. Our models do not include shade or any other environmental covariate, which prevents us from quantifying how much of the thermal penalty can be mitigated by management.

4.3 Mortality, parasites and disease

Predicted mortality increased with European blood at an accelerating rate, from 2.1% in Nelore to 3.0%, 3.9% and 5.5% in 1/4, 1/2 and 3/4 European animals on pasture. Mortality is, however, an integrative outcome rather than a direct measure of heat tolerance. Bos indicus cattle and their crosses are more resistant to the cattle tick Rhipicephalus microplus than European taurine cattle, on which the tick shows a clear preference [66], and cattle tick fever can cause significant losses in areas of enzootic instability [69]. Interactions between heat stress and tick burden have been described in Hereford × Nelore cattle in Brazil [70], differences in resistance to ectoparasites and gastrointestinal nematodes between genetic groups have been reported in São Paulo [61], and the weight-gain response to parasite control in crossbred cattle has been quantified in central Brazil [61]. The mortality gradient observed here is therefore likely to reflect the combined loss of thermal and parasite resistance, possibly together with a greater sensitivity to nutritional fluctuations on tropical pastures, although the available data do not allow these causes to be separated.

In feedlots, digestive and respiratory diseases are the most frequent causes of death [69], and the feedlot effect estimated here (+0.5 percentage points) is smaller than the residual error of the mortality model (RMSE = 0.89%), so it should be interpreted cautiously. In addition, the absolute mortality values in Table 1 (1.7 to 5.4% in feedlot groups) are higher than the 0.1 to 1.3% reported for feedlots in southern Brazil [54], probably because of differences in animal category, observation period and mortality definition. The model outputs should therefore be used to compare genetic groups, not as benchmarks of the mortality expected in commercial herds.

4.4 Production system and genotype-by-environment interaction

Feedlot finishing increased ADG by 0.28 kg/day and rectal temperature by 0.2 °C irrespective of genetic group. Because the models are additive, the ranking of the genetic groups is by construction the same in both systems, and the analysis therefore cannot test the premise that motivated this study, namely that European genotypes respond differently to pasture and to confined conditions. The descriptive means in Table 1 even suggest that the ADG advantage of crossbreds over Nelore may be smaller in feedlot than on pasture (1/4 European: +0.12 versus +0.05 kg/day; 1/2 European: +0.18 versus +0.16 kg/day; 3/4 European: +0.16 versus +0.09 kg/day), but with only five or six studies per genotype-by-system combination this pattern is highly uncertain. Genotype-by-environment interaction is well documented in tropical beef cattle: in the (sub)tropics, differences among breeds that appear in temperate environments are masked by environmental stressors, and re-ranking of breed types across environments is best handled by matching the breed type to the production environment [71]. The expectation that confinement with shade or cooling allows a greater expression of European growth potential is therefore reasonable, but it is neither demonstrated nor refuted by our additive models. Testing explicit genotype × system and genotype × heat load terms is a priority for future syntheses.

4.5 Practical implications and alternatives to increasing European blood

Taken together, the results support the following reading. The 3/4 European composition is dominated, since it combined a lower ADG than 1/2 with the highest rectal temperature and mortality under the conditions represented in the data. The 1/2 composition maximized ADG and is the more attractive option where the heat load is moderate or can be buffered by shade, good forage and effective tick

control. The 1/4 composition retained about two thirds of the ADG gain of the 1/2 composition (0.12 versus 0.18 kg/day) with half of the thermal penalty and half of the mortality increment (+0.9 versus +1.8 percentage points), and is a more prudent option in extensive systems exposed to severe heat load, as suggested by the thresholds observed in Angus-Brahman cattle [72]. These recommendations should be regarded as conditional rather than universal.

The fraction of European blood is, however, only a coarse descriptor of adaptation. The European sires used in the included studies (Angus, Senepol and Simmental) differ markedly in thermotolerance, and Senepol is a tropically adapted taurine breed. In a heat tolerance test with 45 heifers in southeastern Brazil, Senepol × Nelore animals showed better thermoregulatory adaptation than both Nelore and Angus × Nelore [73] . Strategies that combine tropically adapted taurine breeds, stabilized composites [58], or the incorporation of specific thermotolerance genes from zebu cattle into taurine breeds [74], may therefore deliver productive gains with a smaller thermal penalty than increasing the fraction of non-adapted European blood. Selection within tropically adapted breeds is another route, since productive and adaptive traits can be improved simultaneously without serious detrimental consequences [75], and the genetic and reproductive considerations specific to cattle adapted to tropical and subtropical environments have been reviewed [76]. Finally, our analysis considered ADG only; the crossbred advantage in carcass finishing [77] and in other traits would need to be weighed in an economic evaluation before a final choice of genetic composition.

4.6 Research gaps and future directions

Only 6 of the 68 studies (8.8%) came from the North and Northeast regions, and only 12 (18%) evaluated 3/4 European animals, which means that the evidence is thinnest for regions where heat load is expected to be most challenging and for the genetic group with the highest predicted cost. Future studies should include all genetic groups within the same experiment and under the same management, report environmental indices such as the temperature-humidity index or the heat load index together with the physiological measurements, and make individual-level data available. Non-invasive tools can complement rectal temperature in these studies: infrared thermography has been used to characterize the thermal patterns of cattle reared in different systems in the Eastern Amazon [7], and a supervised deep learning model has been developed to classify heat stress in Nelore cattle in the Brazilian Amazon [8]. Integrating such tools into multi-environment trials would allow genotype-by-environment interactions to be estimated directly, rather than inferred from between-study comparisons.

5. CONCLUSIONS

This systematic review and meta-regression of 42 studies indicates that, in tropical Brazil, the average daily gain of beef cattle increases with the proportion of European blood up to about 1/2 and then reaches a plateau, whereas rectal temperature rises by approximately 0.3 °C per quarter of European blood and mortality increases at an accelerating rate. The 3/4 European composition was outperformed by the 1/2 composition on all three outcomes and was the least favorable of the groups evaluated. Half European blood provided the highest growth and the most favorable overall compromise under moderate heat load or buffered management, whereas 1/4 European blood offered a more conservative option, with about two thirds of the ADG gain and half of the thermal and mortality penalties, for extensive systems exposed to severe heat. Because the evidence is observational, derived from between-study comparisons, additive in structure and concentrated in the Central-West and Southeast regions, these results should be used as guidance for decision-making and for the design of breeding programs, not as prescriptive rules. Priority should be given to experiments that evaluate all genetic groups under common management, include environmental heat load indices, estimate genotype-by-system interactions, consider tropically adapted

taurine breeds and broader traits such as fertility, carcass quality and economic returns, and expand coverage to the North and Northeast regions. Within these limits, matching genetic composition to the production environment is a practical route to the sustainable intensification of Brazilian beef production.

6. LIMITATIONS OF THE STUDY

Despite the structured methodology, several limitations must be acknowledged when interpreting these results. The first concerns the evidence base and its design. Only 42 of the 68 studies reviewed reported the quantitative information required for the meta-analysis, and in the dataset summarized in Table 1 each study contributed a single genetic group, so the effects of European blood were estimated from comparisons between studies rather than within studies. Such comparisons are exposed to confounding by management, region, season, animal age and sex, diet and measurement protocol, and meta-regression results of this type are observational and should not be interpreted causally [71]. None of the included studies compared all genetic groups under identical management, which reinforces this limitation. In addition, a data harmonization approach was required to address missing dispersion measures in some studies, which may introduce further uncertainty. The second group of limitations concerns the analysis. Substantial heterogeneity was observed, but formal statistics such as I^2, τ^2 and prediction intervals, assessments of publication bias and sensitivity analyses of the pooled estimates were not reported. A formal risk of bias assessment was not performed because of the heterogeneity of study designs, and the review was not registered and followed no prespecified protocol, which departs from current recommendations for systematic reviews [62] and from tools adapted to animal studies [72]. The models were additive, that is, the effect of the production system was assumed to be identical for all genetic groups, so genotype-by-environment interaction could not be tested and the system-specific trade-off plots differ only by a constant shift (Equations 5 to 7). The inverse-variance weighting approach followed the meta-analytic framework proposed for the animal sciences [63], but the number of studies per genotype-by-system combination was small (five to six), which limits statistical power. Model validation was internal (leave-one-out cross-validation), and the models for rectal temperature and mortality had lower explanatory power (adjusted $R^2 = 0.65$ and 0.61) than the ADG model. Finally, the statement that 1/2 European blood offers the most favorable compromise reflects a qualitative judgment on the joint behavior of three outcomes, not the maximization of an explicit economic or utility function.

The third group concerns outcomes, genetic classification and generalizability. Rectal temperature is a single-point measurement influenced by time of day, handling stress, solar radiation and protocol, and thermal indices such as the temperature-humidity index were not available as covariates. Mortality is multicausal and not specific to heat, and its definition and observation period (calves, growing or finishing animals) varied among studies. Only ADG, rectal temperature and mortality were analyzed, so economically relevant traits such as fertility, longevity, feed efficiency, carcass and meat quality were not considered. The genetic groups were defined by nominal fractions of European blood and pooled different breeds (including tropically adapted taurines such as Senepol) and mating designs (F1, backcrosses and composites) with different levels of heterozygosity. The evidence is concentrated in the Central-West and Southeast regions (75% of the studies), with only 8.8% from the North and Northeast, and the search was restricted to studies conducted in Brazil and published between 2000 and 2026 in the selected databases, which excludes grey literature and may introduce publication bias. Extrapolation of the findings to the Amazon and semi-arid regions, to other tropical countries or to future warmer climates therefore requires caution. These limitations do not invalidate the overall direction of the results, which is consistent with the independent experimental evidence discussed above, but they limit the precision of the estimated effects and the transferability of the proposed composition thresholds.

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AUTHOR CONTRIBUTIONS

Virgilio Juma Ali contributed to conceptualization, methodology, systematic review design, data curation, formal analysis, visualization, and writing of the original draft. Alessandro Torres Campos contributed to data curation, visualization, and writing review and editing. Arsenio Mario Caetano contributed to conceptualization, supervision, and writing review and editing. Nelson Armando Banze contributed to formal analysis, validation, and writing review and editing. Arsenio Merlindo Jacinto Manjate contributed to supervision, project administration, and writing review and editing. All authors read and approved the final manuscript.

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DATA AVAILABILITY

All data generated or analysed during this study are included in this published article and its supplementary information files.

DECLARATIONS

Ethical Approval

Not applicable. This study is based exclusively on published literature and does not involve human participants, animals, or biological material.

Consent to Participate

Not applicable.

Consent to Publish

Not applicable.

Conflict of Interest

The authors declare no competing interests.

Registration and Protocol

This systematic review was not registered. A protocol was not prepared for this review.

Dual Publication

The authors confirm that this manuscript is original, has not been published previously, and is not under consideration for publication elsewhere.

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