



Protein metabolism, feed energy partitioning, behavior patterns and plasma cortisol in Nellore steers with high and low residual feed intake¹

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¹ Funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (Fapesp, #2005/0423-5 and 2005/1448-0).

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ABSTRACT - The objective was to evaluate protein turnover, nitrogen balance, feed energy partitioning, behavior patterns and plasma cortisol in Nellore (*B. indicus*) cattle with high and low residual feed intake (RFI = actual minus expected dry matter intake). Seventy-two Nellore steers (16 to 21 months-old, 334±19 kg initial body weight) were fed a feedlot diet for 70 days *ad libitum*. Daily dry matter intake (DMI) and average daily gain (ADG) were recorded individually and RFI was calculated. The 12 steers of lowest (Low-RFI, most efficient) RFI and the 12 ones of highest RFI (High-RFI, least efficient) were evaluated with respect to their behavior patterns and plasma cortisol concentration. Urine was collected for determination of daily 3-methylhistidine excretion (3MH) and myofibrillar protein breakdown rates. Urinary, gaseous and fecal energy losses were determined as well as the N retention and excretion. High-RFI steers tended to have shorter lying and idle periods and greater feeding time and plasma cortisol levels than low-RFI cattle. No RFI effects were seen for urine 3MH excretion and for rates of protein degradation and synthesis. No effects of efficiency class were observed for N excretion or N retention. No RFI effects were observed for dry matter digestibility, digestible energy (DE) and metabolizable energy (ME) content and DE/ME ratio. Methane energy losses were lower for low- compared with high-RFI steers. Protein turnover seems not to affect feed efficiency in Nellore steers. Improved RFI in Nellore steers is probably associated with lower degrees of activity and responsiveness to stress and lower losses of dietary energy as methane.

Key Words: *Bos indicus*, feed efficiency, methane, net feed intake, 3-methyl-histidine, zebu

Introduction

Improving feed efficiency (FE) in livestock has been recognized as an important tool to decrease production costs and negative environmental impacts. Extensive research regarding residual feed intake (RFI), a FE trait independent of growth rate and body size (Koch et al., 1963), has provided knowledge about the variation among individuals for FE (Herd et al., 2004; Richardson & Herd, 2004), as well as the potential consequences of breeding for improved RFI.

Studies have shown that the lower energy losses as methane during digestion (Nkrumah et al., 2006) and greater energy retention as protein (Basarab et al., 2003) may also contribute to the better efficiency of feed use in low-RFI cattle. Other factors such as physical activity (Barea et al., 2010; Luiting et al., 1994) and responsiveness to stress (Knott et al., 2008; 2010) can also be linked to FE due to their impact on metabolic rate and, consequently, on the requirements of energy for maintenance.

Nonetheless, it is noteworthy that most of those findings were observed in British breeds and that little research has been carried out in *B. indicus*. In general, zebu breeds are

late-maturing (NRC, 1996), more temperamental (Voisinet et al., 1997) and have lower energy requirements for maintenance (NRC, 1996) when compared with *B. taurus*. Lower energy requirements should be partially explained by lower rates of protein turnover (Chizzotti et al., 2008). In summary, although the same mechanisms affecting RFI in British breeds affect FE in *B. indicus*, the differences in aspects significantly associated with FE require that specific investigations be conducted.

Therefore, the objective of this study was to evaluate behavior, protein metabolism, plasma cortisol concentration, feed digestibility and feed energy partitioning in Nellore steers with high (less efficient) and low RFI (more efficient).

Material and Methods

All procedures involving animals were accomplished following ethical principles required by the Brazilian Committee for Animal Experimentation (COBEA). The study was carried out at the Faculdade de Zootecnia e Engenharia de Alimentos da Universidade de São Paulo (FZEA-USP), Pirassununga, SP, Brazil.

Nellore steers (n = 72, 19 months-old \pm 29 d; 334 \pm 19 kg initial BW) were obtained from the beef herd of Universidade de Sao Paulo, in Pirassununga, São Paulo, Brazil. At enrollment, cattle were dewormed with injections of albendazol sulfoxide (Ricobendazole 10%, Ouro Fino, Cravinhos, SP, Brazil) and ivermectin (Ivomec 1%, Merial, Paulínia, SP, Brazil).

The steers were fed in feedlots a diet composed of coastcross hay (25.4%), ground corn (35.8%), soybean hulls (35%), 45% crude protein (CP), soybean meal (2.2%), mineral premix (0.6%) and urea (1%), on a dry basis, with estimated CP and metabolizable energy (ME) content of 14.3% and 2.63 Mcal/kg DM (NRC, 1996). Daily dry matter intake (DMI) was calculated individually in individual pens or using the Calan Broadbent system (American Calan Inc., Northwood, NH, USA) for 70 days. A previous adaptation period of 21 d allowed cattle to adapt to the diet and to learn how to feed from Calan gates. Cattle were weighed after a 18-hour fasting, in the beginning and the end of the feeding period and every 21 days to obtain shrunk body weight (SBW) and average daily gain (ADG). Residual feed intake (RFI) was calculated regressing DMI against the mid-test metabolic BW ($BW^{0.75}$) and ADG as follows:

$$DMI, \text{ kg/d} = \beta_0 + (\beta_1 \times BW^{0.75}) + (\beta_2 \times ADG) + \varepsilon,$$

where ε represents the RFI (actual DMI minus expected DMI).

The 12 highest and 12 lowest RFI steers were referred to as high-RFI and low-RFI steers, where high-RFI are less efficient and low-RFI steers are more efficient. The high- and low-RFI steers were housed in individual pens (5 \times 8 m) and fed the same diet previously offered *ad libitum*. Nine steers from each RFI class were randomly chosen and behavior variables were evaluated for two consecutive periods of 24 hours. Description of animal position (lying or standing) and activity (feeding, ruminating and idle) was accomplished every 15 minutes. Records of feed bunk attendance (events/d), total feeding time (min/day) and mean feeding time (min/event) were also obtained, according to Nkrumah et al. (2006). Bunk attendance was defined as the number of visits by an animal to the feed bunk in a day. A bunk attendance event started every time a steer lowered its head in the bunk to eat and ended when it walked away from the bunk.

Following the behavior study, cattle were bled by puncture of the jugular vein, in vacuum tubes containing heparin on two consecutive days, at 8h00. Plasma was obtained and the cortisol concentration was analyzed using an enzyme immunoassay (DSL-10-2000 ACTIVE Cortisol EIA, Diagnostic Systems Laboratories, Inc., Webster, TX).

Then, the cattle were moved to a barn with rubber-surfaced floor where they were contained with halters.

Cattle had fresh water available all the time and were fed the feedlot diet *ad libitum* in individual concrete feed bunks positioned in front of each animal, for seven days. Following a 5-day adaptation period, individual DMI was monitored and the feed and orts offered were sampled for two days. Concomitantly, total fecal excretion was determined by collecting feces from the floor immediately after defecation. Fecal samples were pooled, identified and frozen (-18 °C) until analysis.

Urine was also totally collected throughout the 48-hour period by positioning buckets below the penis of the animals at urination. Urine pooled samples were stored in identified tubes containing H₂SO₄ and frozen (-18 °C) until analysis of gross energy, nitrogen and 3-methyl-histidine content.

Feces, feed and ort samples were dried in forced-ventilation oven at 55 °C for 72 hours, ground in Wiley mill to pass a 1 mm sieve and once more dried in sterilization oven at 105 °C for 24 hours. The gross energy content in urine (UE), feces (FE), feeds and orts were analyzed using an oxygen bomb calorimeter (C2000 Basic, IKA Works GmbH & Co., Staufen, Germany) and the nitrogen (N) concentration was determined by the Micro-Kjeldahl method (AOAC, 1990).

The metabolizable energy content of the diet (ME, Mcal/kg DM) was determined using outputs from the metabolism trial, according to the NRC (1996) (Eq. 1).

$$ME \text{ (Mcal/kg DM)} = (\text{GEI} - [\text{FE} + \text{UE} + \text{GE}]) / \text{DMI} \quad (\text{Eq. 1})$$

Where GEI is the gross energy intake (Mcal/d), FE is fecal energy output (Mcal/d), UE is urinary energy production (Mcal/d) and GE is the gaseous energy (Mcal/d) throughout the collection days. Gross energy intake was the difference between the gross energy offered as feed and gross energy of orts. Fecal energy was the product between fecal DM excretion and the gross energy of feces. Urine energy was the product between the urinary excreted volume and the urine gross energy content. Gaseous energy was considered the energy lost as methane production, estimated using the equation described by Blaxter & Clapperton (1965):

$$\text{CH}_4 \text{ (Mcal/d)} = (1.30 + 0.112 \times \text{DEm} - \text{DMI level} \times [2.37 - 0.050 \times (\text{DEm})]) * \text{GEI} / 100 \quad (\text{Eq. 2})$$

Where DEm is digestible energy as percentage of GEI at maintenance intake, DMILEvel is the DMI intake level as a multiple of DMI at maintenance (DMI_m, kg/d) and GEI is the gross energy intake (Mcal/d). To calculate DEm, the energy digestibility was adjusted according to Tyrrell & Moe (1979) and NRC (2001) for the level of feed intake, which recommended a 4% decrease in feed digestibility for every

1-fold increase in DMIm. To predict DMIm, the predicted ME content of the diet (ME_{diet_pred}), according to Weiss et al. (1992) and nutritional tables of the NRC (1996), was divided by the ME requirement for maintenance (ME_m), estimated according to Valadares et al. (2006) recommended for Nellore steers (Eq. 3).

$$\text{ME}_m, \text{Mcal/d} = 119.5 \text{ kcal/EBW}^{0.75} \quad (\text{Eq. 3})$$

Where EBW is empty body weight calculated according to Aferri (2007) as:

$$\text{EBW, kg} = -15.74911 + 0.98517 \times \text{SBW, kg} \quad (\text{Eq. 4})$$

Muscle protein metabolism was evaluated through measurements of myofibrillar protein fractional degradation rate (FDR), fractional synthesis rate (FSR) and fractional accretion rate (FAC) (Harris & Milne, 1981; Castro Bulle et al., 2007). Additionally, the nitrogen (N) balance was evaluated by calculating N intake, N excretion in the feces and urine and N retention in the metabolism trial. The FDR (%/d) was determined through the ratio between the daily excretion of 3-methyl-histidine (3MH) in urine and the pool of this amino acid in the skeletal muscle mass (SMM) in the body, as follows:

$$\text{FDR, \%d} = \frac{[\text{3MH}]_{\text{urine}}, \mu\text{mol/L} \times \text{urine volume, L/d}}{\text{muscular mass, kg} \times 180 \text{ g protein/kg} \times 3.5106 \mu\text{mol/g muscle protein}} \times 100 \quad (\text{Eq. 5})$$

The concentration of 3-methyl-histidin (3MH) in urine was determined using high performance liquid chromatography (HPLC), followed by fluorometric detection (Dunnnett & Harris, 1997). To calculate FDR, it was assumed that 3MH concentration in skeletal muscle was 3.5106 $\mu\text{mol/g}$ muscle protein (Nishizawa et al., 1979). The percentage of muscle protein was determined as the mean nitrogen content (Micro-Kjeldahl method) in three longissimus muscle samples (between the 12th and 13th ribs) multiplied by 4.8 (Janney, 1916). The protein content in the skeletal muscle was 18%, which was very close to the value used by previous studies (Castro Bulle et al., 2007).

The SMM in the beginning of the feeding trial (Initial SMM) and in the metabolism trial (Metabolism SMM) was estimated using the following equations, which were generated regressing SBW and SMM data in independent populations of Nellore steers which had similar ages and body weight range to that of cattle evaluated in the present study:

$$\text{Initial SMM, kg} = 0.39817 \times \text{SBW, kg} \quad (\text{Eq. 6})$$

$$\text{Metabolism SMM, kg} = 0.38976 \times \text{SBW, kg} \quad (\text{Eq. 7})$$

The rates of synthesis and degradation of muscle protein were determined taking in account the period from the beginning of the growing phase and the beginning of metabolism trial period. The FAC (%/d) was estimated as

the ratio between the daily protein gain rate (kg/d) and the mean SMM (kg) during the respective period ($[\text{Initial SMM} + \text{Metabolism SMM}]/2$). The FSR (%/d) was calculated as the sum of FDR and FAR.

The data was analyzed for outliers ($>3\text{SD}$), homogeneity of variance (Hartley test) and normality of residuals (Shapiro-Wilk test). Plasma cortisol was analyzed considering a completely randomized design with repeated measures, sample time and RFI class as fixed effects, using restricted maximum likelihood analysis (Proc Mixed). To test the RFI effect on dependent variables, one-way analyses of variance was employed, using the General Linear Models procedure of SAS (version 9.1, SAS Institute Inc., Cary, NC). Treatment difference of $P \leq 0.05$ was considered significant and $0.05 < P \leq 0.10$ was considered a tendency. Means and standard error of mean (SEM) are presented throughout.

Results and Discussion

With respect to the feedlot performance of high- and low-RFI steers, no differences between high and low-RFI was observed ($P > 0.05$) for initial BW (340 vs. 336 kg; SEM = 2.16 kg), final BW (448 vs. 441 kg; SEM = 2.82 kg) and average daily gain (1.48 vs. 1.48 kg/d; SEM = 0.03 kg); however, cattle with low RFI showed lower dry matter intake, feed conversion ratio and residual feed intake than animals with high RFI. These results are consistent with the RFI concept regarding its independence of growth rate and body weight (Koch et al., 1963) and agree with previous studies on *Bos taurus* breeds (Arthur et al., 2001a,b). Low-RFI cattle ate less, had a better feed conversion ratio and presented the same body weight and growth rate as high-RFI cattle, thereby the former are considered more efficient (Gomes et al., 2011).

There were trends (Table 1, $P < 0.10$) towards differences between RFI classes for the length of standing, lying, feeding and idleness periods. High-RFI steers seemed to remain standing and feeding for longer periods whereas low-RFI steers tended to stay lying and idle longer. The RFI classes did not differ for time in rumination, bunk attendance and mean feeding time, but high RFI cattle remained longer periods feeding than low-RFI cattle.

According to Richardson & Herd (2004), differences in feeding patterns and activity should contribute to variation in RFI. The present study observed evidence that low-RFI steers had a lower degree of activity than high-RFI animals, as seen through the longer lying and idle periods and shorter feeding periods for the first group. Moreover, other studies have also reported smaller number of daily meals, shorter feeding time (Robinson & Oddy, 2004; Bingham et al., 2009;

Lancaster et al., 2009) and lower degree of activity (Herd et al., 2004) in low-RFI cattle. These characteristics of behavior that are inherent to most efficient animals would likely enhance energy sparing, thereby decreasing energy requirements for maintenance and finally contributing to improve feed efficiency. Although the observations in this study are limited to cattle fed in individual pens, one can suggest that physical activity is likely to contribute to variation in requirements for maintenance and in RFI in Nellore cattle.

High-RFI steers presented higher plasma cortisol levels than low-RFI steers (21.1 vs. 19.4 ug/dL; SEM = 0.38 ug/dL; P = 0.03). Blood cortisol indicates responsiveness to stress and temperament contributing to variation in RFI in Nellore cattle. These observations agree with previous findings of studies reporting that inefficient sheep present higher cortisol levels and are more responsive to ACTH and insulin infusions (Knott et al., 2008; 2010). The higher responsiveness to exogenous challenges is expected to alter the hypothalamic-pituitary-adrenal (HPA) axis toward an increased metabolic rate and energy use (Brockman & Laarveld, 1986), which would be consistent with lower efficiency and greater energy requirement in high-RFI cattle.

Furthermore, the cortisol level is negatively related to temperament and calmness (Curley et al., 2006; Stahringer et al., 1990), which have potential effects on performance (Voisinet et al., 1997). Therefore, the relationship between cortisol level and RFI in Nellore steers can be based on the negative effects of excitable temperaments on growth and energy use. It is noteworthy that *B. indicus* cattle are more temperamental or excitable than *B. taurus* cattle, and so are females when compared with males (Voisinet et al., 1997). Thus, the effects of temperament on feed efficiency should

be more marked in zebu breeds (such as the Nellore), in females and in herds not selected based on temperament.

No differences between high- and low-RFI steers were observed for initial and final skeletal muscle protein, as well as for skeletal muscle protein gain. The total muscle 3MH and daily 3MH excretion in urine did not differ between RFI classes. Also, there were no RFI effects on FDR, FSR, FAR and FSR:FDR ratio (Table 2).

In addition, there were no RFI effects on nitrogen intake, nitrogen urinary output and fecal excretion. No effects of RFI class were also observed for total N excretion and for N retention, in grams per day, in percentage of ingested N and in percentage of digested N.

Some studies have highlighted that the effects of protein turnover on energy requirements are contributors to variation in feed efficiency (Baldwin et al., 1980). In addition, cortisol activity has been associated with muscle catabolism and nitrogen losses (Raina & Jeejeebhoy, 1998; Larson, 2005). However, in the present study, the differences in plasma cortisol between high- and low-RFI cattle seemed not to lead to changes in protein metabolism and protein turnover was not related to feed efficiency. In agreement with the present study, Castro Bulle et al. (2007) did not observe differences between high- and low-RFI cattle for the fractional rates of protein degradation, synthesis and accretion. It is noteworthy that the estimates using 3-methyl-histidine in the present study were very similar to that found by the referred authors. Also, the protein turnover results are consistent with the observed nitrogen balance since no differences between efficiency groups were seen for nitrogen retention and excretion (Table 3).

Table 1 - Behavior patterns in high- and low-RFI steers

Item	RFI class		SEM	P>F ²
	High	Low		
Position ¹				
Standing, %	41.7	37.9	1.13	0.09
Lying, %	58.3	62.1	1.13	0.09
Activity				
Feeding, %	16.4	14.2	0.68	0.08
Rumination, %	24.4	20.6	1.07	0.12
Others, %	7.4	8.15	0.53	0.46
Idle, %	51.9	57.0	1.22	0.06
Feeding behavior				
Bunk attendance, visits/d	27.3	24.3	1.13	0.18
Mean feeding time, min/visit	8.73	8.89	0.44	0.86
Total feeding time, min/d	231	207	6.12	0.04

RFI - residual feed intake; SEM - standard error of the mean.

¹ Relative to a 24-hour period.

² Probability of a type I error.

Table 2 - Protein metabolism of skeletal muscle in high- and low-RFI steers

Item	RFI class		SEM	P>F ⁴
	High	Low		
Skeletal muscle protein ¹				
Initial, kg	24.4	24.1	0.21	0.48
Final, kg	32.3	31.4	0.49	0.10
Gain, g/d	57.2	55.2	2.71	0.72
Total muscle 3MH, mmol ²	113	110	1.74	0.10
Urine excreted 3MH, mmol/d	1.96	2.06	0.10	0.63
FDR, %/d ³	1.76	1.85	0.10	0.66
FSR, %/d ³	2.01	2.09	0.09	0.65
FAR, %/d ³	0.24	0.24	0.01	0.97
FSR:FDR	1.15	1.14	0.01	0.88

FDR - fractional degradation rate of skeletal protein; FSR - fractional synthesis rate of skeletal protein; FAR - fractional accretion rate of skeletal protein; RFI - residual feed intake; SEM - standard error of the mean.

¹ Relative to the beginning of the first feeding period until the metabolism trial. Values are least square means adjusted for common days on feed, except for the initial protein content.

² 3MH = 3-methyl-histidine. Values are least square means adjusted for common days on feed.

³ Values are least square means adjusted for common shrunk body weight at the collection day.

⁴ Probability of a type I error.

No differences were observed on apparent dry matter digestion, digestible and metabolizable energy content of diet and ME to DE ratio, across the RFI groups ($P>0.05$, Table 4). However, the predicted energy loss as methane was lower for low-RFI steers compared with high-RFI animals ($P<0.05$).

According to Richardson & Herd (2004), differences in digestion may contribute to variation in RFI. In the present study, one hypothesis was that digestibility would be a biological process affecting RFI in Nellore cattle since differences between efficiency classes had been previously described by Australian studies on Angus cattle, by Richardson et al. (1996). This study suggested that the greater efficiency in low-RFI cattle could be partially explained by an enhanced capacity to digest ingested feed. Conversely, no feed digestion differences were observed between cattle with high and low efficiency, which is consistent with the absence of RFI effects on digestibility of high grain diets in high- and low-RFI Angus \times Hereford crossbred steers (Cruz et al., 2010).

With respect to findings reported by Richardson et al. (1996), doubts can arise as to whether the positive relationship between feed digestibility and feed efficiency is a consequence of real differences in digestive capacity between RFI groups or simply a result from large differences in the feed intake level between most and least efficient cattle. Negative effects of DMI level in feed digestibility occur by increasing passage rate of feed throughout the gastrointestinal tract, thereby feed digestibility is decreased four percentage points at every 1-fold DMI required for maintenance (DMI_m) increase, on average (Tyrrell & Moe, 1975; NRC, 2001). In that study, authors did not report DMI for either groups of RFI, and did not allow making such inference. However, in the present study, the feed intake in the feeding trial was equivalent to 2.8-fold and

2.4-fold DMI_m for high- and low-RFI steers, respectively (Nellore DMI_m (Valadares et al., 2006) = $119.5 \text{ kcal ME} \cdot \text{EBW}^{0.75} / 2.63 \text{ Mcal ME kg}^{-1} \text{ DM} \cdot 1000$), a difference of 0.4-fold DMI_m between efficiency groups that could affect feed digestibility by 1.6%, a little greater than the 1% difference in digestion between high- and low-RFI steers given by Richardson et al. (1996). This suggests that small differences in feed digestibility between cattle with divergent feed efficiency are most likely a result of differences in the feed consumption level and not in the ability to digest feed.

Nkrumah et al. (2006) reported no differences between RFI classes for dietary DE, ME and ME to DE ratio. In the same study, the authors reported lower methane production in low-RFI cattle using an indirect calorimetry system. These results corroborate the present findings, although the methane production herein reported was not directly measured but predicted based on diet digestibility and energy intake. Consequently, in the present study, the lower methane production by most efficient cattle is strongly associated with their lower feed consumption.

In the present study, the direct determination of urinary and fecal energy outputs and the estimation of methane production allowed us to obtain the digestible and metabolizable energy content of diet. The calculated ME to DE ratio was 0.79, a value slightly lower than the 0.82 reported by the NRC (1996). Accordingly, the observed dietary ME content was 11% lower than the predicted using the NRC (1996) (2.39 vs. 2.69 Mcal/kg DM). The relationship between DE and ME can vary considerably among feed ingredients or diets as a result of differences in intake, digestion and passage rates and chemical composition (NRC, 1996). These factors should explain the differences in the ME to DE ratio and the difference between observed and predicted ME content of diet. Nkrumah et al. (2006) reported greater DE to ME ratio values and no differences between RFI classes (0.90, 0.91 and 0.92 for high, medium and low-RFI groups, respectively).

Table 3 - Nitrogen balance of high- and low-RFI Nellore steers

Item	RFI class		SEM	P>F ¹
	High	Low		
N intake (g/d)	161	157	6.12	0.71
N excretion				0.37
Urine				
g/d	61.5	55.0	3.50	0.37
% of ingested	37.7	35.1	1.56	0.43
Feces				
g/d	47.3	42.3	2.75	0.38
% ingested	29.0	26.8	1.16	0.37
Total (g/d)	108.8	97.3	5.50	0.31
Retention				
g/d	53.2	60.0	3.44	0.34
% ingested N	33.4	38.1	2.03	0.26
% digested N	46.5	51.9	2.48	0.29

RFI - residual feed intake; SEM - standard error of the mean.

¹ Probability of a type I error.

Table 4 - Dry matter apparent digestibility and feed energy partitioning in high- and low-RFI Nellore steers

Item ¹	RFI class		SEM	P>F ²
	High	Low		
Dry matter apparent digestibility (%)	72.3	75.2	1.06	0.18
Digestible energy (Mcal/kg DM)	2.94	3.09	0.07	0.2723
Methane energy (Mcal/d)	5.74	5.29	0.19	0.0072
DE/ME	0.794	0.793	0.002	0.8260
Metabolizable energy (Mcal/kg DM)	2.34	2.45	0.05	0.2892

RFI - residual feed intake; SE - standard error of the mean; DM - dry matter; DE - digestible energy; ME - metabolizable energy

¹ Means are adjusted for common final shrunk body weight.

² Probability of a type I error.

Conclusions

Selecting Nellore cattle for improved residual feed intake might not influence protein turnover and feed digestibility; however, it is expected to decrease the degree of activity and responsiveness to stress. Furthermore, improving the residual feed intake might diminish dietary energy losses as methane, as well as contribute to mitigate the green house gas emissions from beef production.

Acknowledgments

The contributions of Rodrigo Souza, Fernando Alves, Vinicius Rahmé, Murilo Trettel, Juliana Moraes, Eduardo Telles, Diogo Foratto and Eliza Trickett are gratefully acknowledged.

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