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Authors
Andreini, Emily M
Augenstein, Sheyenne M
Fales, Carrie S
et al.

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Effects of feeding level on efficiency of high- and low-residual feed intake beef steers

Emily M. Andreini,[1] Sheyenne M. Augenstein, Carrie S. Fales, Roberto D. Sainz, and James W. Oltjen

Department of Animal Science, University of California, Davis, Davis, CA 95616

[1]Corresponding author: emandreini@ucdavis.edu

ORCiD number: 0000-0002-6498-0162 (E. M. Andreini).

Abstract

Comparing heat production after ad libitum (**ADLIB**) and restricted (**RESTRICT**) feeding periods may offer insight into how residual feed intake (**RFI**) groups change their energy requirements based on previous feeding levels. In this study, the authors sought to explain the efficiency changes of high- and low-RFI steers after feed restriction. To determine RFI classification, 56 Angus-cross steers with initial body weight (**BW**) of 350 ± 28.7 kg were individually housed, offered ad libitum access to a total mixed ration, and daily intakes were recorded for 56 d. RFI was defined as the residual of the regression of dry matter intake on mid-test $BW^{0.75}$ and average daily gain. High- and low-RFI groups were defined as >0.5 SD above or below the mean of zero, respectively. Fourteen steers from each high and low groups (n = 28) were selected for the subsequent 56-d RESTRICT period. During the RESTRICT period, intake was restricted to 75% of previous ad libitum intake on a $BW^{0.75}$ basis, and all other conditions remained constant. After the RESTRICT period, both RFI groups had decreased maintenance energy requirements. However, the low-RFI group decreased maintenance energy requirements by 32% on a $BW^{0.75}$ basis, more (P < 0.05) than the high-RFI group decreased maintenance requirements (18%). Thus, the low-RFI steers remained more efficient after a period of feed restriction. We conclude that feed restriction decreases maintenance energy requirement in both high- and low-RFI groups that are restricted to the same degree.

Key words: beef cattle, efficiency, residual feed intake

Introduction

Feed inputs are a major cost in most animal production systems, and selecting for animals with improved feed efficiency provides an opportunity to improve producer profits and reduce resource use in beef production (Archer et al., 1999). Residual feed intake (**RFI**) is an efficiency measure used to identify animals that consume less feed than others for a given body weight (**BW**) and rate of gain. RFI is the difference between an individual's actual and predicted feed intake over a measurement period (Arthur and Herd, 2008). RFI is phenotypically independent of the production traits used to calculate expected feed intake (i.e., BW and average daily gain [**ADG**]), which allows for the comparison of individuals of different production levels during the measurement period (Koch et al., 1963; Archer et al., 1999). There are many potential factors that contribute to the variation in RFI, including differences in digestion of feed, protein turnover and tissue metabolism, feed selection, body composition, activity, heat production, and maintenance

Abbreviations

ADF	acid detergent fiber
ADG	average daily gain
ADLIB	ad libitum feeding period
BF	subcutaneous fat over the 12th and13th ribs
BW	body weight
CP	crude protein
Diet ME	diet metabolizable energy
Diet NE_m	diet net energy for maintenance
DM	dry matter
DMI	dry matter intake
EBF	empty body fat
EBP	empty body protein
EBW	empty body weight
EE	ether extract
EQSW	equivalent shrunk body weight
FBW	final body weight
G:F	gain to feed
HE	heat energy
HH	hip height
MBW	metabolic body weight
ME	metabolizable energy
MEI	metabolizable energy intake
NDF	neutral detergent fiber
NE_m	net energy maintenance requirement
OM	organic matter
RE	retained energy
REA	longissimus muscle area
$RE_{protein}$	recovered energy in body protein
RESTRICT	restricted feeding period
RF	subcutaneous rump fat
RFI	residual feed intake
SBW	shrunk body weight
TMR	total mixed ration
YG	USDA yield grade

energy requirement (Herd and Arthur, 2009; Cruz et al., 2010); therefore, differences in RFI among animals are not likely to be explained by a single mechanism. Variation in RFI is related to differences in maintenance energy requirement, which may vary with the level of feeding (Sainz et al., 1995; Castro-Bulle et al., 2007). However, it is unclear how the basal metabolic rate of low- and high-RFI animals differs under or adjusts to certain conditions, and further research can determine how RFI groups will adjust or maintain their maintenance energy requirements in response to variations in feed supply due to a changing climate. For instance, drought-like situations can be simulated through feed restriction, and after determining RFI rank and basal metabolic rates under ad libitum conditions, these measurements can be repeated under restricted feeding. Comparing heat production after each feeding period could offer insight into the adaptability of low- or high-RFI cattle, and through understanding how different RFI groups are able to change their maintenance energy requirements, animals can be selected based on their ability to tolerate environmental changes, such as drought, without compromising the efficiency of production.

Previous research has addressed the hypothesis that low-RFI steers remain more efficient during feed restriction based on BW; Dykier et al. (2019) showed that high- and low-RFI steers performed similarly under feed restriction, which suggested that variation in RFI might be explained by behavior and appetite rather than metabolic efficiency. However, Dykier et al. (2019) suggested that it was unclear if the results of restricted feeding were related to RFI or different levels of restriction (i.e., 68% of adlib intake for high-RFI and 78% of ad lib intake for low-RFI steers). Therefore, in this experiment, the authors sought to explain the efficiency changes during feed restriction based on previous ad libitum intake.

It was hypothesized that low-RFI cattle remain more efficient during feed restriction and adjust their maintenance energy requirements according to environmental conditions, such as feed restriction. The objectives of this study were to determine the differences in performance, heat production, and behavior between low- and high-RFI steers during periods of ad libitum and restricted feed intake and to determine if low-RFI steers remained more efficient during a period of restricted intake.

Materials and Methods

The study was conducted in accordance with the approved University of California, Davis (UC Davis) Institutional Animal Care and Use Committee protocol (number: 19522) at the UC Davis Feedlot (Davis, CA). Fifty-six Angus-cross steers, between 10 and 12 mo of age and initial BW of 350 ± 28.7 kg, were obtained from the UC Sierra Foothill Research and Extension Center herd for the study. The study consisted of a 56-d ad libitum feeding period (**ADLIB**) followed by a 56-d restricted feeding period (**RESTRICT**).

To determine individual RFI classifications during the ADLIB period, steers were individually housed, offered ad libitum access to a total mixed ration (**TMR**; Tables 1 and 2), and individual intakes were recorded daily for 56 d at the UC Davis feedlot trial barn (Figure 1). Individual pens had a roof over half of the pen, measured 2.5 × 10 m, and were bedded with rice hulls. Steers were fed twice daily at 0700 and 1600 hours, and refusals were collected and weighed before each morning feeding. Animals were fed ad libitum with targeted refusals of 10% on an as-fed basis. Shrunk BW was taken every 14 d after 12 to 16 h of solid feed withdrawal but with access to water. ADG was estimated as the slope of the regression of BW vs. time. RFI, defined as the residual of the regression of dry matter intake (**DMI**; kg/d) on mid-test $BW^{0.75}$ and ADG, was calculated using the following equation:

$$DMI = -4.49 + 0.1513\ BW^{0.75} + 1.812\ ADG + \mathcal{E};$$

Table 1. Ingredients of the TMR on a DM basis

Ingredients	% Composition (as-fed basis)
Rolled corn	62.34
Dried distiller's grain	15.00
Alfalfa hay	6.00
Wheat hay	6.00
Molasses	6.00
Fat	2.50
Limestone	1.12
Urea	0.57
Magnesium oxide	0.14
Rumensin	0.015
Beef trace salt (Elanco, Greenfield, IN)	0.314

Table 2. Analysis of the TMR and TMR particle fractions on a DM basis

	TMR	>19 mm	8 to 19 mm	4 to 8 mm	<4 mm
% of TMR (as-fed)	100	9.53	20.38	31.44	38.65
DM, %	95.80	96.16	96.54	96.72	96.90
NDF, %	16.22	47.18	14.39	12.37	15.72
ADF, %	7.48	31.24	8.06	6.16	6.28
CP, %	13.62	11.10	8.60	9.70	18.70
EE, %	5.88	3.90	3.20	4.40	8.80
Ash, %	5.52	6.97	2.53	3.16	7.82
OM, %	94.48	93.03	97.47	96.84	92.18

Figure 1. Steers housed in individual pens and TMR stored in the UC Davis trial barn.

$$R^2 = 0.72, \quad S = 0.51$$

High- and low-RFI groups (18 steers per group) were defined as >0.5 SD above or below the mean of zero, respectively, and intermediate steers were classified as medium. After the high- and low-RFI steers were identified, the 14 most extreme of each high- and low-RFI groups (n = 28) were selected for the subsequent 56-d RESTRICT period, which began after animals were fed in group pens for 60 d. Animals were housed in group pens for additional behavioral measurements and metabolic measurements taken with the GreenFeed System (C-Lock Inc., Rapid City, SD, USA; data not reported). Results are reported for 14 high- and 13 low-RFI steers (n = 27), as 1 steer was removed from the study during the RESTRICT period due to illness. During the RESTRICT period, the feed intake of each steer was restricted to 75% of its previous ad libitum DMI as a percent of $BW^{0.75}$ and adjusted every 2 wk based on the most recent BW. All other conditions remained the same during the RESTRICT period as in the ADLIB period, except for the amount of feed offered. After the RESTRICT period, animals were fed 75% of previous ad libitum DMI as a percent of $BW^{0.75}$ in group pens for 30 d for additional behavioral measurements.

Sampling

For each new batch of TMR, a representative sample was collected and dried for future analysis approximately every 6 d. Dry matter (**DM**) was calculated as the retained weight after drying for 72 h at 60 °C. At the end of the study, a composite sample from all batches of TMR was used for laboratory analysis. Orts of each animal were collected daily, stored in a bag, and composited approximately every 2.5 wk (three periods) during the ADLIB phase. Soiled refusals (i.e., refusals containing urine, feces, or bedding) and large refusals not representative of regular behavior (e.g., refusals > 2 kg due to an animal going off feed) were not retained in the composite bag. The composite sample of orts was dried for 72 h at 60 °C. Orts were composited to one sample per individual. Dried feed and orts samples were ground in a Wiley Mill to pass a 1-mm screen.

Lab analysis

Diet and orts were analyzed for ash, crude protein (**CP**), ether extract (**EE**), neutral detergent fiber (**NDF**), and acid detergent fiber (**ADF**). Ash was measured in duplicate in a muffle furnace at 525 °C for 12 h. Samples were sent to IEH-J L Analytical Laboratories (Modesto, CA) for the determination of total nitrogen and EE. CP was calculated as nitrogen × 6.25. Using fiber bag technology with the Ankom Fiber Analyzer 200, NDF and ADF were analyzed in duplicate. Ankom F57 bags were filled with 0.75 g of sample and used for NDF and subsequent ADF analyses. Both NDF and ADF values were expressed on an ash-inclusive basis.

Body composition measurements

Real-time ultrasound measures were taken of the longissimus muscle area (**REA**), subcutaneous fat over the 12th and 13th ribs (**BF**), and subcutaneous rump fat (**RF**) at the beginning, middle, and end of the ADLIB period and at the beginning and end of the RESTRICT period. Ultrasound measures were taken following the guidelines of R.D.S. (University of California, Davis, personal communication, 2016). Body composition, gain, and energy use were estimated following the equations listed in Table 3 and in the study of Dykier et al. (2019). Body fat estimates were based on ultrasonic BF and were adjusted according to ultrasonic RF. Empty body protein, fat, and energy gains were estimated as the slopes of the regression of each variable vs. time.

Behavior measurements

Feed selection and activity level were assessed as different measures of behavior. Distribution of particle size of orts and TMR were evaluated to determine the differences in diet selection between RFI groups. Particle distribution of orts and TMR were analyzed three separate times throughout the ADLIB period. Orts collected in the composite bag for each animal were analyzed in triplicate after each 2.5-wk collection period for particle distribution using a 4-sieve Penn State Particle Separator (Nasco, Fort Atkinson, WI) following the procedures outlined in "Penn State Particle Separator" (Penn State Extension, 2017). Feed selection was evaluated on the proportion of the offered particle fraction in the TMR that was consumed. The offered particle fraction in the TMR is considered to be 100%. For each RFI group, particle fraction consumed (%) was divided by the particle fraction offered (%). Consumption percentages above 100% indicate a higher preference than what was offered in the TMR. Feed selection was only assessed during the ADLIB period, because there were no orts during the RESTRICT period.

For each steer, the composition of the consumed diet was determined using the nutrient composition of the orts with the following equation:

Table 3. Equations used to estimate body composition, gain, and energy use[1]

Terms	Equations	Literature cited
MBW, kg	$\text{MBW} = \text{SBW}^{0.75}$	Kleiber (1947)
EBW, kg	$\text{EBW} = 0.917 * \text{SBW} - 11.39$	Owens et al. (1995)
Frame score	$\text{Frame score} = -11.548 + (0.192 * \text{HH}) - (0.0289 \times \text{Age}) + (0.00001947 * \text{Age}^2) + (0.00001315 * \text{HH} * \text{Age})$	Cundiff et al. (2010)
FBW, kg	$\text{FBW} = 366.52 + 33.35 * \text{Frame score}$	Fox et al. (2001)
EQSW, kg	$\text{EQSW} = \text{SBW} * (467 / \text{FBW})$	Perry and Fox (1997)
YG	$\text{YG} = 4.38 + 0.991 * \text{BF} - 0.20 * (\text{REA} / (\text{SBW}/100)) + 0.000639 * \text{EQSW}$	Perry and Fox (1997)
EBF, kg	$\text{EBF} = 0.351 * \text{EBW} + 21.6 * \text{YG} - 80.8$	Perry and Fox (1997)
EBP, kg	$\text{EBP} = (\text{EBW} - \text{EBF}) * 0.2201$	Garrett and Hinman (1969)
RE, Mcal	$\text{RE} = \text{EBF} * 9.367 + \text{EBP} * 5.686$	NASEM (2016)
HE, Mcal	$\text{HE} = \text{MEI} - \text{RE}$	NASEM (2016)
Partial efficiency of gain (k_g)	$k_g = 0.75 / (1 + 2.75 * (\text{RE}_{\text{protein}} / \text{RE}))$	Williams and Jenkins (2003)
NE_m reqt., Mcal	$\text{NE}_m\text{reqt.} = [\text{DMI} - ((\text{RE}/k_g) / \text{Diet ME})] * \text{Diet NE}_m$	NASEM (2016)

[1]MBW, metabolic body weight (kg); SBW, shrunk body weight (kg); EBW, empty body weight (kg); HH, hip height (cm); Age (d); FBW, final body weight (kg); EQSW, equivalent shrunk body weight (kg); YG, USDA yield grade; BF, subcutaneous fat over the 12th and 13th ribs (cm); REA, Longissimus muscle area (cm^2); EBF, empty body fat (kg); EBP, empty body protein (kg); RE, retained energy (Mcal); HE, heat energy (Mcal); MEI, metabolizable energy intake (Mcal); $RE_{protein}$, recovered energy in body protein (Mcal); NE_m reqt., net energy for maintenance requirement (Mcal); DMI, dry matter intake (kg); Diet ME, diet metabolizable energy (Mcal/kg DM); Diet NE_m, diet net energy for maintenance (Mcal/kg DM).

$$\textit{Nutrient intake, \%} = \frac{[(\textit{DM offered, kg} * \textit{Nutrient in TMR, \%}) - (\textit{DM refused, kg} * \textit{Nutrient in orts, \%})]}{\textit{DMI}}$$

To determine the differences in activity levels between the RFI groups, accelerometer data loggers (Hobo Pendant G, Onset Computer Corporation, Pocasset, MA) were used to measure the frequency and duration of standing and lying behaviors, while the animals were housed in group pens. The y and z-axes of each data logger were set to record at 1-min intervals following the recommendations of Ledgerwood et al. (2010). Loggers were labeled with a number corresponding to an animal ID. Loggers were placed with the x-axis horizontal to the ground on the outside of the right hind leg below the hock and above the metatarsophalangeal joint, as recommended by Ledgerwood et al. (2010). Before placing the logger, each steer's leg was wrapped with a layer of thick cotton, followed by several layers of self-adherent bandaging tape (Vetrap, 3M Corporation, St. Paul, MN). The logger was placed over the Vetrap, glued in place (Gorilla glue, Sharonville, OH), and secured with additional layers of Vetrap (Figure 2). Loggers were attached at the beginning of each period when steers were moved to group pens, and loggers were removed at the end of each group pen period. Logger placement was checked twice daily at 0700 and 1600 hours.

Statistical analysis

All data were analyzed using the General Linear Model in Minitab (Minitab, Inc., State College, PA) as a repeated measures design, except the logger activity data, which were analyzed using the Proc Glimmix procedure in SAS version 9.4 (SAS Institute Inc., Cary, NC). Models included RFI phenotype (high and low), feed level (ad libitum and restricted), and the interaction of RFI and feed level as fixed effects. Steer was the experimental unit. Residual vs. predicted plots were examined to check the assumption of normality for all models. Least-squares means were compared across periods using a Tukey adjustment. Comparisons were considered statistically significant when $P < 0.05$. Results are presented as the least-squares means estimates ± SE.

Figure 2. Activity loggers attached to the right hind leg of steers in group pens.

Results

Diet description

Composition and analysis of the TMR (Tables 1 and 2) show numerical differences in the diet composition between particle fractions. The largest particle sieve (>19 mm) consisted of hay, the middle sieves (4 to 19 mm) contained corn grain and small hay particles, while the bottom sieve (<4 mm) consisted of the finest diet ingredients (i.e., dried distiller's grain). The finest particles had higher EE and CP values, and the largest particles had higher NDF and ADF values. The TMR was formulated (Taurus, University of California) to contain energy values of 3.22, 2.21, and 1.52 Mcal/kg DM for metabolizable energy (**ME**), net energy for maintenance, and net energy for gain, respectively.

Performance

Initial age (P = 0.160), hip height (P = 0.290), mean $BW^{0.75}$ (P = 0.857), and ADG (P = 0.330) did not differ among the RFI groups in the ADLIB period, which is consistent with the independence of RFI from growth rate and BW (Koch et al., 1963; Table 4). During the ADLIB period, low-RFI steers consumed 12% less feed than the high-RFI steers (9.26 and 10.49 kg DM/d, respectively). On a BW basis, during the ADLIB period, low-RFI steers consumed 2.29% of their BW compared with 2.58% for the high-RFI steers (P = 0.001). During the RESTRICT period, because both groups were restricted to the same degree (75% of ad libitum intake), the 12% difference in DMI was maintained (Period × RFI interaction P = 0.62). Since ME intake (**MEI**; Mcal/d) was estimated based on the diet ME (Mcal/kg DM) and DMI (kg/d), there is a 12% difference in MEI between the groups.

For high-RFI animals, ADG (kg/d) decreased (P = 0.002) between ADLIB (1.75 ± 0.14) and RESTRICT (1.07 ± 0.14) periods; however, the low-RFI group did not significantly decrease ADG when restricted (1.74 to 1.35 ± 0.14 kg/d, P = 0.246). The low-RFI group had greater gain:feed (**G:F**) than the high group (P = 0.020).

Heat production and maintenance energy requirement

The interaction for retained energy (**RE**/BW$^{0.75}$) between the RFI group and period approached significance (P = 0.086; Table 5). However, RE decreased (P = 0.001) during the RESTRICT period compared with the ADLIB period. Heat energy (**HE**/BW$^{0.75}$) was lower (P = 0.001) for both groups during the RESTRICT period compared with ADLIB and was lower (P = 0.001) for the low-RFI group compared with the high group during both periods. Daily HE (Mcal/d) was reduced (P = 0.001) during the RESTRICT period for both groups, but the low-RFI group decreased HE (Mcal/d) by nearly 17% compared with an approximate 6% decrease for the high-RFI group.

Both high- and low-RFI groups reduced net energy maintenance requirements (**NE$_m$**/BW$^{0.75}$) after feed restriction (P = 0.001). However, the low-RFI group had a greater proportional decrease in NE$_m$/BW$^{0.75}$ in response to feed restriction. Between the ADLIB and RESTRICT feeding periods, high-RFI steers decreased NE$_m$/BW$^{0.75}$ by nearly 18%, while the low-RFI steers decreased NE$_m$/BW$^{0.75}$ by approximately 32%.

Behavior

The selection of different particle sizes and consumed diet composition for each RFI group were used to evaluate behavioral differences in feed selection. There were no differences in total diet composition, except for organic matter (**OM**; P = 0.009) between the offered and consumed diet for both the low- and high-RFI groups (Table 6). During the ADLIB period when refusals were collected and separated by particle size, there were no differences (P = 0.256) in selection for the >19-mm particle size fraction between the high-RFI group, low-RFI group,

Table 4. Performance data and characteristics of high- and low-RFI steers for periods of ADLIB and RESTRICT feed intake[1]

	High RFI			Low RFI			P-value		
Period	ADLIB	RESTRICT	SEM	ADLIB	RESTRICT	SEM	Period	RFI	Period × RFI
N	14	14		13	13				
Initial age, d	332^a	453^b	5.78	328^a	465^b	5.99	0.001	0.472	0.160
Hip height, cm	123.1^a	132.2^b	0.82	123.2^a	134.2^b	0.85	0.001	0.223	0.290
Initial BW, kg	355^a	556^b	7.25	353^a	542^b	7.53	0.001	0.289	0.439
Final BW, kg	462^a	617^b	10.60	460^a	619^b	11.00	0.001	0.983	0.849
Mean BW$^{0.75}$, kg$^{0.75}$	91^a	119^b	1.31	90^a	118^b	1.36	0.001	0.635	0.857
DMI, kg/d	10.49^a	9.28^b	0.19	9.26^b	8.24^c	0.20	0.001	0.001	0.616
Intake, % BW	2.58^a	1.58^b	0.03	2.29^c	1.42^d	0.03	0.001	0.001	0.014
MEI, Mcal/d	33.78^a	29.89^b	0.60	29.80^b	26.53^c	0.63	0.001	0.001	0.616
ADG, kg/d	1.75^a	1.07^b	0.14	1.74^a	1.35^{a,b}	0.14	0.001	0.339	0.330
G:F	0.166^{a,b}	0.114^b	0.014	0.189^a	0.161^{a,b}	0.015	0.007	0.020	0.415
RFI, kg/d	0.60^a	—	0.06	−0.59^b	—	0.07	—	0.001	—

[1]RFI cannot be calculated under restricted feeding; therefore, the RFI values and classifications reported are those calculated during the ADLIB period.
[a–d]Means within a row without common superscript letters differ (P < 0.05).

Table 5. Efficiencies of high- and low-RFI steers after periods of ADLIB and RESTRICT feed intake

	High RFI			Low RFI			P-value		
Period	ADLIB	RESTRICT	SEM	ADLIB	RESTRICT	SEM	Period	RFI	Period × RFI
N	14	14		13	13				
RE, Mcal/d	7.81	5.54	0.90	6.63	7.26	0.93	0.378	0.771	0.121
RE, Mcal/BW$^{0.75}$	0.09^a	0.05^b	0.01	0.07^{a,b}	0.06^{a,b}	0.01	0.001	0.871	0.086
RE fat, Mcal/d	6.69	5.07	0.85	5.37	6.57	0.88	0.812	0.913	0.108
RE protein, Mcal/d	1.12^a	0.48^b	0.11	1.26^a	0.68^b	0.11	0.001	0.111	0.766
HE, Mcal/d	25.97^a	24.34^a	0.87	23.17^a	19.27^b	0.90	0.003	0.001	0.204
HE, Mcal/BW$^{0.75}$	0.286^a	0.2^c	0.01	0.26^b	0.16^d	0.01	0.001	0.001	0.466
NE$_m$, Mcal/d	13.23^{a,b}	14.24^a	0.91	11.22^{a,b}	9.85^b	0.95	0.849	0.001	0.206
NE$_m$, Mcal/BW$^{0.75}$	0.146^a	0.120^b	0.008	0.124^b	0.084^c	0.008	0.001	0.001	0.385

[a–c]Means within a row without common superscript letters differ (P < 0.05).

Table 6. Comparison of offered and consumed TMR DM composition between high- and low-RFI steers during the ADLIB feed intake period

	High RFI	SEM	Low RFI	SEM	TMR[1]	SEM	*P*-value
NDF, %	16.23	0.24	16.29	0.25	16.22	0.27	0.979
ADF, %	7.52	0.14	7.62	0.15	7.48	0.16	0.801
CP, %	13.52	0.12	13.20	0.13	13.62	0.14	0.077
EE, %	5.86	0.05	5.77	0.05	5.88	0.05	0.246
OM, %	94.56[a,b]	0.05	94.73[a]	0.05	94.48[b]	0.06	0.009

[1]TMR, offered total mixed ration.
[a,b]Means within row without common superscript letters differ ($P < 0.05$).

Table 7. Selection of each particle fraction of the TMR between high- and low-RFI steers compared with the percentage of each particle fraction in the total ration during the ADLIB feed intake period

	High RFI	SEM	Low RFI	SEM	TMR[1]	SEM	*P*-value
n	14		13		9		
Particle fraction, %							
>19 mm	10.32	0.004	10.50	0.004	9.53	0.005	0.256
8 to 19 mm	21.29[a,b]	0.003	21.70[a]	0.003	20.38[b]	0.004	0.045
4 to 8 mm	32.21[a]	0.002	32.50[a]	0.002	31.44[b]	0.002	0.007
<4 mm	36.18[a]	0.005	35.30[a]	0.005	38.65[b]	0.006	0.001

[1]TMR, offered total mixed ration.
[a,b]Means within row without common superscript letters differ ($P < 0.05$).

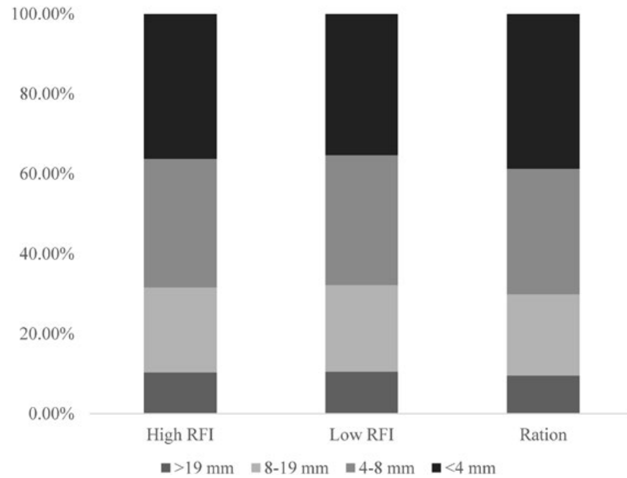

Figure 3. Intake of each particle fraction of the ration between high- and low-RFI steers compared with the percentage of each particle fraction in the total ration during the ADLIB feed intake period.

and the offered TMR (Table 7; Figure 3). For the 8- to 19-mm particle size fraction, the intake by the high-RFI group did not differ from the TMR; however, the low-RFI group consumed more of this fraction ($P = 0.045$) than the offered ration. For both the 4- to 8-mm and <4-mm particle size fractions, there were no differences ($P > 0.05$) in consumption between the high and low groups, but both groups differed from the ration ($P < 0.05$). Both the high- and low-RFI groups consumed more of the 4- to 8-mm particle size fraction and less of the <4-mm particle size fraction than was present in the TMR. The differences in particle size consumption of the groups compared with the offered ration suggest that both groups preferred the particles > 4 mm in size (i.e., corn grain and hay) over the fines (i.e., dried distiller's grain and small particles of corn or hay).

Preference for particle size was evaluated based on the proportion of the offered particle fraction that was consumed. For each RFI group, particle fraction consumed (%) was divided by the particle fraction offered (%). Consumption percentages above 100% indicate a higher preference than consumptions below 100%. Although there were no statistical differences, the high- and low-RFI groups consumed 108.4% and 110.2%, respectively, of the offered >19 mm particles. Of the 8 to 19 mm particles, the high-RFI group selected for 104.5%, and the low-RFI group selected 106.5% of the offered TMR. The high group consumed 102.4%, and the low group consumed 103.4% of the 4 to 8 mm particles. Particles <4 mm in size were not preferred at higher amounts than the offered diet at 93.6% and 91.3% for the high and low groups, respectively.

Lying time (average min lying/d), lying bouts (average number of lying bouts/d), and lying bout duration (average min lying/bout) were assessed as measures of activity to examine behavioral variation between RFI groups. There was no significant interaction between RFI and feeding period for lying time ($P = 0.241$), lying bouts ($P = 0.870$), and lying bout duration ($P = 0.835$). Numerically, the low-RFI group spent more total time lying per day than the high-RFI group during the ADLIB period (Table 8). During both the ADLIB and RESTRICT periods, the low-RFI group had numerically fewer total lying bouts per day than the high group with longer lying bout duration; however, the results are not significant ($P > 0.05$).

Discussion

In this study, the low-RFI steers remained more efficient than the high-RFI steers in response to a resource-challenged situation of feed restriction. At the ADLIB and RESTRICT feeding levels, G:F was 12.2% and 29.2% higher, respectively, for the low group compared with the high group. During the ADLIB period, the high-RFI group consumed 11.8% more ME (Mcal/d), but there were no observed differences in RE (Mcal/kg $BW^{0.75}$) between the two groups. Heat production (Mcal/kg $BW^{0.75}$) was 9.1% and 20.0% lower ($P < 0.05$) for the low-RFI group compared with the high group during the ADLIB and RESTRICT periods, respectively. Maintenance energy requirement (Mcal/ kg $BW^{0.75}$) did not differ between the two groups during the ADLIB period, but it decreased 18% in the high-RFI and 32% in the low-RFI group when the intake was restricted to the same degree.

In a previous study, Dykier et al. (2019) showed that high- and low-RFI steers had similar BW, ADG, and G:F under feed restriction based on BW; however, the RESTRICT period in that study placed all animals at the same level of DMI as a percentage of BW. Therefore, it was unclear if the results of restricted feeding were related to RFI or different degrees of restriction (i.e., 68% and 78% of ad libitum intake for high-RFI and low-RFI steers, respectively). Prior to feed restriction, during ad libitum feeding, Dykier et al. (2019) observed similar RE (Mcal/kg $BW^{0.75}$) between the groups, and 17% lower HE (Mcal/kg $BW^{0.75}$) in low-RFI steers compared with high, which is similar to the ADLIB results of this study. Dykier et al. (2019) concluded that increased DMI and HE (Mcal/ kg $BW^{0.75}$) of high-RFI steers during ad libitum feeding might be due to appetite rather than the metabolic differences between RFI groups based on the similar performance of the groups during restricted feeding. In agreement with Dykier et al. (2019),

Table 8. Means (n = 26) of lying behaviors for each RFI group (low and high) after each feeding period (ADLIB and, RESTRICT)[1]

	High RFI			Low RFI			P-value		
Period	ADLIB	RESTRICT	SEM	ADLIB	RESTRICT	SEM	Period	RFI	Period × RFI
Lying time, min/d	870.9	882.7	22.3	898.5	865.4	24.1	0.001	0.848	0.241
Lying bouts, bouts/d	13.7	13.8	1.2	11.8	11.3	1.3	0.001	0.161	0.870
Bout duration, min/bout	74.4	77.7	10.5	82.9	101.2	11.3	0.034	0.182	0.835

[1]Least-squares means did not differ ($P > 0.05$).

although contrary to the results of this study, Lines et al. (2014) observed no superiority of low-RFI animals to high-RFI animals during feed restriction. Lines et al. (2014) reported no differences in HE or protein metabolism between RFI groups and suggested that differences in RFI can be attributed to increased appetites in high-RFI animals leading to greater energy consumption. In the study by Lines et al. (2014), increased energy intake stored as fat resulted in divergent fat deposition between the groups, and they reported no difference in the efficiency of energy utilization. Therefore, it was concluded that high-RFI animals do not have higher maintenance requirements Lines et al. (2014).

In goat breeds fed at a restricted level of 50% adequacy for maintenance and moderate energy accretion relative to BW, declines in HE (kJ/kg $BW^{0.75}$ per day) were observed by Helal et al. (2011). Over a 10-wk restricted feeding trial, HE declined 20% to 30% compared with HE of goats fed at maintenance (Helal et al., 2011). Maintenance requirements have been shown to be altered by the plane of nutrition rather than acting as a constant function of BW, and differences in fasting energy expenditure have been shown to not be attributable to measurable differences in body composition (Ferrell et al., 1986). Within groups of lambs of similar BW, lambs fed at higher planes of nutrition had greater maintenance requirements (kJ/kg $BW^{0.75}$ per day), but similar body composition (Ferrell et al., 1986). In two consecutive feeding periods, lambs fed at higher planes of nutrition in the first period had higher maintenance requirements in the following feeding period (Ferrell et al., 1986).

Previous studies have suggested that differences in heat production between high- and low-RFI steers might be attributable to variation in metabolic efficiency (Basarab et al., 2003; Nkrumah et al., 2006), and 46% of the variation in RFI can be explained by heat increment of fermentation, protein turnover, tissue metabolism, and stress (Richardson and Herd, 2004; Arthur and Herd, 2008; Herd and Arthur, 2009). Nkrumah et al. (2006) observed greater heat production in high-RFI steers (0.164 ± 0.004 Mcal/kg $BW^{0.75}$) compared with low-RFI steers (0.129 ± 0.005 Mcal/kg $BW^{0.75}$), and Basarab et al. (2003) showed that low-RFI animals compared with high-RFI animals consumed 10.4% less feed (0.55 kg DM d^{-1}) and had lower heat production (0.163 ± 0.002 Mcal/kg $BW^{0.75}$ vs. 0.179 ± 0.002 Mcal/kg $BW^{0.75}$). Basarab et al. (2003) reported that high-RFI steers had greater MEI (0.259 ± 0.001 Mcal/kg $BW^{0.75}$ vs. 0.233 ± 0.001 Mcal/kg $BW^{0.75}$) and RE (0.079 ± 0.001 Mcal/kg $BW^{0.75}$ vs. 0.070 ± 0.001 Mcal/kg $BW^{0.75}$) compared with low-RFI steers. A portion of the greater MEI in high-RFI steers may be accounted for by higher fat gains, but a greater portion may be attributed to increased heat production with one reason being higher maintenance costs (Basarab et al., 2003).

Castro-Bulle et al. (2007) concluded that low-RFI animals used less energy for the physiological processes involved in maintenance, which resulted in more net energy available for tissue accretion. The positive relationship between the rate of muscle protein breakdown and NE_m supports the idea that an animal with a greater protein turnover rate will have a greater NE_m and, therefore, a lower G:F (Castro-Bulle et al., 2007). Lower G:F and higher NE_m were observed for the high-RFI group during both periods of this study. Recent work from our laboratory has shown that skeletal muscle from low-RFI cattle has a greater abundance of mitochondria, with greater energy transduction efficiency, than muscle from high-RFI cattle (Fernandez et al., 2020). Taken together, these data support the notion that low-RFI steers have reduced maintenance energy requirements compared with high-RFI animals due to differences in energy-consuming metabolic processes, as well as the differences in the efficiency of energy capture from the products of digestion.

In the present experiment, both groups decreased NE_m (Mcal/kg $BW^{0.75}$) in response to restricted feeding at 75% of previous ad libitum DMI. Lower NE_m has been observed in steers restricted to 70% of ad libitum intake (Sainz et al., 1995), and improved feed efficiency was observed with 85% to 90% limited intake, possibly due to decreased NE_m, altered behavior, or energy expenditures (Hicks et al., 1990). Physical activity is reported to explain 10% of the variation in RFI, while feeding patterns contribute to 2% of the variation (Richardson and Herd, 2004; Arthur and Herd, 2008; Herd and Arthur, 2009).

Ration sorting and particle selection in this study are similar to the results reported by Dykier (2016). Using a ration similar to the one fed in this study, Dykier (2016) also observed preferential selection (>100%) by steers for particles > 4 mm in size. The high- and low-RFI groups selected for the <4 mm particles at 94.9% and 92.8%, respectively, of the offered diet (Dykier, 2016). Consumption of particles > 4 mm in size above the offered ration for the current study as well as Dykier (2016) suggests that cattle have a preference for larger particles (i.e., rolled corn and hay); however, the reason for this selection is unknown. One hypothesis is that the fines are less desirable for reasons of palatability or digestion, and the animals purposely select for the larger particles. Adequate refusals (10% as-fed basis) to allow for feed sorting were targeted during ADLIB, and Cruz et al. (2010) showed that individual pens may be used without impacting DMI as long as animals are stimulated to visit the bunk more than once per day. In the present study, feeding twice daily provided stimulation for the steers to visit the bunk more than once per day. Steers were fed ad libitum by targeting for adequate refusals and stimulated to eat in this study, giving them the opportunity to select for a preferred diet during the ADLIB period. Further observation of feeding events and behaviors may lend insight into the driving force of feed selection.

Hicks et al. (1990) hypothesized that reduced mobility and activity due to lethargy in limit-fed animals may reduce NE_m. In the study by Hicks et al. (1990), steers spent 54.4% of the time per day lying, which did not alter behavior and could not account for improved feed efficiency in that study. During the ADLIB period, the low-RFI group spent 62.4% of the day lying, and the high group spent 60.5% of the day lying. During the RESTRICT period, the low group spent 60.1% of the day lying, and the high group spent 61.3% of the time lying.

Gomes et al. (2013) showed trends toward differences between high- and low-RFI animals for length of lying, standing, feeding, and idleness periods. High-RFI steers remained standing and feeding for longer periods, whereas low-RFI steers tended to stay lying and idle longer (Gomes et al., 2013). Similar to ADLIB period results, Gomes et al. (2013) observed high-RFI steers lying 58.3% of the day, and low-RFI steers lying 62.1% of the day. Although lying activity results do not show significant differences between the groups, the more-efficient steers spent more time lying per day with longer lying bouts during the ADLIB period. This suggests that the efficient steers were slightly less active than the high-RFI group, which had more frequent, shorter lying bouts per day. However, these results do not explain the decrease in time spent lying for the low group and a slight increase in lying time for the high group during the RESTRICT period.

Feed efficiency and energy expenditure may be influenced by altering physical activity through feeding behaviors (Kelly et al., 2010). Feeding events per day and eating rate (min/d) were positively correlated with DMI and RFI, which indicates that one way efficient animals utilize less energy is by spending more time being inactive (Kelly et al., 2010). Efficient animals typically have less daily feeding activity (Nkrumah et al., 2006), and repeatability estimates for feeding behaviors are strong within and between production phases (Kelly et al., 2010). Nkrumah et al. (2006) showed that high-RFI animals spent approximately 35% more time feeding (min/d) and 49% more time at the bunk (events/d) than low-RFI animals.

Feeding events were not observed in this study, but based on differences in lying activities, it is suggested that the low-RFI steers were less active. High-RFI animals have been shown to spend more time standing and feeding longer than low-RFI animals (Richardson and Herd, 2004). Whole animal energy expenditure increases by 16% to 29% between standing and lying animals, and standing contributes up to 30% of the average daily muscle energy expenditure in ruminants (Richardson and Herd, 2004). Therefore, it is possible that the high-RFI steers may expend more energy due to more time spent standing and eating per day.

During feed restriction, ADG was significantly reduced compared with the ADLIB period in the high-RFI steers but not in the low-RFI steers. Compared with the ADLIB period, feed restriction also resulted in decreased HE (−38% and −30% in low- and high-RFI steers, respectively) and NE_m (−33% and −20% in low- and high-RFI steers, respectively). Although both groups decreased maintenance energy requirements, the higher efficiency of the low-RFI group compared with the less-efficient steers was maintained during feed restriction. This result is in contrast with a previous study (Dykier et al., 2019), in which cattle were fed to the same intake (1.5% of BW) and not the same degree of restriction (75% of ad libitum intake). This study suggests that feed restriction decreases maintenance requirement, which occurs in both high- and low-RFI groups that are restricted to the same degree. Considering the results of previous studies using varying levels of feed restriction, changes in maintenance requirement appear to be sensitive to the level of feed restriction.

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Conflict of interest statement

The authors declare no conflict of interest.

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