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Multi-trait Models with Maternal Effects for Genetic Evaluation of Weaning and Ultrasound Carcass Traits in Nelore Calves

Leonardo de Oliveira Seno

leonardoseno@ufgd.edu.br

Great Dourados Federal University: Universidade Federal da Grande Dourados https://orcid.org/0000-0001-9450-7870

Rusbel Raul Aspilcueta-Borquis

UTFPR: Universidade Tecnologica Federal do Parana

Maria Fernanda Castro Burbarelli

UFGD: Universidade Federal da Grande Dourados

Haylleen Aparecida Oliveira Menezes Sá

UFGD: Universidade Federal da Grande Dourados

Lucas Bernardes Fonseca

UFGD: Universidade Federal da Grande Dourados

Larissa Dias Santos

UFGD: Universidade Federal da Grande Dourados

Brenda Beatriz Dutra Boveda

UFGD: Universidade Federal da Grande Dourados

André Luiz Julien Ferraz

UEMS: Universidade Estadual do Mato Grosso do Sul

Gabriel Lima Borges

ULTRAGEN

Daniel Jordan de Abreu Santos

UNESP: Universidade Estadual Paulista Julio de Mesquita Filho

Humberto Tonhati

UNESP: Universidade Estadual Paulista Julio de Mesquita Filho

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Additional Declarations:
Tables 1 to 6 are available in the Supplementary Files section.

Multi-trait Models with Maternal Effects for Genetic Evaluation of Weaning and Ultrasound Carcass Traits in Nelore Calves

Leonardo de Oliveira Seno[1a], Rusbel Raul Aspilcueta-Borquis[2], Maria Fernanda de Castro Burbarelli[1], Haylleen Aparecida Oliveira Menezes de Sá[1], Lucas Bernardes da Fonsêca[1], Larissa Dias dos Santos[1], Brenda Beatriz Dutra Boveda[1], André Luiz Julien Ferraz[3], Gabriel de Lima Borges[4], Daniel Jordan de Abreu Santos[5], Humberto Tonhati[5]

[1]Grande Dourados Federal University, Agricultural Sciences Faculty – Dourados-MS, Brazil

[2]Federal University of Technology, Dois Vizinhos Campus – Dois Vizinhos-PR, Brazil

[3]Mato Grosso do Sul State University, Aquidauana Campus – Aquidauana-MS, Brazil

[4]ULTRAGEN Carcass Ultrasound, Campo Grande-MS, Brazil

[5]São Paulo State University - Animal Science Department – Jaboticabal-SP, Brazil

[a]*Present address: Agricultural Sciences Faculty, UFGD, P. O. Box 533, Dourados-MS, Brazil*

Corresponding author: Leonardo de Oliveira Seno. E-mail: leonardoseno@ufgd.edu.br

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Running head: Seno, Aspilcueta-Borquis, Burbarelli, Sá, Fonsêca, Santos, Boveda, Ferraz, Borges and Tonhati

Abstract: This study aimed to identify the most appropriate statistical model for the genetic evaluation of Nelore cattle and to estimate genetic parameters for adjusted weaning weight (W210) and ultrasound-measured carcass traits—longissimus muscle area (LMA), marbling (MARB), and backfat thickness (BF). The dataset comprised 2,001 calves born between 2015 and 2025 in a commercial herd in Mato Grosso do Sul, Brazil. Significant ($P < 0.05$) non-genetic sources of variation identified by GLM included sex, recipient breed, birth

month and year, calf age (linear and quadratic), and calving. Variance components were estimated using REML under three models: M1 (direct additive), M2 (M1 + maternal additive), and M3 (M2 + maternal permanent environmental effects). Likelihood ratio tests favored M2 and M3, with maternal effects reducing residual variance. Direct heritability estimates were moderate for LMA (0.31–0.34), MARB (0.24–0.25), and W210 (0.17–0.22), and low for BF (0.08–0.11). Maternal heritability ranged from 0.08 to 0.25. Positive direct additive genetic correlations (0.22–0.70) indicated that selection for increased LMA and BF is expected to generate correlated responses in MARB and W210. Overall, maternal additive and maternal permanent environmental effects should be included in genetic evaluations of weaning and carcass traits in Nelore cattle, and ultrasound proves useful for early selection given the favorable genetic correlations.

Key words: beef cattle, direct and maternal genetic effects, genetic correlations, genetic evaluation, heritability, production system

Introduction

Beef cattle production in tropical regions is characterized by high environmental heterogeneity, which poses substantial challenges for achieving consistent growth performance and carcass quality. In these systems, *Bos indicus* breeds predominate due to their adaptability to heat stress, seasonal forage availability, and extensive management conditions. Among them, Nellore cattle constitute the primary genetic base of beef production in tropical environments, playing a central role in both domestic supply and international beef markets (Luchiari, 2006; Oldenbroek & Van der Waaij, 2014).

Improving carcass quality under tropical conditions requires selection strategies that account for the biological and environmental complexity inherent to early-life traits. Characteristics such as longissimus muscle area, subcutaneous fat thickness, and

intramuscular fat deposition are directly associated with carcass value and meat quality attributes, including tenderness, juiciness, and flavor (Felício, 1999; Londoño-Gil et al., 2022). However, these traits often exhibit substantial phenotypic variability, particularly when measured at or near weaning, reflecting the combined influence of genetic potential, maternal ability, and transient environmental effects.

Real-time ultrasound has become an established, noninvasive, and cost-effective tool for *in vivo* assessment of carcass traits in beef cattle. Numerous studies have demonstrated moderate to strong genetic associations between ultrasound measurements obtained in young animals and carcass traits evaluated at slaughter, supporting their use in genetic evaluation and early selection programs (Crews Jr and Kemp 2001; Yokoo et al. 2008; Duff et al. 2021). In production systems where post-weaning performance records are limited or unavailable, ultrasound measurements collected at weaning represent a particularly valuable source of information for guiding selection decisions (Suguisawa et al., 2013).

Reliable inference on genetic parameters for growth and carcass traits requires proper accounting for nongenetic sources of variation. Factors such as sex, age at measurement, year and season of birth, parity order of the dam, and management conditions can substantially influence phenotypic expression, particularly for traits measured at weaning (Souza et al., 2000; Silva et al., 2015). Failure to account for these effects may bias estimates of genetic parameters and reduce the accuracy of breeding values.

Maternal effects represent an important source of phenotypic variation for early-life traits, especially those expressed before or at weaning. Maternal additive genetic effects and maternal permanent environmental effects, associated with milk production, maternal behavior, and long-term management conditions experienced by the dam, may substantially influence calf growth and early carcass development (Koch, 1972; Garrick, 1990; González-Recio et al., 2012). Therefore, genetic models that partition phenotypic variance into direct

additive genetic, maternal additive genetic, and maternal permanent environmental components are essential for reliable genetic evaluation of traits under maternal influence (Bijma, 2006; Meyer, 1997; Mrode, 2014; Romé et al., 2023).

The relevance of maternal effects tends to decline with age as postweaning genetic and environmental factors become more influential; however, their proper modeling is crucial for traits measured at or near weaning (Räsänen & Kruuk, 2007). In this context, multi-trait analyses may further improve the precision of genetic parameter estimates and mitigate selection bias when multiple correlated traits are evaluated simultaneously (Pollak et al., 1984; Thompson & Meyer, 1986).

Maternal genetic and environmental effects are well recognized as important sources of variation in early-life growth traits in beef cattle. However, their relative contribution to ultrasound-derived carcass traits measured at weaning under tropical commercial conditions remains less documented. Therefore, the objective of this study was to evaluate the importance of maternal additive genetic and maternal permanent environmental effects on weaning weight and ultrasound carcass traits in Nellore cattle raised under commercial tropical conditions, using single-trait and multi-trait animal models, with emphasis on their implications for early selection strategies.

Materials and Methods

Ethical approval

This study was approved by the Ethics Committee on Animal Use (CEUA) of the Federal University of Grande Dourados (UFGD) under protocol number 25/2022.

1. Animals, data, and pedigree information

Phenotypic records were obtained from 4,949 Nelore calves born between 2015 and 2025 at Fazenda Nelore Birigui, located in Bela Vista, Mato Grosso do Sul, Brazil. The

pedigree file comprised 9,051 individuals in the numerator relationship matrix. Only calves with correctly identified dams were retained in the analyses.

The farm is located at approximately 22°04′ S and 56°10′ W, near the Brazilian–Paraguayan border. The region is characterized by a tropical savanna climate (Aw; Köppen classification), with a well-defined dry season. Mean annual temperature is 22.7 °C, and average annual precipitation is 1,416 mm, with July and August being the driest months (Amaral et al. 2009). Animals were raised exclusively on pasture, predominantly *Urochloa brizantha* cv. MG5, with *ad libitum* mineral supplementation.

2. Traits and data editing

The traits evaluated included weaning weight standardized to 210 days, following Beef Improvement Federation (BIF) guidelines, and the following ultrasound-derived carcass traits measured at weaning: longissimus muscle area (LMA), marbling score (MARB), and backfat thickness (BF).

Ultrasound images were obtained from calves approximately 7–8 months of age using a US Aloka 500 New scanner equipped with an 18-cm linear transducer. Image acquisition and interpretation were performed by a certified technician from Designer Genes Technologies (DGT) Brazil using BIA software. LMA was measured from a cross-sectional image of the *Longissimus dorsi* between the 12th and 13th ribs. MARB was obtained from longitudinal images captured between the 11th and 13th ribs and recorded as a numerical score associated with intramuscular fat deposition. BF was measured over the *Longissimus dorsi* muscle at the 12th–13th rib interface.

Data consistency checks were performed prior to analysis. Records from animals whose age at measurement deviated more than ±45 days from the standard weaning age were excluded. Weaning weight records below 150 kg or above 265 kg were also removed. Within

125 contemporary groups, observations exceeding ±3.5 standard deviations from the mean were
126 discarded to reduce the influence of recording errors and biologically implausible values.
127 *3. Fixed effects and contemporary groups*
128 Preliminary analyses of variance were conducted using the GLM procedure of SAS
129 (SAS Institute, Cary, NC) to identify significant non-genetic sources of variation. Fixed
130 effects were considered significant at $P < 0.05$.
131 The initial linear model included the fixed effects of sex (SX), recipient breed (RB),
132 month of birth (MB), year of birth (YB), and the linear and quadratic covariates of calf age
133 at measurement (AGE) and dam calving order (CO).
134 Based on these preliminary analyses, contemporary groups (CG) and covariates
135 included in subsequent genetic analyses were defined. For both weaning weight and
136 ultrasound carcass traits, two alternative CG structures were tested: (1) animals born in the
137 same year and month of birth, and (2) animals grouped by sex and recipient breed. The CG
138 structure providing the best model fit was retained for genetic analyses.
139 Recipient cows, which had unknown pedigree information and unknown age, were
140 not included in the breeding value vector. Their effects were accounted for through fixed
141 and/or random environmental components, following current recommendations for genetic
142 evaluation of embryo transfer progeny in beef cattle (Suárez et al. 2015; Beef Improvement
143 Federation 2023).
144 Contemporary groups containing fewer than 20 animals or fewer than two males
145 were excluded from the analyses. Table 1 summarizes the number of observations, number
146 of sires and dams, number of contemporary groups, and the mean number of animals per CG
147 for both CG definitions across all traits evaluated.
148

4. Genetic and Statistical Analyses

Genetic analyses were performed using both single-trait and multi-trait animal models. Three alternative models were evaluated: (1) a model including only direct additive genetic effects; (2) a model including direct additive and maternal additive genetic effects; and (3) a full model including direct additive, maternal additive genetic, and maternal permanent environmental effects.

In all models, fixed effects included contemporary groups and the linear and quadratic covariates for calf age at measurement and dam calving order.

Maternal effects were explicitly modeled to account for both additive maternal genetic and maternal permanent environmental contributions, following classical and modern developments in beef cattle genetic evaluation (Koch 1972; Quintanilla et al. 1999; Suárez and Cantet 2011). Model comparisons aimed to assess the practical relevance of these effects for weaning weight and ultrasound-derived carcass traits under tropical commercial production conditions. The full model was expressed in matrix notation as:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{d} + \mathbf{Z}_2\mathbf{m} + \mathbf{Z}_3\mathbf{mp} + \mathbf{e},$$

where $\mathbf{y}$ is the vector of observations; $\boldsymbol{\beta}$ is the vector of fixed effects; $\mathbf{d}$ is the vector of random direct additive genetic effects; $\mathbf{m}$ is the vector of random maternal additive genetic effects; $\mathbf{mp}$ is the vector of maternal permanent environmental effects; $\mathbf{e}$ is the vector of random residuals; and $\mathbf{X}$, $\mathbf{Z}_1$, $\mathbf{Z}_2$, and $\mathbf{Z}_3$ are incidence matrices relating observations to their respective effects. The expectations were defined $\mathrm{E}(\boldsymbol{y}) = X\beta \; and \; \mathrm{E}(\boldsymbol{d}) = \mathrm{E}(\boldsymbol{m}) = \mathrm{E}(\boldsymbol{mp}) = \mathrm{E}(\boldsymbol{e}) = \mathbf{0}$. The variance-covariance structure of random effects was assumed to be:

$$Var\begin{bmatrix} d \\ m \\ mp \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_d^2 & A\sigma_{dm} & 0 & 0 \\ A\sigma_{dm} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I_{nc}\sigma_{mp}^2 & 0 \\ 0 & 0 & 0 & I_n\sigma_e^2 \end{bmatrix},$$

where σ_d^2 is the direct additive genetic variance; σ_m^2 is the maternal additive genetic variance; σ_{dm} is the direct–maternal additive genetic covariance; σ_{mp}^2 is the maternal permanent environmental variance; σ_e^2 is the residual variance; **A** is the numerator relationship matrix; $\mathbf{I}_n c$ is an identity matrix of order equal to the number of dams; and $\mathbf{I}_n$ is an identity matrix of order to the number of observations.

Direct and residual effects were assumed independent. Direct and maternal additive genetic effects were assumed correlated, whereas maternal permanent environmental effects were assumed independent of genetic and residual effects.

5. Genetic and Statistical Analyses

Variance components were estimated using a derivative-free restricted maximum likelihood (DF-REML) algorithm implemented in the BLUPF90 family of programs (Misztal et al. 2002). Although derivative-based algorithms are currently preferred for large-scale multi-trait analyses, DF-REML remains appropriate for moderate-sized datasets when model dimensionality is limited and convergence diagnostics are carefully evaluated.

All analyses were initiated from multiple sets of starting values to reduce the risk of convergence to local maxima. Convergence was declared when successive iterations resulted in negligible changes in the log-likelihood function, and likelihood behavior and parameter stability were inspected, following the recommendations of Misztal (1994).

Models were compared using likelihood ratio tests (LRT), in which increases in −2 log-likelihood values were evaluated using a chi-square distribution at a 5% significance level, with degrees of freedom equal to the difference in the number of estimated parameters between models.

Total heritability (h_t^2)was estimated according to Wilham (1972):

$$h_t^2 = \frac{\sigma_d^2 + 0.5\sigma_m^2 + 1.5\sigma_{dm}}{\sigma_p^2},$$

196 with, $\sigma_p^2 = \sigma_d^2 + \sigma_m^2 + \sigma_{mp}^2 + \sigma_e^2$.

197 Genetic and phenotypic correlations were estimated from the multi-trait model.
198 Pearson and Spearman correlations among sire breeding values were computed using SAS
199 (SAS Institute, Cary, NC) to evaluate the consistency of sire rankings across traits.

200

201 **Results**

202 *1. Descriptive Statistics and Fixed Effects*

203 Descriptive statistics and the results of the analyses of variance for the evaluated
204 traits are presented in Table 2. All traits were significantly affected ($P < 0.05$) by the fixed
205 effects of sex, recipient breed, month and year of birth, as well as by the linear and quadratic
206 covariates of calf age at evaluation and dam calving order. Among the evaluated traits, only
207 backfat thickness (BF) exhibited a coefficient of variation (CV%) greater than 24%.

208 The mean weaning weight adjusted to 210 days (W210) was 201.97 kg, which is
209 higher than values previously reported for Nellore cattle (Souza et al., 2000; Silva et al.,
210 2015). Mean longissimus muscle area (LMA) and backfat thickness were 42.66 cm² and 2.61
211 mm, respectively, exceeding those reported by Adamich (2018) for Brangus calves. The
212 average marbling score (MARB) was 2.98.

213 No significant effects of dam calving order were observed for LMA (quadratic effect,
214 $P = 0.070$) or BF (linear effect, $P = 0.300$; quadratic effect, $P = 0.593$), indicating that, in
215 this herd, cow maturity did not substantially influence these carcass traits at weaning.

216 *2. Variance components and model comparison*

217 Estimates of variance components and genetic parameters obtained under the
218 different models are summarized in Tables 3 and 4. Likelihood ratio tests indicated that
219 models including maternal additive genetic effects (M2) and maternal permanent

environmental effects (M3) provided a significantly better fit ($P < 0.05$) than the model including only direct additive genetic effects (M1) for all evaluated traits.

The inclusion of the direct–maternal genetic covariance (σ_{dm}) in Models M2 and M3 markedly reduced the residual variance (σ_e^2), reflecting improved model adequacy. The estimated direct–maternal covariance was positive for all traits, suggesting a favorable association whereby animals with superior genetic merit for growth and carcass traits are produced by dams with enhanced maternal ability.

3. Genetic Parameters

Estimates of direct heritability (h_d^2) were moderate for longissimus muscle area (LMA; 0.31–0.34), marbling score (MARB; 0.24–0.25), and weaning weight adjusted to 210 days (W210; 0.17–0.22), and low for backfat thickness (BF; 0.08–0.11). Maternal heritability (h_m^2) ranged from 0.04 to 0.21 and represented a considerable proportion of the corresponding direct heritability values, reaching up to 95% for W210.

Multi-trait analyses produced more precise and consistent estimates compared with single-trait analyses. Specifically, multi-trait modeling slightly increased the estimated direct heritability for BF and optimized genetic correlation estimates, supporting its application in breeding programs that rely on selection indices combining growth and carcass traits.

4. Genetic Correlations

Direct additive genetic correlations among all traits were positive, with estimates ranging from low to moderate magnitude (0.22 to 0.70; Table 5). Positive correlations were observed between LMA and W210 (0.54) and between LMA and BF (0.50), indicating that selection for increased muscling is associated with heavier calves and improved fat deposition. Likewise, positive correlations between MARB and the other traits (0.35 to 0.51) suggest that simultaneous genetic gains in marbling, growth, and muscling are feasible.

Maternal genetic correlations exhibited a different pattern, with negative estimates observed between W210 and MARB (−0.08) and, more markedly, between LMA and MARB (−0.32). Pearson and Spearman correlations among sire breeding values (Table 6) were positive, high, and significant (0.43 to 0.74), indicating consistency between magnitude-based and ranking-based selection criteria.

Discussion

1. Descriptive Statistics and Fixed Effects

The high CV observed for BF reflects the strong sensitivity of this trait to short-term environmental variation, such as nutritional fluctuations and climatic conditions, which are common in extensive tropical production systems (Oldenbroek and Van der Waaij, 2014). This variability highlights the importance of cautious interpretation of genetic parameters for BF measured at early ages.

The superior W210 observed in this study likely reflects improvements in herd management, including nutrition, health, and reproductive practices, allowing better expression of the animals' genetic potential. The significance of all fixed effects reinforces the multifactorial nature of weaning weight and the need to properly account for environmental sources of variation in genetic evaluation models, as previously reported by Gandra et al. (2019).

The relatively high MARB observed for Nellore calves at weaning suggests that intramuscular fat deposition is influenced by environmental conditions associated with sex, season, and year of birth. These results indicate the presence of genotype x environment interactions affecting early expression of carcass quality traits and emphasize the importance of modeling these effects to ensure unbiased genetic evaluations.

2. Variance components and model adequacy

The superior performance of models incorporating maternal additive genetic and maternal permanent environmental effects confirms the critical role of maternal contribution in traits expressed at weaning. These findings are consistent with both classical and contemporary studies emphasizing the importance of properly partitioning maternal sources of variation in beef cattle genetic evaluations (Bijma, 2006; Mrode, 2014; Javier et al., 2024).

The inclusion of direct–maternal genetic covariance improved model fit by reallocating part of the variation previously attributed to random error. Although positive estimates of σ_{dm} were observed in this study, continuous monitoring of this parameter is essential, as strong negative covariances may indicate biological antagonism arising from resource allocation trade-offs between growth and maternal ability (Robinson, 1996; Feng et al., 2025).

3. Genetic Parameters and breeding implications

The low h_d^2 estimated for BF confirms the predominant influence of non-permanent environmental factors, limiting the expected response to direct genetic selection when measured at weaning (Espinoza-Villavicencio et al., 2015). In contrast, moderate direct heritabilities for LMA, MARB, and W210 indicate meaningful potential for genetic improvement through selection.

The magnitude of h_m^2 estimates, particularly for W210, reinforces the importance of explicitly modeling maternal effects to avoid underestimation of total genetic variance and loss of accuracy in breeding value prediction, as originally proposed by Willham (1972).

The superiority of multi-trait analysis observed in this study reflects its ability to exploit genetic correlations among traits, resulting in increased precision and reduced selection bias. These findings support its use in breeding programs that select animals based

294 on multiple correlated traits, as recommended by Pollak et al. (1984) and Thompson and
295 Meyer (1986).

296 *4. Genetic Correlations and selection strategies*

297 The favorable direct genetic correlations among ultrasound-derived carcass traits and
298 weaning weight demonstrate the feasibility of early selection at weaning for growth and
299 carcass quality in Nellore cattle under tropical conditions. These associations indicate that
300 selection for increased muscling and adequate fat deposition does not compromise marbling
301 or growth performance.

302 From a practical breeding perspective, the development of selection indices
303 integrating W210, LMA, BF, and MARB, while accounting for their heritabilities and
304 genetic correlations, represents an effective strategy to accelerate genetic progress and
305 improve economic efficiency. In this context, ultrasonography proves to be a valuable and
306 practical tool for early genetic selection in beef cattle production systems where early
307 decision-making is essential (Golden et al., 2000).

308 The correct identification and inclusion of environmental effects in statistical models
309 are essential to ensure accuracy in genetic evaluations and to enable fair comparisons among
310 animals. In the present study, the inclusion of maternal additive genetic effects and maternal
311 permanent environmental effects in Models M2 and M3 resulted in a significantly better fit
312 compared with the model that considered only direct additive genetic effects (M1). The high
313 magnitude of maternal heritability, which in some cases approached or exceeded direct
314 heritability, indicates that failure to account for maternal contributions leads to an
315 underestimation of total genetic variance and compromises the accuracy of genetic
316 evaluations for traits measured at weaning.

317 Overall, the multi-trait analysis proved superior to the single-trait approach by
318 providing more precise genetic parameter estimates and reducing potential selection bias,

particularly in breeding programs based on multiple correlated traits. The presence of positive and moderate direct additive genetic correlations among ultrasound-derived carcass traits—longissimus muscle area (LMA), marbling score (MARB), and backfat thickness (BF)—and weaning weight adjusted to 210 days (W210) indicates a favorable genetic association structure. These relationships demonstrate that selection strategies targeting increased musculature and adequate fat deposition are expected to promote correlated genetic gains in marbling and growth performance. Consequently, genetic evaluations based on multi-trait animal models that incorporate both maternal additive genetic and maternal permanent environmental effects are recommended to maximize genetic progress for carcass and growth traits measured at weaning. Under commercial tropical conditions, ultrasound measurements represent a practical and effective tool for early selection of both males and females, contributing to improved efficiency and sustainability of beef cattle breeding programs.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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