

Genetic correlation between feed efficiency and carcass traits in Nelore cattle in Brazil

Correlação genética entre características de eficiência alimentar e de carcaça em bovinos da raça Nelore no Brasil

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Highlights

Genetic correlation of residual feed intake with carcass traits was evaluated.
Selection of efficient animals does not affect subcutaneous fat deposition.
There is no genetic antagonism between feed efficiency traits and carcass traits.

Abstract

The aim was to estimate the genetic correlations between residual feed intake (RFI) and dry matter intake (DMI) with carcass finish (CF), rib eye area (REA), and marbling (MAR) of Nelore cattle. Data from 7,808 animals were considered. In addition, data from 2,261 females included in the complete database were also considered. Estimates of variance and covariance components, as well as heritabilities and genetic correlations were obtained by means of two-character analysis under animal model. Heritability estimates were found to be moderate for the RFI (0.22) and DMI (0.29) traits. It was observed that genetic correlation was close to zero for all traits, except between RFI and REA (-0.11). However, considering the female population, there was an increase in the estimated genetic correlation between RFI and DMI, although still a favorable genetic association of low magnitude (-0.30). There was also an increase in the genetic association of REA with RFI (-0.21). It can be concluded that the direct selection for RFI and DMI will not influence the CF, MAR, or REA of Nelore cattle. However, this selection may generate some favorable responses in MAR and REA in Nelore females.

Key words: Beef cattle. Carcass quality. Direct selection. Profitability.

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Resumo

Objetivou-se estimar as correlações genéticas entre consumo alimentar residual (CAR) e ingestão de matéria seca com acabamento de carcaça (ACAB), área de olho de lombo (AOL) e marmoreio (MAR) para bovinos da raça Nelore. Foram consideradas informações de 7.808 animais. Além disso foram consideradas informações de 2.261 animais fêmeas que compunham o banco de dados completo. As estimativas dos componentes de variâncias e covariâncias, bem como das herdabilidades e correlações genéticas foram obtidas por meio de análises bicaracterísticas sob modelo animal. Verificou-se que as estimativas de herdabilidade foram moderadas para as características de CAR (0,22) e IMS (0,29). Observou-se que as estimativas de correlação genética foram próximos a zero para todas as Características, exceto entre CAR e AOL (-0,11). No entanto, considerando a população de fêmeas, houve um aumento na estimativa de correlação genética com CAR e IMS, apesar de ainda ser uma associação genética favorável de baixa magnitude (-0,30). Também houve um aumento na associação genética da AOL com o CAR (-0,21). Concluiu-se, assim, que a seleção direta para o CAR e IMS não influenciará no ACAB, MAR e AOL de bovinos da raça Nelore. No entanto, essa seleção poderá gerar alguma resposta favorável em MAR e AOL em fêmeas Nelore.

Palavras-chave: Bovino de corte. Qualidade de carcaça. Rentabilidade. Seleção direta.

Introduction

Feed stands out as the main economic variable within a beef cattle production system, since it represents the highest variable cost (Zorzi et al., 2013). Feed efficiency is the ability of an animal to ingest less feed than expected without compromising productive performance (Gomes et al., 2012). Residual feed intake (RFI) is a measure proposed by Koch et al. (1963) and defined as the difference between observed food intake and that expected to support maintenance of body weight and growth. This is the most used feed efficiency trait in breeding programs (BP) of beef cattle, for the purpose of predicting the genetic values of animals in order to select animals that are more efficient in food consumption (Cantalapiedra-Hijar et al., 2018; Kenny et al., 2018).

According to previous studies, heritability estimates for RFI are moderate to high (Berry & Crowley, 2013; Santana et al., 2014; Moraes et al., 2019) indicating a rapid response to direct selection. Despite the attention RFI has received, there is no consensus on the genetic relationships between growth traits, carcass traits, and feed efficiency (Berry & Crowley, 2013; Torres-Vázquez et al., 2018).

It is important to emphasize that the genetic associations between feed efficiency and productive traits, of economic interest, should be estimated to generate the necessary information for the constitution of selection indices. In case of genetic antagonism of feed efficiency with carcass traits (yield and carcass finish), there may be a reduction of economic benefits achieved with the direct selection for RFI, since the quality of the bovine carcass is determinant in the commercial valuation of animals intended for slaughter (Kenny et al., 2018).

There are few studies that portray the genetic association of traits related to feed efficiency with those of the carcass in growing cattle, especially from the Nelore breed (Santana et al., 2014; Ceacero et al., 2016; Moraes et al., 2019), and none depicting the associations between genetic differences among these traits for heifers. Studies by Picard et al. (2019) and Baharun et al. (2021) noted differences in fat deposition in the carcass of females, therefore, it is essential to evaluate the genetic associations between the characteristics of feed efficiency and the carcass in different genders. These results contribute to the understanding of the different heritability estimates for this trait. Therefore, research involving carcass characteristics and RFI need to be expanded, as this field involves recent findings and divergences presented in the literature (Savietto et al., 2014).

Thus, it is essential to know the estimates of these genetic parameters in order to define the best genetic strategy to achieve the expected economic objectives. Therefore, this study aimed to estimate the genetic correlations between RFI and dry matter intake and carcass characteristics both in a population of Nelore cattle and in another population containing only Nelore females.

Material and Methods

Data from 7,808 cattle of the Nelore breed, of pure origin (PO) were used. They were aged between 240 and 685 days, sons of 397 bulls and 4,307 dams. The animals were evaluated in 142 trials or feed efficiency tests,

from 2011 to 2020, on 15 farms participating in the Nelore Brazil program of the National Association of Breeders and Researchers (*Associação Nacional de Criadores e Pesquisadores - ANCP*). The traits considered were residual feed intake (RFI, kg DM day⁻¹), dry matter intake (DMI, kg DM day⁻¹), rib eye area (REA, cm²), carcass finish (CF, mm), and marbling (MAR, %). It is important to emphasize that all the carcass information used in this study was also collected during feed efficiency trials, at the beginning or end of each trial, and the animals were subjected to the same environmental factors for all traits evaluated.

All data from the tests were collected according to the criteria of the guideline manual for execution of feed efficiency tests (Mendes et al., 2020) in Brazil. Thus, the evaluated animals comprised a contemporary group (CG), presenting the same breed, same birth season (maximum age interval of 90 days), same sex, and previous conditions of feeding and management lot. In terms of age, the animals were evaluated at a minimum age of eight months at the beginning of the test and a maximum age of 24 months at the end of the test.

The DMI characteristic was calculated as the average of all information obtained daily for each animal through the use of electronic troughs. The RFI characteristic was measured using the equation described by Koch et al. (1963):

$$RFI = DMI_{obs} - DMI_{est}$$

where DMI_{obs} represents the average dry matter intake observed and DMI_{est} is the expected dry matter intake.

According to Koch et al. (1963), the DMI_{est} is obtained through the following formula:

$$DMI_{est} = \beta_0 + (\beta_1 \times ADG) + (\beta_2 \times MMW)$$

where information regarding the average observed dry matter intake (DMI_{obs}), average daily weight gain (ADG), and mean metabolic live weight (MMW) from all test animals is used to predict the coefficients (β) of the multiple linear regression equation.

The average daily weight gain (ADG) was estimated by the linear regression equation:

$$Y_i = \alpha + \beta \times DET_i + E_i$$

where Y_i is the weight of the animal at the i th observation, α is the intercept, β is the linear regression coefficient and represents the ADG, DET_i is the day under test at the i th observation, and E_i is the random error associated with each observation. The MMW was calculated as:

$$MMW = [\alpha + \beta \times (DET \div 2)]^{0,75}$$

where α is the intercept of the equation, β is the linear regression coefficient, and DET represents the days under test.

In order to measure the carcass characteristics, ultrasound images were collected using an ALOKA 500 v device, with a 17.2 cm, 3.5 MHz linear probe and an acoustic

coupler in conjunction with an image capture system (Blackbox, Bionitrics, Inc., Ames, IA, USA).

The rib eye area (REA) was measured as the cross-sectional area of the *Longissimus dorsi* muscle between the twelfth and thirteenth ribs. Subcutaneous fat thickness (SFT) and marbling (MAR) were measured in the *Longissimus dorsi* muscle between the twelfth and thirteenth ribs. The subcutaneous rump fat thickness (SRFT) was measured between the ilium and ischium bones at the intersection of the *Gluteus medius* and *Biceps femoris* muscles (Yokoo et al., 2008). These images were collected and interpreted by the laboratory responsible for data quality assurance. The carcass finish (CF) characteristic was calculated as the sum of the weights at 0.35 for SFT and 0.65 for SRFT (Associação Nacional dos Criadores e Pesquisadores [ANCP], 2022).

For the structuring of the data files, the Statistical Analysis System program (Statistical Analysis System Institute [SAS Institute Inc.], 2004) was used. For the verification of environmental effects, the GLM and RE procedures of the SAS software were considered. For analysis purposes with all animals evaluated and also with a female-only population, two files were generated: (a) Nellore population (males and females); and (b) Nellore female population. The descriptive analysis of the characteristics studied in the Nellore cattle population is presented in Table 1.

Table 1
Descriptive analysis of residual feed intake (RFI), dry matter intake (DMI), rib eye area (REA), marbling (MAR), and carcass finish (CF) of Nellore cattle

Variable	N	Mean	SD	CV (%)	Min	Max
<i>Complete database</i>						
RFI (kg DM day ⁻¹)	7,808	0.00	0.72	NE	-4.93	4.69
DMI (kg DM day ⁻¹)	7,808	8.45	1.98	23.51	3.32	18.75
REA (cm ²)	5,158	68.21	10.79	15.82	37.18	122.34
MAR (%)	3,857	2.62	1.02	38.99	1.00	7.73
CF (mm)	5,041	6.26	2.97	47.44	1.00	23.45
<i>Female database</i>						
RFI (kg DM day ⁻¹)	2,261	0.000	0.76	NE	-3.78	2.68
DMI (kg DM day ⁻¹)	2,261	7.95	1.58	19.95	3.44	12.88
REA (cm ²)	1,830	66.91	10.54	15.76	37.18	103.35
MAR (%)	1,485	3.02	1.17	38.88	1.00	7.73
CF (mm)	1,841	8.39	3.68	43.86	1.00	23.45

SD: standard deviation; CV: coefficient of variation; NE: not evaluated; DM: dry matter.

In order to verify the association between feed efficiency and carcass traits in a population of only Nellore females, the following set of data, described as the female database in Table 1, was also used. It should be noted that the population of Nellore females studied came from herds that prioritize selection for sexual precocity, obtaining significant genetic progress over generations.

The estimates of variance and covariance components, as well as heritabilities and genetic correlations were obtained by means of two-characteristic analysis under animal model, considering the Derivative Free Restrict Maximum Likelihood methodology, through the Multiple Traits Derivate Free Restrict Maximum Likelihood (MTDFREML) application developed by Boldman et al. (1995). The complete model can be represented in matrix notation as:

$$Y = X\beta + Zu + e$$

where Y is the vector of observations (evaluated characteristics), β is the vector of fixed effects (environmental effects), u is the vector of random effects (genetic values obtained for each animal), e corresponds to the vector of residual random effects, X and Z are the incidence matrices that relate the observations to the fixed effects and the direct additive genetic random effect, respectively. The genealogy file included 30,918 animals of the Nellore breed. The kinship matrix was built up to the generation of founder animals.

According to Lopes et al. (2005), heritability is a parameter that varies from zero to one or from zero to 100%. It is considered low when it is between 0-0.20, moderate when between 0.20-0.40, and high when above 0.40. Correlations with correlation coefficient

values close to 0.5 (regardless of whether positive or negative) are medians; while those with values close to zero are very low, which indicate practically no correlation between the characteristics. Correlations with a value close to one are high (of high magnitude/intensity), according to Falconer (1960).

For the RFI and DMI traits, the fixed effects considered the CG of contemporary animals, the cow's age class at calving (CACC), and the animal's age as a covariate of linear effect. For the CF trait, the fixed effects were the same as for DMI and RFI; however, without the inclusion of the CACC.

For the REA and MAR, the CG and the age of the animal were considered as covariates of linear and quadratic effect. For the formation of CG, the farm of origin, the feed efficiency test, and the age group of animals with a maximum interval of 90 days were considered.

The CACC was constituted according to the following criteria: cow's age at calving up to 27 months (class 1); from 28 to 47 months (class 2); from 48 to 72 months (class 3); from 72 to 120 months (class 4); above 120 months (class 5).

In the analysis to estimate the variance and covariance components of the direct and residual additive genetic effects, using multicharacter models between carcass traits and feed efficiency, the following two-character matrix model was used:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1\beta_1 & Z_1u_1 \\ X_2\beta_2 & Z_2u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

wherein:

Y_i = vector of characteristic observations;

β_i = the vector of fixed effects;

u_i = vector of the direct additive genetic effects associated with the matrices X_i and Z_i , respectively;

e_i = vector of residual effects. The hopes of Y_i are $X_i\beta_i$.

The variance and covariance structure of the random effects matrix was assumed as:

$$\text{Var} \begin{bmatrix} u_1 \\ u_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{u_1}^2 & 0 & 0 & 0 \\ A\sigma_{u_1u_2} & A\sigma_{u_2}^2 & 0 & 0 \\ 0 & 0 & I\sigma_{e_1}^2 & 0 \\ 0 & 0 & I\sigma_{e_1e_2} & I\sigma_{e_2}^2 \end{bmatrix}$$

wherein:

$\sigma_{u_1}^2$ = direct additive genetic variance for characteristic 1;

$\sigma_{u_2}^2$ = direct additive genetic variance for characteristic 2;

$\sigma_{e_1}^2$ = variance of residual effects of characteristic 1

$\sigma_{e_2}^2$ = variance of residual effects of characteristic 2;

A = parentage matrix numerator;

I = appropriate identity matrix;

$\sigma_{u_1u_2}$ = genetic covariance between direct genetic effects for traits 1 and 2;

$\sigma_{e_1e_2}$ = covariance between residual effects for traits 1 and 2.

Results and Discussion

The highest coefficient of variation in the characteristics of CF and MAR are shown in Table 1, which can be explained by the difference in age of the animals that comprised the evaluation database, since

body composition is influenced by several factors, including animal age (Osório et al., 2012).

It was found (Table 2) that the estimated heritability for the DMI (0.29) and RFI (0.22) were of moderate magnitude, which proves the existence of genetic variability in the evaluated Nelore population. It was observed that the estimated heritability for the DMI was higher than that obtained for the RFI, indicating more significant genetic gains through the selection of DMI in relation

to RFI. This higher estimate for the DMI was expected, since the calculation of RFI is adjusted for the MMW and ADG of the animal, and in comparison, to the lot of the animals evaluated. Thus, the RFI is a composite trait that may lead to reduced heritability estimates, while the DMI is measured directly on the animal, without adjustments with other variables. In this context, one can suggest the inclusion of DMI in the composition of selection indices, seeking animals with high performance and low DMI, characterized as efficient.

Table 2

Estimates of additive genetic variance (α_a^2), residual variance (α_r^2), phenotypic variance (α_p^2), and heritability (h^2) of residual feed intake (RFI), dry matter intake (DMI), rib eye area (REA), marbling (MAR), and carcass finish (CF) of Nelore population

Characteristic	α_a^2	α_r^2	α_p^2	h^2
RFI	0.12	0.42	0.54	0.22
DMI	0.27	0.66	0.94	0.29
REA	11.45	36.62	48.07	0.24
MAR	0.17	0.35	0.52	0.33
CF	0.70	2.50	3.20	0.22

The moderate heritability estimate obtained in this study for RFI corroborates that found by Ceacero et al. (2016), considering information on Nelore cattle. However, in other experiments with cattle of the same breed, high magnitude heritability estimates were obtained, ranging from 0.30 to 0.37 (Santana et al., 2014; Grion et al., 2014; Grigoletto et al., 2017; Moraes et al., 2019). In taurine breeds, moderate to high magnitude heritability estimates have also been reported, with values of 0.22, 0.28, and 0.50, respectively (Zhang et al., 2017; Polizel et al., 2018).

These divergences in heritability can be attributed to the tendency for heritability estimates from smaller samples or samples with a weak family structure (with higher standard error) to have higher values than heritability estimates from larger samples (Del Claro et al., 2012). In the current study, RFI heritabilities were estimated based on information from 7,808 animals, resulting in a lower estimate compared to these other studies. In addition, for Moraes et al. (2019), heritability estimates were based on single trait analyses, resulting in higher values than those estimated in multitrait analyses.

The estimates of variance components and heritability for feed efficiency and carcass traits obtained in a population of Nellore females are presented in Table 3. It

was observed that the values obtained from this population related to DMI and RFI traits were 0.30 and 0.22, respectively.

Table 3

Estimates of additive genetic variance (α_a^2), residual variance (α_r^2), phenotypic variance (α_p^2), and heritability (h^2) of residual feed intake (RFI), dry matter intake (DMI), rib eye area (REA), marbling (MAR), and carcass finish (CF) of Nellore females

Characteristic	α_a^2	α_r^2	α_p^2	h^2
RFI	0.14	0.47	0.61	0.22
DMI	0.29	0.66	0.95	0.30
REA	9.48	33.71	43.19	0.22
MAR	0.36	0.37	0.73	0.49
CF	1.67	4.66	6.33	0.26

Regarding the heritability estimates for CF, moderate values were observed for the Nellore population (0.22; Table 2) and Nellore female population (0.26; Table 3), corroborating the heritability estimates obtained in studies with Nellore animals (Faria et al., 2015). However, the heritability estimates obtained in this study were lower than estimated by Moraes et al. (2019), who reported an heritability estimate of 0.32 for CF, when analyzing data from Nellore males, suggesting that the higher estimate obtained may be due to the selection of this herd for carcass traits, presenting higher additive genetic variance for fat deposition in the carcass.

Moderate values of 0.24 and 0.22 were observed in the heritability estimates for REA of the Nellore population (Table 2) and the Nellore female population (Table 3), respectively. A heritability estimate of 0.35 (high magnitude) for REA was reported by

Santana et al. (2014). Moraes et al. (2019) estimated a heritability of 0.46 for this trait, resulting from herd selection for carcass traits. It is important to highlight that the number of animals evaluated by these authors was half that evaluated in the present study, so it is likely that this divergence of estimates is due to the small numbers of records and data structure.

When comparing the heritability estimates for MAR and CF from the database of Nellore cattle (Table 2) with the heritability estimates for these same traits evaluated in the population of Nellore females (Table 3), we noted an increase in the heritability estimate obtained in the evaluation of females. The heritability estimate for MAR in the Nellore population (Table 2) was 0.33 and in the Nellore female population (Table 3) it was 0.49, showing estimates of high magnitude. This higher heritability estimate (Table 3) obtained in the female population

for MAR can be explained by the composition of fatty acids in females used in the formation of subcutaneous fat and MAR, and the presence of genes that have the highest fat storage capacity (Reddy et al., 2015). Picard et al. (2019) and Baharun et al. (2021) found that sexual hormones affect both hyperplasia and hypertrophy of intramuscular adipocytes in cattle. Male hormones inhibit the differentiation of intramuscular adipocytes and decrease the secretion of an adipose tissue-specific secretory protein. While progesterone, a female hormone, upregulates the expression of a gene, which provides a potential mechanism for the lipogenic actions of this tissue. These results contribute to the understanding of the different heritability estimates for this trait.

The heritability estimates of medium to high magnitude reported for MAR is reaffirmed by the work found in the literature for Nellore (0.47) (Moraes et al., 2019) and Angus (0.37) (Mao et al., 2013). Thus, these results show that genetic gains are obtained for these characteristics when used as selection criteria, inferring, therefore, that additive genetics is responsible for a large part of the total variation of the characteristic, also subject to selection, considering its variability. Chen et al. (2019) reported the relevance of greater intramuscular fat content, justifying that this greater fat deposition is one of the most important factors that influences the palatability and quality of beef. MAR is positively correlated with meat sensory characteristics, including juiciness, color, tenderness, and flavor (Stewart et al., 2021). In view of this, it is highlighted that the selection of females favorable to this trait would have a greater impact on the quality and palatability of the meat when compared

to the selection of males also favorable to this trait, since females have a greater effect of the direct additive genes than males.

The estimated heritabilities in this study for carcass traits, DMI, and RFI for the evaluations of the database of Nellore cattle (Table 2) as well as the database composed of Nellore females, were lower than those estimated in several works on Nellore cattle (Grion et al., 2014; Santana et al., 2014; Faria et al., 2015; Moraes et al., 2019). This can be explained by differences in carcass composition, since males generally produce heavier and leaner carcasses compared to heifers, which have less muscle and more fat deposition (Nogalski et al., 2018). Irshad et al. (2013) defended those estrogens produced by the ovaries as generally having little or no effect on skeletal muscle protein synthesis but being effective in promoting body fat deposition.

The genetic correlation coefficients between traits related to feed efficiency (RFI and DMI) and carcass traits (CF, REA, and MAR) are presented in Table 4. It was found that the estimates were of low magnitude, with values close to zero for all traits, except between RFI and REA. In general, the results found in this study regarding the genetic correlation estimates for RFI and CF were of low magnitude for both the Nellore population and Nellore female population (Table 4), corroborating the findings of Mao et al. (2013), who obtained a genetic correlation estimate of 0.02 in Angus steers. This estimate found by the authors also showed that there is no genetic association between RFI and CF in this breed. In the studies of Fitzsimons et al. (2014) with Simmental cattle, the authors also did not find a genetic association of RFI with CF. Similarly, Gomes et al. (2012) did not

observe a genetic association of RFI with carcass fat deposition in Nellore cattle. In a study conducted in Nellore herd selection, Moraes et al. (2019) found a favorable and low magnitude (-0.11) genetic correlation

between RFI and CF. Novo et al. (2021) also found a negative correlation (-0.23) in Senepol cattle. In general, these results infer that the selection for RFI and DMI does not alter the carcass traits in Nellore cattle.

Table 4

Estimates of genetic correlations of residual feed intake (RFI) and dry matter intake (DMI) with rib eye area (REA), marbling (MAR), and carcass finish (CF) of Nellore cattle

Characteristic	RFI	DMI
<i>Complete database</i>		
REA	-0.11	0.05
MAR	-0.07	-0.07
CF	0.05	0.06
<i>Female database</i>		
REA	-0.21	0.05
MAR	-0.30	-0.30
CF	0.03	0.02

Some antagonistic results to those found in this study have been observed in the literature. The study conducted by Ceacero et al. (2016) in a Nellore herd considered 955 RFI observations, 2,285 SFT observations, and 1,817 SRFT observations. In the evaluated population from a single herd, the genetic correlation estimates were 0.37 and 0.30 for RFI with SFT and SRFT, respectively. The authors concluded that there is medium magnitude genetic antagonism between RFI and carcass fat deposition. However, when considering the information on RFI adjusted for fat deposition, the genetic correlation coefficients remained at practically the same magnitude, which was not expected and can be explained by the genetic profile of the herd studied. A similar moderate genetic correlation (0.42) between RFI and carcass fat in Charolais steers was found. These

discrepant estimates between RFI and CF with the present study may be explained by the genetic differences that exist between beef cattle breeds for CF.

The estimates of genetic correlation between DMI and CF were of low magnitude in this study (Table 4), which indicates that there are practically no genes in pleiotropy with DMI and CF. Therefore, the selection of efficient animals for DMI would not imply any increase or decrease in fat thickness in these cattle, emphasizing the importance of building selection indices that add desirable carcass characteristics. Some contrary results were reported by Mao et al. (2013), who found a genetic correlation estimate of 0.36 for fat deposition with DMI in Angus, and 0.44 in Charolais, corroborating the studies of Nkrumah et al. (2007), who estimated a

correlation of 0.49 with fat deposition in the carcass of taurine cattle. Ceacero et al. (2016), in a study with a Nellore herd, reported correlations of DMI with SFT and SRFT of 0.29 and 0.39, respectively.

The estimates of genetic correlations between RFI and REA (-0.21) in Nellore females (Table 4) were close (-0.30) to those of Berry and Crowley (2013), in a meta-analysis with beef cattle. These results are desirable for selection because some genes that influence feed efficiency improvement (negative RFI), also lead to increased muscle area (REA), an indicator of carcass yield (Yokoo et al., 2008).

In contrast to these studies, Mao et al. (2013) found a positive correlation in Charolais (0.19) and in Angus (0.09), to those found by Novo et al. (2021) in Senepol heifers (0.19). Studies by Sun et al. (2019) suggest a differential regulation of gene expression linked to muscle, adipose tissue, and rumen tissue deposition in efficient feeding animals, as well as the same mechanisms in the last two at the epithelial level. This can improve nutrient absorption, as the rumen is responsible for the uptake of volatile fatty acids, a primary and metabolizable energy source in ruminants.

Regarding the genetic association of RFI with REA, a negative genetic correlation of -0.11 was observed (Table 4). However, despite being a favorable genetic association of low magnitude, only 1.21% of the additive effect genes affecting RFI have an influence on REA. Thus, it can be inferred that the selection of efficient animals (negative RFI) leads to some improvement in carcass yield of animals, but it is not significant. This is because when selecting efficient animals for RFI indirectly at low intensity, genes for better

REA will be selected, therefore, to obtain a more qualified genetic progress for feed efficiency and carcass yield, selection indices for these two traits must be considered.

As shown in Table 4, there is practically no genetic association of RFI and DMI with CF. The estimated values indicate that only 0.25% and 0.36% of additive effect genes influence the RFI and DMI, respectively, also affecting CF. This result shows that there is no genetic antagonism between these characteristics, so it can be inferred that the selection of efficient animals does not lead to reduced fat deposition in the carcasses of Nellore cattle.

A negative genetic correlation estimate (-0.07) regarding MAR was observed, in which 0.49% of the additive effect genes that interfere in the RFI and DMI characteristics also influence MAR. Thus, despite being a favorable correlation (negative), the selection of efficient animals does not cause significant changes in the MAR of Nellore cattle.

The genetic associations of RFI and DMI with the carcass traits (CF, REA, and MAR), considering the population of Nellore females, are also presented in Table 4. For the trait CF, the estimated genetic correlation with RFI and DMI was of low magnitude, 0.03 and 0.02, respectively. Thus, the selection of efficient females does not cause changes in fat deposition in the carcass, as it was confirmed that there was practically no genetic association between these characteristics. Regarding MAR, the genetic correlation estimates with RFI and DMI was -0.30, a favorable association of low magnitude. Thus, the selection of efficient females (negative RFI and low DMI) may lead to some increase in carcass MAR.

In the evaluation of the genetic association between DMI and REA (Table 4), some previous results were different from those obtained in this previously. Mao et al. (2013) estimated values of 0.16 in Charolais and 0.36 in Angus, whereas Nkrumah et al. (2007) found values of 0.21 and Ceacero et al. (2016) estimated 0.40. It was reported by Del Claro et al. (2012) that more than 60% of the variation in RFI estimates in a study with a meta-analysis of 22 articles was due to the factors of sex and breed of these animals. The low magnitude genetic association between RFI and MAR (-0.07) obtained in the Nellore population is reaffirmed in the work of Mao et al. (2013), who estimated a low magnitude genetic correlation between both traits for Angus (0.18) and Charolais (0.14) animals. Moraes et al. (2019) also found genetic associations between RFI and MAR of low magnitude (0.10) for Nellore cattle, suggesting that genes that present an influence on efficient animals have no relationship with genes for intramuscular fat deposition.

However, Nkrumah et al. (2007) estimated genetic correlations between feed efficiency and carcass traits of Angus and Charolais crossbred animals of medium magnitude (0.32), as did Torres-Vázquez et al. (2018), who evaluated Angus animals in Australia from 2013 to 2017 and estimated a genetic correlation of 0.31, inferring that selecting efficient animals can lead to lower MAR deposition, although not very expressive. The genetic correlation estimate found in this study for the Nellore female population (Table 4) was favorable and of medium magnitude (-0.30) between RFI and MAR, pointing out that selecting efficient animals may influence a higher intramuscular fat deposition.

As shown in Table 4, there is practically no genetic association of RFI and DMI with CF. The estimated values indicate that only 0.25% and 0.36% of additive effect genes influence the RFI and DMI, respectively, also affecting CF. This result shows that there is no genetic antagonism between these characteristics, so it can be inferred that the selection of more efficient animals does not lead to reduced fat deposition in the carcasses of Nellore cattle.

In the female population (Table 4), the genetic association of REA with RFI (-0.21) presented a low magnitude, which indicates a favorable response of selecting efficient animals with improved carcass yield. However, it should be emphasized that such changes were minor.

Given the results obtained in this study, it was possible to observe that RFI is not antagonistic to carcass traits, such as CF, MAR, and REA. However, in Nellore females the selection for RFI may generate some favorable response in deposition of both intramuscular fat and muscle tissue, since estimates of favorable genetic correlations of low magnitude for RFI with MAR and REA were found. In this case, the inclusion of RFI as a selection criterion will not develop more productive animals with higher carcass quality for the producer. Thus, it is necessary that the breeder contemplates a selection index that adds desirable characteristics for the objective of production, correlated with an economic impact.

Conclusion

Direct selection for RFI and DMI will not influence subcutaneous fat deposition, intramuscular fat, or carcass yield in Nellore

cattle. However, selection for RFI may generate some favorable response in intramuscular fat deposition in the Nelore female population. There is no genetic antagonism between feed efficiency traits and carcass traits. Therefore, the selection of efficient animals will provide greater profitability to the producer due to the reduction of feed costs, without leading to a loss of genetic carcass characteristics.

Acknowledgments

To the breeders and to ANCP for the data provided and to FAPEMIG for the financial support.

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