

Feed efficiency negatively associated with reproductive traits in Nellore cattle

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ABSTRACT. Various studies have been conducted to improve feed efficiency in Nellore beef cattle, as well as to select for more sexually precocious animals. In order to understand how reproduction is affected by selection for feed efficiency, we analyzed a database containing phenotypic information from 194,063 Nellore animals, a pedigree file containing 331,752 animals, and a genotyping file of 7,631 animals. The evaluated traits were probability of pregnancy at 14 months (PP14), stayability (STAY), cumulative annual productivity (COWPROD), residual feed intake (RFI), residual body weight gain (RG), and residual intake and gain (RIG). The (co)variance components were estimated through a multi-trait Bayesian linear-threshold model combination. The heritability estimates were: 0.38 ± 0.03 for PP14, 0.23 ± 0.02 for STAY, 0.14 ± 0.00 for COWPROD, 0.18 ± 0.05 for RFI, 0.21 ± 0.05 for RG and 0.18 ± 0.05 for RIG. Estimates of genetic correlation coefficients

between feed efficiency and reproduction traits were unfavorable for selection, 0.10 (RFI and PP14), -0.16 (RG and PP14), -0.11 (RIG and PP14), 0.12 (RFI and STAY), -0.21 (RG and STAY), -0.13 (RIG and STAY), and -0.16 (RG and COWPROD), indicating that selection for these feed efficiency traits could reduce the probability of early pregnancy of heifers and decrease the number of cows that remain in the herd for at least six years. Considering the importance of reproduction for beef cattle production and the costs of feeding the cattle, examining their genetic association with better modeling strategies could help breeders and researchers to overcome such unfavorable relationships between feed efficiency and reproduction.

Key words: Beef cattle; Genetic association; Linear-threshold model; Sexual precocity; Stayability

INTRODUCTION

Increasing the efficiency of production systems should be the goal of any breeding program. It is well known that increases in efficiency are achieved through management, nutrition, and genetic selection (Van Vleck, 1987). From the genetic selection perspective, it is necessary to establish a breeding goal emphasizing all the traits that influence productivity and profitability; both genetic and economic issues must be considered.

Reproduction and feed efficiency traits are directly linked to economic success. We can highlight the sexual precocity and fertility of the cow, which might boost its output and profitability. Selecting heifers for sexual precocity helps to anticipate female productive life by allowing for a greater number of progenies during their lifespan, higher levels of selection intensity, and a shorter generation time (Martín Nieto et al., 2003).

Feed is the major economic factor that influences the production and profitability of beef cattle (Nielsen et al., 2013). Furthermore, given climate change, reduced grazing grounds, and a need for increased meat output, selecting for feed efficiency could provide long-term advantages. As a result, genetic selection is appealing to improve the economic and environmental sustainability of agro-industrial systems (Kenny et al., 2018). The effective use of genetic variation in livestock populations is necessary and must be considered for the continual genetic improvement of economically important traits. For this, it is necessary to know about genetic relationships and the environment. As information is limited, estimations of genetic parameters are required, to reduce the possibility of introducing unforeseen changes in traits that are not under direct selection.

According to Randel and Welsh (2013), selection for efficient animals using residual feed intake might result in the selection of late-maturing heifers, which has a negative consequence in that females calve later in the first and subsequent calvings. It has also been reported that there is an inverse relationship between measures that relate fertility of young bulls and feed efficiency with lower sperm motility (Awda et al., 2013) and decreased semen quality (Fontoura et al., 2016).

There are few studies in beef cattle that explore genetic associations of reproduction traits with feed efficiency traits. Previous research has primarily focused on reproductive traits such as first service conception rate, pregnancy rate, days to calving, age at puberty,

age at conception, and scrotal circumference (Basarab et al., 2011; Donoghue et al., 2011; Shaffer et al., 2011; Randel and Welsh et al., 2013; Mu et al., 2016). These traits differ from the specific traits investigated in this study, which include heifer pregnancy, stayability, and cumulative annual productivity. Therefore, the aim of this study was to estimate variance components and genetic parameters under a multi-trait analysis using a linear-threshold model under Bayesian procedures for feed efficiency and reproductive traits in Nelore cattle.

MATERIAL AND METHODS

Pedigree and phenotypic data

The feed efficiency traits were provided from the experimental design defined by Grigoletto et al. (2017). The reproductive traits were measured in animals belonged to 12 farms located in the Midwest, Southeast and Northeast regions of Brazil. The dataset consisted of 194,063 animals, measured for feed efficiency (2,058) or female reproductive (192,005) traits. The pedigree file contained a total of 331,752 animals, including 3,631 sires and 102,929 dams, 106,560 individuals with progeny, and 225,192 individuals without progeny.

A genotype file of 7,631 animals was utilized, which had been genotyped by commercial panels of SNP molecular markers, with a density of 50,000 markers. They were subjected to quality control using the PREGSF90 software (Aguilar et al., 2014), which removed SNPs with call rate < 0.90 (0), frequency of minor alleles (MAF) < 0.03 (7,359), monomorphic (321) and SNPs with a difference between the observed and expected frequencies for the balance test Hardy-Weinberg > 0.15 (119). After quality control, 44,214 SNPs remained for analysis.

The analyzed traits were the probability of pregnancy at 14 months (PP14); stayability (STAY); cumulative annual productivity (COWPROD); residual feed intake (RFI); residual body weight gain (RG); and residual intake and gain (RIG). The descriptive statistics of the dataset are presented in Table 1.

Table 1. Number of animals within each category for different criteria for categorical traits and descriptive statistics for feed efficiency and reproductive traits in Nelore cattle.

Trait	N	Min	Max	NCG	Mean ± SD	Category*	
						0	1
RFI	2,058	-3.48	3.91	32	0.00 ± 0.99	-	-
RG	2,058	-1.04	1.25	32	0.00 ± 0.28	-	-
RIG	2,058	-4.47	4.48	32	0.00 ± 1.20	-	-
COWPROD	159,320	50.00	260.20	334	127.08 ± 30.20	-	-
PP14	35,533	0.00	1.00	94	-	29,069	6,464
STAY	127,398	0.00	1.00	546	-	90,960	36,438

N: Number of individuals; Min: Minimum; Max: Maximum; NCG: Number of contemporary group; SD: Standard deviation; RFI: Residual feed intake; RG: Residual body weight gain; RIG: Residual intake and gain; PP14: Probability of pregnancy at 14 months; STAY: stayability; and COWPROD: cumulative annual productivity. *Data presented as count of the number of animals per category: 0 (unsuccess) and 1 (success).

Phenotypic description

PP14 is related to sexual precocity, being the probability of the heifer becoming pregnant. The females were challenged, that is they were exposed to bulls in natural mating settings, for the first time around 14 months of age. The heifers were submitted to a pregnancy diagnosis about 60 days after the breeding season. This trait is treated as a binary outcome: 0 if the heifer is not pregnant and 1 otherwise (Eler et al., 2002). STAY is related to the fertility of the adult female, which is defined as the ability to remain in the herd, producing (at least) one calf per year, with no failures, up to six years of age (Silva et al., 2006). This trait was also treated as a binary outcome, i.e., if the cow is still productive at six years of age, it receives the code one, and zero otherwise. Finally, COWPROD is an estimate of the average annual productivity of weaned calves, measured in kg. The female's phenotype is the mean of calf weaning weights, each calf adjusted for fixed and sire effects (Eler et al., 2008).

The dry matter intake (DMI) and average daily weight gain (ADG) (needed for estimating the feed efficiency traits), were measured according to Grigoletto et al. (2017). The RFI (proposed by Koch et al., 1963) was calculated by subtracting the estimated DMI from the observed DMI. The estimated DMI was calculated as follows:

$$\text{DMI} = \beta_0 + \beta_1 \text{ADG} + \beta_2 \text{MBW}^{0.75} + \varepsilon_{1i}, \quad (\text{Eq. 1})$$

where: DMI is the expected dry matter intake; β_0 is the intercept of the model; β_1 and β_2 are the partial regression coefficients of DMI on ADG and $\text{MBW}^{0.75}$, respectively; ADG is the observed average weight daily gain, $\text{MBW}^{0.75}$ is the mid-test metabolic body weight, defined as the average of the initial and final body weight, to the power of 0.75; and ε_{1i} is the residual associated with the i^{th} observation (estimated RFI). The RG was measured as the difference between observed and estimated ADG. The estimated ADG was obtained by the following regression equation (Koch et al., 1963):

$$\text{ADG} = \beta_0 + \beta_1 \text{DMI} + \beta_2 \text{MBW}^{0.75} + \varepsilon_{2i}, \quad (\text{Eq. 2})$$

where: ADG is the average daily gain; β_0 is the intercept of the model; β_1 and β_2 are the partial regression coefficients of ADG on DMI and $\text{MBW}^{0.75}$, respectively; DMI is the observed dry matter intake, $\text{MBW}^{0.75}$ is the mid-test metabolic body weight; and ε_{2i} is the residual associated with the i^{th} observation, that is, RG.

Berry and Crowley (2012) proposed a measure for feed efficiency, called residual intake and gain (RIG), which relates RFI and RG to generate a parameter that has a favorable correlation with consumption and weight gain. The same authors highlighted that the animals selected for the RIG have superior weight gain performance than those selected for the RFI. RIG was calculated by subtracting RG from RFI, that is:

$$\text{RIG} = \varepsilon_{2i} - \varepsilon_{1i}, \quad (\text{Eq. 3})$$

where: RIG is the estimated residual intake and gain; ε_{2i} is the residual body weight gain, and ε_{1i} is the residual feed intake.

Statistical models

To analyze the traits, three different models were used in this study (to estimate variance components and genetic parameters). Those were as follows:

$$y_{ij} = \mu + CG_i + \beta_1 \text{Age}_j + u_j + e_{ij}, \quad (\text{Eq. 4})$$

$$y_{ijk} = \mu + CG_i + \beta_2 \text{Dtjn}_j + u_j + \text{Gmand}_k + e_{ijk}, \quad (\text{Eq. 5})$$

$$y_{ij} = \mu + CG_i + u_j + e_{ij}, \quad (\text{Eq. 6})$$

where: y_{ij} in equation (4) represents the phenotypic information for feed efficiency traits (RFI, RG, and RIG); y_{ijk} (on equation 5) represents the phenotypic information for PP14, and y_{ij} in equation (6) represents the phenotypic information for STAY and COWPROD. μ in all models represents a constant. CG_i represents the systematic effect of the i^{th} contemporary group (defined later); β_1 is the regression coefficient of age at the beginning of the experiment for feed efficiency trait of the j^{th} animal in the model (4); β_2 is the regression coefficient of Julian date of birth (Dtjn) of the j^{th} animal in the model (5); u_j in all models represents the additive random effect of the j^{th} animal; Gmand_k on the model (5) represents the uncorrelated random effect of the k^{th} management group at weaning; e_{ij} and e_{ijk} represent the residual random terms.

For the feed efficiency traits, contemporary groups (CG) were defined based on the significance level ($P < 0.001$) of a mixed model using the SAS PROC MIXED procedure. The CG consisted of the farm, experiment year, sexual condition (steers, young bulls, and heifers), days of confinement, and installation (individual pens, Calan Gate, or GrowSafe systems). For reproductive traits, the CG consisted of the farm, year of birth, management group and sex.

Assuming a matrix notation, the model can be expressed as:

$$y = X\beta + Z_1u + Z_2g + e, \quad (\text{Eq. 7})$$

where: y is the vector of phenotypic observations; ordered by the animal within traits; β represents the vector of systematic effects, ordered by trait; u represents the vector of the additive genetic effect of the animal; g represents the vector of the Gmand random effect (only for PP14); e represents the vector of residual random terms; X , Z_1 , and Z_2 are the incidence matrices of systematic, additive genetic and Gmand effects, respectively.

Assuming random effects as multivariate normally distributed, the (co)variance matrix for them was assumed to be as follows:

$$\text{Var} \begin{bmatrix} u \\ g \\ e \end{bmatrix} = \begin{bmatrix} G_0 \otimes A & 0 & 0 \\ 0 & G_1 \otimes I & 0 \\ 0 & 0 & R_0 \otimes I \end{bmatrix}, \quad (\text{Eq. 8})$$

where: u , g , and e were defined above; G_0 is a 6 by 6 matrix of additive genetic (co)variances for the studied traits; G_1 is a 6 by 6 matrix with all zero elements except one that corresponds to the Gmand variance component for PP14, and R_0 is a 6 by 6 matrix with the residual (co)variance among all traits. It must be noticed that residual covariances among reproductive and feed efficiency traits were assumed to be zero. A is the additive genetic relationship matrix, and finally, I is an identity matrix with proper order, and \otimes is the Kronecker product. Given those assumptions, y (conditionally on systematic and random effects) was assumed as normally and independently distributed as $y|\beta, u, g, G_0, G_1, R_0 \sim \text{MVN}\{X\beta + Z_1u + Z_2g, R_0 \otimes I\}$. Additionally, the vector of systematic

effects was assumed as $\beta \sim \text{MVN}\{0, \Sigma_\beta \otimes I\}$. For PP14 and STAY, instead of y , the vector l was used, which contains the liability for these two characteristics, making the same assumptions as above. It was further assumed that G_0 , G_1 and R_0 follow an inverse Wishart distribution, $WI^{-1}(v, V)$, with hyperparameters (chosen to be non-informative) v and V .

Estimation of variance components

The (co)variance components were estimated through a multi-trait analysis, in a linear-threshold model combination, using the THRGIBBS1f90 software (Misztal et al., 2018). For the Bayesian inference, a single chain was generated with 1,000,000 samples, with the first 500,000 samples being discarded as *burn-in*. The remaining samples were saved every 200 samples. Thus, the inference was made on 2,500 samples from the posterior distribution of all parameters. The convergence of Markov chains was evaluated by Geweke's test (Geweke, 1992), by checking the autocorrelation (Heidelberger and Welch, 1983) of the generated samples, and by applying a visual evaluation of the chains.

RESULTS

The heritability estimates for the feed efficiency traits ranged from 0.18 to 0.21 and for the reproductive traits ranged from 0.14 to 0.38 (Table 2). The highest estimate was obtained for the PP14 trait, demonstrating that selective breeding for this reproductive trait may increase the probability of early pregnancy in heifers.

Table 2. Estimates of variance components and heritability coefficient of feed efficiency and reproductive traits under multi-trait analysis via Bayesian inference in Nellore cattle.

Trait	Estimates	Mean \pm PSD	HPD (95%)	Geweke (Z score)	<i>r-lag 50</i>
RFI	$\hat{\sigma}_a^2$	0.12 \pm 0.04	[0.06; 0.19]	-0.18	0.46
	$\hat{\sigma}_e^2$	0.53 \pm 0.03	[0.47; 0.58]	0.13	0.28
	\hat{h}^2	0.18 \pm 0.05	[0.09; 0.28]	-0.18	0.47
RG	$\hat{\sigma}_a^2$	0.01 \pm 0.00	[0.01; 0.01]	0.23	0.38
	$\hat{\sigma}_e^2$	0.04 \pm 0.00	[0.03; 0.04]	-0.21	0.17
	\hat{h}^2	0.21 \pm 0.05	[0.13; 0.31]	0.24	0.28
RIG	$\hat{\sigma}_a^2$	0.18 \pm 0.05	[0.09; 0.28]	-0.11	0.41
	$\hat{\sigma}_e^2$	0.81 \pm 0.04	[0.72; 0.89]	0.07	0.22
	\hat{h}^2	0.18 \pm 0.05	[0.10; 0.27]	-0.11	0.41
PP14	$\hat{\sigma}_a^2$	0.73 \pm 0.08	[0.57; 0.89]	-0.18	0.06
	$\hat{\sigma}_{gmand}^2$	0.19 \pm 0.02	[0.15; 0.23]	-0.05	0.00
	$\hat{\sigma}_e^2$	1.00 \pm 0.00	[0.99; 1.01]	0.00	0.02
	\hat{h}^2	0.38 \pm 0.03	[0.33; 0.43]	-0.18	0.06
STAY	$\hat{\sigma}_a^2$	0.31 \pm 0.04	[0.25; 0.38]	-0.04	0.05
	$\hat{\sigma}_e^2$	1.00 \pm 0.00	[0.99; 1.01]	0.01	-0.03
	\hat{h}^2	0.23 \pm 0.02	[0.20; 0.28]	-0.04	0.04
COWPROD	$\hat{\sigma}_a^2$	93.18 \pm 3.12	[87.18; 99.39]	0.00	0.01
	$\hat{\sigma}_e^2$	580.75 \pm 3.44	[574.20; 587.40]	-0.05	0.02
	\hat{h}^2	0.14 \pm 0.00	[0.13; 0.15]	0.01	0.02

RFI: Residual feed intake; RG: Residual body weight gain; RIG: Residual intake and gain; PP14: Probability of pregnancy at 14 months; STAY: stayability; and COWPROD: cumulative annual productivity; $\hat{\sigma}_a^2$: Additive genetic variance estimate; $\hat{\sigma}_e^2$: Estimate of residual genetic variance; $\hat{\sigma}_{gmand}^2$: Management group variance estimate; \hat{h}^2 : Estimate of the heritability coefficient; Mean: Posterior means; PSD: Posterior standard deviation; HPD: Highest posterior density; and *r-lag50*: Autocorrelation at lag 50.

Geweke's diagnostic was used to evaluate the convergence for the Markov chains, in which, the hypothesis of chain convergence is rejected, considering a 5% level of significance if the value of the Z statistic in modulus is higher than $|1.96|$ (Geweke, 1992). Therefore, there was an indication of convergence for all parameters' estimates (Table 2).

Autocorrelation values (r-lag50) were observed for the variance components of all traits; however, feed efficiency traits had a higher value than reproductive traits, implying less accurate inferences; this may be because we have less information for feed efficiency compared to reproductive traits.

The genetic correlation coefficients (Supplementary 1) obtained in this study between the feed efficiency traits ranged from -0.98 (between RFI and RIG) to 0.82 (between RG and RIG). The high correlation coefficient among feed-efficiency traits was expected because RIG is derived from both RG and RFI. In addition, RFI and RG are supposed to be correlated since ADG and DMI are correlated measures. ADG is considered for RFI estimation, while DMI is included in the model for calculating RG.

The genetic correlation coefficients (Supplementary 1) between the reproductive traits ranged from 0.40 (between STAY and PP14) to 0.83 (between STAY and COWPROD). There was a strong association between STAY and COWPROD and a medium association between PP14 and COWPROD. Given this genetic correlation, it is plausible to hypothesize that selection for sexual precocity will lead to choosing highly productive cows (in terms of kilograms of weaned calves per year) along with remaining at least six years (given at least one birth/year) in the herd. Therefore, selecting for PP14 is favorable since it should contribute positively to increasing cow production in the herd, as well as being one of the traits evaluated that can be measured early in the animal's life, allowing selection to occur more swiftly.

When we analyze the correlation coefficients between the feed efficiency and reproduction traits, the posterior estimator high-density interval includes the zero value; in practical terms, it is assumed that the parameter is not significantly different from zero. Our results are not conclusive; rather they should be utilized to hypothesize the probable links between reproduction and feed efficiency in beef cattle, at least from a genetic perspective. In this population, selection for feed efficiency may not affect the aforementioned reproductive traits. However, we can speculate on possible links between fat deposition, feed efficiency, and reproduction (explained below).

The genetic correlations found between RFI and PP14, RFI, and STAY were detrimental (0.10 and 0.12, respectively), since selection for PP14 and STAY will enhance breeding values for RFI; in other words, producing inefficient animals in terms of food consumption. In the same way, the selection of highly efficient animals for RG and RIG will decrease the heifer pregnancy probability, the cow's ability to stay in the herd, and the cow's average annual productivity as the estimated genetic correlations were negative between these traits. Based on this reasoning, selection for feed efficiency traits could adversely affect female reproductive traits.

Concerning the environmental and non-additive effects, residual correlations were negative between RG and RFI, and RIG and RFI. This could mean that those non-additive effects act in opposite ways on those traits, while the environmental effect acts in the same direction for RIG and RG since their residual correlation was 0.90 (Supplementary 1). On other hand, all residual correlations among reproductive traits were positive, which should indicate that environmental and non-additive forces affecting PP14, STAY and COWPROD

act in the same way for different traits. In addition, all residual correlation estimates were significantly different from zero since their high-density interval did not include the zero value.

DISCUSSION

Heritability estimates

The heritability estimates for RFI were similar to those reported by Ceacero et al. (2016), Benfica et al. (2020) and Brunes et al. (2021). However, were lower than the estimates found by Santana et al. (2014) and Grigoletto et al. (2017), 0.37 and 0.30 respectively. This discrepancy could be explained by the different statistical models, since those authors included the sexual condition as a covariate to estimate the RFI.

RG and RIG showed heritability estimates of 0.21 and 0.18, respectively. Those values are in accordance with the previous results (ranging between 0.14 and 0.54) from Berry and Crowley (2012); Santana et al. (2014); Ceacero et al. (2016); and Benfica et al. (2020). The most discrepant values were presented by Santana et al. (2014), who found heritability estimates of 0.40 (RG) and 0.54 (RIG), since the statistical model used to estimate the RG was different from that used in our study.

The highest heritability estimate was obtained for PP14 (0.38). Our estimate was close to previous studies in which PP14 had heritability ranging from 0.30 to 0.42 (Santana Jr et al., 2012; Irano et al., 2016; Kluska et al., 2018), depending on the implemented model. PP14 is an early puberty indicator that is related to sexual precocity.

Concerning the ability of a cow to remain productive (in terms of giving birth at least one calf a year until a certain point – STAY), the desired age of selection defines which class of STAY is being used. Several studies showed different heritability estimates at different ages ranging from 0.14 to 0.25 (Santana Jr et al., 2014; Paterno et al., 2017; Schmidt et al., 2018, Bonamy et al., 2019). In our study, STAY was measured at six years of age and our heritability estimate was 0.23, which falls in the previous range reported for different definitions of stayability. The adoption of the trait as a selection criterion should increase the number of cows that stay in the herd and calve regularly, meaning a lower cost of heifer replacement as cow culling decreases over time.

Finally, the estimate of heritability for COWPROD was the lowest (0.14). Our result was similar to the coefficients reported previously for Nellore cattle (Baldi et al., 2008; Eler et al., 2008; Schmidt et al., 2018) which falls between 0.15 and 0.19.

Genetic correlation estimates

The high correlation coefficients among feed-efficiency traits were close to those found in the reviewed literature (Berry and Crowley, 2012; Santana et al., 2014; Figueiredo et al., 2019). Low RIF animals are expected to be RG/RIG highly efficient, as well as animals presenting high RG values may have low RFI values.

The genetic correlation coefficients between the reproductive traits obtained in our study were moderate to high, in accordance with reports for Nellore cattle (Santana Jr et al., 2012, 2014; Schmidt et al., 2018). Terakado et al. (2014) also found that precocious females remain in the herd longer and may produce slightly heavier calves at weaning. A strong

positive correlation was observed between COWPROD and STAY, which may indicate that it is not necessary to include both traits as a selection criterion. Selection for COWPROD seems to be more advantageous, despite the low heritability estimate, since its measurement is faster than STAY. It is possible to obtain phenotypes for COWPROD in young females and young sires, but not for stayability.

The genetic correlation coefficients between feed efficiency and reproductive traits were unfavorable and of low magnitude (Supplementary 1). Other studies have also found evidence of an unfavorable relationship between fertility and RFI. There were significant differences in calving dates; low RFI dams had their calves later than inefficient dams (Donoghue et al., 2011; Randel and Welsh, 2013; Mu et al., 2016). Shaffer et al. (2011) observed an unfavorable association between age at puberty and RFI, indicating that a 7.54 days reduction in age at puberty would increase RFI by one unit.

Complex factors control puberty, including genetics, nutritional status, physiological status, and environment. According to D'Occhio et al. (2019), the nutritional factor has a great impact on the onset of puberty interaction, by influencing the metabolic state of the animal through changes in insulin, insulin-like growth factor, glucose, and reproductive hormones. Changes in intermediary metabolism associated with oscillations in body weight and different degrees of body fat may influence luteinizing hormone release, and consequently puberty (Schillo et al., 1992).

The relationship between the amount of body fat and the other traits studied may be one of the possible reasons for the unfavorable associations. Several studies showed that body fat is associated with RFI (Donoghue et al., 2011; Lines et al., 2018) as well as puberty age in beef cattle (Caetano et al., 2013; Pereira et al., 2017); thus efficient heifers (presenting low RFI values) may have a lower amount of body fat and consequently may negatively affect puberty age. Shaffer et al. (2011) and Crowley et al. (2011) also related delayed puberty to decreased fat deposition in low RFI heifers.

Leptin is a peptide synthesized and secreted by adipocytes and works as a metabolic signal of nutritional status for the reproductive axis (Williams et al., 2002; Hausman et al., 2012). It acts in the hypothalamus as a regulator of hunger and satiety, stimulating or decreasing food consumption (Gamba and Pralong, 2006) and can act centrally in the hypothalamus or peripherally in the ovary to increase the reproductive function of females (Williams et al., 2002; Hausman et al., 2012). Therefore, reduction of adipose tissue could cause changes in the synthesis and release of leptin, which is supported by Foote et al. (2015), who showed a positive association between leptin concentration and body and carcass composition.

The plasma leptin concentration was positively associated with RFI; thus animals presenting high levels of RFI will have higher concentrations of leptin and high percentages of body fat (Nkrumah et al., 2007; Foote et al., 2015). Different results were presented by Mota et al. (2017), who found a negative association between plasma leptin concentration and RFI. On the other hand, Gillis et al. (2004), reported no significant association between leptin concentration and performance (DMI and ADG) and carcass traits. There still are many limitations to the relationship between other feed efficiency traits and reproduction because the main trait researched was RFI; also, there is a lot of divergence regarding the association of body fat and efficient animals for RG and RIG.

To see if there is a relationship between feed efficiency traits and the amount of body fat, it could be possible to look for the genetic correlation between feed efficiency

traits and backfat (BF) and rump fat thicknesses (RF). Santana et al. (2014) and Ceacero et al. (2016) found negative genetic correlations between RG and BF, and between RG and RF. However, Buarque (2018) reported a negative weak association between RG and BF and a positive correlation between RG and RF, disagreeing with what was found by Brunes et al. (2021), who reported a positive association between RG and BF and a negative association between RG and RF. Concerning RIG, its genetic correlation with fat thickness was previously reported as being negative (Ceacero et al., 2016; Buarque, 2018), showing that selection for low RIG values will lead to reduced fat deposition. However, there still are some disagreements; for example, Crowley et al. (2011), Santana et al. (2014) and Brunes et al. (2021) found a positive genetic correlation between RIG and fat thickness.

Concerning the environmental and non-additive effects, residual correlations were negative between RG and RFI, and RIG and RFI. This could mean that those non-additive effects act in opposite ways on those traits, while the environmental effect acts in the same direction for RIG and RG since their residual correlation was 0.90 (Supplementary 1). On other hand, all residual correlations among reproductive traits were positive, which should indicate that environmental and non-additive forces affecting PP14, STAY and COWPROD act in the same way for different traits. In addition, all residual correlation estimates were significantly different from zero since their high-density interval did not include the zero value.

CONCLUSIONS

Based on our results, we may speculate on possible links between feed efficiency and precocity, demonstrating that selection for low residual feed intake values, along with high values of residual gain and residual intake and gain, will result in decreases in the probability of a heifers becoming pregnant early and the cows' ability to remain productive in the herd for up to six years. Further studies still are needed to confirm or refute our hypothesis, because there seems to be a controversial relationship between feed efficiency and reproductive traits in Nellore beef cattle. Considering the importance of reproduction for beef cattle production and the costs of feeding, studying their genetic association with better modeling strategies could help breeders and researchers to overcome possible unfavorable relationships between feed efficiency and reproduction.

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DATA AND MODEL AVAILABILITY STATEMENT

Since the pedigree and phenotypic data used are from a commercial breeder's association, the authors have no permission to share the data.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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