Apparent digestibility and ingestive behavior of Nellore bulls with low and high residual feed intake

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Abstract
The objective of this study was to determine the correlation between ingestive behavior, 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 were used. Fecal production and nutrient digestibility were calculated using indigestible neutral detergent fiber as an internal marker. The feeding behavior was evaluated over 24 h by direct observation every 5 min. 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 behavior ($P>0.05$). Animals spent, on average, 3 h 28 min feeding, 7 h 32 min ruminating, and 13 h 40 min in idle time. In the present study, ingestive behavior and dry matter digestibility were not responsible for between-animal variation in residual feed intake in Nellore bulls fed a high concentrate diet.

Keywords Beef cattle · Ingestive behavior · Feed efficiency · Digestibility · RFI

Introduction

In cattle production, especially in feedlots, feed represents the largest input cost. Therefore, improving feed efficiency aims to maximize profitability by reducing costs and lowering the environmental footprint of beef production by reducing the use of natural resources (Kenny et al., 2018). Improved ability to digest food can interfere positively in the efficiency of transforming feed into meat by Nellore cattle.

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 of 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 use as feed efficiency criteria in animal breeding programs of Nellore cattle (Santana et al., 2014), which is the dominant breed in tropical regions.

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). Gomes et al. (2012) found that low-RFI Nellore bulls had lower energy intake. 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 behavior might be evasive, especially due to differences in the 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. Aldrighi et al. (2019) found that in Nellore bulls, digestibility is responsible for significant differences in RFI. 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.

The biological determinants of animal-to-animal variation in feed efficiency are not fully understood. In face of contradictory information, further research is needed to better understand the biological mechanism between divergent classes of RFI, and to validate datasets covering different environmental conditions and genetic background of the animals. The present study hypothesizes that RFI is related to the digestibility and ingestive behavior of Nellore bulls on finishing rations. Therefore, this study aimed to determine the correlation between ingestive behavior, apparent digestibility, and residual feed intake (RFI) of finishing Nellore 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 Goias, Goiania, Goias, Brazil (16° 40’ S, 49° 15’ W), where the climate is classified as Aw according to Köppen-Geiger — tropical wet and dry climate.

All animals involved in this study were cared for according to the rules of the Ethics Committee on Animal Use of Federal University of Goias and the National Council of Animal Experimentation Control (protocol approval number 078/12).

The performance trial lasted 84 days after a 14-day adaptation period. One hundred and twenty bulls, participants in Nelore Qualitas® genetic improvement program, were chosen (20 months of age and initial body weight of 394.33 ± 37.42 kg) from 13 farms. Bulls were pre-selected by performance indices such as weaning weight, weight gain post-weaning, scrotal circumference at 15 months, muscularity, and 17 other morphometric measurements.

Animals were dewormed and randomly allocated to individual pens (12.5 m²). Bulls were weighed every 28 days after 16-h fast. Metabolic weight was calculated as BW⁰.⁷⁵.

The diet was formulated to meet a predicted gain of 1.6 kg/day (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. The chemical and nutrient compositions of diets are presented in Table 1.

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

\[ eDMI = \beta_0 + (\beta_1 \times ADG) + (\beta_2 \times BW^{0.75}) + \varepsilon_i \]

where \(\beta_0\) and \(\beta_1\) are the partial regression coefficients of DMI on ADG and metabolic weight, and \(\varepsilon\) 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, bulls were classified into three groups, according to the methodology of Basarab et al. (2003), as follows: high residual feed intake (RFI), low RFI, and medium RFI. Data from RFI, carcass traits, and temperament were published elsewhere (Guimarães, 2013). Then, 30 bulls (10 animals of each RFI group) were selected among the 120 animals to investigate digestibility and ingestive behavior.

Table 1  Diet composition and nutritional characteristics

| Ingredients                      | g kg⁻¹ DM⁰⁺⁺ |
|----------------------------------|-------------|
| Corn silageab                    | 180         |
| Sugarcane bagasse                | 50          |
| Sorghum meal                     | 468         |
| Soybean hulls                    | 243         |
| Soybean meal                     | 35          |
| Urea                             | 8           |
| Mineral premix                   | 16          |
| Chemical composition (g kg⁻¹ DM) |             |
| Dry matter (g kg⁻¹ 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         |

⁺⁺Dry matter
⁺⁺Corn silage without cob
Digestibility trial

The digestibility trial lasted 10 days. During that time, feed and orts were measured. Indigestible NDF (iNDF) was used as an internal marker to estimate fecal output. Fecal collection occurred twice a day during the last 3 consecutive days at 12–14-h intervals (Ferreira et al.; 2009). Feces were collected after spontaneous defecation or manual collection direct from the rectum. Fecal samples were pooled per animal.

Samples of feed ingredients, orts, and feces were dried in a ventilated oven at 55 °C for 72 h and 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 (TCs) were calculated according to NRC (2000) as follows: 

\[
TC = 100 - (%CP + %EE + %Ash).
\]

Non fiber carbohydrates (NFCs) 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 (TDNs) were calculated according to National Research Council (2001): 

\[
TDN = % \text{digestible CP} + 2.25 \times % \text{digestible EE} + % \text{digestible NDFomp} + % \text{digestible NFC}.
\]

For iNDF quantification, feed samples, orts, and feces were put in non-woven textile bags at a 20-mg DM/cm² of surface (Nocek, 1988). The bags were kept for 264 h (Casali et al., 2008) in the rumen of two cannulated bulls, and samples were replicated by bull. After that, the bags were cleaned with tap water, and sequentially oven-dried. The bags were then submitted to extraction with neutral detergent. Fecal output was calculated as marker intake divided by the concentration of marker in feces. Ingestion was calculated as the amount of feed offered minus orts:

\[
\text{Digestibility was calculated as follows: DMD (\%) = (ingested nutrient amount-amount nutrient excreted in the feces) / ingested nutrient amount \times 100.}
\]

Ingestive behavior trial

Ingestive behavior was evaluated for 24 h at intervals of 5 min on the last day of the trial in 10 bulls per RFI group. The following behavioral categories were evaluated: feeding, ruminating, and idling (ingestion of water, interaction with other animals, rest). Feeding efficiency (FE) and ruminating efficiency (RE) were calculated as 

\[
\text{FE (kg) = DMI (kg)/ feeding time (h); RE = DMI (kg)/ ruminating time (h).}
\]

Statistical analysis

Data were analyzed as a completely randomized design with three treatments and ten replicates, using the “easyanova” 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 \(P < 0.05\). Pearson’s linear correlation analysis was performed between the behavior variables, apparent digestibility, performance data, and RFI.

Results

Residual feed intake

The equation obtained to estimate dry matter intake was:

\[
e_{\text{DMI}} = -3.123 + 2.04 \times ADG + 0.089 \times BW^{0.75} \ (R^2 = 0.71; P < 0.01)
\]

where \(e_{\text{DMI}}\) is the estimated DMI in kg DM day\(^{-1}\), ADG is average daily live weight gain in kg day\(^{-1}\), and BW is the body weight in kg.

The mean RFI was \(-1.13, -0.07, \) and \(0.96 \) kg DM day\(^{-1}\) for low, medium, and high RFI, whose difference between the lowest and the greatest was 2.09 kg DM day\(^{-1}\). There were no differences in ADG, initial BW, final BW, and average metabolic weight between RFI groups (Table 2).

The most efficient animals (low RFI; 8.58 kg DM day\(^{-1}\)) consumed, on average, 21.65 % less feed than the least efficient animals (high RFI, 10.95 kg DM day\(^{-1}\)). Animals with medium efficiency (mean RFI, 9.49 kg DM day\(^{-1}\)) 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).

The 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 day\(^{-1}\)) and DMI (%BW) was 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 was high (r = 0.78, P < 0.01, Table 3).

No differences in ingestive behavior and FE were observed between the most (low RFI) and the least (high RFI) efficient animals. Animals spent, on average, 3.15 h feeding, 7.35 h ruminating, and 13.5 h in idle time (Table 4). No correlations were found between divergent feed efficiency animals and ingestive behavior.

No differences were observed for apparent digestibility of nutrients, except for the ether extract coefficient (Table 5) which was 7.86% higher for the least efficient animals (high-RFI) than animals with medium and low RFI. 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).

### Discussion

The average amplitude of 2.07 kg day⁻¹ of DMI detected between low and high RFI classes indicated the potential 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

| Table 2 | Performance of Nellore cattle with different residual intake |
|---------|-------------------------------------------------------------|
| Variables | Residual feed intake | SEM² | p-value |
|          | Low | Medium | High |
| N        | 10 | 10 | 10 | – | – |
| RFI⁴, kg day⁻¹ | – 1.13 C | – 0.07 B | 0.96 A | 0.17 | < 0.01 |
| Initial BW, kg | 400.2 | 409.6 | 413.3 | 5.34 | 0.69 |
| Final BW, kg | 555.9 | 556.5 | 572.9 | 6.77 | 0.54 |
| BW⁰.⁷⁵, kg | 102.6 | 103.3 | 105.0 | 1.70 | 0.60 |
| Total live-weight gain, kg | 155.7 | 146.8 | 159.6 | 6.63 | 0.51 |
| Average daily LW gain, kg day⁻¹ | 1.86 | 1.75 | 1.89 | 0.05 | 0.48 |
| Dry matter intake, kg day⁻¹ | 8.58B | 9.49B | 10.95A | 0.23 | < 0.01 |
| Dry matter intake, % BW | 1.78C | 1.96B | 2.21A | 0.04 | < 0.01 |
| Gain/feed, kg ADG kg⁻¹ DMI | 0.22A | 0.18B | 0.17B | 0.05 | < 0.01 |
| Feed conversion, kg DMI kg⁻¹ ADG | 4.61B | 5.43A | 5.79A | 0.13 | < 0.01 |

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

RFI residual feed intake; BW body weight; ADG average daily gain, DMI dry matter intake

| Table 3 | Correlations between performance data and RFI (rRFI) and feed conversion ratio (rFCR) of Nellore cattle |
|---------|--------------------------------------------------------------------------------------------------|
| Variable | rRFI | rFCR |
| Initial BW, kg | 0.215 | 0.571** |
| Final BW, kg | 0.203 | 0.240 |
| Body weight⁰.⁷⁵ | 0.018 | – 0.015 |
| Average daily gain, kg day⁻¹ | – 0.021 | – 0.511** |
| Dry matter intake, kg day⁻¹ | 0.803** | 0.515** |
| Dry matter intake, % BW | 0.858** | 0.379* |
| Gain/feed, kg ADG kg⁻¹ DMI | – 0.766** | – 0.983** |
| Feed conversion, kg DMI kg⁻¹ ADG | 0.782** | – |

*P < 0.05; **P < 0.01

BW body weight, ADG average daily gain, DMI dry matter intake

### Table 4 Ingestive behavior of Nellore cattle with different residual feed intake

| Activity (min day⁻¹) | 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 |
| Feeding efficiency, kg DMI h⁻¹ | 2.71 | 3.35 | 3.25 | 0.26 | 0.19 |
| Ruminating efficiency, kg DMI h⁻¹ | 1.23 | 1.33 | 1.48 | 0.07 | 0.06 |

DMI dry matter intake
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; according to the authors, it may be a consequence of several biological mechanisms. 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.

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, 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 behavior 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. Batalha et al. (2020) found no differences in ingestive behavior in Nellore bulls with divergent feed efficiency although they did not find differences in DMI. 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 behavior and RFI were close to zero except for ruminating efficiency and idle time. But, in their experiment, animals were fed a 45% forage-55% concentrate diet with higher NDF content.

In the present work, the diet offered to animals had high digestibility and probably a high passage rate through the rumen, which caused a decrease in activities such as rumination, so that differences in the digestive process could not be detected. These results, collectively, indicate that in feedlot systems, differences in feeding behavior-related traits between low- and high-RFI cattle are largely a reflection of differences in intake (Cantalapiedra-Hijar et al., 2018).

Digestibility has been reported to explain up to 10% of phenotypic variation in RFI (Herd and Arthur, 2009). On the contrary, Cantalapiedra-Hijar et al. (2018) argued that digestive mechanisms are associated with RFI because they co-vary with feed intake.

The impact of feed digestion in low and high RFI has been reported to be controversial. Previous studies reported higher apparent digestibility for low-RFI Nellore animals fed a high-concentrate diet (Bonilha et al. 2017) or
high-roughage diet (Magnani et al. 2013). In agreement with our findings, previous works reported no differences in diet apparent digestibility in Brangus heifers and Santa Gertrudis steers fed a high roughage-based diet (Johnson et al. 2019) and Angus-Hereford steers fed a high-concentrate diet (Dykier et al. 2020).

In our study, animals from different RFI classes were fed the same diet, and considering that the apparent digestibility of nutrients depends on the feedstuff evaluated, it can be inferred that differences in RFI may be due to metabolic mechanisms involved with nutrient absorption throughout the gastrointestinal tract (Bonilha et al., 2017). Although we have not found differences in apparent digestibility, high-RFI consumed more digestible nutrients and energy, suggesting that more efficient animals require less digestible nutrients and energy, presumably because they have fewer maintenance requirements and therefore regulate intake and digestibility to supply their required intake according to the diet.

The increase of EE apparent 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 a high-energy metabolic process in high-RFI animals (Kenny et al., 2018). Moreover, the increase of the maintenance requirements of high RFI might be resulted from the enlargement of the organs as well as from the amount of energy spent by the tissues per unit of animal weight (Batalha et al., 2020).

Discrepancies among literature reports are certainly exacerbated by variation among studies in breed, gender, and stage of maturity coupled with a huge disparity in methodologies used. In addition, discrepancies between studies may be influenced by genotype-by-environment interactions (Cantalapiedra-Hijar et al., 2018). Genotype-by-environment interaction is a function of the extent of the differences between environments and between genotypes of animals (Berry and Crowley, 2013).

Carcass traits from all the animals used in the present work showed that high-RFI animals had thicker subcutaneous fat than low-RFI animals (Guimarães, 2013). The deposition of the same weight of lean tissue and fat has different energy costs. According to Herd and Arthur (2009), protein turnover, tissue metabolism, and stress explain 37% of the phenotypic variation. It is recommended to include ultrasound measures of fat and protein gain as regressor variables in the multiple regression model when deriving RFI (Basarab et al., 2003). Animals depositing proportionally more protein than fat for the same ADG will be deemed more efficient, and if all animals are of similar age, then this may result in long-term selection for later-maturing animals, which may have implications for the overall efficiency of the cowherd (Berry and Crowley, 2013).

The findings of the present study do not support our previous hypothesis that RFI is related to apparent digestibility and ingestive behavior. We concluded that the RFI of genetically improved Nellore bulls fed a high-concentrate diet does not correlate to their digestion ability and ingestive behavior. Other metabolic processes rather than digestibility and ingestive behavior seem to be the source of variations in efficiency.

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

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 to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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