Relationship of efficiency indices with performance, heart rate, oxygen consumption, blood parameters, and estimated heat production in Nellore steers

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ABSTRACT: The objective of this study was to examine the relationship of efficiency indices with performance, heart rate, oxygen consumption, blood parameters, and estimated heat production (EHP) in Nellore steers. Eighteen steers were individually lotfed diets of 2.7 Mcal ME/kg DM for 84 d. Estimated heat production was determined using oxygen pulse (O₂P) methodology, in which heart rate (HR) was monitored for 4 consecutive days. Oxygen pulse was obtained by simultaneously measuring HR and oxygen consumption during a 10- to 15-min period. Efficiency traits studied were feed efficiency (G:F) and residual feed intake (RFI) obtained by regression of DMI in relation to ADG and midtest metabolic BW (RFI_{REG}). Alternatively, RFI was also obtained based on equations reported by the NRC's Nutrient Requirements of Beef Cattle to estimate individual requirement and DMI (RFI calculated by the NRC [1996] equation [RFI_{NRC}]). The slope of the regression equation and its significance was used to evaluate the effect of efficiency indices (RFI_{REG}, RFI_{NRC}, or G:F) on the traits studied. A mixed model was used considering RFI_{REG}, RFI_{NRC}, or G:F and pen type as

fixed effects and initial age as a covariate. For HR and EHP variables, day was included as a random effect. There was no relationship between efficiency indices and back fat depth measured by ultrasound or daily HR and EHP (P > 0.05). Because G:F is obtained in relation to BW, the slope of G:F was positive and significant (P < 0.05). Regardless of the method used, efficient steers had lower DMI (P < 0.05). The initial LM area was indirectly related to RFI_{REG} and RFI_{NRC} (P < 0.05); however, the final muscle area was related to only RFI_{NRC}. Oxygen consumption per beat was not related to G:F; however, it was lower for RFI_{REG}and RFI_{NRC}-efficient steers, and consequently, oxygen volume (mL min $^{-1}$ kg $^{-0.75}$) and O_2P (μL O_2 ·beat⁻¹·kg^{-0.75}) were also lower (P < 0.05). Blood parameters were not related to ${\rm RFI}_{\rm REG}$ and ${\rm RFI}_{\rm NRC}$ (P> 0.05); however, G:F-efficient steers showed lower hematocrit and hemoglobin concentrations (P < 0.05). Differences in EHP between efficient and inefficient animals were not directly detected. Nevertheless, differences in oxygen consumption and O₂P were detected, indicating that the O₂P methodology may be useful to predict growth efficiency.

Key words: bioenergetic, feed efficiency of feed utilization, heat rate, oxygen consumption, residual feed intake

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J. Anim. Sci. 2015.93:5036–5046 doi:10.2527/jas2015-9066

INTRODUCTION

According to the Brazilian Institute of Geography and Statistics (IBGE, 2014), Brazil has the world's largest commercial cattle herd, with approximately 211 million *Bos indicus* steers accounting for nearly 80%

¹Corresponding author: amaliaschaves@yahoo.com.br Received March 4, 2015. Accepted August 4, 2015. of the total, of which the Nellore breed makes up 90% (ABIEC, 2014). Therefore, feed efficiency is an important factor to reduce feed costs and increase profitability. Different methods have been indicated to measure efficiency, with feed efficiency (G:F) and residual feed intake (RFI) being the most common. One difficulty in measuring and incorporating efficiency in beef cattle breeding programs is measuring individual animal feed intake, which is a very laborious task (Herd et al., 2003; Arthur et al., 2004). An alternative would be to identify

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steers with lower requirements of ME for maintenance for the same BW and gain; that is, steers that produce less heat at a certain weight are more efficient at converting feed. Heat loss can represent 70 to 75% of the total energy consumed (Ferrell and Jenkins, 1984; NRC, 1984). Variation of maintenance measures is 10 to 12%, making it an important component of efficiency variance in beef cattle (Hotovy et al., 1991; Swanson and Miller, 2008). The calorimetric chamber is used to estimate heat production (estimated heat production [EHP]); however, this methodology is very laborious and expensive. Heat production can be indirectly estimated from heart rate (HR) calibrated to oxygen consumed per HR, because most oxygen used by homoeothermic steers is transported to the tissues by the heart. Estimated heat production in humans obtained by this methodology is highly correlated to that obtained by calorimetric chamber (r = 0.943; Ceesay et al., 1989). In this context, the objective of this study was to examine the relationships between different efficiency indices and performance, HR, oxygen consumption, blood parameters, and EHP in Nellore steers.

MATERIALS AND METHODS

Steers and Diet

Steers were handled and managed according to the Institutional Animal Care and Use Committee Guidelines (Brazilian Agricultural Research Corporation [EMBRAPA], São Carlos, SP, Brazil). Eighteen Nellore steers of 20 mo of age and 281 ± 22 kg were used in this study. Steers were randomly distributed in individual pens (sheltered or unsheltered) where they were given excess feed twice daily to result in 5% orts for 84 d with diet containing 15% CP and 2.7 Mcal ME/kg DM (Table 1).

Samples of diet and individual orts were collected weekly, dried in forced ventilation oven (55°C ± 5°C/72 h), and then ground in a 1 mm screen using a Wiley mill (Arthur H. Thomas, Philadelphia, PA, USA) to obtain composite samples at the end of the experimental period. Samples were then analyzed with an Ankom fat analyzer (model XT20; Ankom Technology Corp., Macedon, NY) DM at 105°C (method 930.15; AOAC, 1986); ash (method 942.05; AOAC, 1986); CP Kjeldahl N (method 984.13; AOAC, 1986), NDF, ADF, and lignin (Van Soest et al., 1991); NDIN and ADIN (Licitra et al., 1996); and ether extract with an fat analyzer (Ankom XT20, method 2, 01–30–09, Ankom Technology Corp., Macedon, NY).

Total digestible nutrients were obtained using the equation proposed by Weiss et al. (1992); afterward, TDN was converted to DE, considering that 1 kg of TDN corresponds to 4,409 Mcal of DE, and finally,

Table 1. Ingredients and composition of experimental diet

Ingredient	Ra	ite, % DM
Corn silage		44.03
Grounded corn grain		29.45
Soybean hull		9.25
Cotton seed		7.76
Soybean meal 45%		8.17
Limestone		0.45
Urea		0.23
Mineral premix ¹		0.63
Monensin ²		0.03
Composition ³	Diet	Corn silage
DM^4	59.19	38.50
Ash	4.19	5.25
CP	15.73	8.43
NDIN ⁴	16.65	17.31
ADIN ⁵	7.95	15.77
EE	4.22	4.90
NDF	43.39	47.54
NDFp	40.78	46.07
ADF	31.14	30.26
Lignin	3.76	4.60
NFC	35.09	35.35
TDN^6	71.03^{7}	65.73
ME^8	2.63	2.51

¹Composition by kilogram: 85 g phosphorus, 130 g calcium, 5 g magnesium, 25 g sulfur, 156 g sodium, 240 g chlorine, 5,000 mg zinc, 1,500 mg copper, 1,700 mg iron, 1,250 mg manganese, 120 mg cobalt, 120 mg iodine, and 15 mg selenium.

 3 NDIN = neutral detergent insoluble nitrogen; ADIN = acid detergent insoluble nitrogen; EE = ether extract; NDF $_p$ = NDF corrected for protein; NFC = non-fibrous carbohydrate.

DE was converted to ME, where ME corresponds to 0.82 of the DE, according to the NRC (1984; Table 1).

Performance and Intake

Body weight was measured every 2 wk in the morning before feeding (no food or water restriction). Initial BW (kg) and final BW (kg) of the RFI evaluation period as well as preslaughter weight were taken after a 16-h period of feed and water fasting. Midtest metabolic BW was calculated as the average of initial BW and final BW.

Average daily gain (kg/d) was estimated for the period of RFI evaluation by regression between BW and days on feed using PROC REG (SAS Inst. Inc., Cary, NC), where the slope represents the growth rate.

Individual DMI (kg/d) was obtained as the difference between offer and refusal DM. The DM content

²28 mg/kg of DM.

⁴Percent DM basis.

⁵Percent CP basis.

⁶Estimated according to Weiss et al. (1992).

⁷Processing factor (0.95) used according to Van Soest et al. (1991).

 $^{^{8}}$ Megacalories per kilogram of DM, in which 1 kg of TDN = 4.409 kcal DE and ME = DE × 0.82 (NRC, 1984).

of the diet and orts was determined weekly. At the end of the experimental period, DM was corrected to definitive DM (105°C) using individual composite samples of refusals and diet samples.

Efficiency Indices

Feed efficiency and RFI were evaluated as efficiency parameters. Feed efficiency was calculated by the ratio between ADG (kg) and DMI (kg/d), and RFI was obtained by 2 different approaches. The first is a classical approach computed by regression of DMI, BW^{0.75}, and ADG (Koch et al., 1963) using the MIXED procedure (SAS Inst. Inc.). The difference between observed and predicted DMI by the regression was denominated **RFI**_{REG} (RFI obtained by regression of DMI in relation to ADG and midtest metabolic BW).

The second approach is based on equations to predict DMI proposed by the NRC, taking into account the amount of energy and feed required for both gain and maintenance (NRC, 1996). Net energy for maintenance per kilogram of shrunk BW and NEg per kilogram of shrunk body gain were also determined using equations indicated by the NRC. Those values were then divided by the concentration of NEm (Mcal/kg) and NEg (Mcal/kg) of the diet to determine the feed required to meet maintenance and energy gain requirements. The difference between actual and expected DMI, according to requirements, was denominated RFI_{NRC} (RFI calculated by the NRC [1996] equation) in agreement with Fan et al. (1995).

Body Gain Composition

Back fat (**BF**) depth and LM area between the 12th and 13th ribs were measured by ultrasound (Aquila; Pie Medical, Inc., Maastricht, The Netherlands) at the beginning (the first day of the trial period), middle (42 d after the beginning of the trial period), and end of the trial period (84 d after the beginning of the trial period). Images were collected, processed, and interpreted by ODT Eview software (Pie Medical, Inc.).

Heat Production Estimated by Oxygen Pulse Methodology

Heat production was estimated according to Brosh et al. (1998b). To obtain average beats per minute (**bpm**) and total daily beats, HR per minute was recorded using heart monitors (POLAR RS400; Kempele, Finland) for at least 4 consecutive days, between 42 and 52 d after the beginning of the trial period. Electrodes were fitted to steers with stretch belts. To calculate oxygen pulse (**O₂P**), oxygen consump-

tion and HR were simultaneously measured for 10 to 15 min. Oxygen consumption was collected by an EXHALYZER (ECOMedics, Zurich, Switzerland) on different days and periods using an open respiratory system (Taylor et al., 1982) consisting of a facemask connected to the gas analyzer, previously calibrated with gases with a known oxygen concentration and a syringe of known volume (3 L).

Because O₂P is constant only under stress-free conditions, calibration of oxygen consumption per beat was taken only when HR was up to 20% greater than the HR previously obtained under normal conditions (4 d) to avoid biased results.

Daily oxygen consumption was calculated by multiplying the volume of $\rm O_2$ per beat by total daily beats. The result was multiplied by constant 4.89 kcal/L of $\rm O_2$ (Nicol and Young, 1990) to estimate daily heat production in relation to metabolic BW (kcal.kg₋₁ BW^{0.75}·d⁻¹). Daily EHP was determined as follows:

EHP = (TDB
$$\times$$
 O₂ per beat \times 4.89 kcal/L O₂)/ kg BW^{0.75}, [1]

in which EHP is expressed in kilocalories/kilogram BW^{0.75}, TDB = total daily beats, and O_2 per beat is liters of O_2 per beat).

Blood Parameters

To analyze hematocrit and hemoglobin, blood samples (5 mL) were collected using vacuum tubes with EDTA, between 42 and 52 d after the beginning of the trial period. The blood sample was partially transferred into a capillary tube and centrifuged using a micro hematocrit centrifuge at $1,077 \times g$ for 5 min at ambient temperature. The packed cell volume as percentage of each specimen was determined using a graduated scale in millimeters. Hemoglobin was determined by colorimetric methodology using commercial kits (Labtest Diagnóstica, Lagoa Santa, Brazil) and spectrophotometer (UV-1601PC, Shimadzu, Japan) at 525 nm.

Statistical Analysis

Average daily gain was estimated by regression between BW and days on feed using PROC REG (SAS, Inst. Inc.), where the slope represents growth rate. Regression of DMI, BW^{0.75}, and ADG was computed as RFI_{REG} (Koch et al., 1963) considering pen type as a fixed effect using the MIXED procedure (SAS Inst. Inc.). Variables were analyzed by multiple linear regression in which studied traits were considered dependent or response variables (*y*) and RFI_{REG}, RFI_{NRC}, or G:F as independent variables (*x*) using the PROC MIXED function of

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SAS. Initial age was considered a covariate and pen type and RFI_{REG}, RFI_{NRC}, or G:F were considered fixed effects according to the statistical model described below:

$$y_{ijkt} = \mu + \beta i + \gamma_j + \rho_k + \alpha_t + e_{ijkt}$$

in which μ is the fixed overall mean effect; β_i is the fixed RFI_{REG}, RFI_{NRC}, or G:F effect; γ_j is the fixed pen type effect; ρ_k is the covariate effect of initial age; αt is the random effect of sire; and e_{ijkt} is the random residual error associated with y_{iikt} .

Variables related to HR and EHP did not show normal distribution and, for this reason, generalized mixed models (PROC GLIMMIX in SAS) were used. Following recommendations of Gbur (2012), in accordance with characteristic data, γ distribution was assumed for those variables. The effects of RFI_{REG}, RFI_{NRC}, or G:F and pen type (sheltered and unsheltered) were considered a fixed effect, initial age was considered a covariate, and time of day (morning or afternoon) when oxygen consumption was measured was considered a random effect.

$$y_{ijkt} = \mu + \beta_i + \gamma_j + \rho_k + \eta_t + e_{ijtk}$$

in which μ is the fixed overall mean effect; β_i is the fixed RFI_{REG}, RFI_{NRC}, or G:F effect; γ_j is the fixed pen type effect; ρ_k is the covariate effect of initial age; η_t is the random effect of day of the period when the measurement was made; and e_{ijkt} is the random residual error associated with y_{ijkt} . Gamma distribution was assumed and critical probability level of 5% was adopted for type I error in all tests realized.

RESULTS AND DISCUSSION

Performance, DMI, and Efficiency Indices

Average daily gain, DMI, and DMI as percent of BW (Table 2) were similar to those reported in the literature for *Bos taurus* and *B. indicus*. Nkrumah et al. (2007), working with 464 *B. taurus* crosses, obtained values of 1.46 kg/d for ADG and 10.45 kg/d for DMI, whereas Lancaster et al. (2009a) detected values of 1.40 kg/d for ADG and 8.45 kg/d for DMI in Angus cattle. Zorzi et al. (2013), working with 59 Nellore steers, detected DMI of 7.13 kg/d and 1.67% BW.

Although the RFI_{REG} mean was very close to zero, the RFI_{NRC} mean was 0.70 kg/d (Table 2). A positive RFI_{NRC} mean indicates that the equation to predict DMI by the NRC underestimated DMI. A RFI_{NRC} mean different from zero was also reported by Fan et al. (1995), wherein the averages obtained were -1.30 ± 0.10 , -0.76 ± 0.10 , and 0.11 ± 0.10 ME Mcal/d for a 3-yr test. Hennessy and Arthur (2004) reported a negative

Table 2. Mean, SD, and range of performance traits of Nellore steers during the feed efficiency evaluation period

Trait	Mean	SD	Minimum	Maximum
Initial age, d	614.2	25.84	568	649
Final age, d	697.2	25.84	651	732
Initial BW, kg	280.6	22.46	241	313
Final BW, kg	421.0	27.47	361	464
ADG, kg/d	1.72	0.159	1.48	2.06
DMI, kg/d	9.07	0.701	7.70	10.3
DMI, % BW	2.59	0.210	2.22	3.02
TDN intake, 1 kg/d	6.01	0.529	4.89	6.91
RFI_{REG}^{2}	0.00	0.634	-1.26	0.84
RFI _{NRC} ³	0.70	0.645	-0.46	1.72
G:F ⁴	0.19	0.022	0.15	0.23

¹TDN intake according to Weiss et al. (1992).

RFI_{NRC} mean, indicating that the expected consumption was overestimated in relation to the NRC equation.

The RFI $_{\rm REG}$ and RFI $_{\rm NRC}$ indices ranged from -1.26 to 0.84 and -0.46 to 1.72 kg/d with an amplitude of 2.10 and 2.19 kg/d, respectively, indicating phenotypic variability for this characteristic (Table 2). Smith et al. (2010) reported that the most efficient steers had -0.65 and 0.98 kg/d whereas the least efficient had 0.90 and 0.90 kg/d for RFI $_{\rm REG}$ and RFI $_{\rm NRC}$, respectively. Phenotypic RFI variance in Nellore has also been reported (Gomes et al., 2012; Costa e Silva et al., 2013). Gomes et al. (2012) detected minimum and maximum values of -2.72 and 1.54 kg/d for RFI in Nellore, an increase of 4.26 kg/d consumption among steers, whereas Costa e Silva et al. (2013) detected a difference of 2.0 kg/d.

No significant difference was detected between efficiency groups for initial and final live weight, live weight gain, and metabolic average daily weight when RFI_{REG} and RFI_{NRC} were used (Table 3). This result was expected because RFI is known to be independent of the weight characteristics. Still, Smith et al. (2010) observed that bulls with low RFI_{NRC} had significantly greater weight gain and were consequently heavier at 140 d of the experimental period compared with steers with medium and high RFI_{NRC}.

The regression slope between G:F and ADG was positive (P < 0.001), meaning that efficient steers had 17.4% greater ADG than inefficient ones (Table 3). Smith et al. (2010) also observed a negative correlation between G:F and ADG (r = -0.56, P < 0.001) and final BW after 140 d of the test period, indicating that bulls with lower G:F showed faster growth rate and greater final BW compared with bulls with greater G:F values.

 $^{^{2}}$ RFI_{REG} = residual feed intake obtained by regression of DMI in relation to ADG and midtest metabolic BW.

³RFI_{NRC} = residual feed intake calculated by the NRC (1996) equation. ⁴Feed efficiency (ADG/DMI).

Differences between efficient and inefficient groups based on RFI_{REG}, RFI_{NRC}, and G:F were highly significant for DMI, DMI as percent of BW, and TDN intake (Table 3). Therefore, efficient steers had lower DMI regardless of the method used to calculate efficiency of feed utilization.

Efficient RFI_{REG}, RFI_{NRC}, and G:F steers consumed 13.9, 11.6, and 10.31% less feed (kg/d), respectively, compared with inefficient ones. The same pattern was observed for TDN intake. Smith et al. (2010) also observed lower DMI in efficient steers regardless of the method used to calculate feed efficiency; however, the authors detected no correlation between total DMI and RFI_{NRC}, indicating that phenotypic selection based on RFI_{NRC} could slightly affect DMI. Arthur et al. (2001a) also reported weak phenotypic and genotypic correlations with DMI when RFI was calculated using standard models instead of regression between DMI, ADG, and metabolic BW.

Arthur et al. (2001b) observed an annual decrease of 0.240 kg/d in DMI in the low-RFI selection line steers compared with those selected for high RFI. Several studies confirmed a positive relationship between RFI, RFI_{NRC}, and G:F and DMI in different breeds (Arthur et al., 2001a,b; Castro Bulle et al., 2007; Lancaster et al., 2009a,b; Smith et al., 2010; Ahola et al., 2011; Lucila Sobrinho et al., 2011; Gomes et al., 2012; Santana et al., 2012; Welch et al., 2012; Zorzi et al., 2013). Smith et al. (2010) detected a difference of 13.9% (9.72 vs. 8.36 kg/d) in DMI between low- and high-RFI_{NRC} Angus steers, and Zorzi et al. (2013) reported a difference of 10% between lowand high-RFI Nellore steers.

Efficient steers had lower DMI for maintenance and gain when RFI_{REG} and RFI_{NRC} were used (P < 0.01; Table 3). This shows that DMI difference would be more related to a possible change in gain composition or metabolic factors that determine inefficiency in energy use for weight gain over the simple reduction in maintenance requirement.

Fable 3. Means for efficient and inefficient steers; SEM; linear regression coefficients (θ_v) for residual feed intake obtained by regression of DMI in relation to ADG and midtest metabolic BW (RFI_{REG}; β_1), residual feed intake calculated by the NRC (1996) equation (RFI_{NRC}; β_2), and feed efficiency (G:F; β_3); and probability level for performance traits of 18 Nellore steers

•			$\mathrm{RFI}_{\mathrm{REG}}$					RFI_{NRC}					G:F		
Trait ¹	Efficient	Inefficient	SEM	β ₁	P > F	Efficient	Inefficient	SEM	β2	P > F	Efficient	Inefficient	SEM	β3	P > F
IBW, kg	281	280	5.62	-0.195	86.0	287	274	5.44	-8.951	0.36	270	289	5.31	-11.04	0.22
FBW, kg	423	419	6.83	-3.152	0.80	431	412	6.54	-13.00	0.27	424	418	6.82	4.424	0.75
MMBW, kg	81.3	8.08	1.04	-0.322	98.0	82.5	79.7	1.00	-1.937	0.28	80.4	81.5	1.04	-18.99	0.71
Hip height, m	1.42	1.44	0.01	0.012	0.58	1.43	1.43	0.01	0.001	96.0	1.43	1.43	0.01	-0.089	0.88
ADG, kg/d	1.74	1.71	0.04	-0.023	0.76	1.74	1.71	0.04	-0.022	92.0	1.90	1.58	0.03	5.617	<0.001
DMI, kg/d	8.36	9.72	0.07	0.958	<0.0001	8.49	09.6	0.11	0.781	<0.001	8.71	9.48	0.13	0.548	0.03
DMI, % BW	2.37	2.79	0.03	0.296	<0.0001	2.36	2.81	0.01	0.316	<0.0001	2.45	2.70	0.04	-4.382	90.0
TDN intake, ² kg/d	5.45	6.52	0.05	0.754	< 0.0001	5.54	6.44	80.0	0.629	<0.001	5.57	6.37	0.10	-13.99	0.01
ME,3 Mcal/kg MS	2.36	2.43	0.01	0.049	<0.01	2.36	2.43	0.01	0.046	<0.01	2.36	2.42	0.01	-1.036	0.03
NEm, ⁴ Mcal/kg MS	2.04	1.77	0.03	-0.191	<0.01	1.48	1.54	0.01	0.041	<0.01	2.10	1.74	0.02	6.276	< 0.0001
NEg, ⁵ Mcal/kg MS	1.38	1.15	0.02	-0.167	<0.01	68.0	0.95	0.01	0.037	<0.01	1.44	1.12	0.02	5.524	< 0.0001
DMI_{m} , 6 kg/d	3.06	3.51	0.04	0.313	<0.01	3.11	3.46	90.0	0.248	0.02	2.92	3.59	0.02	-11.71	< 0.0001
DMIg,7 kg/d	5.29	6.21	0.07	0.651	< 0.001	5.37	6.14	0.09	0.537	<0.01	5.59	5.92	0.12	-5.881	0.32

IBW = initial BW; FBW = final BW; MMBW = midtest metabolic BW; DMI_m = DMI for maintenance; DMI_g = DMI for gain

6Estimated per NEm requirement/diet NEm

²According to Weiss et al. (1992).

³Estimated per kilogram DM intake.

⁴According to Zinn and Shen (1998) ⁵According to Zinn and Shen (1998)

Estimated per difference between DMI and DMI_m.

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able 4. Means for efficient and inefficient steers; SEM; linear regression coefficients (β_x) for residual feed intake obtained by regression of DMI in relation to ADG and midtest metabolic BW (RFI_{REG}; β_1), residual feed intake calculated by the NRC (1996) equation (RFI_{NRC}; β_2), and feed efficiency (G.F; β_3); and probability level for LM and back fat thickness traits of 18 Nellore steers

Trait Efficient		$\mathrm{RFI}_{\mathrm{REG}}$					$\mathrm{RFI}_{\mathrm{NRC}}$					G:F		
-	ent Inefficient	int SEM	β1	P > F	Efficient	Inefficient	SEM	β2	P > F	Efficient	Inefficient	SEM	β_3	P > F
LM area,¹ cm²														
Initial 46.9	41.1	1.07	-4.044	0.05	47.6	40.5	0.95	-4.908	<0.01	42.9	44.8	1.23	-33.33	0.58
Final 56.9	52.0	1.35	-3.430	0.18	57.9	51.1	1.25	-4.733	0.05	54.7	54.1	1.44	10.09	68.0
Deposition 9.99	9 10.6	1.29	0.451	0.84	10.3	10.4	1.28	0.055	86.0	11.8	60.6	1.26	46.31	0.46
Back fat thickness,1 mm														
Initial 2.36	5 2.72	0.19	0.254	0.48	2.47	2.62	0.20	0.101	0.77	1.96	3.02	0.17	-18.44	0.04
Final 5.15	5 6.04	0.21	0.622	0.13	5.27	5.93	0.22	0.455	0.25	5.11	6.02	0.22	-15.83	0.16
Deposition 2.79	9 3.30	0.23	0.365	0.38	2.79	3.30	0.23	0.354	0.38	3.13	2.99	0.23	2.502	0.82

Measured by ultrasound between the 12th and 13th ribs.

There were no differences between the G:F animal groups in DMI for gain, although DMI for the maintenance of G:F-efficient steers was 18.7% lower (P < 0.0001), showing that the observed difference in DMI can be partially explained by a greater dilution of maintenance. Furthermore, although efficient steers showed the same DMI for gain as inefficient steers (P > 0.05), ADG was 17.4% greater (Table 3).

Body Gain Composition

There was no relationship between RFI_{REG} and RFI_{NRC} groups for initial and final BF depth and BF deposition, measured by ultrasound (P > 0.05). However, the initial LM area was indirectly proportional to ${\rm RFI}_{\rm REG}$ and ${\rm RFI}_{\rm NRC}$ (P < 0.05), whereas the final LM area was not related to RFI_{NRC}. This relationship may indicate that efficient steers had greater ability to deposit muscle (Table 4). Smith et al. (2010) detected no correlation between RFI_{NRC} and BF depth measured by ultrasound at the end of the trial. However, smaller LM area deposition on high-RFI steers was also reported by Trejo et al. (2010), who observed differences between the LM area (92.88, 87.88, and 89.46 cm², respectively) in lower-, medium-, and high-RFI steers with similar subcutaneous BF depth (1.32, 1.28, and 1.26 mm, respectively).

Furthermore, G:F was not related to the LM area nor was it related to final and deposited BF depth; however, G:F was observed in lower initial BF depth in efficient steers (P < 0.05; Table 4). Smith et al. (2010) detected no correlation between G:F and BF depth at the end of 140 d on feed for efficient and inefficient steers, indicating that selection for low G:F may not affect this characteristic. Nevertheless, some authors observed greater BF depth in inefficient steers in trials using *B. taurus* (Herd and Bishop, 2000; Arthur et al., 2001a; Carstens et al., 2002; Lancaster et al., 2009a) and Nellore (Gomes et al., 2012; Santana et al., 2012).

Estimated Heat Production Measured by the Oxygen Pulse Methodology

During calibration, HR was similar to the average daily mean during the 4-d measurement period, indicating that the steers were not under stress during oxygen collection (Table 5).

During the 4-d evaluation period, HR was 89.8 ± 8.04 bpm and mean O_2P was 227.6 ± 52.5 μL $O_2 \cdot BW^{-0.75} \cdot beat^{-1}$. Brosh et al. (1998b), in a study of 6 Hereford steers weighing 345 ± 10.8 kg, detected an average similar to that of the present study, in which HR was 94 bpm and O_2P was $238 \mu L$ $O_2 \cdot BW^{-0.75} \cdot beat^{-1}$ in steers fed 80% concentrate and 20% sorghum si-

Table 5. Mean, SD, and range of heart rate, oxygen consumption, and heat production traits of 18 Nellore steers during the feed efficiency evaluation period

Trait ¹	Mean	SD	Minimum	Maximum
O ₂ calibration period ²				
Heart rate, bpm	88.5	12.21	65.9	118.3
O2 consumption, mL/beat	21.5	5.84	11.8	31.5
${ m O_2}$ volume, mL·min $^{-1}$ ·kg PV $^{-0.75}$	19.8	4.07	13.5	28.9
${ m O_2P}$, ${ m \mu L~O_2 \cdot beat^{-1} \cdot kg}$ ${ m PV^{-0.75}}$	227.6	52.49	140.2	329.5
Trial period ³				
Heart rate, bpm	89.8	8.04	78.6	106.9
O ₂ consumption, L/d	2,739	626.7	1,606	3,809
EHP, Mcal/d	13.4	3.06	7.9	18.6
EHP, kcal·d ⁻¹ ·kg PV ^{-0.75}	142.5	27.61	83.5	194.9
EHP, $kJ \cdot d^{-1} \cdot kg \ PV^{-0.75}$	596.2	115.6	349.7	815.7
EHP, Mcal/kg gain	8.31	1.95	5.23	12.02

¹bpm = beats per minute; O₂P = oxygen pulse; EHP = estimated heat production.

lage. In addition, HR in cows ranged from 61 to 88 bpm. Oxygen volume values reported by Brosh (2007) of 20 to 30 mL·min⁻¹·kgBW^{-0.75} were also similar to those observed in the present study.

Daily EHP was $13.4 \pm 3,06\,$ Mcal/dia and $596.2 \pm 115.6\,$ kJ·d₋₁·kg BW_{-0.75}). Brosh et al. (2002) observed EHP as $340 \pm 18.4\,$ kJ·d⁻¹·kg BW^{-0.75} in a study on the use of HR to estimate heat production in 6 cows in different reproductive stages. Additionally, Brosh et al. (2004) observed an average of $481 \pm 53\,$ kJ·d⁻¹·kg BW^{-0.75} in pasture-fed nonlactating cows. Heat production differences between studies may be attributed to differences in breed, seasonal, age, metabolism, HR, and ME intake of the steers studied. The steers in the study conducted by Brosh et al. (2002) showed HR of $44.9 \pm 1.81\,$ bpm, whereas the average observed in the present study was $89.4 \pm 8.27\,$ bpm. Greater EHP can be observed in steers with greater HR and steers fed a ME-rich diet (Brosh et al., 2002).

The nycterohemeral profile of HR was within the normal pattern established for the conditions of the trial, whose peaks were equivalent 2 h after feeding, which happened at 0800 and 1500 h (Fig. 1). Under stable conditions, that is, without stress factors or sudden changes in feed intake, the daily pattern of HR is similar over time throughout the days (Brosh, 2007).

Although daily HR during calibration and the 4-d evaluation period were numerically lower for efficient steers, they were not related to the efficiency of feed utilization indices studied (Table 6). Inefficient steers showed HR 6.9% greater at the calibration time in relation to the rate measured in the 4-d evaluation period, whereas this

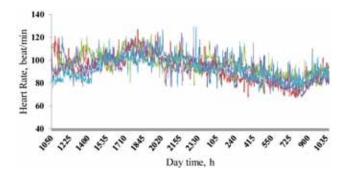


Figure 1. Profile of diurnal heart rate of 4 Nellore for 24 h. Each color represents an animal.

variation in efficient steers was only 1.5%. This may be attributed to greater response to stress in these steers. Some studies show (Lancaster et al., 2005; Hafla et al., 2013) that steers with high RFI had greater HR compared with steers with low RFI. Factors related to this difference in HR are not clear, but they may be related to increased requirements for maintenance or greater response to stress in inefficient steers. Cortisol blood circulation is negatively related to temperament and calmness in steers, indicating great responsiveness to stress, which may contribute to variation of RFI in Nellore (Gomes et al., 2013). Some studies on sheep (Knott et al., 2008, 2010) and Nellore (Gomes et al., 2013) reported high cortisol levels in plasma of inefficient steers.

Oxygen consumption (mL/beat) was not related to G:F; however, it was lower for efficient RFI_{REG} and RFI_{NRC} steers, and consequently, $\rm O_2$ volume (mL·min⁻¹·kg^{-0.75}) and $\rm O_2$ P values were lower in this group of steers (Table 6). A study of 16 heifers classified as high or low RFI indicated that steers with high RFI also presented greater $\rm O_2$ P and $\rm O_2$ consumption in relation to those with low RFI (Paddock, 2010).

Because O_2P is an individual characteristic, for some authors (Brosh et al. (1998a,b, 2004), it may change during the day if the steers are under intense physical activity or stress. In the present study, steers did not undergo any heavy physical exercise or stress, because they were kept in individual pens throughout the trial. This indicates that the use of a constant value of O_2P to calculate heat can properly represent daily heat production.

There was no significant effect of RFI_{REG}, RFI_{NRC}, and G:F on EHP (Table 6). Paddock (2010), using the O₂P methodology, observed that EHP was 17.4% greater in steers with high RFI compared with those with low RFI. However, Aharoni et al. (2003) observed that EHP increased proportionally with RFI in lactating cows. Furthermore, Aharoni et al. (2006) studied EHP to characterize use efficiency of protein and NE in Holstein or Holstein × Montbeliarde and observed that crossed steers had lower HR but that this was not reflected in differences in O₂P and heat production.

²Minimum 15 min.

³Minimum 4 d.

Table 6. Means for efficient and inefficient steers; SEM; linear regression coefficients (β_x) for residual feed intake obtained by regression of DMI in relation to ADG and midtest metabolic BW (RFI_{REG}; β₁), residual feed intake calculated by the NRC (1996) equation (RFI_{NRC}; β₂), and feed efficiency (G.F; β₃); and probability level for heart rate, oxygen consumption, and heat production traits of 18 Nellore steers

			$\mathrm{RFI}_{\mathrm{REG}}$					$\mathrm{RFI}_{\mathrm{NRC}}$					G:F		
$Trait^1$	Efficient	Efficient Inefficient	SEM	β1	P > F	Efficient	Inefficient	SEM	β ₂	P > F	Efficient	Inefficient	SEM	β_3	P > F
O_2 calibration period ²															
HR, bpm	83.3	89.7	3.42	0.052	0.41	81.5	91.2	3.50	0.079	0.23	9.98	92.3	1.34	-0.058	0.16
O ₂ C, mL/beat	19.1	23.8	2.19	0.155	<0.01	19.1	24.2	2.32	0.165	<0.01	21.6	21.0	1.88	-0.020	0.81
VO_2 , mL·min ⁻¹ ·kg BW ^{-0.75}	16.2	21.8	1.59	0.211	0.04	15.3	23.1	1.75	0.286	<0.01	19.8	19.1	1.18	-0.025	0.79
O_2P , μL O_2 -beat ⁻¹ -kg BW ^{-0.75} Trial period ³	202	245	18.9	0.137	0.05	200	252	19.9	0.161	<0.01	228	220	16.9	0.027	0.43
HR, bpm	89.2	90.3	1.4	0.784	0.77	89.5	90.1	1.44	0.409	0.87	87.5		1.32	-3.561	0.43
O_2C , L/d	2,445	3,014	255	0.147	80.0	2,513	2,964	255	0.115	0.19	2,673		230	-0.025	0.71
EHP, Mcal/d	12.0	14.7	1.25	0.147	80.0	12.3	14.5	1.25	0.115	0.19	13.1		1.12	-0.025	0.71
EHP, kcal·d ⁻¹ ·kg BW ^{-0.75}	126	154	11.2	0.137	80.0	128	154	11.4	0.128	0.10	138	143	10.3	-0.025	0.78
EHP, kJ·d ⁻¹ ·kg BW ^{-0.75}	529	643	46.7	0.137	80.0	536	643	47.6	0.128	0.10	577		43.0	-0.025	0.78
EHP, Mcal/kg gain	7.71	8.69	0.64	0.084	0.40	7.95	8.49	0.63	0.046	0.65	7.39	90.6	0.64	-0.147	0.14

 $^{^{\}prime}$ HR = heart rate; bpm = beats per minute; $^{\prime}$ O₂C = $^{\prime}$ C consumption; $^{\prime}$ VO₂ = $^{\prime}$ C volume; BW= Body weight; $^{\prime}$ O₂P = oxygen pulse; EHP = estimated heat production.

Table 7. Means for efficient and inefficient steers; SEM; linear regression coefficients (β_x) for residual feed intake obtained by regression of DMI in relation to ADG and midtest metabolic BW (RFI_{REG}; β_1), residual feed intake calculated by the NRC (1996) equation (RFI_{NRC}; β_2), and feed efficiency (G:F; β_3); and probability level for blood traits of 18 Nellore steers

	P > F	<0.01	0.03
	β_3	ľ	-1.882
G:F	SEM	0.924	0.443
,	Inefficient	45.7	15.5
	Efficient	36.8	12.6
	P > F	0.42	0.19
	β_2	1.744	1.175
$\mathrm{RFI}_{\mathrm{NRC}}$	SEM	1.22	0.49
	Inefficient	43.0	15.0
	Efficient	40.5	13.3
	P > F	0.28	0.17
	β_1	2.425	1.287
$\mathrm{RFI}_{\mathrm{REG}}$	SEM	1.20	0.49
	Inefficient	43.4	15.1
	Efficient	40.0	13.3
	Trait ¹	Hct, %	Hb, g/dL

 $^{^{1}}$ Hct = hematocrit; Hb = hemoglobin.

 $^{^2}$ Minimum 15 min.

³Minimum 4 d.

Blood Parameters

There was no significant relationship between RFI_{REG}, RFI_{NRC}, and blood parameters; however, G:Fefficient steers had lower hematocrit percentage and lower hemoglobin concentration (P < 0.05; Table 7). Richardson et al. (1996), in search of possible physiological indicators for feed efficiency, also studied blood constituents of Angus heifers and bulls with high and low efficiency. These authors observed that the most efficient steers had a greater number of red blood cells. On the other hand, the proportion of hemoglobin and hematocrit in those cells was lower compared with inefficient steers. Richardson et al. (2000) also observed a lower concentration of hemoglobin (11.7 \pm 0.15 vs. 12.3 \pm 0.13 g/dL, respectively; P < 0.01) and hematocrit (31.4 \pm 0.50 vs. 33.3 ± 0.42 %, respectively; P < 0.01) in Angus bulls with low RFI compared with those with high RFI.

Therefore, the lower hematocrit percentage in the most efficient steers indicates that they may have a greater number of red cells compared with inefficient steers. These differences may be associated with oxygen-carrying capacity.

Conclusions

Efficient steers had lower DMI regardless of the method used to calculate efficiency of feed utilization.

Although no relationships were detected for G:F, RFI_{REG}, and RFI_{NRC} with EHP, classifying the steers based on those indices facilitated the identification of differences in oxygen consumption and O₂P, indicating that the O₂P method may be useful to identify efficient steers.

The observed differences in hematocrit and hemoglobin concentrations between efficient and inefficient G:F steers may be associated with oxygen-carrying capacity. Further studies should evaluate theses 2 parameters as alternative markers to estimate biological variation in feed efficiency as well as to understand the physiological basis for this relationship.

LITERATURE CITED

- Aharoni, Y., A. Brosh, and E. Kafchuk. 2006. The efficiency of utilization of metabolizable energy for milk production: A comparison of Holstein with F1 Montbeliarde × Holstein cows. J. Anim. Sci. 82:101–109. doi:10.1079/ASC200515.
- Aharoni, Y., A. Brosh, P. Kourilov, and A. Arieli. 2003. The variability of the ratio of oxygen consumption to heart rate in cattle and sheep at different hours of the day and under different heat load conditions. Livest. Prod. Sci. 79:107–117. doi:10.1016/S0301-6226(02)00147-1.
- Ahola, J. K., T. A. Skow, C. W. Hunt, and R. A. Hill. 2011. Relationship between residual feed intake and end product palatability in longissimus steaks from steers sired by Angus bulls divergent for intramuscular fat expected progeny difference. Prof. Anim. Sci. 27:109–115.

- AOAC. 1986. Official Methods of Analysis. 14th ed. Assoc. Off. Anal. Chem., Arlington, VA.
- Arthur, P. F., J. A. Archer, and R. M. Herd. 2004. Feed intake and efficiency in beef cattle: Overview of recent Australian research and challenges for the future. Aust. J. Exp. Agric. 44:361–369. doi:10.1071/EA02162.
- Arthur, P. F., J. A. Archer, R. M. Herd, and G. J. Melville. 2001a. Response to selection for net feed intake in beef cattle. In: Proc. 14th Conf. Assoc. Advancement Anim. Breed. Genet., Queenstown, New Zealand. p. 135–138.
- Arthur, P. F., J. A. Archer, D. J. Johnston, E. C. Richardson, and P. F. Parnell. 2001b. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency and other post weaning traits in Angus cattle. J. Anim. Sci. 79:2805–2811.
- Associação Brasileira das Indústrias Exportadoras de Carne (ABIEC). 2014. Statistic reports. http://www.abiec.com.br/estatisticas/. http://www.abiec.com.br/estatisticas/ (Accessed 14 August 2014.)
- Brosh, A. 2007. Heart rate measurements as an index of energy expenditure and energy balance in ruminants: A review. J. Anim. Sci. 85:1213–1227. doi:10.2527/jas.2006-298.
- Brosh, A., Y. Aharoni, A. Degen, D. Wright, and B. A. Young. 1998a. Effects of solar radiation, dietary energy, and time of feeding on thermoregulatory responses and energy balance in cattle in a hot environment. J. Anim. Sci. 76:2671–2677.
- Brosh, A., Y. Aharoni, A. Degen, D. Wright, and B. A. Young. 1998b. Estimation of energy expenditure from heart rate measurements in cattle maintained under different conditions. J. Anim. Sci. 76:3054–3064.
- Brosh, A., Y. Aharoni, and Z. Holzer. 2002. Energy expenditure estimation from heart rate: Validation by long-term energy balance measurement in cows. Livest. Prod. Sci. 77:287–299. doi:10.1016/S0301-6226(02)00033-7.
- Brosh, A., Y. Aharoni, E. Shargal, B. Sharir, M. Gutman, and I. Choshniak. 2004. Energy balance of grazing beef cattle in Mediterranean pasture, the effects of stocking rate and season. 2. Energy expenditure as estimated from heart rate and oxygen consumption, and energy balance. Livest. Prod. Sci. 90:101–115. doi:10.1016/j.livprodsci.2004.03.008.
- Carstens, G. E., C. M. Theis, M. B. White, T. H. Welsh Jr., B. G. Warrington, R. K. Miller, R. D. Randel, T. D. A. Forbes, H. Lippke, L. W. Greene, and D. K. Lunt. 2002. Relationships between net feed intake and ultrasound measures of carcass composition in growing beef steers. Beef Cattle Research in Texas. Nutrition. p. 31–34.
- Castro Bulle, F. C., F. C. P. Paulino, A. C. Sanches, and R. D. Sainz. 2007. Growth, carcass quality, and protein and energy metabolism in beef cattle with different growth potentials and residual feed intakes. J. Anim. Sci. 85:928–936. doi:10.2527/jas.2006-373.
- Ceesay, S. M., A. M. Prentice, K. C. Day, P. R. Murgatroyd, G. R. Goldberg, W. Scott, and G. B. Spurr. 1989. The use of heart rate monitoring in the estimation of energy expenditure: A validation study. Br. J. Nutr. 61:175–186. doi:10.1079/BJN19890107.
- Costa e Silva, L. F., S. C. Valadares Filho, E. Detmann, P. P. Rotta, D. Zanetti, F. A. C. Villadiego, S. C. Pellizzoni, and R. F. G. Pereira. 2013. Performance, growth, and maturity of Nellore bulls. Trop. Anim. Health Prod. 45:795–803. doi:10.1007/s11250-012-0291-1.

- Fan, L. Q., D. R. C. Bailey, and N. H. Shannon. 1995. Genetic parameter estimation of postweaning gain, feed intake, and efficiency for Hereford and Angus bulls fed two different diets. J. Anim. Sci. 73:365–372.
- Ferrell, C. L., and T. G. Jenkins. 1984. Energy utilization by mature, nonpregnant, nonlactating cows of different types. J. Anim. Sci. 58:234–243.
- Gbur, E. E. 2012. Analysis of generalized linear mixed models in the agricultural and natural resources sciences. American Society of Agronomy, Soil Science Society of America, and Crop Science Society of America, Madison, WI.
- Gomes, R. C., R. D. Sainz, and P. R. Leme. 2013. Protein metabolism, feed energy partitioning, behavior patterns and plasma cortisol in Nellore steers with high and low residual feed intake. R. Bras. Zootec. 42:44–50. doi:10.1590/S1516-35982013000100007.
- Gomes, R. C., R. D. Sainz, S. L. Silva, M. C. Cesar, M. N. Bonin, and P. R. Leme. 2012. Feedlot performance, feed efficiency reran king, carcass traits, body composition, energy requirements, meat quality and calpain system activity in Nellore steers with low and high residual feed intake. Livest. Prod. Sci. 150:265–273. doi:10.1016/j.livsci.2012.09.012.
- Hafla, A. N., G. E. Cartens, T. D. A. Forbes, L. O. Tedeschi, J. C. Bailey, J. T. Walter, and J. R. Johnson. 2013. Relationships between postweaning residual feed intake in heifers and forage use, body composition, feeding behavior, physical activity, and heart rate of pregnant beef females. J. Anim. Sci. 91:5353–5365. doi:10.2527/jas.2013-6423.
- Hennessy, D. W., and P. F. Arthur. 2004. The effect of preweaning growth restriction on the feed intake and efficiency of cattle on a grain-based diet before slaughter. Aust. J. Exp. Agric. 44:483–488. doi:10.1071/EA02110.
- Herd, R. M., J. A. Archer, and P. F. Arthur. 2003. Reducing the cost of beef production through genetic improvement in residual feed intake: Opportunity and challenges to application. J. Anim. Sci. 81:9–17.
- Herd, R. M., and S. C. Bishop. 2000. Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. Livest. Prod. Sci. 63:111–119. doi:10.1016/S0301-6226(99)00122-0.
- Hotovy, S. K., K. A. Johnson, D. E. Johnson, G. E. Carstens, R. M. Bourdon, and G. E. Siedel. 1991. Variation among twin beef cattle in maintenance energy requirements. J. Anim. Sci. 69:940–946.
- Instituto Brasileiro de Geografia e Estatística (IBGE). 2014. Integrated dataset and livestock reports. http://www.sidra. ibge.gov.br/bda/pecua/default.asp?t = 4&z = t&o = 24&u1 = 1&u2 = 1&u3 = 1&u4 = 1&u5 = 1&u6 = 1&u7 = 1. (Accessed 14 August 2014.)
- Knott, S. A., L. J. Cummins, F. R. Dunshea, and B. J. Leury. 2008. Rams with poor feed efficiency are highly responsive to an exogenous adrenocorticotropin hormone (ACTH) challenge. Domest. Anim. Endocrinol. 34:261–268. doi:10.1016/j. domaniend.2007.07.002.
- Knott, S. A., L. J. Cummins, F. R. Dunshea, and B. J. Leury. 2010. Feed efficiency and body composition are related to cortisol response to adrenocorticotropin hormone and insulininduced hypoglycemia in rams. Domest. Anim. Endocrinol. 39:137–146. doi:10.1016/j.domaniend.2010.03.003.
- Koch, R. M., L. A. Swinger, D. Chambers, and D. K. E. Gregory. 1963. Efficiency of feed use in beef cattle. J. Anim. Sci. 22:486–494.

- Lancaster, P. A., G. E. Carstens, D. H. Crews, T. H. Welsh Jr., T. D. A. Forbes, D. W. Forrest, L. O. Tedeschi, R. D. Randel, and F. M. Rouquette. 2009b. Phenotypic and genetic relationships of residual feed intake with performance and ultrasound carcass characteristics of Brangus heifers. J. Anim. Sci. 87:3887–3896. doi:10.2527/jas.2009-2041.
- Lancaster, P. A., G. E. Carstens, F. R. B. Ribeiro, L. O. Tedeschi, and D. H. Crews. 2009a. Characterization of feed efficiency traits and relationships with feeding behavior and ultrasound carcass characteristics in growing bulls. J. Anim. Sci. 87:1528–1539. doi:10.2527/jas.2008-1352.
- Lancaster, P. A., B. R. Schilling, G. E. Carstens, E. G. Brown, T. M. Craig, and D. K. Lunt. 2005. Correlations between residual feed intake and carcass traits in finishing steers administered anthelmintic treatments. J. Anim. Sci. 83(Suppl. 1):263 (Abstr.).
- Licitra, G., T. M. Hernandez, and P. J. Van Soest. 1996. Standardization of procedures for nitrogen fractionation of ruminant feeds. Anim. Feed Sci. Technol. 57:347–358. doi:10.1016/0377-8401(95)00837-3.
- Lucila Sobrinho, T., R. H. Branco, S. F. M. Bonilha, A. M. Castilhos, L. A. Figueiredo, A. G. Razook, and M. E. Z. Mercadante. 2011. Residual feed intake and relationships with performance of Nellore cattle selected for post weaning weight. R. Bras. Zootec. 40:929–937. doi:10.1590/S1516-35982011000400030.
- Nicol, A. M., and B. A. Young. 1990. Short-term thermal and metabolic responses of sheep to ruminal cooling: Effects of level of cooling and physiological state. Can. J. Anim. Sci. 70:833–843. doi:10.4141/cjas90-102.
- Nkrumah, J. D., J. A. Basarab, Z. Wang, C. Li, M. A. Price, E. K. Okine, D. H. Crews, and S. S. Moore. 2007. Genetic and phenotypic relationships of feed intake and different measures of feed efficiency with growth and carcass merit of beef cattle. J. Anim. Sci. 85:2711–2720. doi:10.2527/jas.2006-767.
- NRC. 1984. Nutrient requirements of beef cattle. 6th rev. ed. Natl. Acad. Press, Washington, DC.
- NRC. 1996. Nutrient requirements of beef cattle. 7th rev. ed. Natl. Acad. Press, Washington, DC.
- Paddock, Z. D. 2010. Energy expenditure in growing heifers with divergent residual feed intake phenotypes: Effects and interactions of metaphylactic treatment and temperament on receiving steers. MS Thesis, Texas A&M Univ., College Station. http://oaktrust.library.tamu.edu/handle/1969.1/ETD-TAMU-2010-08-8264 (Accessed 20 June 2013.)
- Richardson, E. C., R. M. Herd, P. F. Arthur, J. Wright, G. Xu, K. Dibley, and V. H. Oddy. 1996. Possible physiological indicators for net feed conversion efficiency in beef cattle. Proc. Aust. Soc. Anim. Prod. http://asap.asn.au/livestockli-brary/1996/Richardson96.PDF. 21:103–106. (Accessed 23 June 2013.)
- Richardson, E. C., R. M. Herd, I. G. Colditz, V. H. Oddy, J. A. Archer, and P. F. Arthur. 2000. Red cell profiles of Angus steers selected for and against residual feed intake. Asian Aus. J. Anim. Sci. 13 Supplement J. p. 195.
- Santana, M. H. A., P. Rossi Jr., R. Almeida, and D. C. Cucco. 2012. Feed efficiency and its correlations with carcass traits measured by ultrasound in Nellore bulls. Livest. Prod. Sci. 145:252–257. doi:10.1016/j.livsci.2012.02.012.
- Smith, S. N., M. E. Davis, and S. C. Loerch. 2010. Residual feed intake of Angus beef cattle divergently selected for feed conversion ratio. Livest. Prod. Sci. 132:41–47. doi:10.1016/j. livsci.2010.04.019.

Swanson, K., and S. Miller. 2008. Factors regulating feed efficiency and nutrient utilization in beef cattle. In: J. France and E. Kebreab, editors, Mathematical modelling in animal nutrition. CAB International, Cambridge, MA. p. 419–441.

- Taylor, C. R., N. C. Heglund, and G. M. O. Maloiy. 1982. Energetics and mechanics of terrestrial locomotion as a function of speed and body size in birds and mammals. J. Exp. Biol. 97:1–21.
- Trejo, C. O., D. Faulkner, J. M. Dahlquist, and T. G. Nash. 2010. Influence of residual feed intake, breed of sire and dam on the performance and carcass characteristics of early weaned steers during the feedlot phase. J. Anim. Sci., 88, E-Suppl. 2, 685.
- Van Soest, P. J., J. B. Robertson, and B. A. Lewis. 1991. Methods for dietary fiber, neutral detergent fiber, and no starch polysaccharides in relation to animal nutrition. J. Dairy Sci. 74:3583–3597. doi:10.3168/jds.S0022-0302(91)78551-2.

- Weiss, W. P., H. R. Conrad, and N. R. Pierre. 1992. A theoretically-based model for predicting total digestible nutrient values of forages and concentrates. Anim. Feed Sci. Technol. 39:95–110. doi:10.1016/0377-8401(92)90034-4.
- Welch, C. M., J. K. Ahola, J. B. Hall, G. K. Murdoch, D. H. Crews Jr., L. C. Davis, M. E. Doumit, W. J. Price, L. D. Keenan, and R. A. Hill. 2012. Relationships among performance, residual feed intake, and product quality of progeny from Red Angus sires divergent for maintenance energy EPD. J. Anim. Sci. 90:5107–5117. doi:10.2527/jas.2012-5184.
- Zinn, A., and Y. A. Shen. 1998. An evaluation of ruminal degradable intake protein and metabolizable amino acid requirements of feedlot calves. J. Anim. Sci. 76:1280–1289.
- Zorzi, K., S. F. M. Bonilha, A. C. Queiroz, R. H. Branco, T. Lucila Sobrinho, and M. S. Duarte. 2013. Meat quality of young Nellore bulls with low and high residual feed intake. Meat Sci. 93:593–599. doi:10.1016/j.meatsci.2012.11.030.