

# Apparent Digestibility and Ingestive Behavior of Nellore Bulls With Low and High Residual Feed Intake

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## Research Article

**Keywords:** beef cattle, ingestive behavior, feed efficiency, digestibility, RFI

**Posted Date:** September 14th, 2021

**DOI:** <https://doi.org/10.21203/rs.3.rs-849493/v1>

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# Abstract

The objective of this study was to determine the correlation between ingestive behaviour, apparent digestibility and residual feed intake (RFI) of finishing Nellore bulls fed a high concentrate diet. One hundred and twenty Nellore bulls, housed in individual pens, were evaluated in individual performance tests. The animals were fed a high concentrate diet (23:77 roughage/concentrate ratio). The animals were classified as: low RFI, medium RFI, and high RFI. Data from ten animals from each group was used. Faecal production and nutrient digestibility were calculated using indigestible neutral detergent fiber as an internal marker. The feeding behaviour was evaluated over twenty-four hours by direct observation every five minutes. The most efficient animals (low RFI, 8.58 kg DM/day) consumed 27.62% less feed than the least efficient animals (high RFI, 10.95 kg DM/day). Animals with medium efficiency (mean RFI, 9.49 kg DM/day) consumed 15.39% less than high RFI. Nutrient digestibility coefficients were similar except for ether extract ( $P < 0.03$ ) which was 8% greater for the high-RFI animals. No effect was observed for ingestive behaviour ( $P > 0.05$ ). Animals spent, on average, three hours twenty-eight minutes feeding, seven hours thirty-two minutes ruminating and thirteen hours forty minutes in idle time. In the present study, ingestive behaviour and dry matter digestibility were not responsible for between-animal variation in residual feed intake in Nellore bulls fed a high concentrate diet.

## Introduction

In cattle production, especially in feedlots, feed represents the largest input cost. So, improving feed efficiency aims to maximize profitability through reducing costs and lowering the environmental footprint of beef production through reducing the use of natural resources (Kenny et al., 2018).

There are different approaches to measure feed efficiency, among which the most studied measure in beef cattle lately is residual feed intake (RFI; (Kenny et al., 2018). Residual feed intake is calculated as the difference between measured and predicted feed intake estimated through a regression equation as a function of metabolic body weight and weight gain (Basarab et al., 2003). The RFI is independent on growth rate and body size which allows comparison between individuals differing in levels of production during the measurement period (De La Torre et al., 2015). Moreover, genetic parameter estimates have demonstrated that RFI is moderately heritable for Nellore cattle and is feasible for using as feed efficiency criteria in animal breeding programmes of Nellore cattle (Santana et al., 2014).

At least five major processes have been reported to be involved in the variation of efficiency: feed intake, feed digestion, animal activity, thermoregulation, and energy metabolism (Herd and Arthur, 2009). Kenny et al. (2018) in a meta-analysis of growing beef cattle fed high concentrate diets described that high-RFI animals spent more time eating than low-RFI animals. However, the relationship between RFI and feeding behaviour might be evasive, especially due to differences of type of diet offered when analyzing its contribution to RFI and the limited literature (Kenny et al., 2018).

Also, the impact of digestion of feed to explain differences in RFI has been controversial. For instance, Potts et al. (2017) observed that digestibility explained none of the variation in RFI for dairy cows eating high starch diets, but it explained 9 to 31% of the variation in RFI with cows fed low starch diets. (De La Torre et al., 2015) found that in Charolais cows, digestibility is responsible for significant differences in RFI, irrespective of the type of diet. On the contrary, Dykier et al. (2020) stated that digestibility was not responsible for feed efficiency in beef steers. However, it is unclear if the improved ability of feed-efficient animals is inherent or a function of a slower passage of feed through the rumen due to lower intake.

Further research is needed to better understand the biological mechanism between divergent classes of RFI in respect to breed, type of diet, sex, age and environmental conditions. The present study hypothesises that RFI is related to the digestibility and ingestive behaviour of Nelore bulls on finishing rations. Therefore, this study aimed to determine the correlation between ingestive behaviour, apparent digestibility and residual feed intake (RFI) of finishing Nelore bulls fed high concentrate diet.

## Material And Methods

### Performance trial and residual feed intake estimative

The experiment was conducted from April to August 2013 at the Federal University of Goiás, Goiania, Goiás, Brazil (16° 40 ' S, 49° 15' W), where the climate is classified as Aw according to Köppen-Geiger - tropical wet and dry climate.. The performance trial lasted 84 days after a 14-day adaptation period. One-hundred-and-twenty Nelore bulls (20 months of age and initial body weight of 394.33 ± 37.42 kg) from 13 farms, participants in Nelore Qualitas® genetic improvement programme, were used. They were dewormed and randomly allocated to individual pens (12.5 m<sup>2</sup>). Bulls were weighed every 28 days after a 16-h water and feed withdraw. Metabolic weight was calculated as  $BW^{0.75}$

The diet was formulated to meet a predicted gain of 1.6 kg/d (National Research Council, 2000) and an estimated intake of 2.5% BW. Feed was offered once a day at 13.00 and feed offered and refused was recorded daily. The diet was adjusted to allow approximately 10% of orts. Feed and orts were collected weekly, and samples were composed over a 28-day period. Chemical and nutrient compositions of diets are presented in Table 1.

### Table 1: Diet composition and nutritional characteristics

Ingredients	g kg <sup>-1</sup> DM <sup>a</sup>
Corn silage <sup>b</sup>	180
Sugarcane bagasse	50
Sorghum meal	468
Soybean hulls	243
Soybean meal	35
Urea	8
Mineral premix	16
Chemical composition (g kg <sup>-1</sup> DM)	
Dry matter (g kg <sup>-1</sup> as fed)	618
Crude protein	147
Neutral detergent fiber	360
Acid detergent fiber	240
Ether extract	25
Mineral salts	45
Total carbohydrates	780
Non fibrous carbohydrates	420
Total digestible nutrients	669

<sup>a</sup> dry matter; <sup>b</sup> corn silage without cob

Daily dry matter intake (DMI) of each animal was calculated as the difference between feed offered andorts. The following linear regression model was adjusted to estimate DMI (eDMI) according to Archer et al. (1997):

$$eDMI = \beta_0 + (\beta_1 \times ADG) + (\beta_2 \times BW^{0.75}) + \epsilon_i,$$

where  $\beta_0$  and  $\beta_1$  are the partial regression coefficients of DMI on ADG and metabolic weight, and  $\epsilon$  is the random error (which represents RFI). Residual feed intake was calculated as the difference between observed DMI and expected DMI (eDMI).

After 84 days in the feedlot, animals were classified into three groups, according to the methodology of Basarab et al. (2003), as follow: low residual feed intake (RFI), medium RFI and high RFI. Data from ten bulls from each group were used to estimate digestibility and to evaluate ingestive behaviour.

### **Digestibility trial**

Indigestible NDF (iNDF) was used as an internal marker to estimate faecal output. Faecal collection from all 120 animals occurred during three consecutive days, at 0800h, 12h00 and 16h00, respectively, according to Ferreira et al. (2009), during the experiment. Faeces were collected after spontaneous defecation or manual collection direct from rectum. Composite samples were elaborated per animal. Analyses of faeces were done in 30 selected animals.

Samples of feed ingredients, orts and faeces were dried in a ventilated oven at 55°C for 72 h, ground in a Wiley mill (sieve of 1 mm). Dry matter (DM, method 934.01), ash (method 942.05), ether extract (EE, method 920.39) and crude protein (CP, method 945.18) were determined according to AOAC, (1990). Neutral detergent fiber (NDF), NDF exclusive of protein and residual ash (NDFomp) and acid detergent fiber (ADF) were determined according to Detmann et al. (2012). Total carbohydrates (TC) were calculated according to NRC (2000) as follows:  $TC = 100 - (\%CP + \%EE + \%Ash)$ . Non fiber carbohydrates (NFC) were calculated according to Hall (2000):  $NFC = 100 - [\% Ash + \%EE + \%aNDF + (\%CP - \%CPu + U)]$ , in which CPu is the CP from urea and U is the urea content. Total digestible nutrients (TDN) were calculated according to National Research Council (2001):  $TDN = \% \text{ digestible CP} + 2.25x \% \text{ digestible EE} + \% \text{ digestible NDFap} + \% \text{ digestible NFC}$ .

For iNDF quantification, composite samples (feed, orts and feces) were put in non-woven textile bags (100g/m<sup>2</sup>) at a ratio of 20 mg DM/cm<sup>2</sup> of surface (Nocek, 1988). The bags were kept for 264 h (Casali et al., 2008) in the rumen of a cannulated bull. After that, the bags were cleaned with tap water, sequentially oven dried. The bags were then submitted to extraction with neutral detergent.

Digestibility was calculated as follows:  $DMD (\%) = 100 - [100 \times (Mfd / Mfc)]$ , where Mfd is the marker concentration in the feed and Mfc is the marker concentration in faeces.

### **Ingestive behaviour trial**

Ingestive behaviour was evaluated for 24 h at intervals of five minutes for the selected animals at d 85. The following behavioural categories were evaluated: feeding, ruminating, and idling (ingestion of water, interaction with other animals, rest). Feeding efficiency (FE) and rumination efficiency (RE) were calculated as  $FE (kg) = DMI (kg) / \text{feeding time (h)}$ ;  $RE = DMI (kg) / \text{ruminating time (h)}$ .

### **Statistical Analysis**

Data was analyzed as a completely randomized design with three treatments and ten replicates, using "easynova" procedure of R (Arnhold, 2013). The statistical model was as follows:

$$Y_{ij} = \mu + T_i + e_{ij}$$

where  $Y_{ij}$  is the dependent variable,  $\mu$  is the overall mean for each parameter,  $T_i$  is the effect of treatment and  $e_{ij}$  is the residual error.

The Tukey test was used to compare treatment means, and significant differences were declared at  $P \leq 0.05$  and tendency at  $P \leq 0.10$ . Pearson's linear correlation analysis was performed between the behaviour variables, apparent digestibility, performance data and RFI.

## Results

### Residual Feed Intake

The equation obtained to estimate dry matter intake was:

$$eDMI = -3,1232 + 2,01439 \cdot ADG + 0,08862 \cdot BW^{0.75}; (R^2 = 0.7052; P < 0,01).$$

The mean RFI was -1.13, -0.07 and 0.96 kg DM day<sup>-1</sup> for -low, -medium and -high RFI, whose difference between the lowest and the greatest was 2.09 kg DM day<sup>-1</sup>. There were no differences for ADG, initial BW, final BW, and average metabolic weight between RFI groups (Table 2). Animals gain 1.81 kg day<sup>-1</sup> and weighted 563 kg on average at the end.

The most efficient animals (low RFI; 8.58 kg DM day<sup>-1</sup>) consumed, on average, 21.65% less feed than the least efficient animals (high RFI, 10.95 kg DM day<sup>-1</sup>). Animals with medium efficiency (mean RFI, 9.49 kg DM day<sup>-1</sup>) consumed, on average, 13.3% less feed than high RFI animals. In terms of percentage of body weight, the most efficient animals consumed 9.18% less feed (1.78% of BW) than medium efficient animals (1.96% of BW) and 19.46% less than low efficient animals (2.21% of BW).

**Table 2.** Performance of Nellore cattle with different residual intake

Variables	Residual Feed Intake			SEM <sup>f</sup>	p-value
	Low	Medium	High		
<i>N</i>	10	10	10	-	-
RFI <sup>a</sup> , kg d <sup>-1</sup>	-1.13 C	-0.07 B	0.96 A	0.17	<0.01
Initial BW <sup>b</sup> , kg	400.17	409.65	413.32	5.34	0.69
Final BW, kg	555.88	556.46	572.88	6.77	0.54
BW <sup>0.75</sup> , kg	102.61	103.30	104.99	1.70	0.60
TG <sup>c</sup> , kg	155.71	146.81	159.56	6.63	0.51
ADG <sup>d</sup> , kg d <sup>-1</sup>	1.86	1.75	1.89	0.05	0.48
DMI <sup>e</sup> , kg d <sup>-1</sup>	8.58 B	9.49 B	10.95 A	0.23	<0.01
DMI, % BW	1.78 C	1.96 B	2.21 A	0.04	<0.01
Gain : Feed, kg ADG kg <sup>-1</sup> DMI	0.22 A	0.18 B	0.17 B	0.05	<0.01
Feed conversion, kg DMI kg <sup>-1</sup> ADG	4.61 B	5.43 A	5.79 A	0.13	<0.01

ABC Means with a common letter did not differ ( $P>0.05$ ) from each other.

<sup>a</sup> residual feed intake; <sup>b</sup> body weight;; <sup>c</sup> total gain <sup>d</sup> average daily gain; <sup>e</sup> dry matter intake; <sup>f</sup> standard error of the mean

Gain to feed ratio was higher for low RFI animals. Feed conversion was similar between medium and high RFI groups, and both were on average 18% less efficient than low-RFI animals.

Metabolic weight and ADG approached zero correlation ( $r=0.018$  and  $r=-0.021$ , respectively) with RFI (Table 3). The correlation between RFI and DMI (kg d<sup>-1</sup>) and DMI (%BW) were high and positive ( $r=0.80$  and  $r=0.86$ , respectively,  $P < 0.01$ ). Feed conversion correlated ( $P<0.01$ ) positively with initial BW and negatively, with ADG (Table 3). The correlation between RFI and feed conversion were high ( $r=0.78$ ,  $P<0.01$ , Table 3)

**Table 3.** Correlations between performance data and RFI ( $r_{RFI}$ ) and feed conversion ratio ( $r_{FCR}$ ) of Nellore cattle

Variable	r <sub>RFI</sub>	r <sub>FCR</sub>
Initial BW <sup>a</sup> , kg	0.215	0.571**
Final BW, kg	0.203	0.240
BW <sup>0.75</sup>	0.018	-0.015
ADG <sup>b</sup> , kg d <sup>-1</sup>	-0.021	-0.511**
DMI <sup>c</sup> , kg d <sup>-1</sup>	0.803**	0.515**
DMI (%BW)	0.858**	0.379*
Gain : Feed, kg kg <sup>-1</sup>	-0.766**	-0.983**
Feed conversion, kg kg <sup>-1</sup>	0.782**	-

\*P<0.05; \*\*P<0.01

<sup>a</sup> body weight; <sup>b</sup> average daily gain; <sup>c</sup> dry matter intake.

No differences in ingestive behaviour and FE were observed between the most (low RFI) and the least (high RFI) efficient animals. The RE tended (P=0.06) to be greater in high-RFI than low-RFI animals.

Animals spent, on average, 3.15 hours feeding, 7.35 hours ruminating and 13.5 hours in idle time (Table 4).

**Table 4.** Ingestive behaviour of Nellore cattle with different residual feed intake

Activity (min day <sup>-1</sup> )	Residual Feed Intake			SEM	p-value
	Low	Medium	High		
Feeding	195.50	168	203	12.45	0.11
Ruminating	433	436	454	20.30	0.72
Idle time	811.50	835.50	783	24.49	0.33
FE <sup>a</sup> , kg h <sup>-1</sup>	2.71	3.35	3.25	0.26	0.19
RE <sup>b</sup> , kg h <sup>-1</sup>	1.23	1.33	1.48	0.07	0.06

<sup>a</sup> Feeding efficiency, <sup>b</sup> ruminating efficiency.

No differences were observed for apparent digestibility of nutrients, except for ether extract coefficient (Table 5) which was 7.86% higher for the least efficient animals (high-RFI) than animals with medium and low-RFI. Apparent protein digestibility tended (P=0.10) to be greater for low RFI animals compared to others. Pearson`s correlations between RFI and digestibility are presented in Table 6. There was a

moderate positive correlation between RFI and ether extract digestibility. A moderate negative correlation was observed between feed conversion ratio and non-fibrous carbohydrate digestibility ( $r = -0.398$ ).

**Table 5.** Total tract apparent digestibility of nutrients of Nellore cattle with different residual feed intake

Total tract apparent digestibility, %	Residual Feed Intake			SEM	p-value
	Low	Medium	High		
Dry matter	76.20	75.01	74.79	0.69	0.31
Crude protein	72.85	69.42	70.77	1.08	0.10
NDF <sup>a</sup>	62.82	61.35	61.81	0.68	0.31
NFC <sup>b</sup>	94.88	94.55	93.22	0.74	0.26
Ether extract	72.93 b	72.16 b	78.25 a	1.61	0.03
TDN <sup>c</sup>	77.89	76.77	76.54	0.65	0.30

Means with a common letter did not differ ( $P > 0.05$ ) from each other a – neutral detergent fiber; b – non-fiber carbohydrate; c – total digestible nutrients.

**Table 6.** Correlations between digestibility and RFI ( $r_{RFI}$ ) and feed conversion ratio ( $r_{FCR}$ ) of Nellore cattle

Digestibility, %	$r_{RFI}$	$r_{FCR}$
DM <sup>a</sup>	-0.287	-0.246
CP <sup>c</sup>	-0.231	-0.310
NDF <sup>d</sup>	-0.178	-0.020
NFC <sup>e</sup>	-0.339	-0.398*
EE <sup>f</sup>	0.443*	0.252
TDN <sup>g</sup>	-0.298	-0.266

\* $P < 0.05$

<sup>a</sup>dry matter; <sup>b</sup>apparent digestibility of minerals; <sup>c</sup>crude protein; <sup>d</sup>neutral detergent fiber; <sup>e</sup>non-fiber carbohydrate; <sup>f</sup>ether extract; <sup>g</sup>total digestible nutrients.

## Discussion

The average amplitude of  $2.07 \text{ kg day}^{-1}$  of DMI detected between low and high RFI classes indicated the impact of genetic selection on this characteristic in reducing feed inputs without compromising growth performance (Moraes et al., 2019). Feed intake was significantly different between divergent classes of RFI and they were highly correlated. These findings corroborate the results from Basarab et al. (2003) and McGee et al. (2014), indicating that the selection for RFI, unlike feed conversion, seems to select lower intake animals and lower maintenance demands. According to (Herd and Arthur (2009), a variation in feed intake *per se* has been associated with a variation in maintenance requirements, and they hypothesized that low-RFI animals could expend less energy as heat increment. Gomes et al. (2012) found similar results in Nellore bulls, as low-RFI animals had lower energy intake and it was consistent with decreased heat production and, according to the authors, it may be a consequence of several biological mechanisms such as lower methane production (Johnson et al., 2019). Indeed, the selection of animals with lower maintenance requirements is a desired feature, especially in countries with a tropical climate that suffer from long periods of drought in poorly managed pastures.

The lack of differences in final BW, ADG and metabolic weight between RFI groups were expected due to their explicit use to calculate RFI. The feedlot performance agreed with the concept of RFI, which is defined to be phenotypically independent on body size and average daily gain (Bonilha et al., 2017).

Although feed conversion improved in low-RFI animals and it has been a typical index of feed efficiency in feedlots, its use as a parameter for genetic selection can lead to an increase in body size which may be undesirable, mainly because it compromises reproductive efficiency in cows under limited nutrition as well as reduced feed conversion in the rearing phase (Lanna et al., 2003). This relationship between body size and feed conversion is supported by our results in which FCR was positively correlated to initial BW and ADG, while RFI was not.

Feeding is an activity that is strictly related to the physical characteristics of the diet, the feeling of fulfillment, physiological factors that include hunger control and satiety, and psychogenic factors such as the palatability of the food and environmental factors such as temperature and stress (Santana et al., 2014). Adam et al. (1984) hypothesized that the rate of ingestion and duration of the meal determined the energy cost of eating in cattle. Therefore, more efficient animals might save energy by reducing feed intake and feeding duration. Nonetheless, in the present study, ingestive behaviour did not relate to the difference between RFI groups, although high-RFI animals tended to be more efficient in ruminating than low-RFI animals, which could be due to lower DMI observed for low-RFI animals. Contrary to our results, Aldrighi et al. (2019) studying Nellore bulls, observed that more feed efficient animals spent a longer time feeding and ruminating, but correlations between ingestive behaviour and RFI were close to zero except for rumination efficiency and idle time. But, in their experiment, animals fed 45% forage – 55% concentrate diet with higher NDF content. Which provided greater chewing stimulus and differences between RFI classes could be detected.

Digestibility has been reported to explain up to 10% of phenotypic variation in RFI (Herd and Arthur, 2009). However, the findings of the present study do not support our previous hypothesis that RFI is

related with digestibility. In the present study, there were no differences for DMD except for digestibility of ether extract that was significantly correlated with RFI.

The augment of EE digestibility observed in animals with high intake (high-RFI animals) was counterintuitive because generally as DMI increases, digestibility decreases, primarily due to an increased rate of passage and a corresponding reduction in rumen retention time (Kenny et al., 2018). A possible explanation for this might be that the extra energy due to the increased EE intake might have been driven to attend maintenance requirements and directed toward high energy metabolic process in high-RFI animals, such as protein turnover as well as less efficient mitochondrial activity (Delveaux Araujo Batalha et al., 2020).

Moreover, the absence of differences in DMD between cattle of varying RFI phenotype, in some cases, may be related to the nature of the diets offered, as the effect of feed intake on digestion is less with forage than concentrate-based diets (Kenny et al., 2018).

Otherwise, it is unclear if the improved ability of feed-efficient animals is inherent or a function of a slower passage of feed through the rumen due to lower intake. The impact of feed digestion in low and high RFI has been reported to be controversial. Bonilha et al. (2017) found higher dry matter and NDF digestibility for low-RFI Nellore bulls fed high concentrate diet. Magnani et al. (2013) found higher DM, NDF and CP digestibility for Nellore heifers fed high roughage diet. In agreement with our findings, Johnson et al. (2019) found no differences for Brangus heifers and Santa Gertrudes steers fed a high roughage-based diet; and Dykier et al. (2020) found no differences for Angus-Hereford steers fed a high concentrate diet.

In summary, the high correlation between intake and RFI supports that increased DMI in high-RFI animals reflects an increased need to fulfill the energy intake required for maintenance and growth. Ingestive behaviour does not contribute to between-animal variation in residual feed intake of Nellore bulls fed a high concentrate diet. Further studies evaluating the correlation between breed, sex, and type of diet and RFI are recommended.

## **Declarations**

### **Ethics approval**

The study was approved by the Ethics Committee on Animal Use, protocol no. 078/12, at the Federal University of Goias.

### **Consent for publication**

Not applicable

### **Data availability statement**

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request

## Declaration of interest

## Funding

This study was funded by Nelore Qualitas. The funders had no role in data collection, analysis and interpretation or decision to publish the manuscript.

## Author's contributions

Conceptualization: Victor Rezende Moreira Couto; Methodology: Victor Rezende Moreira Couto; Formal analysis and investigation: Rayanne Galdino Menezes; Writing - original draft preparation: Rayanne Galdino Menezes; Writing - review and editing: Alana Maria Menezes Di Calaça, Marcia Helena Machado da Rocha Fernandes; Funding acquisition: Juliano José de Resende Fernandes; Supervision: Juliano José de Resende Fernandes; Project administration: Juliano José de Resende Fernandes; Software: Emmanuel Arnhold

## Acknowledgements

The authors thank Nelore Qualitas.

## References

1. Adam, I., Young, B.A., Nicol, A.M. and Degen, A.A., 1984. Energy cost of eating in cattle given diets of different form *Animal Science*, 38, 53–56
2. Aldrighi, J., Branco, R.H., Cyrillo, J.N. dos S.G., Magnani, E., Nascimento, C.F. do, Bonilha, S.F.M. and Mercadante, M.E.Z., 2019. Ingestive behavior and temperament of Nelore cattle classified for residual feed intake *Semina: Ciências Agrárias*, 40, 457
3. AOAC, 1990. Official methods of analysis, 15th ed. A. International (ed), (Arlington)
4. Archer, J.A., Arthur, P.F., Herd, R.M., Parnell, P.F. and Pitchford, W.S., 1997. Optimum postweaning test for measurement of growth rate, feed intake, and feed efficiency in British breed cattle. *Journal of Animal Science*, 75, 2024
5. Arnhold, E., 2013. Pacote em ambiente R para análise de variância e análises complementares *Brazilian Journal of Veterinary Research and Animal Science*, 50, 488
6. Basarab, J.A., Price, M.A., Aalhus, J.L., Okine, E.K., Snelling, W.M. and Lyle, K.L., 2003. Residual feed intake and body composition in young growing cattle *Canadian Journal of Animal Science*, 83, 189–204
7. Bonilha, S.F.M., Branco, R.H., Mercadante, M.E.Z., dos Santos Gonçalves Cyrillo, J.N., Monteiro, F.M. and Ribeiro, E.G., 2017. Digestion and metabolism of low and high residual feed intake Nelore bulls

8. Casali, A.O., Detmann, E., Valadares Filho, S. de C., Pereira, J.C., Henriques, L.T., Freitas, S.G. de and Paulino, M.F., 2008. Influência do tempo de incubação e do tamanho de partículas sobre os teores de compostos indigestíveis em alimentos e fezes bovinas obtidos por procedimentos in situ Revista Brasileira de Zootecnia, 37, 335–342
9. De La Torre, A., Recoules, E., Blanc, F., Ortigues-Marty, I., D'Hour, P. and Agabriel, J., 2015. Changes in calculated residual energy in variable nutritional environments: An indirect approach to apprehend suckling beef cows' robustness Livestock Science, 176, 75–84
10. Delveaux Araujo Batalha, C., Morelli, M., Branco, R.H., Santos Gonçalves Cyrillo, J.N., Carrilho Canesin, R., Zerlotti Mercadante, M.E. and Figueiredo Martins Bonilha, S., 2020. Association between residual feed intake, digestion, ingestive behavior, enteric methane emission and nitrogen metabolism in Nellore beef cattle Animal Science Journal, 91, 1–9
11. Detmann, E., Souza, M.A., Valadares Filho, S.C., Queiroz, A.C., Berchielle, T.T., Saliba, E.O.S., Cabral, L.S., Pina, D.S., Ladeira, M.M. and Azevedo, J.A.G., 2012. Métodos para Análise de Alimentos, 1st ed. (Suprema: Visconde do Rio Branco)
12. Dykier, K.C., Oltjen, J.W., Robinson, P.H. and Sainz, R.D., 2020. Effects of finishing diet sorting and digestibility on performance and feed efficiency in beef steers Animal, 14, 59–65
13. Ferreira, M. de A., Valadares Filho, S. de C., Marcondes, M.I., Paixão, M.L., Paulino, M.F. and Valadares, R.F.D., 2009. Avaliação de indicadores em estudos com ruminantes: digestibilidade Revista Brasileira de Zootecnia, 38, 1568–1573
14. Gomes, R.C., Sainz, R.D., Silva, S.L., César, M.C., Bonin, M.N. and Leme, P.R., 2012. Feedlot performance, feed efficiency reranking, carcass traits, body composition, energy requirements, meat quality and calpain system activity in Nellore steers with low and high residual feed intake Livestock Science, 150, 265–273
15. Hall, M.B., 2000. Neutral detergent-soluble carbohydrates: nutritional relevance and analysis, a laboratory manual, (Gainesville)
16. Herd, R.M. and Arthur, P.F., 2009. Physiological basis for residual feed intake. Journal of animal science, 87, 64–71
17. Johnson, J.R., Carstens, G.E., Krueger, W.K., Lancaster, P.A., Brown, E.G., Tedeschi, L.O., Anderson, R.C., Johnson, K.A. and Brosh, A., 2019. Associations between residual feed intake and apparent nutrient digestibility, in vitro methane-producing activity, and volatile fatty acid concentrations in growing beef cattle1 Journal of Animal Science, 97, 3550–3561
18. Kenny, D.A., Fitzsimons, C., Waters, S.M. and McGee, M., 2018. Invited review: Improving feed efficiency of beef cattle – the current state of the art and future challenges Animal, 12, 1815–1826
19. Lanna, D., Calegare, R., Almeida, R. and Berndt, A., 2003. Conversão alimentar – Eficiência econômica de vacas de corte de raças puras e cruzadas. In: Anais do III Simpósio de Pecuária de Corte, (Lavras)
20. Magnani, E., Nascimento, C.F., Branco, R.H., Bonilha, S.F.M., Ribeiro, E.G. and Mercadante, M.E.Z., 2013. Relações entre consumo alimentar residual, comportamento ingestivo e digestibilidade em

novilhas Nelore *Boletim de Indústria Animal*, 70, 187–194

21. McGee, M., Welch, C.M., Ramirez, J.A., Carstens, G.E., Price, W.J., Hall, J.B. and Hill, R.A., 2014. Relationships of feeding behaviors with average daily gain, dry matter intake, and residual feed intake in Red Angus–sired cattle<sup>1</sup> *Journal of Animal Science*, 92, 5214–5221
22. Moraes, G.F., Abreu, L.R.A., Toral, F.L.B., Ferreira, I.C., Ventura, H.T., Bergmann, J.A.G. and Pereira, I.G., 2019. Selection for feed efficiency does not change the selection for growth and carcass traits in Nelore cattle *Journal of Animal Breeding and Genetics*, 136, 464–473
23. National Research Council, 2001. *Nutrient Requirements of Dairy Cattle*, 7th ed. (National Academies Press: Washington, D.C.)
24. National Research Council, 2000. *Nutrients requirements of beef cattle.*, 7th ed. (National Academic Press: Washington)
25. Nocek, J.E., 1988. In situ and Other Methods to Estimate Ruminant Protein and Energy Digestibility: A Review *Journal of Dairy Science*, 71, 2051–2069
26. Potts, S.B., Boerman, J.P., Lock, A.L., Allen, M.S. and VandeHaar, M.J., 2017. Relationship between residual feed intake and digestibility for lactating Holstein cows fed high and low starch diets *Journal of Dairy Science*, 100, 265–278
27. Santana, M.H.A., Oliveira, G.A., Gomes, R.C., Silva, S.L., Leme, P.R., Stella, T.R., Mattos, E.C., Rossi, P., Baldi, F.S., Eler, J.P. and Ferraz, J.B.S., 2014. Genetic parameter estimates for feed efficiency and dry matter intake and their association with growth and carcass traits in Nelore cattle *Livestock Science*, 167, 80–85