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Is apparent digestibility associated with residual feed intake and enteric methane emission in Nellore cattle?

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ABSTRACT - This study was conducted to evaluate the relationship among digestibility, residual feed intake (RFI), and enteric methane emission in growing Nellore cattle (*Bos indicus*) divergently classified based on RFI phenotype and breeding value (EBV-RFI). Animals (n = 122) subjected to performance testing (forage:concentrate ratio of 60:40) in two test groups were classified based on RFI. A sample of 80 animals classified as low (−0.748±0.076 kg DM/day) or high (0.775±0.075 kg DM/day) RFI was evaluated regarding feed compounds digestibility, fecal excretion, and methane emission (CH_4, g/day). Statistical mixed models included fixed effects of RFI (or EBV-RFI), linear effect of initial age as covariate, and the random effects of the test group. There was no difference in the digestibility of feed compounds between the most and least efficient animals. However, dry matter intake (DMI; 6.92 vs. 8.66 kg DM/day) and feed conversion (7.93 vs. 9.42 kg/kg) were lesser in low RFI animals. On average, low RFI animals emitted 14.3 g less CH_4 per day (174 vs. 188 g CH_4/day); however, CH_4 emission expressed as g/kg DMI (23.1 vs. 20.1) and the percentage of gross energy intake lost as CH_4 (8.13 vs. 7.08%) were greater for these animals. These results showed the benefits of using more feed efficient animals in the beef production chain, i.e., animals that exhibit lower feed intake, lower fecal excretion, and lower enteric methane emission without differences in weight gain or body weight. However, the variations in feed efficiency among them cannot be explained by differences in dry matter or feed compounds digestibility. More efficient animals emit less enteric methane than less efficient animals, probably as a result of lower DMI.

Keywords: beef cattle, digestion, feed efficiency, greenhouse gases emissions

1. Introduction

The growth of the world population and the global demand for food raise concerns regarding climate change, since the increase in the emission of greenhouse gases from agricultural production systems is proportional to the increase in food production (O'Mara, 2011). Enteric methane emissions from ruminants and manure management practices account for over 32% of global anthropogenic methane emissions. The production of enteric methane is a natural process for ruminants, and the enteric methane emission from cattle represents about 11.17% of total anthropogenic methane emissions (United Nations Environment Programme, 2021).

Low residual feed intake (RFI) detects animals that consume less dry matter (DM) adjusted for weight gain and metabolic body weight. Animals exhibiting lower RFI demonstrate a more efficient conversion of consumed feed into body weight, resulting in reduced enteric fermentation and, consequently, lower methane production. Therefore, RFI may be a potential measure to identify animals that emit less methane (CH_4, g/day) without affecting production (Hegarty et al., 2007; Jones et al., 2011; Manafiazar et al., 2020).

Differences in digestibility may explain the differences in RFI among contemporaneous cattle (Herd and Arthur, 2009). Studies have reported a negative correlation of RFI with DM digestibility (Nkrumah et al., 2006; Krueger et al., 2009; Oliveira et al., 2016; Herd et al., 2019), as well as with the digestibility of other feed compounds (Johnson et al., 2019), i.e., more efficient animals in terms of reducing feed intake without changing the average daily gain (ADG) exhibit greater digestibility. However, other studies failed to show this relationship (Lawrence et al., 2011, 2012; Rius et al., 2012) or even reported a positive correlation between digestibility and RFI (Batalha et al., 2020). It is not clear whether the increase in the digestive capacity of efficient animals (low RFI) is inherent to the individual or is due to the slower passage of digesta through the rumen caused by lower dry matter intake (DMI) when compared with inefficient animals (high RFI) (Kenny et al., 2018).

The emission of methane resulting from the digestive process reduces the efficiency of energy utilization and performance of animals (Subepang et al., 2019). Methane emission expressed as a function of gross energy intake in beef cattle is around 7.01±2.50% (varying from 5.97 to 8.79% in low-forage diets to all-forage diets) (Congio et al., 2023). More efficient diet utilization is particularly important, since it reduces feed intake and methane emission for the same production level (Fitzsimons et al., 2013), as well as fecal production (Herd et al., 2002).

The hypothesis of this study is that efficient animals (low RFI) exhibit greater digestibility and, consequently, greater utilization of feed compounds (DM, crude protein (CP), ether extract (EE)) associated with lower enteric methane emission than inefficient animals (the most efficient tercile compared with the least efficient tercile). The novelty of the present study, in relation to those reviewed by Kenny et al. (2018) and Cantalapiedra-Hijar et al. (2018), whose studies were based on *Bos taurus* fed low forage diet, is that it involves a considerable number of animals of indicine cattle fed a high forage diet. The objective of the present study was to evaluate the relationship between digestibility, RFI, and enteric methane emission in growing Nellore cattle (*Bos indicus*) divergently classified based on RFI phenotypes and on RFI breeding value.

2. Material and Methods

The study was approved by the institutional Ethics Committee on Animal Experimentation (Protocol 86 Number 278–19), Nova Odessa, SP, Brazil. The animals included in the study were from a Nellore breeding program established in 1980 in Sertãozinho, SP, Brazil (21°10' South latitude and 48°5' West longitude). Since 2004, the animals have been measured for feed efficiency traits after weaning (Benfica et al., 2020). The climate is wet tropical with a rainy season in summer from October to March, receiving 80.5% of the total rainfall (1,485 mm), and a dry season in winter from April to September with a precipitation of 359 mm. Except during performance tests, animals were on *Brachiaria brizantha* (*Urochloa* spp) pasture.

2.1. Performance test

A total of 122 contemporary non-castrated Nellore males born in 2018 were evaluated in two consecutive test groups (TG1, n = 60, mean±standard deviation [SD] of 249±31.1 days of age and

224±33.2 kg of live weight at the beginning of the test; TG2, n = 62, mean±SD 329±24.1 days of age and 285±48.6 kg of live weight at the beginning of the test). The performance tests lasted 83 days, preceded by 28 days of adaptation to the diet. The animals were weighed every 15 days without previous fasting as recommended by Archer et al. (1997), always before morning feed. They were kept in a collective pen equipped with ten electronic feed bunks (GrowSafe System®, Airdrie-AB, Canada) for the automatic recording of individual daily feed intake, with *ad libitum* access to diet and water. GrowSafe system is a set of feed bunks equipped with load bars to measure feed disappearance and with an antenna within each feed bunk to record the presence of the animal through detection of an electronic identification tag. Assigned feed disappearance (AFD) rates were computed daily by the GrowSafe system for each feed bunk to assess data quality, and the daily intake records were discarded when AFD was less than 90%.

The diet (Table 1) was formulated for an ADG of 1,100 kg/animal (NRC, 2000) and supplied twice a day (09:00 and 15:00 h) as a total mixed ration. Forage was weekly sampled, while concentrate feeds were monthly sampled for quantification of the DM content of the diet and chemical analysis. The metabolizable energy was calculated by multiplying the digestible energy intake by 0.82 (NRC, 2000).

Table 1 - Ingredients and chemical composition of the experimental diet

Item	
Ingredients (g/kg dry matter (DM))	
Sorghum silage	600
Ground corn	250
Soybean meal	130
Mineral premix[1]	17.5
Urea	2.5
Chemical composition (g/kg DM)	
Dry matter (g/kg)	517
Organic matter	954
Crude protein	112
Neutral detergent fiber	406
Acid detergent fiber	244
Ether extract	20.7
Ash	46.3
Non-fibrous carbohydrates	416
Gross energy (MJ/kg of DM)	15.8
Metabolizable energy (MJ/kg of DM)	8.9

[1] Composition: phosphorus, 80 g/kg; calcium, 140 g/kg; sodium, 137.2 g/kg; sulfur, 12 g/kg; copper, 1,600 mg/kg; cobalt, 210 mg/kg; iodine, 180 mg/kg; manganese, 1,400 mg/kg; selenium, 27 mg/kg; zinc, 4,500 mg/kg; nickel, 11 mg/kg; fluoride, 800 mg/kg.

Dry matter intake (kg/day) was obtained as the average of all valid days (66 valid days for TG1 and for TG2). Average daily gain (kg/day) was estimated by the linear regression coefficient of weights on days in test (DIT) according to the equation 1:

$$y_i = \alpha + \beta \times DIT_i + \varepsilon_i, \quad (1)$$

in which y_i is the weight of the animal in the i-th observation; α is the intercept representing the initial body weight of the animal (BW_i); β is the linear regression coefficient representing ADG; DIT_i is the day in test in the i-th observation; and ε_i is the random error associated with each observation.

Midpoint body weight (mBW, kg) was estimated according to equation 2:

$$mBW = BW_i + (0.5\ DOT \times ADG), \quad (2)$$

in which DOT is the total of days on test; and ADG is the average daily gain. Midpoint metabolic body weight ($mBW^{0.75}$, kg) was calculated as $(mBW)^{0.75}$.

The RFI was calculated as the difference between observed DMI and predicted DMI (DMIp), which was estimated by multiple regression of DMI on ADG and $mBW^{0.75}$ within each test group using the GLM procedure of SAS software (Statistical Analysis System, version 9.3), according to equation 3 for TG1 and equation 4 for TG2:

$$DMIp = 1.298\ (\pm 1.107) + 2.706\ (\pm 0.860) \times ADG + 0.060\ (\pm 0.024) \times mBW^{0.75}\ (R^2 = 0.53) \quad (3)$$

$$DMIp = -0.055\ (\pm 0.719) + 2.151\ (\pm 0.584) \times ADG + 0.087\ (\pm 0.013) \times mBW^{0.75}\ (R^2 = 0.75) \quad (4)$$

Feed conversion ratio was obtained as the ratio between DMI and ADG. At the end of the performance tests, the animals were classified based on RFI. Forty animals of each extreme tercile were used for the analysis of feed compounds digestibility (DM, CP, EE, neutral detergent fiber, gross energy, and total digestible nutrients) and enteric methane emission: low RFI (mean: −0.774±0.068 kg DM/day; 17 animals from TG1 and 23 animals from TG2) and high RFI (mean: 0.782±0.068 kg DM/day; 22 animals from TG1 and 18 animals from TG2). Next, the breeding values for RFI (EBV-RFI) were estimated for these animals in a genetic evaluation of 1,878 animals with the RFI phenotype, 2,256 animals with genomic data, and 12,594 animals in the relationship matrix using the single-step GBLUP method, as described by Benfica et al. (2020). Since the herd has been selected for lower RFI and higher body weight since 2008, the EBV-RFI was expressed as a deviation of the average EBV-RFI of all animals born in 2008 (−0.0384 kg DM/day), and there were more negative EBV-RFI animals (n = 56) than positive EBV-RFI animals (n = 24).

2.2. Digestibility estimates

To estimate fecal excretion using indigestible neutral detergent fiber (iNDF) as the internal marker, diurnal feces samples were collected from the rectum of the animals for two consecutive days at defined times (7:30 and 13:30 h, and 10:30 and 16:30 h) (Sampaio et al., 2011) in the first (initial period) and last week (final period) of the performance test of each test group. Dietary ingredients were also collected in both periods (initial and final period). The feces samples (300 g/animal) and dietary ingredients were stored at −20 °C and then pre-dried in a forced ventilation oven at 60±5 °C for 72 h and ground in a Wiley mill (2-mm sieves). For the determination of iNDF, dietary ingredient and fecal samples were incubated (six replicates per period + one blank) in four Nellore animals fed the same diet as used in the performance test by the *in situ* non-woven textile bag method (TNT; 100 g/m^2, 4 × 5 cm at a proportion of 25 mg DM/cm^2 surface area) for 264 h, as described by Casali et al. (2008). Subsequently, the bags were removed, washed until completely whitened, and then subjected to extraction in neutral detergent (Mertens, 2002), as recommended by the manufacturer, using a fiber analyzer (TE 149; TECNAL, Piracicaba, SP, Brazil), dried in an oven at 105 °C for 2 h, placed in desiccators, and weighed for quantification of iNDF.

Total daily fecal excretion of the animal (FE, g DM/day) was estimated with the following equation (equation 5), as described by Detmann et al. (2001):

$$FE = IM/[M], \quad (5)$$

in which IM is the daily intake of the internal marker (g DM/day) of the percentage of dietary iNDF and DMI during fecal collection (DMIc), and [M] is the content of the marker in the fecal sample (g/g). The DMIc was obtained as the average of feed intake during each week (period) of the fecal collection (four days prior to collection, two days of collection, and one day post-collection). The FE was expressed as the average of the initial and final periods.

Apparent DM and feed compounds digestibility (D, g/kg) was obtained and expressed as the average apparent digestibility of the initial and final periods with the following equation (equation 6), as described by Cochran and Galyean (1994):

$$D = [(consumed - excreted)/consumed] \quad (6)$$

2.3. Measurement of enteric methane emission

Enteric methane emission (CH_4, g/day) was estimated using the sulfur hexafluoride (SF_6) tracer gas technique, adapted to the local conditions, following the recommendations of Berndt et al. (2014). The animals were allowed to adapt for 10 days to the sampling apparatus, leather halter, and light saddle. Permeation tubes (brass capsule) containing SF_6 were maintained in an oven at 39 °C and calibrated by weekly weighing on an analytical scale for eight weeks before the beginning of sampling to ensure constant and linear emission of SF_6. Eighty capsules with an average release of 4.598±0.040 and 2.460±0.039 mg SF_6/day in the first (TG1) and second (TG2) samplings, respectively, were selected and administered five days before the beginning of the gas sampling period.

Starting between 7:30 and 8:00 h, methane was collected on consecutive days [June 24 to July 02, 2019 for TG1; October 15 to 23, 2019 for TG2], with exchange of the cylinder every 24 h to ensure five samples per animal. The collection was extended up to eight days due to losses. The gases expelled from the mouth and nostrils of the animals were captured in a controlled and continuous manner through a stainless-steel capillary tube, which was calibrated as described by Deighton et al. (2014) and protected by a flexible hose fixed to the halter and connected to the collection cylinder (Figure 1).

Figure 1 - Uncastrated Nellore males, in a feed efficiency test group, with the apparatus (halter, saddle, and cylinder) for methane collection by sulfur hexafluoride (SF6) tracer gas technique.

The collection cylinder was subjected to vacuum (<0.03-0.50 atm) and attached to the animal's back. The pressures (initial and final) of the cylinders were monitored daily to ensure the quality of the sample. Environmental gas concentrations were collected daily in two cylinders every 24 h in the same environment as the animals. At the end of each sampling period, CH_4 concentrations (ppm, parts per million) were measured by gas chromatograph (HP6890, Agilent, Wilmington, DE, USA) equipped with a flame ionization detector at 280 °C, helium as carrier gas, and megabore column (HP-Plot Al_2O_3 0.53 mm × 30 m × 15 μm). The SF_6 concentrations (ppt, parts per trillion) were determined by an electron capture detector (μ-ECD) at 300 °C, helium as carrier gas, and megabore column (HP-MolSieve

0.53 mm × 30 m × 25 µm). The columns were in parallel, with two loops 0.5 cm^3 maintained at 80 °C coupled to six-way valves, as the method described by Johnson et al. (1994).

The amount of enteric methane (CH_4, g/day) was estimated as a function of SF_6 concentrations, relating the results to the known rate of tracer gas release by the capsule deposited in the rumen, with correction for sampled environmental concentrations and molecular weights as described by Berndt et al. (2014), using equation 7:

$$CH_4 = SF_6 \times \frac{\text{animal sample } [CH_4] - \text{background air } [CH_4]}{\text{animal sample } [SF_6] - \text{background air } [SF_6]} \times \frac{\text{molecular weight } [CH_4]}{\text{molecular weight } [SF_6]} \times 1000 \quad (7)$$

in which CH_4 is daily methane emission (g/day), SF_6 is sulfur hexafluoride emission (mg/day), animal sample [CH_4] is the concentration of CH_4 in the cylinder in ppm, animal sample [SF_6] is the concentration of SF_6 in the cylinder in ppt, background air [CH_4] is the concentration of CH_4 in the environment in ppm, background air [SF_6] is the concentration of SF_6 in the environment in ppt, molecular weight [CH_4] is 16 g/mol, molecular weight [SF_6] is 146 g/mol, and 1000 is the conversion factor to express the CH_4 emission in g/day.

The daily methane emission (CH_4, g/day) of each animal was considered as the arithmetic mean of emissions estimated in the five samples. Methane emission was also obtained in relation to mBW (CH_4/mBW, g/kg/day), ADG (CH_4/ADG, g/kg/day), and DMI (CH_4/DMI, g/kg/day). The percentage (%) of gross energy intake lost in the form of methane was calculated as described by Wilkerson et al. (1995): $CH_4/GEI = [(CH_4 \times 0.0133)/GEI] \times 100$, in which GEI is the gross energy intake and 0.0133 is the gross energy in Mcal/g CH_4 (Holter and Young, 1992).

2.4. Chemical analyses (diet and feces)

The diet and feces samples were ground to pass a 1-mm screen (Wiley mill) and analyzed for DM (method 934.01), ash, and organic matter (method 938.08), and EE (method 954.02) content according to the AOAC (1990). Total nitrogen (total N × 6.25 = CP) was analyzed using a combustion assay (DUMATHERM® N Analyzer, Gehart, Germany) according to AOAC (2005) method 990.13. For neutral detergent fiber (NDF), samples were treated with alpha thermo-stable amylase omitting sodium sulfite, determined according to the method of Van Soest et al. (1991), and adapted for fiber analyzer (TE-149; TECNAL, Piracicaba, 187 SP, Brazil). For NDF correction, the neutral detergent-insoluble ash was determined in the residue after sequential fiber analysis following the methods described by Detmann et al. (2012). Crude protein was performed by Dumas method based on the release of nitrogen by combustion at high temperature in pure oxygen in DUMATHERM® analyzer (AOAC, 2005). The NDF and acid detergent fiber were expressed exclusive of ash.

Non-fibrous carbohydrates (NFC) were obtained by %NFC = 100% − (%CP + %EE + %ash + %NDF). Total digestible nutrients (TDN) were estimated according to the NRC (2000): TDN = %CPD + %NFCD + %NDFD + 2.25 × %EED, in which D is the digestibility (NRC, 2000). Gross energy was determined with an adiabatic calorimeter (IKA WERKE Model C5003) according to the method of Parr Instrument Company (1960). Digestible energy of the diet was calculated by subtracting total fecal gross energy from total dietary gross energy.

2.5. Statistical analysis

The effect of RFI class was estimated with the MIXED procedure of SAS, fitting a model that included the fixed effect of RFI class (i = 1, 2), and the linear effect of initial age of the animal as covariate, and the test group (j = 1, 2) as random effects. The quadratic effect of initial age was included when the linear effect was significant (P<0.05). The fixed interactions between RFI class (or EBV-RFI class) and test group class were tested and included in the final models when significant (P<0.05). Different variance residuals for the test group (i = 1, 2) were modeled using the GROUP option of the REPEATED command for all variables studied. The mixed model can be described as equation 8:

$$yijk = \mu + RFIi + TGj + \beta_1(age\text{-}aage)k + \beta_2((age\text{-}aage)k)^2 + (RFI*TG)ij + eijk, \quad (8)$$

in which y is the variable analyzed, μ is the overall mean, RFI is a fixed effect of RFI class i, TG is a random effect of test group j, β_1 and β_2 are the linear and quadratic regression coefficients of y on initial age k, aage is the average of initial age, (RFI*TG) is a fixed interaction effect of RFI class i with TG j, and eijk is random error. The TGj is assumed independent with variance σ^2_{TG}, and the eijk is assumed independent with variance σ^2_e.

Means were adjusted by the least squares method (LSMEANS). Complementary analyses were performed that included the fixed effect of EBV-RFI (i = 1, 2) instead of the RFI class, since the experimental animals came from a selection herd as described above.

The phenotypic correlations of CH_4 (g/day) and CH_4/DMI (g/kg/day) with apparent DM and feed compounds digestibility were estimated by Pearson correlation using the CORR procedure of SAS. Statistical significance was declared when P<0.05.

3. Results

Performance, feed efficiency, estimated fecal excretion, and apparent digestibility were analyzed in Nellore males with extreme RFI phenotypes and EBV-RFI (positive and negative). There was no significant difference in apparent digestibility between most and least efficient animals (Table 2). Dry matter intake (6.92 vs. 8.66 kg DM/day) and feed conversion ratio (7.93 vs. 9.42 kg/kg) were −20.1 and −15.8%, respectively, in low RFI animals compared with their high RFI counterparts; consequently, estimated fecal excretion were also lower in low RFI animals. There was no difference in the performance of low and high RFI animals. As a complementary analysis, negative and positive EBV-RFI classes were compared, confirming the results obtained for the comparison of extreme RFI phenotype classes in terms of performance, excretion, and digestibility. The rank correlation between RFI phenotype and EBV-RFI of these 80 animals was r = 0.79.

Table 2 - Least squares means for performance, feed efficiency, estimated fecal excretion, and apparent digestibility of Nellore males with extreme RFI phenotypes (the most and the least efficient terciles) and classified as negative or positive EBV-RFI

Item	Low RFI	High RFI	SEM	P-value	Negative EBV-RFI	Positive EBV-RFI	P-value
Number of animals	40	40			56	24	
Performance and feed efficiency traits							
BWi (kg)	256	263	11.16	0.26	258±11.4	263±12.2	0.39
mBW (kg)	298	305	5.57	0.33	300±4.82	306±7.11	0.42
ADG (kg/day)	1.000	1.024	0.03	0.60	0.994±0.028	1.038±0.043	0.39
DMI (kg/day)	6.92	8.66	0.16	<0.01	7.34±0.15	8.82±0.23	<0.01
DMI (% mBW/day)	2.39	2.82	0.07	<0.01	2.50±0.06	2.86±0.07	<0.01
FCR	7.28	8.70	0.21	<0.01	7.66±0.19	8.87±0.29	<0.01
RFI (kg/day)	−0.748	0.775	0.08	<0.01	−0.345±0.093	0.833±0.141	<0.01
EBV-RFI (kg/day)	−0.276	0.043	0.03	<0.01	−0.217±0.020	0.121±0.029	<0.01
Fecal excretion (kg DM/day)	2.43	3.01	0.09	<0.01	2.55±0.08	3.10±0.12	<0.01
Apparent digestibility (g/kg)							
DMD	661	669	7.61	0.46	665±6.42	667±9.86	0.87
CPD	607	597	13.29	0.51	606±12.5	592±16.0	0.37
EED	564	573	15.84	0.64	563±13.0	586±20.5	0.35
NDFD	461	466	31.36	0.81	461±30.2	470±33.1	0.69
GED	631	634	8.53	0.75	632±7.17	631±11.1	0.97
TDN	697	699	13.22	0.87	697±12.5	700±14.3	0.78

EBV - estimated breeding value; SEM - standard error of the mean; BWi - initial body weight; mBW - midpoint body weight; ADG - average daily gain; DMI - dry matter intake; FCR - feed conversion ratio; RFI - residual feed intake; DMD - dry matter digestibility; CPD - crude protein digestibility; EED - ether extract digestibility; NDFD - neutral detergent fiber digestibility; GED - gross energy digestibility; TDN - total digestible nutrients.
For EBV-RFI class, least squares means are followed by the standard error of the mean.

The animals emitted on average 180.2 g CH_4/day. High RFI animals emitted 14 g CH_4/day more than low RFI animals, i.e., low RFI animals (more efficient) emitted −7.4% than the high RFI animals (least efficient). However, low RFI animals emitted more CH_4 expressed as g/kg DMI (23.1 vs. 20.1 g/day) and lost more gross energy in the form of methane (8.13 vs. 7.08%) when compared with high RFI. There were no differences in methane emission per mBW or ADG. When the animals were classified based on EBV-RFI, no difference in CH_4 emission (g/day) was observed between more and less efficient animals (Table 3).

There was a negative correlation between EE digestibility with CH_4 (g/day) and CH_4 (g/kg DM/day) (Table 4).

Table 3 - Least squares mean for enteric methane emission of Nellore males with extreme RFI phenotypes (the most efficient tercile and the least efficient tercile) and classified as negative or positive EBV-RFI

Item	Low RFI	High RFI	SEM	P-value	Negative EBV-RFI	Positive EBV-RFI	P-value
Number of animals	40	40			56	24	
CH_4 (g/day)	174	188	4.39	0.02	177±3.70	189±5.82	0.11
CH_4 (g/kg mBW/day)	0.601	0.622	0.01	0.27	0.608±0.011	0.621±0.018	0.55
CH_4 (g/kg ADG/day)	180	186	4.98	0.39	183±4.21	185±6.33	0.78
CH_4 (g/kg DMI/day)	23.1	20.1	0.45	<0.01	22.2±0.39	19.8±0.62	<0.01
CH_4 (Mcal/100 Mcal GEI/day)	8.13	7.08	0.16	<0.01	7.83±0.14	6.98±0.22	<0.01

EBV - estimated breeding value; SEM - standard error of the mean; mBW - midpoint body weight; ADG - average daily gain; DMI - dry matter intake; GEI - gross energy intake.
For the EBV-RFI class, least squares means are followed by the standard error of the mean.

Table 4 - Phenotypic correlations between digestibility variables and enteric methane emission

Item	CH_4 (g/day)	CH_4 (g/kg DM/day)
Dry matter digestibility	−0.067 NS	−0.112 NS
Crude protein digestibility	−0.135 NS	−0.144 NS
Ether extract digestibility	−0.305 (P<0.05)	−0.460 (P<0.01)
Neutral detergent fiber digestibility	−0.075 NS	−0.107 NS
Gross energy digestibility	−0.058 NS	−0.102 NS
Total digestible nutrients	−0.075 NS	−0.112 NS

NS - non-significant.

4. Discussion

There was no difference in the initial body weight, mBW, or ADG between animals with extreme RFI phenotypes (the most efficient tercile and the least efficient tercile) despite the large difference in DMI. This can be explained by the fact that RFI is an efficiency measure that is independent of the growth rate and weight (Koch et al., 1963). The average difference in DMI between animals classified as more and less efficient (1.74 kg DM/day) was similar to those reported in other studies involving different animal categories—Fitzsimons et al. (2014), 1.91 kg DM/day for Simmental cows; McGee et al. (2014), 1.60 kg DM/day for Red Angus steers in the growth phase and 1.80 kg DM/day in the finishing phase.

Various factors might be related to the higher DMI of the least efficient animals, including digestibility (Herd and Arthur, 2009; Herd et al., 2019). In general, an increase in DMI reduces diet digestibility because of the increased passage rate of digesta in the rumen; consequently, DM and feed compounds digestibility are expected to be lower in high RFI cattle than in low RFI animals (Kenny et al., 2018).

In addition, a greater nutrient supply is lost in feces. In a review of 14 studies on the DM digestibility of low versus high RFI animals, Kenny et al. (2018) found only one study that reported higher DM digestibility in more efficient animals. The lack of difference in DM digestibility among cattle with varying RFI phenotypes might be related to the type of diet offered, since the effect of feed intake on digestion is lower for high-forage diets than for high-concentrate diets.

Recent studies have shown higher DM and organic matter digestibility (De La Torre et al., 2019) and higher DM and feed compounds digestibility (Johnson et al., 2019) in low RFI animals, even those receiving high-forage or high-grain diets (Herd et al., 2019), and similar digestibility in low and high RFI animals (Johnson et al., 2019). In indicine cattle, studies have demonstrated higher DM and feed compounds digestibility in low RFI animals than in high RFI animals fed either a high-forage (Oliveira et al., 2016; Magnani et al., 2013) or a high-concentrate diet (Bonilha et al., 2017). On the other hand, Batalha et al. (2020) reported lower digestibility for low RFI (most efficient) animals, i.e., a negative relationship between RFI and digestibility. Therefore, the results of the present study showing similar digestibility between animals classified based on extreme phenotypes for RFI and also genetically classified as negative and positive RFI, whose RFI was obtained for a high-forage diet, do not confirm the hypothesis that more efficient animals have higher digestibility, in agreement with the majority of the results reported in the review by Kenny et al. (2018).

Low RFI animals excreted 0.581 kg DM/day in feces less compared with high RFI animals. This finding was expected because low RFI animals consumed less DM, which leads to less waste excretion. The lower DMI in low RFI animals may also indicate that these animals utilized feed efficiently. Considering the test period of 83 days, the 40 most efficient animals produced almost two tons (1,929 kg DM) less feces than the least efficient animals, corresponding to 19.3% less excretion and potentially less methane and nitrous oxide release into the soil (Herd et al., 2002). In addition, this fact reduces concerns regarding waste management (Montes et al., 2013). Rius et al. (2012) reported lower fecal nitrogen production and higher feed compounds digestibility in lactating cows classified as low RFI. Therefore, the lower fecal output of low RFI animals compared with high RFI animals, despite similar digestibility, can be attributed to their more efficient utilization of nutrients from the feed.

The benefits of using more efficient animals can be extended to reducing enteric methane emissions while maintaining the same level of production (Jones et al., 2011; Johnson et al., 2019; Fitzsimons et al., 2013). The average daily methane emission from beef cattle ranges from 150 to 450 g/day (Hristov et al., 2013). In recent studies, Escobar-Bahamondes et al. (2017) and van Lingen et al. (2019) reported averages for methane emission ranging from 37.0 to 372 g/day. Among the factors that influence methane emission, feed intake is the main factor responsible for the variation in daily emissions. In the present study, the phenotypic correlation between DMI and CH_4 (g/day) was 0.375 ($P<0.01$). Methane emission increases 15 min after a feeding event and subsequent fermentation, and this elevated emission can persist for several hours (de Haas et al., 2017). If there is a moderate to high positive correlation (phenotypic and genetic) of methane emissions with feed intake, RFI should also show a moderate positive correlation with methane emission since negative RFI cattle consume less than expected for their live weight and weight gain. It is therefore expected that methane emission will be lower in negative RFI animals proportionally to the lower DMI.

Indeed, Manafiazar et al. (2020) evaluating a considerable number of animals (heifers and cows) concluded that low RFI animals (from both categories) emit less daily enteric CH_4 and CO_2, mainly due to lower feed intake at equal body weight, gain, and fatness. However, the authors also reported that low RFI heifers and cows had higher CH_4 and CO_2 per kg of DM than the high RFI counterparts. The significance of this event lies in its implications for sustainable livestock production, as the reduction of methane emissions from ruminants is critical in mitigating the impact of agriculture on climate change.

Over the last decade, studies have strongly recommended the use of more efficient animals (low RFI) as an indirect measure to reduce methane emissions from production. However, some authors showed that the association between methane emission and RFI is positive for high-digestibility diets (Nkrumah et al., 2006; Hegarty et al., 2007; Jones et al., 2011) and that negative RFI animals have lower

CH_4 expressed as g/day and g/kg DM/day. On the other hand, in cattle fed low-digestibility diets such as those that predominate in Brazil, the phenotypic association between methane emission (CH_4, g/day) and RFI is highly variable (positive, zero, or even negative; Jones et al., 2011; Manafiazar et al., 2020; Freetly and Brown-Brandl, 2013; Mercadante et al., 2015; Velazco et al., 2016), and individual enteric methane emission in relation to DMI may be higher in more efficient animals (low RFI). Herd et al. (2019) also estimated a negative correlation (−0.54) between CH_4 expressed in relation to DMI and RFI, even in animals fed a high-digestibility diet.

The associations between the enteric methane emission variables (CH_4, g/day, and CH_4, g/kg DM/day) and DM and feed compounds digestibility were close to zero, except for EE digestibility (EED, %) which was low to moderate and negative. Ellis et al. (2007) observed a negative effect of dietary EE content when this variable was included in the regression equation for predicting methane emission. Dietary addition of lipids influences CH_4 production in ruminants (Beauchemin et al., 2008) due to the process of biohydrogenation by ruminal microorganisms that adds H_2 to the double bonds of unsaturated fatty acids (Machmuller and Kreuzer, 1999), draining the element necessary for the formation of methane (Jenkins, 1993). In their review of studies involving cattle and sheep, Beauchemin et al. (2008) observed a 5.6% decrease in methane production with every 1% increase in supplemental fat. Furthermore, fiber degradation is reduced by the dietary addition of lipids due to the formation of a layer that surrounds the fiber and impairs the adhesion of microorganisms (Valadares Filho and Pina, 2006).

Residual feed intake is an important tool for evaluating the factors responsible for variations in feed efficiency and selecting the most efficient beef cattle. However, the mechanisms related to RFI are complex and still not fully understood. In the current study, we investigated the relationship among digestibility, RFI, and enteric methane emission in bovine with extreme RFI phenotype (low and high) and classified as negative or positive EBV-RFI. A possible limitation of the present study was the impossibility of analyzing individual leftovers from the animals' diet, as the animals' feed intake were measured in electronic feed bunks in collective pens. Although the diet has a high percentage of forage and is offered as a complete diet with little possibility of selection in intake, this makes nutrient intake dependent on DMI. On the other hand, the feed intake data obtained in collective pens is adequate because it represents the natural pattern of feed intake of pasture-fed cattle.

5. Conclusions

Taken together, the present results demonstrate the environmental benefits of using more efficient animals in the beef production chain, i.e., animals that exhibit lower feed intake, lower fecal excretion, and lower enteric methane emission without differences in weight gain or body weight. In cattle farming, feed costs account for the largest part of the production costs and increasing feed efficiency is extremely important because of the reduction in the amount of feed consumed per kilogram of meat produced. Increasing feed efficiency also becomes more important as the production of environmental pollutants such as feces and methane is reduced, meeting the global demands for minimizing the use of inputs and production of waste. However, the variations in RFI cannot be explained by differences in DM or nutrient digestibility. More efficient animals emit less enteric methane (CH_4, g/day) than less efficient animals, probably as a result of lower DMI.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Conceptualization: Sakamoto, L. S.; Canesin, R. C. and Mercadante, M. E. Z. **Data curation:** Gianvecchio, S. B.; Sakamoto, L. S.; Souza, L. L. and Mercadante, M. E. Z. **Formal analysis:** Sakamoto, L. S. and Mercadante, M. E. Z. **Funding acquisition:** Bonilha, S. F. M. and Albuquerque, L. G. **Investigation:** Gianvecchio, S. B.; Sakamoto, L. S.; Souza, L. L.; Benfica, L. F.; Marcatto, J. O. S. and Canesin, R. C.

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