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Article

The effect of feed efficiency classification on visceral organ mass in finishing steers

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Abstract

Individual feed intake of crossbred beef steers (one contemporary group/year, 2 years) was recorded during finishing to investigate visceral organ mass in steers divergent for feed efficiency. Based on residual feed intake (RFI), the 20% most efficient (HE, $n = 8$/year) and 20% least efficient (LE; $n = 8$/year) steers with 12th rib fat $\geq$1.02 cm were slaughtered. High efficiency steers had less DM intake ($P < 0.001$), greater G:F ($P < 0.001$), and similar ADG and hot carcass weight (HCW). High efficiency steers tended to have less ($P \leq 0.10$) small intestinal mass (actual and relative to BW and HCW) in year 1. In year 2, HE steers tended to have greater ($P \leq 0.10$) large intestinal actual and relative masses. Low efficiency steers tended to have greater ($P = 0.06$) actual omasum mass and had greater ($P \leq 0.03$) relative omasum masses compared with HE. Stomach complex, total gastrointestinal tract, liver, and kidney masses tended to be greater ($P \leq 0.10$) relative to BW, and were greater ($P \leq 0.05$) relative to HCW, in LE. Data suggest that visceral organ mass, especially of the gastrointestinal tract, plays a role in overall metabolic efficiency of finishing steers.

Key words: beef cattle, feed efficiency, gastrointestinal tract, residual feed intake, ruminant

Résumé

La consommation alimentaire individuelle des jeunes bœufs croisés de boucherie (un groupe contemporain/année, 2 années) a été enregistrée lors de la finition afin d'étudier la masse des organes viscéraux chez les bovins qui divergent en matière d'indice de consommation. Basé sur l'ingestion alimentaire résiduelle (RFI — « residual feed intake »), 20 % des bouvillons les plus efficaces (HE — « high efficiency », $n = 8$/année) et 20 % des moins efficaces (LE — « low efficiency »; $n = 8$/année) ayant une valeur de gras à la 12^{e} côte $\geq$1,02 cm ont été abattus. Les bouvillons HE montraient moins de consommation de matières sèches (DM — « dry matter ») ($P < 0,001$), des indices de consommation (G:F — « gain feed ratio ») plus élevées ($P < 0,001$), et des gains moyens quotidiens (ADG — « average daily gain ») et poids de la carcasse chaude (HCW — « hot carcass weight ») semblables. Les bouvillons HE tendaient vers des masses d'intestins grêles plus faibles ($P \leq 0,10$) autant les masses réelles et les masses relatives au poids corporel (BW — « body weight ») et au HCW dans l'année 1. Dans l'année 2, les bouvillons HE tendaient vers de plus grandes ($P \leq 0,10$) masses réelles et relatives du gros intestin. Les bouvillons LE tendaient vers de plus grandes ($P = 0,06$) masses réelles d'omasum et avaient de plus grandes ($P \leq 0,03$) masses relatives d'omasum par rapport aux bouvillons HE. Les masses du complexe d'estomacs, du tractus digestif complet, du foie, et du rein tendaient a être plus élevées ($P \leq 0,10$) relative au BW, et elles étaient plus élevées ($P \leq 0,05$) relatives au HCW, chez les bouvillons LE. Les données suggèrent que la masse des organes viscéraux, surtout celle du tractus digestif, joue un rôle important dans l'efficacité métabolique générale des bouvillons en finition. [Traduit par la Rédaction]

Mots-clés : bovins de boucherie, indice de consommation/efficience alimentaire, tractus digestif/tube digestif, ingestion alimentaire résiduelle, ruminant

Introduction

Meat production is projected to increase by 48 000 kg by the year 2027, and beef production specifically is projected to be 21% greater in developing countries and 9% greater in developed countries in 2027 (OECD-FAO 2018). To allow for this increase in production, improvements in feed efficiency will be required to maintain or reduce input costs while increasing productivity. Residual feed intake (RFI) has been used as a measure of feed efficiency in both research and production fields, as it allows for selection of improved animal feed efficiency without increasing mature body weight (BW; Herd and Arthur 2009).

Herd and Arthur (2009) hypothesized that the major processes contributing to variation in RFI include feeding patterns (2%), digestibility (10%), body composition (5%), animal metabolism and protein turnover (37%), activity (10%), heat increment of feeding (9%), and various other factors (27%). Despite being a major research area since that time, physiological mechanisms underlying individual differences in feed efficiency are still largely speculative due to the multiple physiological processes involved and variation in results observed in the research setting (reviewed by Fitzsimons et al. 2017; Kenny et al. 2018). Visceral organs are vital to nutrient digestion, absorption, and assimilation; thus, changes in their mass could lead to altered nutrient and energy acquisition and use, tissue function, and ultimately efficiency of metabolism. The gastrointestinal tract and liver account for 40%–55% of total energy used in ruminants (Ferrell 1988; Caton et al. 2000), while also being responsible for nutrient acquisition and initial metabolism. It is known that feed intake influences visceral organ mass in ruminants, and nutrient restriction in growing beef cattle and sheep has resulted in decreased visceral organ mass (Burrin et al. 1990; Johnson et al. 1990; Fluharty and McClure 1997). This is likely a mechanism that decreases nutrient and energy expenditure for tissue maintenance during times of low nutrient availability (Johnson et al. 1990), but decreased visceral mass is accompanied by poor animal growth and productivity in nutrient restriction models. It has previously been reported that high RFI (low efficiency) bulls tended to have greater reticulo-rumen masses compared with low RFI bulls, and that for every 1 kg/day increased in RFI, reticulo-rumen weight was expected to increase by 1 kg (Fitzsimons et al. 2014). Other researchers hypothesized that nutrient utilization is improved with increased visceral tissue mass, indicated by the positive correlation between G:F and visceral organ mass, outweighing the increased maintenance requirements associated with increased mass (Mader et al. 2009).

Despite these contrasting theories and results (reviewed by Fitzsimons et al. 2017 and Kenny et al. 2018), limited research has been conducted to determine the visceral organ mass and function in beef cattle with similar body size, gain, and body composition but divergent feed intake, such as high and low efficiency animals based on RFI. Because body composition influences efficiency of nutrient utilization (e.g., RFI), it is important to consider carcass quality when evaluating other potential physiological changes in animals divergent for feed efficiency. Additionally, studying the role of visceral organ mass in feed efficiency within a contemporary group of similar breed-type and sex allows for control of other genetic and environmental factors (e.g., previous nutrition and dam nutrition) that contribute to an individual animal's efficiency. It was hypothesized that individual differences in feed efficiency of finishing steers are affected by visceral organ mass due to the relationship of organ size with function and energy use. The specific objective of this study was to investigate visceral organ mass of finishing steers that were classified as high and low efficiency based on RFI rankings within contemporary groups and slaughtered at a similar carcass composition endpoint.

Table 1. Average ingredient and analyzed nutrient composition of diet fed to steers during feed intake period in years 1 and 2.

Item	Year 1	Year 2
DM (%)	79.8	67.5
Nutrient composition (DM basis)		
CP (%)	11.4	133
NE_m (Mcal/kg)	2.00	1.91
NE_g (Mcal/kg)	1.34	1.25
TDN (%)	82.0	78.7
ADF (%)	8.9	13.2
Ingredient composition (% DM basis)		
Whole Shelled Corn	84.8	70.4
Alfalfa hay	5.1	6.3
Alfalfa haylage	6.7	14.5
Straw	–	5.0
Protein, mineral, and vitamin supplement[a]	3.4	3.8

Note: DM, dry matter; CP, crude protein; NE_m, net energy for maintenance; NE_g, net energy for gain; TDN, total digestible nutrients; ADF, acid detergent fiber. Weighted average of the finishing period rations within each year is presented.

[a] 40% CP minimum, 2% crude fat minimum, 11% crude fiber maximum, 5.5%–6.5% Ca, 1.3% P, 4.5%–5.5% NaCl, 1% K minimum, and 88 000 IU/kg vitamin A minimum; DM basis. Contained monensin delivered at 350 mg/hd/day as monensin sodium.

Materials and methods

All animal procedures were approved by the University of Wyoming Institutional Animal Care and Use Committee.

Animal management and diets

Hereford-Angus crossbred steers (year 1: $n = 59$, initial BW $= 461 \pm 4.5$ kg, average age $= 379 \pm 1.5$ days; year 2: $n = 75$, initial BW $= 412 \pm 3.8$ kg, average age $= 370 \pm 1.1$ days) from a single contemporary group in each year (birth to slaughter) were used in a 2-year study. The steers were born into the University of Wyoming (UW; Laramie, WY) spring-calving beef herd, weaned at approximately 200 days of age, and allowed to graze grass meadow pasture (22 days in year 1; 43 days in year 2) until being transported to the UW Sustainable Agriculture Research and Extension Center (SAREC) in Lingle, WY. Upon arrival at SAREC, steers were placed in drylot pens and offered a growing ration that was gradually transitioned (5 rations in year 1; 4 rations in year 2) to a finishing diet consisting of 84.7% corn, 5.1% hay, 6.8% haylage, and 3.4% supplement (year 1; dry matter [DM] basis; Table 1) or 62.5% corn, 5.8% hay, 23.7% haylage, 4.3% straw, and 3.7% supplement (year 2; DM basis; Table 1). Monensin (Rumensin, Elanco Animal Health, Indianapolis, IN) was included in the diet to deliver 350 mg/hd/day in each year. Ingredient inclusion changed between years due to commodity pricing and availability.

Individual feed intake of the finishing diet (Table 1) was monitored using the GrowSafe system (model 4000E, GrowSafe Systems Ltd. Airdrie, AB, Canada) at SAREC for 57 (year 1) or 80 days (year 2). Performance and intake data (average daily gain [ADG], dry matter intake [DMI], gain:feed [G:F], and RFI) were calculated using data collected from the feeding period utilizing the GrowSafe system and BW measures. Average daily gain was calculated as (final BW − initial BW)/days on feed. DMI was calculated using daily feed intake data and diet DM composition, averaged over the feeding period. G:F was calculated as ADG (kg)/DMI (kg). RFI was calculated as the difference between actual feed intake and expected feed intake of each individual within each year's contemporary group. Expected feed intake was determined for each year using the model:

$$Y_i = \beta_0 + \beta_1 \mathrm{ADG}_i + \beta_2 \mathrm{MBW}_i + e_i,$$

with the intercept β_0, partial regression coefficient β_1 for ADG as calculated above, partial regression coefficient β_2 for metabolic midweight (MBW, average $\mathrm{BW}^{0.75}$), and the error term e_i for each animal. The model R_2 were 0.56 ($P < 0.001$) and 0.46 ($P < 0.001$) for years 1 and 2, respectively.

At the end of the feeding period in each year, 12th rib fat thickness was determined by ultrasound. RFI was only calculated for steers with 12th rib fat thickness $\geq$ 1.02 cm (year 1: 1.02–1.55 cm; year 2: 1.02–1.52 cm) to select animals with divergent efficiency that were of similar body composition. From this group in each year ($n = 40$ in year 1, $n = 45$ in year 2), the 20% most efficient (HE, low RFI; $n = 8$/year) and 20% least efficient (LE, high RFI; $n = 8$/year) were selected for slaughter and detailed dissection after the end of the feeding period. This 12th rib fat thickness was used to prevent selection of animals that appeared to be more efficient due to being earlier in their growth curve with less fat deposition.

Organ mass collection

The high and low efficiency steers selected for slaughter data collection ($n = 16$ total/year) were randomly allocated by efficiency group to one of the two slaughter dates occurring 6 and 8 days (year 1) or 5 and 7 days (year 2) after the end of the feeding period. Four steers from both high and low efficiency groups were slaughtered in a random order on each day. Feed and water were not withheld from steers before transport, and steers were transported (204 km) on the morning of slaughter. Steers were slaughtered at the UW Meat Laboratory in Laramie, WY (completed in $\leq$ 8 h for each slaughter date) using standard commercial methods inspected by the Wyoming Department of Agriculture Consumer Health Service division (delegated authority from USDA-Food Safety and Inspection Service), and visceral organs were removed for dissection and sampling immediately following inspection (<20 min post-exsanguination). After dissection, visceral organs were stripped of fat and digesta, including rinsing with tap water for the rumen, reticulum, and omasum. Organ masses were recorded for the small intestine (sectioned into the duodenum, jejunum, and ileum as described below), large intestine, reticulum, rumen, omasum, abomasum, liver, pancreas, spleen, lungs, heart, and kidneys after being stripped of fat and (or) digesta as appropriate. Lastly, mass of the mesenteric and omental fat was also collected in year 1 (the year 2 measurement was incorrect and therefore not presented).

Using identification and dissection methods adapted for cattle from Meyer et al. (2012), demarcations for sections of the small intestine were determined. The duodenum began after the pyloric sphincter and ended at a point on the small intestine adjacent to the junction of the mesenteric and gastrosplenic vein. The juncture of the ileocecal and mesenteric veins was identified, and a sampling point was identified by measuring 15 cm caudal down the mesenteric vein. The jejunum began after the duodenum and ended 300 cm caudal (along the jejunal tissue, measured with a string without stretching the small intestine) to a point adjacent to this sampling location. The ileum was considered from the end of the jejunum to the ileocecal junction.

Carcass composition collection

Carcass data were collected as described in Underwood et al. (2008) after carcasses were held at 2–4 °C for 48 h. One trained, experienced technician collected all carcass measurements. After carcasses were held at 2–4 °C for 14 days, a two-rib portion was removed from the rib primal of the left side and frozen at −40 °C until Warner-Bratzler shear force could be completed. The semitendinosus (ST) was dissected from each carcass side during normal fabrication, trimmed of visible external fat, and weighed.

Steaks were cut from the frozen rib sections to a thickness of 3.175 cm for Warner-Bratzler shear force determination as described in Underwood et al. (2008) after being cooked to an internal temperature of 71 °C. Cores were cut parallel to muscle fiber orientation, then were visually examined and discarded if excess connective tissue or holes due to thermocouple/thermometer placement were present. A minimum of 6 cores and maximum of 10 cores were sheared once in the middle using a Warner-Bratzler machine (G-R Electric Manufacturing Co.; Manhattan, KS) equipped with an electric load cell (Dillion Basic Force Gauge, BFG500N; EU) using a crosshead speed of 225 mm/min. Shear force of individual cores were averaged to obtain the shear force for each steak.

Calculations

The rumen, reticulum, omasum, and abomasum were summed to determine the total stomach complex mass, while the total gastrointestinal mass was calculated as the sum of the stomach complex, small intestine, and large intestine. Relative organ masses were calculated as visceral organ mass (g) divided by BW (kg) or hot carcass weight (HCW, kg). Dressing percentage was calculated as the HCW divided by final BW. Relative ribeye area was calculated as the ribeye area divided by the HCW. Relative ST weight was calculated as the sum of the ST weight from both sides of the carcass divided by the HCW. Yield grade was calculated using the formula: $2.5 + (2.50 \times \text{adjusted fat thickness, inches}) + (0.20 \times \%\ \text{KPH}) + (0.0038 \times \text{HCW, pounds}) - (0.32 \times \text{ribeye area, square inches})$ according to the USDA (1997).

Statistical analysis

Performance, carcass, and organ mass data were analyzed in PROC MIXED of SAS 9.3 (SAS Inst., Inc., Cary, NC) with RFI class (low efficiency [high RFI] versus high efficiency [low RFI]), year (1 and 2), and their interaction included in the model as fixed effects. Least square means were separated using LSD and considered significant when $P \le 0.05$ or a tendency when $0.05 < P \le 0.10$. When an RFI class × year interaction was present, RFI classes were compared within year only, as that is the only meaningful comparison in the current study. In the absence of interactions, main effects were discussed.

Results

Finishing performance data

RFI averaged −1.42 kg DM/day (range: −0.93 to −1.93 kg DM/day) and 1.27 (range: 0.89 to 1.98 kg DM/day) for high efficiency and low efficiency steers, respectively, in year 1. In year 2, RFI averaged −1.17 kg DM/day (range: -0.58 to -2.11 kg DM/day) and 1.31 kg DM/day (range 0.85 to 2.00 kg DM/day) for high and low efficiency steers, respectively. There was no effect ($P \ge 0.40$) of year or RFI class × year for animal performance measures (Table 2). DMI was 25% greater ($P < 0.001$) for low efficiency than high efficiency steers. There was no difference ($P = 0.63$) in ADG between RFI classes, but G:F was greater ($P < 0.001$) in high efficiency steers compared with low efficiency steers.

Carcass composition

There was an RFI class × year interaction ($P = 0.05$) for marbling score, where high efficiency steers tended ($P = 0.09$) to have greater marbling than low efficiency steers within year 2, but there was no difference ($P = 0.25$) in year 1 (Table 3). No other RFI class × year interactions ($P \ge 0.35$) were observed in carcass data. Dressing percentage tended ($P = 0.10$) to be greater (<1% difference) in high efficiency steers compared with low efficiency steers. Additionally, high efficiency steers tended ($P = 0.06$) to have greater cumulative semitendinosus weight than low efficiency steers, despite there being no difference ($P \ge 0.13$) for HCW or semitendinosus weight relative to HCW between RFI classes. The main effect of RFI class did not affect ($P \ge 0.13$) yield grade; 12th rib fat thickness; ribeye area (actual or relative to HCW); kidney, pelvic, and heart fat; or ribeye shear force.

There was a year effect ($P \le 0.02$) for ribeye area and relative ribeye area, where steers in year 1 had greater muscling. Kidney, pelvic, and heart fat was greater ($P = 0.007$) for steers in year 2. Additionally, yield grade tended to be improved ($P = 0.06$) in year 1 compared with year 2.

Actual visceral organ mass

There tended ($P \le 0.09$) to be an interaction of RFI class × year for small intestinal and large intestinal masses (Table 4). Small intestinal mass tended ($P = 0.10$) to be 11% greater in low efficiency than high efficiency steers in year 1, but there was no difference ($P = 0.42$) in year 2. There was no difference ($P = 0.32$) in large intestinal mass between RFI classes in year 1, but large intestinal mass tended ($P < 0.10$) to be 17% greater in high efficiency than low efficiency steers in year 2.

Omasum mass tended ($P = 0.06$) to be 13% greater in low efficiency than high efficiency steers (Table 4). Actual total gastrointestinal tract mass, stomach complex, rumen, reticulum, abomasum, small intestinal sections, omental and mesenteric fat, liver, pancreas, spleen, lungs, heart, and kidney mass were not affected ($P \ge 0.14$) by RFI class.

Steers in year 2 had greater ($P \le 0.02$) total gastrointestinal tract, stomach complex, omasum, jejunum, and ileum masses compared with steers in year 1. Abomasum mass also tended to be greater ($P = 0.06$) in year 2 steers. Conversely, steers in year 1 had greater ($P = 0.04$) pancreas mass.

Visceral organ mass relative to BW

Final BW was not affected ($P \ge 0.22$) by RFI class, year, or their interaction (Table 5). The RFI class × year interaction affected ($P \le 0.05$) small intestinal and large intestinal masses relative to BW and tended ($P = 0.06$) to affect ileal mass relative to BW (Table 5). In year 1, low efficiency steers had 13% greater ($P = 0.02$) relative small intestinal mass and tended ($P = 0.06$) to have 13% greater relative ileal mass compared with high efficiency steers. In year 2 there was no difference ($P \ge 0.44$) in small intestinal or ileal mass relative to BW. There was no difference ($P = 0.24$) in relative large intestinal mass between high efficiency and low efficiency steers in year 1, but in year 2 high efficiency steers tended ($P < 0.10$) to have 14% greater large intestinal mass than low efficiency steers.

Total gastrointestinal and stomach complex mass relative to BW tended ($P \le 0.07$) to be 4.4% and 5.9% greater, respectively, in low efficiency steers compared with high efficiency steers (Table 5). The stomach complex difference observed may be explained by a 14% greater ($P = 0.03$) relative mass of the omasum in low efficiency compared with high efficiency steers. Liver and kidney mass relative to BW tended ($P \le 0.10$) to be greater (5.9% and 4.8%, respectively) in low efficiency than high efficiency steers. Masses of the reticulum, rumen, abomasum, duodenum, jejunum, omental and mesenteric fat, pancreas, spleen, lungs, and heart relative to BW were not different ($P \ge 0.24$) between high efficiency and low efficiency steers.

Steers in year 2 had greater ($P \le 0.01$) total gastrointestinal tract, stomach complex, rumen, omasum, abomasum, jejunum, spleen, and kidney masses. Pancreas mass tended to be greater ($P = 0.09$) in year 1 than year 2, however.

Visceral organ mass relative to HCW

Hot carcass weight was not affected ($P \ge 0.14$) by RFI class, year, or their interaction (Table 6). Small intestinal and large intestinal masses relative to HCW tended ($P \le 0.10$) to be affected by the RFI class x year interaction (Table 6). In year 1, relative small intestinal mass to HCW was 13% greater ($P = 0.02$) in low efficiency compared with high efficiency steers but did not differ ($P = 0.99$) in year 2. Within year, large intestinal mass was not affected ($P \ge 0.16$) by RFI class.

Similar to mass relative to BW, total gastrointestinal mass and stomach complex mass relative to HCW were greater ($P \le 0.03$; 6.1% and 7.2%, respectively) in low efficiency steers compared with high efficiency steers (Table 6). Again, this appeared to be driven by the 15% greater ($P = 0.02$) omasum mass relative to HCW in low efficiency steers. In addition, liver and kidney masses relative to HCW were greater ($P \le 0.05$; 6.9% and 5.7%, respectively) in low efficiency than

Table 2. Effects of residual feed intake (RFI) classification on steer finishing period performance data during feed intake period.

	Year 1		Year 2			*P*-values		
Item	Low efficiency	High efficiency	Low efficiency	High efficiency	SEM	RFI	Year	RFI × Year
Average daily gain (kg/day)	1.51	1.56	1.46	1.51	0.09	0.63	0.58	>0.99
DM intake (kg/day)	12.16	9.62	12.18	9.78	0.37	<0.001	0.82	0.85
Gain:feed (kg/kg)	0.124	0.162	0.120	0.154	0.007	<0.001	0.40	0.79

Note: DM, dry matter. Low efficiency = 20% highest RFI steers ($n = 8$/year); High efficiency = 20% lowest RFI steers ($n = 8$/year).

Table 3. Effects of residual feed intake (RFI) classification on steer carcass data at market weight.

	Year 1		Year 2			*P*-values		
Item	Low efficiency	High efficiency	Low efficiency	High efficiency	SEM	RFI	Year	RFI × Year
Hot carcass weight (kg)	337	342	321	332	9	0.39	0.14	0.74
Dressing percentage (%)	62.3	63.2	62.5	62.9	0.4	0.10	0.86	0.44
Marbling Score[a]	494	449	429[x]	495[y]	27	0.70	0.73	0.05
Yield grade	3.45	3.29	3.78	3.78	0.21	0.70	0.06	0.70
12th rib fat (cm)	1.42	1.43	1.30	1.38	0.12	0.73	0.49	0.77
Ribeye area (cm^2)	77.3	81.9	68.6	70.9	2.1	0.13	<0.001	0.60
Relative ribeye area (cm^2/kg)	0.231	0.240	0.214	0.214	0.008	0.60	0.02	0.60
KPH (%)	2.81	2.88	3.52	3.24	0.18	0.55	0.007	0.35
Semitendinosus weight[b] (kg)	3.85	4.24	3.76	3.98	0.16	0.06	0.26	0.57
Semitendinosus weight[b] (% of HCW)	1.15	1.24	1.17	1.20	0.04	0.13	0.89	0.40
Ribeye shear force (kg)	4.40	4.54	4.10	4.22	0.30	0.67	0.32	0.99

Note: KPH, Kidney pelvic and heart fat; HCW, hot carcass weight. Low efficiency = 20% highest RFI steers ($n = 8$/year); High efficiency = 20% lowest RFI steers ($n = 8$/year).

[a] Marbling score: 100 = practically devoid, 200 = traces, 300 = slight, 400 = small, 500 = modest, 600 = moderate, and 700 = slightly abundant, 800 = moderately abundant, 900 = abundant.

[b] Cumulative semitendinosus weight from both carcass sides.

[x,y] Within a year, RFI class means tend to differ ($0.05 < P \leq 0.10$).

high efficiency steers as well. All other visceral organ masses relative to HCW were not affected ($P \geq 0.11$) by RFI class.

Masses of the total gastrointestinal tract, stomach complex, omasum, abomasum, jejunum, ileum, and spleen were greater ($P \leq 0.02$) for steers in year 2 than year 1. Steers in year 1 had greater ($P = 0.05$) pancreas mass.

Discussion

Performance and carcass data

Performance data in this study are in agreement with previous research in terms of the relationship of ADG, DMI, and G:F with RFI. When using RFI, low efficiency animals consume more feed, but have similar gain and BW, compared with high efficiency animals. Moreover, RFI is correlated with G:F, so high efficiency animals in this study were still more efficient using the more traditional measure (Arthur et al. 2001; Nkrumah et al. 2004).

Overall carcass composition differences between RFI classes observed in the current study were minimal and all present as tendencies. The tendencies for both dressing percentage and semitendinosus weight to be greater for high efficiency steers suggest that more efficient cattle in the current study may have had somewhat leaner body composition despite the lack of difference in yield grade. This is in agreement with genetic correlations between RFI and carcass lean measures which indicate that high efficiency cattle generally have greater muscling (Berry and Crowley 2013). Despite this, muscle accretion differences between high and low RFI cattle were not observed in a recent meta-analysis conducted by Kenny et al. (2018), highlighting the inconsistency of carcass results in divergent RFI studies. Backfat thickness was not different between RFI classes in the current study, although this may have been influenced by the preslaughter ultrasound backfat measure to eliminate thin steers earlier in their growth curve. In 1 year of the current study, high efficiency steers tended to have greater marbling, although marbling has generally been reported to have a positive genetic correlation with RFI (Berry and Crowley 2013).

The lack of consistent differences between efficiency groups across years in our data could be a result of selection of animals based on similar ultrasound backfat or limited biological replicates. The main purpose of the current study was not to determine effects of RFI class on carcass composition, as that has been researched extensively, and the current study was not adequately powered to do so. However, carcass characteristics influence interpretation of gastrointestinal and visceral organ mass data; thus, it is important to consider them in this context. Slaughter of animals at a common endpoint based on backfat thickness appears to have been successful in minimizing body composition differences that could overshadow other physiological drivers of feed ef-

Table 4. Effects of residual feed intake (RFI) classification on steer actual visceral organ mass (kg) at market weight.

Item	Year 1		Year 2		SEM	*P*-values		
	Low efficiency	High efficiency	Low efficiency	High efficiency		RFI	Year	RFI × Year
Total gastrointestinal tract	25.0	23.1	27.6	28.0	0.9	0.42	<0.001	0.23
Stomach complex	18.4	17.2	19.9	19.4	0.8	0.25	0.02	0.65
Reticulum	1.15	1.22	1.21	1.17	0.11	0.87	0.90	0.61
Rumen	10.1	9.9	10.9	10.7	0.5	0.65	0.11	>0.99
Omasum	5.48	4.38	6.00	5.76	0.34	0.06	0.009	0.21
Abomasum	1.59	1.66	1.95	1.76	0.12	0.63	0.06	0.30
Small intestine	4.60^x	4.13^y	5.57	5.80	0.21	0.56	<0.001	0.09
Duodenum	0.665	0.661	0.604	0.701	0.048	0.33	0.83	0.30
Jejunum	1.22	1.06	1.60	1.63	0.10	0.50	<0.001	0.37
Ileum	2.72	2.40	3.36	3.52	0.15	0.61	<0.001	0.14
Large intestine	2.01	1.80	2.16^x	2.52^y	0.15	0.62	0.006	0.06
Other viscera								
Omental and mesenteric fat[a]	26.0	28.4	–	–	1.1	0.14	–	–
Liver	6.79	6.51	6.52	6.25	0.29	0.35	0.37	>0.99
Pancreas	0.515	0.600	0.464	0.445	0.048	0.48	0.04	0.27
Spleen	0.758	0.760	0.786	0.843	0.040	0.48	0.18	0.50
Lungs	2.94	2.54	2.55	2.62	0.15	0.27	0.30	0.13
Heart	2.41	2.45	2.28	2.39	0.09	0.42	0.29	0.68
Kidneys	0.918	0.890	0.913	0.893	0.032	0.45	0.98	0.90

Note: Low efficiency = 20% highest RFI steers ($n = 8$/year); High efficiency = 20% lowest RFI steers ($n = 8$/year).

[a] Measured only in year 1.

[x,y] Within a year, RFI class means tend to differ ($0.05 < P \leq 0.10$).

Table 5. Effects of residual feed intake (RFI) classification on steer visceral organ mass relative to BW at market weight.

Item	Year 1		Year 2		SEM	*P*-values		
	Low efficiency	High efficiency	Low efficiency	High efficiency		RFI	Year	RFI x Year
Final BW (kg)	551	556	535	536	14	0.82	0.22	0.91
Mass (g/kg BW)								
Total gastrointestinal tract	45.2	41.6	54.3	53.5	1.2	0.06	<0.001	0.21
Stomach complex	33.2	30.9	39.1	37.3	1.1	0.07	<0.001	0.81
Reticulum	2.10	2.20	2.38	2.27	0.23	0.98	0.46	0.64
Rumen	18.3	17.9	21.4	20.5	0.6	0.31	<0.001	0.76
Omasum	9.94	7.89	11.65	11.08	0.57	0.03	<0.001	0.21
Abomasum	2.89	2.99	3.80	3.42	0.25	0.57	0.01	0.33
Small intestine	8.35^a	7.42^b	10.83	11.08	0.29	0.24	<0.001	0.04
Duodenum	1.22	1.20	1.18	1.35	0.10	0.43	0.56	0.30
Jejunum	2.24	1.90	3.12	3.11	0.19	0.33	<0.001	0.36
Ileum	4.89^x	4.33^y	6.53	6.76	0.21	0.43	<0.001	0.06
Large intestine	3.65	3.24	4.21^y	4.80^x	0.24	0.72	<0.001	0.05
Other viscera								
Omental and mesenteric fat[a]	47.5	51.2	–	–	2.2	0.24	–	–
Liver	12.3	11.7	12.7	12.0	0.4	0.10	0.40	0.83
Pancreas	0.920	1.074	0.901	0.844	0.075	0.50	0.09	0.15
Spleen	1.37	1.37	1.53	1.62	0.06	0.50	0.003	0.47
Lungs	5.41	4.58	4.97	5.02	0.33	0.25	>0.99	0.19
Heart	4.38	4.41	4.44	4.59	0.12	0.48	0.31	0.64
Kidneys	1.67	1.60	1.78	1.71	0.04	0.10	0.01	0.98

Note: Low efficiency = 20% highest RFI steers ($n = 8$/year); High efficiency = 20% lowest RFI steers ($n = 8$/year).

[a] Measured only in year 1.

[a,b] Within a year, RFI class means differ ($P \leq 0.05$).

[x,y] Within a year, RFI class means tend to differ ($0.05 < P \leq 0.10$).

Table 6. Effects of residual feed intake (RFI) classification on steer visceral organ mass relative to hot carcass weight (HCW) at market weight.

	Year 1		Year 2			*P*-values		
Item	Low efficiency	High efficiency	Low efficiency	High efficiency	SEM	RFI	Year	RFI × Year
HCW (kg)	337	342	321	332	9	0.39	0.14	0.74
Mass (g/kg HCW)								
Total gastrointestinal tract	73.9	67.6	86.6	83.7	1.9	0.02	<0.001	0.37
Stomach complex	54.3	50.3	62.4	58.5	1.7	0.03	<0.001	0.97
Reticulum	3.43	3.58	3.79	3.55	0.35	0.90	0.64	0.59
Rumen	29.9	29.0	34.1	32.3	1.0	0.18	<0.001	0.62
Omasum	16.2	12.8	18.6	17.4	0.9	0.02	<0.001	0.26
Abomasum	4.73	4.86	6.08	5.37	0.39	0.46	0.02	0.29
Small intestine	13.7^{a}	12.1^{b}	17.3	17.3	0.5	0.11	<0.001	0.10
Duodenum	2.00	1.95	1.88	2.13	0.16	0.54	0.84	0.37
Jejunum	3.66	3.08	5.00	4.85	0.29	0.21	<0.001	0.44
Ileum	7.99	7.03	10.45	10.62	0.36	0.28	<0.001	0.12
Large intestine^{b}	6.00	5.27	6.74	7.56	0.40	0.88	<0.001	0.07
Other viscera								
Omental and mesenteric fat^{a}	77.6	83.3	–	–	3.7	0.30	–	–
Liver	20.1	19.0	20.3	18.8	0.6	0.04	>0.99	0.67
Pancreas	1.50	1.75	1.44	1.33	0.12	0.57	0.05	0.14
Spleen	2.24	2.22	2.45	2.54	0.11	0.73	0.02	0.59
Lungs	8.81	7.44	7.95	7.88	0.50	0.16	0.68	0.20
Heart	7.15	7.16	7.11	7.20	0.19	0.78	0.99	0.83
Kidneys	2.73	2.60	2.85	2.69	0.07	0.05	0.14	0.85

Note: Low efficiency = 20% highest RFI steers ($n = 8$/year); High efficiency = 20% lowest RFI steers ($n = 8$/year).

[a] Measured only in year 1.

[b] No RFI class means differ within year, despite RFI class × year interaction.

[a,b] Within a year, RFI class means differ ($P \leq 0.05$).

ficiency in finishing cattle. Overall, given the minimal carcass differences observed, it is unlikely that any differences in body composition were great enough to affect the interpretation of visceral organ mass results.

Visceral organ mass

Visceral organ mass can impact both function and nutrient requirements of the tissues, which has implications for divergence in feed efficiency. Organ masses relative to BW or usable end product (e.g., HCW) provide more useful measures, as organs generally scale with BW but can deviate from this to make up an increased or decreased proportion of animal size. Based on the current results, masses of the small intestine, large intestine, stomach complex, liver, and kidney may influence individual differences in feed efficiency. All of these organs appear to be smaller in more efficient animals, with the exception of the large intestine.

Previous work comparing organ masses in high and low RFI cattle is inconsistent. Basarab et al. (2003) observed that low and moderate RFI steers had decreased combined small and large intestinal mass (with digesta) as well as liver and gastrointestinal mass compared with high RFI steers, and Fitzsimons et al. (2014) observed that low RFI bulls had decreased stomach complex mass. Our laboratory previously demonstrated that more efficient cattle may have less small intestinal mass, as small intestinal mass (actual and relative to BW) was positively correlated with RFI in finishing steers (Meyer et al. 2014). Additionally, rumen and heart masses were less for low RFI, and total intestinal (small and large) mass was less for low G:F Charolais bulls (Meale et al. 2017). Conversely, there was no relationship between RFI and total visceral, gastrointestinal, or individual visceral organ weight, even though G:F was negatively correlated with total visceral weight and positively correlated with gastrointestinal weight in another study (Mader et al. 2009). High RFI Nellore bulls had greater kidney and blood masses (Bonilha et al. 2013), and gastrointestinal fat (equivalent to omental and mesenteric fat in the current study) was greater for high RFI Nellore steers (Gomes et al. 2012), but total gastrointestinal and other visceral organ masses did not differ in either study. In feedlot lambs, Meyer et al. (2015) reported a tendency for spleen and pancreas actual mass to be greater in high efficiency lambs compared with low efficiency lambs, but no differences in gastrointestinal or other visceral masses due to RFI classification.

These contradictory observations in gastrointestinal and visceral organ masses between high and low efficiency ruminants may be due to differences in species, breed type, age of animal or stage of growth, animal sex (bulls versus steers), groups of animals used (highly homogenous groups versus highly heterogeneous groups), methods utilized (gastrointestinal tract organs with digesta or without, sections combined or separated), and specific diets or nutrient densities used in these studies. Gastrointestinal tract organs were not separated and (or) emptied of digesta, or methodology was unclear, in several studies cited above (Basarab et al. 2003; Gomes et al. 2012; Bonilha et al. 2013; Fitzsimons et al. 2014; Meale et al. 2017); thus, drawing conclusions about the gastrointestinal tract is difficult from these studies. Furthermore, animals used in Basarab et al. (2003), Mader et al. (2009), and Meyer et al. (2015) include multiple breed types and contemporary groups formed postweaning. This likely resulted in animals for which body composition and growth due to breed makeup, genetics, previous nutrition and management, or stage of growth may have had a larger influence on RFI classification than other underlying physiological mechanisms. In the current study, these animals were similar in age, genetics, and previous management as they were from one contemporary group from birth to slaughter in each year.

In general, where differences exist among RFI class in studies cited above, low efficiency (high RFI) animals had greater gastrointestinal and liver mass. This follows the general observation that gastrointestinal tract and other visceral organ masses increase with feed intake (Johnson et al. 1990), but challenges the notion that organ mass is constant relative to body size. Interestingly, differences in organ masses between RFI classes became more apparent when expressed relative to BW or HCW in the current study. Using the divergent RFI model, growing animals with similar ADG and BW have gastrointestinal tract and visceral organ masses that align with DM intake in spite of body size and growth. This suggests that high efficiency cattle may have 1) smaller gastrointestinal and visceral organs that are more functional per unit of mass, and (or) 2) decreased energy and nutrient expenditure from less organ mass that makes up for decreased overall organ function.

Some recent research has posed these questions in various feed efficiency models. For example, differential gene expression has been associated with improved feed efficiency and gain in the ruminal epithelium (Kern et al. 2016 and 2017) and small intestine of beef cattle (Lindholm-Perry et al. 2016; Foote et al. 2017). These genes were associated with functions of immune response, inflammation, stress response, metabolism, digestion, and nutrient absorption. Supporting evidence in pigs has identified decreased inflammation and improved detoxification and antimicrobial activity in the liver and small intestine of more efficient pigs compared with less efficient pigs (Mani et al. 2013). Additionally, hepatocyte size was increased in more efficient steers (Montanholi et al. 2017). These data suggest that beyond organ mass, functional aspects of these tissues may be key components of differences in efficiency.

Histomorphic traits of the small intestine were affected by divergence in feed efficiency, where duodenal crypt area and perimeter tended to be larger in low RFI steers, and crypt region nuclei number in the duodenum and ileum were greater in low RFI than high RFI steers (Montanholi et al. 2013). In another study, more dense jejunal mucosa and increased jejunal mucosal DNA concentration and RNA content were associated with more efficient cattle (Meyer et al. 2014). In these studies, more crypt nuclei (active proliferation region) and more mucosa relative to other small intestinal tissue types with less digestive and absorptive function (serosa and muscularis) may lead to less functional difference due to mass in high efficiency steers. Overall, previous research suggests that small intestinal tissue composition differs between efficiency classes.

Energy and nutrient use of the gastrointestinal and visceral organs has not been well studied in divergent RFI or feed efficiency models. Despite this, it is generally accepted that decreased visceral organ mass reduces energy requirements (Ferrell et al. 1986; Burrin et al. 1989) for the animal, which could explain why low efficiency animals may have increased organ mass and thus increased feed intake despite a lack of improvement in gain. A major source of these increased energy requirements may be via the Na^+, K^+-ATPase activity, which is an energy demanding process utilized for transport of nutrients across the plasma membrane and contributes to O_2 consumption and maintenance energy expenditure of the tissue (Milligan and McBride 1985; Huntington and McBride 1988). Increased feed intake resulted in increased Na^+, K^+-ATPase activity in both small intestine and liver of sheep (Milligan and McBride 1985). Conversely, diet type and feed intake did not affect this activity in steers which showed differences in gastrointestinal tract weight (Kelly et al. 2001). These contradicting data suggest that while level of feed intake can alter these activities, sometimes O_2 consumption and energy use may be altered only by response in organ mass (McLeod and Baldwin 2000).

The presence of year effects may be due to the difference in diets utilized. Forage:concentrate ratio has previously been shown to affect gastrointestinal tract masses in both cattle (Sainz and Bentley 1997; McCurdy et al. 2010) and sheep (McLeod and Baldwin 2000; Meyer et al. 2015); thus, greater gastrointestinal masses in year 2 may have been due to the presence of greater dietary fiber. Previous studies had much larger differences in diet type than the 4.3% difference in ADF between years of the current study, however. In fact, the higher fiber diet in year 2 is often more like the high concentrate diet in other studies, and small differences in fiber concentration of corn-based diets have not been greatly studied.

The presence of small intestinal mass differences only in year 1, when the lower fiber diet was used, is interesting and suggests that diet type may influence the role of the small intestine in feed efficiency. Additionally, greater large intestinal mass in high efficiency steers in year 2 suggests that more hindgut capacity improves efficiency with greater fiber content of the diet. Often the reported differences in previous studies are confounded with DMI differences between concentrate and forage-based diets, even if energy or protein intake is similar among or between diet types. Dry matter intake was not affected by year but was affected by RFI class in the current study, indicating that RFI class differences are likely more related to DMI whereas year differences may be due to fiber content.

In the current study, ADG, G:F, final BW, and hot carcass weight were similar among years, with less differences in carcass composition than organ masses, which is rarely true in previous studies investigating diet type differences. Overall, it is important to consider that factors other than diet differed between years, as is common with any study replicated over years. Although from the same cowherd and sires, steers in each year were their own contemporary group that experienced different environments from conception to slaughter, which likely also influenced their organ masses and carcass composition. To meet the objective of comparing divergent RFI phenotypes within a contemporary group, 2 years were needed in the current study to obtain adequate power for organ mass differences.

In summary, small intestinal, stomach complex, liver, and kidney visceral organ masses relative to BW and HCW in this study were less in high efficiency than low efficiency finishing steers from a single contemporary group per year from birth to slaughter. This occurred even when steers of divergent RFI classification had similar BW, HCW, and ADG, as well as minimal carcass differences. Less gastrointestinal and visceral organ mass could lead to decreased energy expenditure for the maintenance of tissues in high efficiency steers. Greater understanding of tissue mass and function differences underlying variation in feed efficiency will allow for development of management strategies to improve efficiency and provide insight for more accurate selection of efficient animals.

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The authors have no conflicts of interest.

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