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Selection criteria for frame score and its association with growth-, reproductive-, feed efficiency- and carcass-related traits in Nellore cattle

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Abstract

Context: A frame score prediction equation developed specifically for Nellore cattle could be an auxiliary tool to improve mating decisions based on feed resources and production system objectives. Aims: Estimate genetic parameters for frame using a prediction equation developed for Nellore cattle and genetic associations between frame score (FRAME) with growth, reproductive, carcass, feed efficiency-related traits and five bioeconomic indexes. Methods: Birth weight (BW), adjusted weight at 120 (W120), 210 (W210) and 450 (W450) days of age, adult eight (AW), age at first calving (AFC), probability of precocious calving (PPC30), stayability (STAY), accumulated cow productivity (ACP), adjusted scrotal circumference at 365 (SC365) and 450 (SC450) days of age, rib eye area (REA), subcutaneous backfat thickness (BFT), rump fat thickness (RFT), intramuscular fat percentage (IMF), residual feed intake (RFI) and dry matter intake (DMI) were included in the analyses. Frame score was calculated using the Multiple Linear Regression (MLR) prediction method. The estimation of genetic parameters was performed using a linear animal model, except for PPC30 and STAY, which were estimated through a threshold animal model. The correlated response in FRAME considering selection for growth, reproductive, carcass and feed efficiency-indicator traits were obtained in the context of single-trait selection and a multiple trait context. Key results: Heritability estimated for FRAME was moderate (0.30 ± 0.09) . Frame score showed moderate genetic correlations with growth traits, BW (0.51 ± 0.08), adjusted weight at 120 (0.41 ± 0.07), 210 (0.35±0.07) and 450 (0.29±0.08) days of age. The genetic correlation estimates between FRAME and RFT was high (-0.84 \pm 0.02), but low with ACP (0.25 \pm 0.08) and RFI (0.10 \pm 0.13). In the single-trait and multi-trait contexts, there was a lower correlated gain for FRAME when the selection was applied for traits commonly measured in beef cattle breeding programs. Conclusion: Selection to increase growth traits would lead to an increase in frame size and herd nutritional requirements and it would reduce the carcass fatness level and early heifer sexual precocity. FRAME could be an alternative trait to monitor calf birth weight. Implications: Selection for FRAME is feasible, and the most suitable frame score value depends on the production system objectives and feed resources.

Online Short Summary

The specific frame score prediction equation developed for Nellore cattle could be an auxiliary tool to improve mating decisions based on feed resources and production-system objectives. The results support the concept that under unrestrictive nutritional management conditions, a favourable relationship between frame score and beef production is expected; nevertheless, under irregular feed supply, range conditions and cow–calf systems, it is important to control the frame size due to potential genetic antagonism between fertility and reproductive traits with frame score.

Keywords: animal size, *Bos indicus*, beef cattle, fertility, genetic parameters, genetic correlation, response to selection, selection indexes.

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Introduction

Frame score is defined as a numerical and categorical descriptor, ranging from one to nine, to evaluate the animal's skeletal size reflecting growth patterns, carcass composition, and potential mature size (BIF-Beef Improvement Federation 2002). It is frequently used as information additional to the animal's liveweight and other performance records to meet the herd nutritional requirements with feed resources, production-system objectives, and market endpoints (Mota *et al.* 2015). Large frame cattle tend to be heavier at all ages with a higher muscle:fat ratio and growth potential, producing leaner carcasses, displaying delayed puberty and greater mature-cow size. Large-frame animals have higher maintenance-energy requirements and, consequently, may be less resistant to periods of feed deprivation than are moderate- to low-frame animals. It is important to emphasise that in tropical and subtropical regions, beef cattle production is characterised by low-input and extensive systems with pasture-based feeding, with high levels of environmental variation inducing challenges and constraints not normally posed to animals in more intensive feeding environments. Therefore, the use of moderate- to low-frame animals is desirable in limited-resource production systems and environments (Jenkins and Ferrell 2002).

There is a growing concern regarding the selection for higher growth rates and liveweight at young ages and their impacts on mature size, carcass composition, fertility and herd productivity. In this regard, published reports of unfavourable genetic correlations between female liveweight and reproductive traits and stayability suggest that cow productivity would decline as a correlated response to selection for growth traits (Mwansa *et al.* 2002; Baldi *et al.* 2008; Berry and Evans 2014). Vargas *et al.* (1999) observed an unfavourable impact of large frame size on the sexual puberty and female's reproductive efficiency in Brahman (*Bos taurus indicus*) cattle reared under tropical conditions. Hence, selection criteria for beef cattle should be based not only on growth-related traits or final animal size, but should encompass several traits, including carcass composition, sexual precocity, feed efficiency, adaptation, and temperament-related traits (Vicente *et al.* 2015).

Frame score standards have been proposed for taurine cattle (*Bos taurus taurus*; BIF – Beef Improvement Federation 2002); however, they may not be applicable to predict frame score in Nellore cattle (*Bos taurus indicus*), since Nellore cattle are taller at similar weights or ages than are taurine cattle. In this regard, Horimoto *et al.* (2007) proposed frame score equations for Nellore cattle, including height (cm), weight (kg), and age of the animal measured at 18 months of age, and compared those to the frame score equations recommended by the BIF – Beef Improvement Federation (2002). The authors reported higher heritability estimates and phenotypic variance for frame score by using the equations developed for Nellore cattle than estimates obtained with the BIF equation for taurine cattle. Recently, Guimarães (2020) proposed a novel frame score prediction equation for Nellore cattle, with values ranging from 1 to 12, and by considering height, age, and ultrasound records (i.e. *Longissimus dorsi* muscle area, backfat, and rump fat deposition) so as to calibrate frame scores to ideal carcass weight and fatness in Brazil.

The development of a frame score prediction equation specific for Nellore cattle could be an auxiliary tool to improve mating and culling decisions on the basis of feed resources, production-system objectives, and productive potential related to precocity, growth, and fertility-related traits. However, studies aimed at quantifying the genetic associations between frame score and growth-, reproductive-, carcass-, and feed efficiency-related traits in Nellore beef cattle are scarce. This information is essential to evaluate the feasibility of frame score as a large-scale selection criterion in Nellore cattle breeding programs. Moreover, many livestock breeding programs use multi-trait selection approaches using selection indexes for breeding stock, and there is concern about the impact of multi-trait selection approaches for productive traits on animal frame size. Therefore, the objective of the present

study was to estimate (co)variance components and genetic parameters for growth-, reproductive-, carcass-, feed efficiency-related traits and frame score in Nellore cattle. Additionally, the direct and correlated responses to selection for frame score were estimated using single-trait and multi-trait approaches, applying five commercial selection indexes for cow–calf, backgrounding and fattening systems.

Materials and methods

Data

Phenotypic records from approximately 400000 Nellore animals born between 2010 and 2017 comprising growth, reproductive-, feed efficiency-, and carcass-related traits were used. These animals belonged to 18 farms located in four Brazilian geographical regions (Midwest, Southeast, Northeast, and North). Animals were raised in pasture-based production systems, with or without the use of creep feeding and supplementation. The mating season occurred from February to April and mid-November to January. Artificial insemination, controlled breeding, and multiple breeding systems were used, with a bull cow ratio of 1:30. The females were exposed to reproduction at 10–14 months of age in an average 3-month breeding season. Heifers were evaluated for pregnancy by rectal palpation roughly 60 days after the end of the breeding season, and those that did not conceive were exposed again at 2 years of age. The pedigree contained information from 644256 animals born between 1990 and 2018, including 16283 sires and 180995 dams from eight generations.

Traits

The growth traits considered were birth weight (BW), adjusted weights at 120 (W120), 210 (W210) and 450 (W450) days of age, and adult weight (AW), all in kilograms. For reproductive traits, the age at first calving (AFC, months), probability of precocious calving (PPC30, %), stayability (STAY, %), accumulated cow productivity (ACP, kg calf weaned/cow.year), and adjusted scrotal circumference (cm) at 365 (SC365) and 450 (SC450) days of age, were considered. The rib eye area (REA, cm²), subcutaneous backfat thickness (BFT, mm), rump fat thickness (RFT, mm), and intramuscular fat (IMF, %) carcass traits were also considered. For feed efficiency-related traits, residual feed intake (RFI, kg of dry matter/day) and dry-matter intake (DMI, kg/day) were used. The number of records and descriptive statistics for the studied traits are shown in Table 1.

Table 1.	Numbers	of conten	nporary	groups	(NCG),	records	(NOBS)	and	descriptive	statistics	for	growth-,
reproduct	tive-, feed o	efficiency-	and car	cass-rela	ated trait	s in Nell	ore cattle.					

Trait	NOBS	N sires	N dams	NCG	Mean ± s.d.
BW	46807	656	19100	1595	33.60 ± 4.64
W120	157636	2582	63609	5345	129.92 ± 20.47
W210	135135	1965	60701	4590	190.40 ± 31
W450	73739	1382	53559	2491	283.20 ± 54.31
AW	44507	2538	28561	2101	476.44 ± 76.22
SC365	125423	1805	59076	6613	20.74 ± 2.6
SC450	127693	1815	59124	6858	23.71 ± 3.35
AFC	188743	2151	87159	7667	36.99 ± 59.32
PPC30	48938	1421	23639	1251	$41.0\pm20.1\%$
STAY	104610	2125	66475	3632	$37.0 \pm 18.3\%$
ACP	96824	2075	59158	3971	144.02 ± 32.68
REA	85271	1737	36807	5563	55.88 ± 11.99
BFT	90783	1801	37205	5671	2.86 ± 1.86
IMF	26579	802	12278	1026	1.55 ± 1.54
RFT	90578	1790	36989	5671	3.97 ± 2.45
DMI	6645	566	3035	156	8.16 ± 1.89
RFI	6633	560	3015	156	0.00 ± 0.66
FRAME	12049	1226	8435	920	5.40 ± 2.056

FRAME, frame score; ACP, cow accumulated productivity; BW, birth weight; W120, weight at 120 days of age; W210, weight at 210 of age; W450, weight at 450 days of age; AW, adult weight; SC365, scrotal circumference at 365 days of age; SC450, scrotal circumference at 450 days of age; AFC, age first calving; PPC30, probability of precocious calving at 30 months of age; STAY, stayability; REA, rib eye area; BFT, subcutaneous backfat

thickness; IMF, intramuscular fat %; RFT, rump fat thickness; DMI, dry-matter intake; RFI, residual feed intake; s.d., standard deviation.

For W120, W210, W450 and ACW, weights ranging from 90 to 150, 165 to 255, 405 to 495 days age and from 2 to 16 years of age were considered respectively. The standardised weights were calculated from a linear regression considering the average daily gain assessed from 90 to 150, 165 to 255, 405 to 495 days of age for W120, W210, W450 respectively. Heifers evaluated for sexual precocity were exposed to reproduction in the weaning year. Heifers that had pregnancy confirmed and calved up to 30 months of age had their phenotypes categorised as a success (2), or otherwise as failure (1). For STAY, dams with at least three calvings at 76 months of age had their phenotypes categorised as success (2), or otherwise as failure (1). The ACP was calculated to express the annual cow productivity, as the average weight of the weaned calf over time integrates sexual precocity, maternal ability, and reproductive periodicity of the cow.

Body composition or carcass traits were recorded on live animals at an average age of 485 ± 155 days by ultrasound using ALOKA 500V equipment with a 3.5 MHz linear probe. The animals were scanned for REA and BFT between the 12th and 13th ribs, and RFT was measured at the junction of the *Gluteus medius* and *Biceps femoris* muscles, between the ileum and ischium. The IMF was measured from a longitudinal arrangement of the transducer over the 12th and 13th ribs.

To obtain the feed efficiency-related traits, the animals were held in individual pens or in group pens equipped with automated feed-intake measurement systems (GrowSafe[®] or Intergado[®]). In the group pens, the number of animals varied from 26 to 226 animals per pen and the number of animals per trial with individual pens varied from 20 to 50 animals. In total, 125 feed-efficiency tests were performed between 2011 and 2018. During the tests, animals were kept in the test for 70 days, preceded by a period of 21 days for adaptation, and the average weight of each animal was obtained by periodic manual weighing or by automated weighing platforms (Intergado[®]). The animals were evaluated under similar management and environmental conditions in the feedlot with an average of 423 ± 122 days of age at the beginning of the tests.

The diets offered over the years differed in composition and ingredients but were formulated on the basis of silage and commercial concentrate, with an average of 64% total digestible nutrients (TDN), 13% crude protein (CP), 76% dry matter (DM), and formulated for gains of 1.2 kg/day. To ensure *ad libitum* feed intake, food supply was adjusted daily, allowing refusals varying from 5 to 10% of offered.

The following feed intake records were not considered in the analyses: days when animals were handled outside of facilities for many hours, equipment failure and when no refusals were found. Dry matter percentage was determined from weekly samples of offered feed and refusals. The average daily gain (ADG) in each test was considered as the linear regression coefficient of body weight on days in test (DIT):

$y_{ij} = \alpha + \beta \times DI \ T + \epsilon_i$

where y_i is the weight of the *i*th animal on the *j*th day; α is the intercept of the regression equation whic represents the initial weight; β is the linear regression coefficient which represents the ADG; DIT_i is the day in the performance test of the *i*th observation; and ε is the error associated with each observation.

The DMI (kg/day) was obtained by calculating the average daily intake values during the test period. In individual stalls, this parameter was calculated as the difference between the dry matter offered and the refusal. In group pens, the DMI was calculated from the amount of individually consumed feed automatically recorded by the electronic systems.

Metabolic weight MW (kg^{0.75}) was retrieved from the liveweight and ADG, as follows:

$$MW^{0.75} = [\alpha + \beta \times (DIT /2)]^{0.75}$$

where MW is the metabolic weight; α is the intercept of the regression equation which represents the initial weight; and β is the linear regression coefficient that represents the ADG, as described and obtained above in estimating ADG.

The RFI was estimated as the residual from a multiple-regression model regressing DMI on ADG and $MW^{0.75}$, in the following model:

where, y is the individual DMI; $\beta 0$ is the intercept; $\beta 1$ and $\beta 2$ are the linear regression coefficients for ADG and MW, respectively; and ϵ is the residual error (i.e., RFI).

The prediction equation for frame score developed by Guimarães (2020) was applied to calculate the animal frame score, using a multiple linear regression prediction method and different equations were applied to males (Eqn 1) and females (Eqn 2), as follows:

 $FRAME_{MALES} = -20.35 + 0.1305 \times REA + 0.2633 \times BFT - 0.5901 \times RFT + 0.1139 \times HH + 0.0056 \times AGE (1)$

 $FRAME_{FEMALES} = -11.87 + 0.1316 \times REA - 0.2457 \times BFT - 0.6218 \times RFT + 0.1139 \times HH + 0.0009507 \times AGE (10.1139 \times HH) - 0.0009507 \times HH) - 0.$

where REA, BFT, RFT, HH and AGE are ribeye area (cm²), subcutaneous backfat thickness (cm), rump fat thickness (cm), hip height (cm) and age (days) at ultrasound measurement respectively.

Genetics parameter estimation

For growth and carcass-related traits, the contemporary group (CG) was composed of farm, management group, sex, year and birth season (dry season: April–September, and rainy season: October–March). For reproductive traits, the CG were composed of farm, year and birth season. For feed efficiency-related traits, the farm, management group, sex, identification of feed-efficiency test, year, and birth season were considered to form the CG. Records within ± 3.5 s.d. of the CG mean were considered in the analysis, and CG with at least four animals were kept for performing the analyses.

The (co)variance components for AFC, BW, W120, W210, W450, AW, SC365, SC450, ACP, REA, BFT, RFT, IMF, RFI, and DMI were estimated considering a bivariate linear animal model:

$y = X\beta + Zg + Mm + Wmpe + e$

where, y is a vector of dependent variables; $\boldsymbol{\beta}$ is a vector of fixed effects, including the CG; g is a vector of random effects of the direct additive genetic effects; **m** is a vector of random maternal additive effects (only for BW, W120 and W210); **mpe** is a random maternal effect vector of permanent environment effects (only for BW, W120 and W210); e is a vector of random residual effects; **X** is the incidence matrix associating $\boldsymbol{\beta}$ with y; **Z** is the incidence matrix associating g with y; **M** is the incidence matrix associating **m** with **y**, and **W** is the incidence matrix associating **mpe** with y. It was assumed that $E(y)=X\beta$. Genetic, maternal, permanent environment, and residual effects were assumed to be normally distributed with mean equal to zero and a covariance structure equal to

$$\operatorname{Var}\begin{bmatrix}\mathbf{g}\\\mathbf{m}\end{bmatrix} = \begin{bmatrix} \sigma_{g1}^2 & \sigma_{g12} & 0\\ \sigma_{g12} & \sigma_{g2}^2 & 0\\ 0 & 0 & \sigma_m^2 \end{bmatrix} \otimes \mathbf{A} = \mathbf{G}_{\mathbf{U}} \otimes \mathbf{A}$$
$$\operatorname{Var}[\mathbf{mpe}] = \mathbf{I} \ge \sigma_{mpe}^2$$
$$\operatorname{Var}[\mathbf{e}] = \mathbf{I} \ge \begin{bmatrix} \sigma_{e1}^2 & \sigma_{e12}\\ \sigma_{e12} & \sigma_{e2}^2 \end{bmatrix}$$

where: σ_{g1}^2 and σ_{g2}^2 are the additive genetic variances for trait 1 and trait 2, respectively; σ_{g2}^2 is the additive genetic covariance between trait 1 and trait 2; **Gu** is a 3 × 3 additive genetic and maternal additive genetic variance–covariance matrix and \otimes is the Kronecker product operator; σ_{mpe}^2 is the maternal permanent environmental variance matrix; σ_{e1}^2 and σ_{e2}^2 are the residual variances for trait 1 and trait 2, respectively; σ_{g12} is the residual covariance between trait 1 and trait 2; **A** corresponds to the pedigree-based relationship matrix, and **I** is the identity matrix. The covariance between direct and maternal genetic effects was set to zero.

The (co)variance components and genetic parameters for PPC30 and STAY were estimated using a threshold animal model (Mrode and Thompson 2005), assuming an underlying scale with a normal distribution:

$\mathbf{U}|\theta \sim N(\mathbf{W}\theta, \mathbf{I}\sigma_{e}^{2})$

where, **U** is the vector of the scale with order r (number of animals); $\theta = (\beta, g, m, mpe)$ is the parameter vector with order s (number of class); β is a vector of fixed effects with order s; **g** is the vector of direct genetic additive effects; **m** is the vector of maternal additive effects; **mpe** is the vector of maternal permanent environmental effects; **W** is the incidence matrix with order r x s; **I** is the identity matrix with order r x r; and σ_e^2 is the residual variance. For binary models, the residual variance is fixed in $\sigma_e^2 = 1$ (Sorensen and Gianola 2002). The link between the

base and the subjacent scale was made by the probity link function (Gianola and Foulley, 1983).

The (co)variance components for the linear traits were obtained by the restricted maximum-likelihood method by using the REMLF90 software (Misztal *et al.* 2002) and applying the average information-restricted maximum-likelihood algorithm by using the AIREMLF90 software (Misztal *et al.* 2002). The (co)variance components for the categorical traits were obtained using the THRGIBBS1F90 software (Misztal *et al.* 2014) by means of 1000000 Gibbs sampling iterations generated with an initial burn-in of 50000 and a thinning interval of 100. Convergence assessment for the parameter estimates was verified by visual inspection of the trace plots and by using Geweke's Diagnostic (Geweke 1992) implemented in the R package Bayesian Output Analysis BOA (Smith 2008). Further, the heritability and genetic correlation estimates were computed as the mean of selected Gibbs samples. The heritability estimates were classified as low (below 0.20), moderate (ranging from 0.20 to 0.40) and high (above 0.40), following the recommendation of Bourdon (1997). The genetic and phenotypic correlation estimates were classified as low (below 0.30), moderate (ranging from 0.30 to 0.70) and high (above 0.70), according to the recommendations of Hill (2013).

Correlated response

The correlated responses in FRAME considering selection for growth-, reproductive-, carcass- and feed efficiencyindicator traits were obtained in the context of single-trait selection. The expected response to direct single-trait selection was estimated for all evaluated traits by using the following equation (Falconer and Mackay 1996):

 $\Delta G_{\rm Y} = (r_{\rm ti \ Y} \times i_{\rm Y} \times \sigma_{a \rm Y}) / GI$

where ΔG_Y is the genetic gain in Trait Y per generation; r_{tiY} is the accuracy of the genetic prediction of Y obtained as the square root of heritability; i_Y is the intensity of selection for Trait Y; σ_{aY} is the genetic variation obtained as the s.d. of the additive genetic effect in Trait Y; and GI is the generation interval.

The GI assumed for FRAME, SC365, SC450, BW, W120, W210, W450, AW, REA, BFT, RFT, RFI and DMI was 1.5 years. The GI considered for PPC30, AFC, STAY and ACP were 2.5, 2.0, 6.0 and 6.0 years respectively. The GIs were defined by considering the age at evaluation for each trait. For growth, carcass, scrotal circumference, and FRAME traits, a selection intensity equal to 1.2 was considered, corresponding to the selection of 10% and 60% of males and females respectively. To estimate the correlated response for PPC30, STAY and ACP, a smaller number of animals were measured, and thus, a selection intensity equal to 0.875 was used, corresponding to the selection of 20% and 80% of males and females respectively.

For the correlated responses in the context of single-trait selection, the following two scenarios were considered: (1) for traits commonly measured and evaluated (growth, carcass, and scrotal circumference), direct selection was applied, and the correlated responses in FRAME were evaluated; and (2) for traits that have a lower number of phenotypic records and are not usually measured (DMI, RFI, PPC30, STAY, and ACP), direct selection for FRAME was applied, and the correlated responses in such traits were evaluated. The correlated responses were estimated by the following equation (Falconer and Mackay 1996):

$\Delta G_{Y|X} = (r_{gXY} \times r_{ti|X} \times i_X \times \sigma_{aY}) / GI$

where, $\Delta G_{Y|X}$ is the genetic gain per generation in trait Y given selection for X; r_{gXY} is the genetic correlation between X and Y; r_{tiX} is the accuracy of the genetic prediction of X; i_X is the intensity of selection for Trait X; σ_{aY} is the s.d. of the additive genetic effect on Trait Y; and GI is the generation interval. In Scenario 1, the Y traits were growth, scrotal circumference, and carcass, while X was FRAME. In Scenario 2, the Y trait was FRAME, while DMI, RFI, AFC, PPC30, STAY, and ACP were used as X traits. The relative efficiency of selection (RES) was calculated as the ratio between the direct and indirect response to selection, as follows:

$\text{RES} = \Delta G_{\text{Y}} / \Delta G_{\text{Y}|\text{X}} \times 100$

Most beef cattle breeding programs use multi-trait selection approaches through selection indexes rather than single-trait selection. Thus, the correlated responses for FRAME using a multi-trait approach were obtained applying five selection indexes for cow–calf, backgrounding and fattening systems. The selection indexes used in the Nellore Brazil breeding program were applied in the multi-trait selection context (Table 2) and are described as follows:

Table 2. Traits included in the customised selection indexes and their respective we	eights (9	%)	١.
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Trait	MGTe	MGTeCR	MGTeRE	MGTeCO	MGTeF1
AFC	6.00				
PPC30	9.00	28.00			
SC365	3.00	5.00			
SC450	3.00				
STAY	22.00	34.00			
MA120	3.00				
MA210	5.00	8.00			
W210	16.00	25.00			
W450	24.00		59.00	14.00	14.00
REA	9.00		34.00	34.00	25.00
BFT			7.00	22.00	30.00
IMF				10.00	14.00
RFI				20.00	17.00

MGTe, index of total economic genetic merit for beef cattle production and lifecycle; MGTeCR, index for semiintensive cow–calf operation; MGTeRE, index for grass-fed semi-intensive backgrounding and finishing system; MGTeCO, index for intensive grain-fed in feedlot for backgrounding and finishing system of Nellore breed, with a bonus for higher carcass weight and fat thickness; MGTeF1, index for intensive grain-fed in feedlot for backgrounding and finishing system of crossbred animals (taurine breed × Nelore breed), with a bonus for higher carcass weight and fat thickness; AFC, age first calving; PPC30, probability of precocious calving at 30 month of age; SC365, scrotal circumference at 365 days of age; SC455, scrotal circumference at 450 days of age; STAY, stayability; MA120, maternal milk ability at 120 days of age (maternal component of weight at 120 days of age); MA210, maternal milk ability at 210 days of age; REA, rib eye area; BFT, subcutaneous backfat thickness; IMF, intramuscular fat %; RFI, residual feed intake; DMI, dry-matter intake.

- 1. MGTe: total economic genetic merit index for a semi-extensive beef cattle production lifecycle proposed by Baldi *et al.* (2016). The MGTe includes the following traits and their respective weights (%): direct EPD for W450 (24%); EPD for STAY (22%); direct EPD for W210 (16%); EPD for PPC30 (9%); EPD for REA (9%); EPD for AFC (6%); maternal EPD for W120 (3%); maternal EPD W210 (5%); and EPD for SC365 (3%) and SC450 (3%);
- 2. MGTeCR: index for semi-intensive cow–calf operations, including the following traits and their respective weights (%): EPD for stayability (34%), EPD for probability of precocious calving (28%); direct EPD for adjusted weight at 210 days of age (25%); maternal EPD for adjusted weight at 210 days of age (8%); and EPD for adjusted scrotal circumference at 365 days of age (5%);
- 3. MGTeRE: index for grass-fed semi-intensive backgrounding and finishing systems, including the following traits ant their respective weights (%): direct EPD for W450 (59%); EPD for REA (34%); and EPD for RFT (7%);
- 4. MGTeCO: index for intensive grain-fed in feedlot for backgrounding and finishing systems of Nellore breed, with a bonus for higher carcass weight and fat thickness. The MGTeCO includes the following traits and their respective weights (%): EPD for REA (34%); EPD for RFT (22%); EPD for RFI (20%); direct EPD for W450 (14%); and EPD for IMF (10%);
- 5. MGTeF1: index for intensive grain-fed in feedlot for backgrounding and finishing systems of crossbred animals (taurine breed × Nelore breed), with a bonus for higher carcass weight and fat thickness. The MGTeF1 includes the following traits and their respective weights (%): EPD for REA (25%); EPD for RFT (30%); EPD for RFI (17%); direct EPD for W450 (14%); and EPD for IMF (14%).

These five selection indexes were developed using specific bioeconomic models for each production system to calculate the economic values for each trait, according to the methodology proposed by Hazel (1943). For more information about the bioeconomic indexes, see: https://www.ancp.org.br/programas/conceitos-basicos/m gte-merito-genetico-total-economico. A deterministic simulation model written in R (R Core Team 2018) was used to predict the direct and correlated genetic gains for FRAME by using the methodology proposed by Rutten *et al.* (2002) to assess selection responses under a multiple-trait context.

Results and discussion

The variance component and heritability estimates for growth-, reproductive-, feed efficiency- and carcass- related traits are presented in Table 3. The heritability estimated for FRAME was moderate (0.30) and comparable to that reported by Horimoto *et al.* (2007) (0.26), also working with Nellore cattle but using a prediction equation for frame, including height and weight at 18 months of age. In the same study, the authors reported a moderate heritability estimate (0.24) for frame score by using the formulas recommended by BIF – Beef Improvement Federation (2002). Bonin *et al.* (2015), using the Nellore cattle-specific equation proposed by Horimoto *et al.* (2007), also obtained a moderate heritability for frame score (0.31) for Nellore cattle. Ríos- Utrera *et al.* (2018) reported a moderate heritability estimate (0.25) for frame score in Charolais and Charbray cattle breeds. Higher heritability estimates for frame score (0.63 and 0.48) were reported by Mercadante *et al.* (2007) in a single Nellore cattle herd (3948 animals) by using the BIF equations (BIF – Beef Improvement Federation 2002). The heritability estimate for FRAME in this study indicates that selection based on frame score is feasible.

Traits ¹	σ^2_a	σ^2_m	σ^2_{mpe}	σ^2_{e}	h ² ±SD	$h^2_m \pm SD$
BW	2.23	0.32	0.96	7.40	0.20 ± 0.06	0.03±0.01
W120	32.76	19.70	42.15	132.38	0.14 ± 0.05	0.09 ± 0.02
W210	68.26	36.58	89.49	247.78	0.15 ± 0.07	0.08 ± 0.02
W450	203.69			575.27	0.26±0.10	
AW	821.60			2199	0.27±0.12	
SC365	1.07			1.91	0.36±0.02	
SC450	1.86			3.10	0.38 ± 0.02	
AFC	1.71			20.31	0.08 ± 0.02	
PPC30	0.38			1.00	0.28 ± 0.02	
STAY	0.20			1.00	0.17 ± 0.02	
ACP	70.92			511.97	0.12±0.03	
REA	10,734			24,822	0.30±0.03	
BFT	0.15			0.76	0.17 ± 0.02	
IMF	0.05			0.24	0.16±0.02	
RFT	0.37			1.09	0.25 ± 0.03	
DMI	0.23			0.61	0.28 ± 0.06	
RFI	0.09			0.36	0.19±005	
FRAME	0.47			1.09	0.30±0.09	

Table 3. Estimates of additive genetic (σ_a^2) ; residual (σ_e^2) ; maternal genetic (σ_m^2) ; maternal permanent environmental (σ_{mpe}^2) variances; maternal heritability (h^2) and direct heritability (h^2) , for growth, reproductive, carcass and feed efficiency indicator traits in Nellore cattle.

The direct heritability estimate was moderate for W450 (0.26) and low for W120 (0.14) and W210 (0.15). Higher heritability estimates for weaning (0.23 and 0.46) and yearling weight (0.49 and 0.49) were reported by Knights *et al.* (1984) and Yokoo *et al.* (2010) for Angus and Nellore cattle respectively, and similar for yearling weight (0.22 ± 0.025) in Brangus cattle (Neser *et al.* 2012). According to Mercadante *et al.* (2007), direct selection for post-weaning growth traits evaluated in Nellore cattle is feasible. Maternal heritability and maternal permanent environmental effects estimated for W120 and W210 were low (0.09 and 0.08 respectively), indicating that gains by direct selection for these traits should be low. Additionally, maternal effects are difficult to improve since maternal weaning weight EPD is expressed in the weaning weight of a bull's grand-progeny.

The heritability estimates for scrotal circumference were moderate (0.36 and 0.38 for SC365 and SC450 respectively), and similar to those previously reported for Nellore cattle (Kluska *et al.* 2018; da Silva Neto *et*

al. 2020). For PPC30 (0.28) and STAY (0.17), the heritability estimates were moderate and low respectively, like those reported in previous studies for Nellore cattle (Bonamy *et al.* 2019; da Silva Neto *et al.* 2020). The estimated heritability for AFC was low (0.08), a value similar to those reported in previous studies in Nellore cattle, ranging from 0.08 to 0.16 (Kluska *et al.* 2018; da Silva Neto *et al.* 2020).

The heritability estimates for REA (0.30) and RFT (0.25) were moderate and higher than that obtained for BFT (0.17). These results agreed with those reported by Kluska *et al.* (2018), namely 0.34, 0.33 and 0.17 for REA, RFT and BFT respectively, also in Nellore cattle. For REA, BFT and RFT, similar heritability estimates have been reported in the literature for Nellore cattle (Caetano *et al.* 2013; Gordo *et al.* 2018). The estimated heritability for IMF was low (0.16), and lower than those reported in the literature for Zebu animals (Tonussi *et al.* 2015; Magalhães *et al.* 2016).

The genetic and phenotypic correlation estimates among growth-, reproductive-, feed efficiency- and carcassrelated traits are presented in Table 4. The genetic correlation estimated between FRAME and BW was positive and moderate (0.51). The BW is an economically important trait in beef cattle and is associated with growth, structure, and calving difficulty (Utsunomiya *et al.* 2013). Johanson and Berger (2003) reported a 13% increase in probability of dystocia per kilogram increment of birth weight. The FRAME could be applied as a selection criterion to monitor BW and avoid dystocia due to excessive calf size or birth weight, since the measurement of BW is sometimes not feasible in extensive production systems or it generates additional management needs during calving season.

Traits	$rg \pm s.d.$	$rp \pm s.d.$
BW	0.51 ± 0.08	0.15 ± 0.04
W120	0.41 ± 0.07	0.21 ± 0.04
W210	0.35 ± 0.07	0.13 ± 0.03
W450	0.29 ± 0.08	0.13 ± 0.04
AW	0.39 ± 0.08	0.12 ± 0.04
SC365	0.06 ± 0.07	0.08 ± 0.03
SC450	0.04 ± 0.07	0.08 ± 0.03
AFC	0.18 ± 0.09	0.03 ± 0.02
PPC30	-0.24 ± 0.08	-0.11 ± 0.05
STAY	0.06 ± 0.12	0.03 ± 0.04
ACP	0.25 ± 0.08	0.06 ± 0.03
REA	0.50 ± 0.04	0.26 ± 0.04
BFT	-0.25 ± 0.10	-0.004 ± 0.01
IMF	-0.15 ± 0.08	-0.06 ± 0.03
RFT	-0.84 ± 0.02	-0.32 ± 0.05
DMI	0.29 ± 0.11	0.11 ± 0.04
RFI	0.10 ± 0.13	-0.02 ± 0.02

Table 4. Genetic (rg) and phenotypic (rp) correlation estimates with their respective standard deviation (±s.d.) between frame score and growth-, reproductive-, carcass- and feed efficiency-indicator traits in Nellore cattle.

FRAME, frame score; ACP, cow accumulated productivity; BW, birth weight; W120, weight at 120 days of age; W210, weight at 210 days of age; W450, weight at 450 days of age; AW, adult weight; SC365, scrotal circumference at 365 days of age; SC450, scrotal circumference at 450 days of age; AFC, age first calving; PPC30, probability of precocious calving at 30 months of age; STAY, stayability; REA, rib eye area; BFT, subcutaneous backfat thickness; IMF, intramuscular fat %; RFT, rump fat thickness; DMI, dry-matter intake; RFI, residual feed intake.

The estimated genetic correlation between FRAME and W120 was positive and moderate (0.41), indicating that selection to increase pre-weaning weight would lead to increased frame size in Nellore cattle. For growth

traits assessed after weaning, the genetic correlations with FRAME were moderate to low (0.35 and 0.29 for W210 and W450 respectively). Higher genetic correlation estimates between frame score and post-weaning growth traits have been reported in the literature. Horimoto *et al.* (2007) obtained a moderate genetic correlation estimate (0.40) between frame score and weaning weight in Nellore cattle. Similarly, Ríos-Utrera *et al.* (2018) obtained a moderate genetic correlation (0.41) between frame score and yearling weight in Charolais and Charbray cattle. In those studies, a moderate genetic correlation was obtained between frame score and adult cow weight (0.39), suggesting that selection for higher frame score would increase the adult cow weight. In the present study, the genetic correlation estimates between growth traits and FRAME were moderate to low, suggesting that selection to increase growth traits after weaning would not affect the frame size in the short term.

The genetic correlation obtained between RFI and FRAME was low (0.10), indicating that selection for frame size would not affect the feed efficiency. A low and positive genetic correlation between DMI and FRAME was obtained (0.29), thus selection to increase the frame size would lead to increased nutritional requirements and feed intake. Vargas Jurado *et al.* (2015) compared the feed intake among Angus crossbred heifers with different ages and frame sizes and reported that heifers with a larger frame size displayed a higher DMI at all ages (P<0,05). According to Walker *et al.* (2015), the typical perception that larger animals are less efficient is not appropriate. The results of our study indicated independence between frame score and feed efficiency, so that even though large frame-score cattle were associated with a higher feed intake, they were not necessarily less efficient.

A moderate genetic correlation between FRAME and REA (0.51) was obtained, indicating that selection to

increase FRAME would lead to improvements in carcass cut yield and commercial value (Mota *et al.* 2015). Low genetic correlation estimates between FRAME and IMF (-0.15) and BFT (-0.25) were achieved, suggesting that selection for larger-frame animals, in the short term, would not affect intramuscular fat deposition and subcutaneous backfat thickness. Reuter Pas *et al.* (2011) evaluated the performance and profitability of a commercial herd composed of *Bos taurus* cattle, and reported that as frame score increased, the REA also increased and IMF decreased linearly. The estimated genetic correlation between FRAME and RFT was high and negative (-0.83), indicating that selection for higher FRAME would decrease the RFT. Reports by other authors in the literature corroborate our results, where selection to increase body structure resulted in animals with later maturation and lower fat deposition (Riley *et al.* 2002). Berg and Butterfield (1976) hypothesised that the muscles and body shape create variable pressures and that the hindquarter intermuscular fat as fattening progresses. Subcutaneous fat depots expand under the skin in the less resistant areas, gradually resulting in the overall smooth appearance of very fat animals; thus, the rump fat thickness is a more appropriate trait to assess the pattern of finishing precocity.

For reproductive traits, the genetic correlations between FRAME and SC365 and SC450 were close to zero, 0.06 and 0.04 respectively; thus, the selection to increase the scrotal circumference would not influence the frame score. The genetic correlation estimates between FRAME with PPC30 (-0.24) and AFC (0.18) were also low. Vargas *et al.* (1999) reported that large-frame Brahman heifers were less sexually precocious; in other words, low- and medium-size Brahman heifers reached puberty earlier (626–633 days) than did large-size heifers (672 days). Animals with a large frame size tend to have higher nutritional requirements for maintenance than do small frame-size animals, therefore, under drought conditions or restricted-feeding, large frame size would delay sexual precocity since reproductive functions have a low priority in nutrient partitioning (Short and Bellows 1971). In this study, the estimates of genetic correlations between FRAME and sexual precocity of females suggest a non-antagonistic relationship between them, indicating that the selection for higher FRAME would not affect heifer sexual precocity. It is important to highlight that the herds analysed in the present study were subjected to nutritional management that largely met their requirements for maintenance, growth and reproduction, that is, to non-restrictive nutritional conditions.

The genetic correlation between FRAME and ACP was positive and low (0.25), suggesting that the selection for large-frame animals would not affect cow productivity in the short term. It is important to consider maximum limits of the cow's body size, nutritional requirements, and feed resources, as well as incidence of dystocia (Grossi *et al.* 2016). In this sense, Taylor *et al.* (2008) analysed the phenotypic effect of frame size on the reproductive performance of Santa Gertrudis cattle and reported that large frame cows produced calves with higher birth weights, longer gestation periods, and fewer calves per calving season, and stated that the reproductive performance of large-frame cows was lower than that of medium- to low-frame size cows. The genetic correlation between FRAME and STAY was close to zero (0.06); thus, selection for higher FRAME would not influence dam longevity. The present study showed evidence of moderate genetic synergism between frame score and cow productivity, but we must consider the context of feed management of the animals analysed, which came from environments considered to be non-restrictive. The null genetic association between FRAME and STAY might be a consequence of the management conditions of the analysed herds, which differ from most beef cattle production systems, especially low-input commercial extensive systems, where dams would suffer periodic moderate to

severe nutritional restriction.

The phenotypic correlation estimates between FRAME and W120, W210, SC365, SC450, BFT and REA were low (Table 4), indicating that these traits were not useful indicator traits of FRAME in Nelore cattle. The RFT displayed a moderate phenotypic antagonism with FRAME, suggesting that animals with a higher frame score displayed lower levels of carcass fat coverage. The FRAME could be used as an indicator trait for carcass composition to identify animals before slaughter with a higher fat coverage, quality grade and price bonus before slaughter. Low phenotypic correlation estimates between FRAME and sexual heifer precocity, and reproductive- and dam productive-related traits were obtained, indicating that FRAME is not an appropriate indicator trait to select heifer replacements and longer-lived cows. However, Brunes *et al.* (2022) pointed out that rump fat thickness obtained by ultrasound can be used as an indicator trait to improve the female sexual precocity in Nellore cattle, since the level of body fat showed the highest discrimination power (discrimination analyses) between early and late-pregnancy heifers.

The relative selection efficiencies for FRAME using single-trait selection for growth, carcass and scrotal circumference traits are presented in Table 5. The results indicated lower correlated gains for FRAME when the selection was applied for traits commonly measured in beef cattle breeding programs. This implies that if the objective is the adequacy of the frame score, this trait must be included as a criterion for direct selection to achieve greater responses. The relative selection efficiencies for traits not commonly used as selection criteria in Nellore cattle and with a lower number of records (low selection intensity), such as DMI, RFI, AFC, PPC30, STAY and ACP, using the FRAME score as an indicator trait, are presented in Table 6. The results indicated that FRAME is not an effective selection criterion to improve DMI, RFI, AFC, PPC30 and STAY. However, for ACP, FRAME appears to be an efficient selection criterion, since ACP is determined late in the animal's life; thus, adopting frame score as a selection criterion earlier in life may provide an opportunity to achieve correlated genetic gains to increase dam productivity.

Trait	Direct	Correlated	Relative selection
	response	response	efficiency
BW	0.808	0.086	235.93
W120	99 573	0.058	348.59
W210	21.455	0.050	403.39
W450	83.327	0.056	365.49
AW	342.794	0.0768	266.96
SC365	0.509	0.014	1457.95
SC450	0.912	0.008	2408.80
REA	4.718	0.103	197.89
BFT	0.050	-0.038	-537.55
IMF	0.015	-0.022	-895.96
RFT	0.146	-0.157	-130.46
FRAME	0.205	_	

Table 5. Direct and correlated responses, and relative selection efficiency (%) for frame scores when selection was performed for growth, scrotal circumference and carcass traits in a single-trait context.

FRAME, frame score; SC365, scrotal circumference at 365 days of age; SC450, scrotal circumference at 450 days of age; REA, rib eye area; BFT, subcutaneous backfat thickness; IMF, intramuscular fat %; RFT, rump fat thickness; BW, birth weight; W120, weight at 120 days of age; W210, weight at 210 days of age; W450, weight at 450 days of age; AW, adult weight.

Trait	Direct	Correlated	Selection relative		
	response	response	efficiency		
AFC	0.208	0.099	205.09		
PPC30	0.069	-0.029	-703.26		
STAY	0.011	0.004	5344.80		
ACP	197.91	78.639	2.61		
DMI	0.096	0.029	690.73		
RFI	0.030	0.004	5435.53		
FRAME	0.205	-			

Table 6. Direct and correlated responses for feed efficiency- and reproductive-related traits when selection is performed for frame score in a single-trait context.

FRAME, frame score; DMI, dry-matter intake; RFI, residual feed intake; AFC, age at first calving; PPC30, probability of precocious calving at 30 months of age; STAY, stayability; ACP, accumulated cow productivity.

The approach proposed by Rutten *et al.* (2002) was applied to assess the effect of multi-trait selection approach on FRAME by using customised selection indexes for different beef production systems. The direct selection responses for growth-, reproductive-, carcass-, frame- and feed efficiency-indicator traits and the correlated responses using selection indexes are presented in Table 7. The results indicated lower correlated gains for FRAME by using the five selection indexes (0.017, 0.020, 0.031, 0.034 and 0.028 for MGTe, MGTeCR, MGTeRE, MGTeRE and MGTeF1, respectively) than with the direct selection for FRAME (0.206) and implied that if the objective is the adequacy of the frame score, this trait should be included as a criterion for direct selection to attain a greater response. As expected, the backgrounding and fattening selection indexes for intensive production systems (MGTeRE, MGTeCO and MGTeF1) displayed higher genetic correlated responses with FRAME than with MGTe and MGTeCR. The backgrounding and fattening selection indexes placed greater emphasis on growth, carcass and finishing traits, which displayed moderate to high genetic correlation estimates with FRAME. Selection using the MGTe and MGTeCR indexes customised for low-input systems or range conditions would not influence FRAME in the short term, which means that these selection indexes would have less impact on mature size, carcass composition and nutritional requirements.

Trait	Direct ΔG Correl			lated ΔG			
		MGTe	MGTeCR	MGTeRE	MGTeCO	MGTeF1	FRAME
FRAME	0.206	0.017	0.020	0.031	0.034	0.028	
BW	0.798	0.120	0.111	0.184	0.274	0.335	0.498
W120	9.806	1.651	1.635	6.935	9.561	12.467	5.885
W210	21.150	3.686	3.124	14.984	20.707	26.709	10.469
W450	83.090	9.533	10.168	49.505	66.484	85.159	25.883
AW	341.533	35.493	34.179	56.282	47.803	46.883	40.403
SC365	0.514	0.050	0.053	0.180	0.255	0.344	0.028
SC450	0.917	0.060	0.085	0.328	0.429	0.578	0.033
AFC	0.290	-0.037	0.059	-0.096	-0.182	-0.247	0.101
PP30	0.070	0.009	0.016	0.020	0.034	0.049	-0.024
STAY	0.012	-0.005	-0.004	0.007	0.009	0.011	0.001
ACP	3.583	-1.915	0.959	3.336	3.949	5.227	1.942
REA	4.702	0.618	0.759	1.767	2.884	3.968	2.351
BFT	0.049	-0.006	0.009	0.013	0.029	0.047	-0.016
IMF	0.016	0.002	0.002	0.001	0.002	0.005	-0.003
RFT	0.148	0.017	0.025	0.036	0.078	0.133	-0.136
DMI	0.097	0.020	0.025	0.002	0.021	0.027	0.029
RFI	0.031	0.002	0.004	0.000	-0.003	-0.004	0.004

Table 7. Direct selection responses ($\Delta G - \sigma_a$, trait unit) for growth-, reproductive-, carcass-, frame- and feed efficiency-indicator traits and correlated responses by using selection indexes in the multi-trait context.

MGTe, index of total economic genetic merit; MGTeCR, index for a semi-intensive cow-calf and rearing system; MGTRE, index for a semi-intensive rearing and finishing system; MGTN, index for a rearing and finish system for the Nellore breed with feedlot (intensive) and bonus for fat thickness; MGTF1, index for a rearing and finish system for crossbred cattle with feedlot (intensive) and bonus for fat thickness; FRAME, frame score; ACP, cow accumulated productivity; BW, birth weight; W120, weight at 120 days of age; W210, weight at 210 days of age; W450, weight at 450 days of age; AW, adult weight; SC365, scrotal circumference at 365 days of age; SC450, scrotal circumference at 450 days of age; AFC, age first calving; PPC30, probability of precocious calving at 30 month of age; STAY, stayability; REA, rib eye area; BFT, subcutaneous backfat thickness; IMF, intramuscular fat %; RFT, rump fat thickness; DMI, dry- matter intake; RFI, residual feed intake.

The FRAME may be an auxiliary or complementary trait for Nellore breeding programs to perform better breeding and mating decisions for different market and production conditions. The classification of FRAME is not only important for Nellore cow–calf systems, but also for backgrounding and finishing systems, due to potential genetic antagonisms among growth-, reproductive-, feed efficiency- and carcass-related traits. Under unrestrictive nutritional management conditions, a favourable relationship between frame score and beef production is expected; however, under discontinuous feed supply, such as most commercial beef cattle production systems, particularly extensive systems, it is advisable to avoid large-frame sires and dams.

Conclusions

The heritability for FRAME indicates that selection for this trait in Nellore cattle is feasible, and the most suitable frame-score value depends on feed resources, production-system objectives, and market needs. Selection to increase growth traits would lead to an increase in frame size and herd nutritional requirements, and, consequently, a reduction in carcass fatness level and early heifer sexual precocity. FRAME could be an alternative trait to monitor calf birth weight to avoid problems related to dystocia. Despite there being a favourable genetic association between FRAME and cow productivity, it is important to be cautious about these results because it is not possible to predict the response in dam productivity when their nutritional requirements increase, and the environment and management conditions lack the capacity to meet them. There is no evidence about any possible genetic antagonism between FRAME and feed efficiency evaluated through RFI. The

implementation of FRAME as a selection criterion to improve beef quality and productivity in tropical conditions would depend on the production-system objectives and feed resources.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request. The data are not publicly available due to privacy or legal restrictions, and due to belonging to the National Association of Breeders and Researchers (ANCP).

Conflicts of interest

The authors declare that they do not have any conflicts of interest.

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