Characterization and evaluation of residual feed intake measured in mid- to late-gestation mature beef cows and relationships with circulating serum metabolites and linear body measurements

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Wood, K. M., Montanholi, Y. R., Fitzsimmons, C. F., Miller, S. P., McBride, B. W. and Swanson, K. C. 2014. **Characterization and evaluation of residual feed intake measured in mid- to late-gestation mature beef cows and relationships with circulating serum metabolites and linear body measurements**. Can. J. Anim. Sci. **94**: 499–508. To evaluate the use of residual feed intake (RFI) models measured in mid-to-late gestating beef cows, a dataset was used combining data from five experiments containing nine treatment and/or replicate groups for a total of 321 animal records. Investigations of RFI models included the effects of age, ultrasound measures of body composition, pregnancy corrected gain, and dietary treatment group. A subset of animals had serum analyzed for circulating metabolites (glucose, non-esterified fatty acids, urea, beta-hydroxybutyrate; $n = 227$) and/or linear body measures (hip height and width, body length, body circumference at the heart, mid-body and at flank; $n = 114$) for correlation analysis with efficiency traits. Goodness-of-fit for all RFI models was assessed using R^2, CV, and Bayesian information criteria. Across treatment/replicate groups, the largest improvements in model fit were made by accounting for management group and dietary treatment. Circulating urea concentrations were positively correlated ($P \leq 0.05$) with average daily gain, dry matter intake, gain:feed, and group RFI model. Linear body measures and circulating metabolites measured (with the exception of urea) were not correlated ($P > 0.05$) with economically relevant traits. Measures of RFI as an indication of feed efficiency may be challenging for use in gestating beef cows. Large variation in efficiency between cows remain, and may be related to mechanisms influencing maintenance and energy expenditures.

Key words: Cow, feed efficiency, residual feed intake, metabolites, body dimensions

Wood, K. M., Montanholi, Y. R., Fitzsimmons, C. F., Miller, S. P., McBride, B. W. et Swanson, K. C. 2014. **Caractérisation et évaluation de l'alimentation résiduelle mesurée dans les phases intermédiaires et tardives de la gestation des vaches de boucherie matures et la relation avec les métabolites sériques circulants et les mesures linéaires du corps**. Can. J. Anim. Sci. **94**: 499–508. Pour évaluer l'utilisation des modèles d'alimentation résiduelle (RFI – « residual feed intake ») chez les vaches dans les phases intermédiaires et tardives de la gestation des vaches de boucherie, une série de données a été utilisée qui combine les données de cinq expériences, donc neuf groupes de traitements ou de réplicats, pour un total de 321 fiches d'animaux. L'investigation des modèles RFI tient compte des effets de l'âge, des mesures de la composition corporelle par ultrasons, des gains de gestation corrigés et du groupe de traitement alimentaire. Un sous-groupe d'animaux a subi une analyse de sérum pour déterminer les niveaux de métabolites circulants (glucose, acides gras non estérifiés, urée, béta-hydroxybutyrate; $n = 227$) et/ou les mesures corporelles linéaires (hauteur aux hanches et largeur aux hanches,

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Abbreviations: **ADF**, acid detergent fibre; **ADG**, average daily gain; **BIC**, Bayesian information criteria; **BHBA**, β-hydroxybutyrate; **BW**, bodyweight; **cBF**; change in real-time ultrasound predicted backfat; **CP**, crude protein; **cRF**, change in real-time ultrasound predicted rump fat; **CV**, coefficient of variation; **DM**, dry matter; **DMI**, dry matter intake; **EBRC**, Elora Beef Research Centre; **F:G**, feed to gain; **G:F**, gain to feed; **iBF**, initial real-time ultrasound predicted backfat; **iRF**, initial real-time ultrasound predicted rump fat; **NDF**, neutral detergent fibre; **NEFA**, non-esterified fatty acid; **NE**, net energy; **NEm**, net energy for maintenance; **NLARS**, New Liskeard Agricultural Research Station; **pcADG**, pregnancy corrected average daily gain; **pcBW**, pregnancy-corrected mid-point body weight; **RFI**, residual feed intake; **RMSE**, root mean square error; **SD**, standard deviation; **TMR**, total mixed ration; **TRMT**, treatment group

longueur du corps, circonférence corporelle au coeur, au milieu du corps et au flanc; $n = 114$) pour l'analyse de corrélation avec les caractéristiques d'efficacité. La qualité d'ajustement pour tous les modèles RFI a été évaluée selon les critères R^2, CV et information bayésienne. Dans tous les groupes de traitement/réplicats, les plus grandes améliorations dans la qualité d'ajustement ont été faites en tenant compte du groupe de gestion et du traitement alimentaire. Il y avait une corrélation positive ($P \leq 0,05$) entre les concentrations circulantes d'urée et le gain moyen quotidien, l'ingestion de matières sèches, l'indice de consommation alimentaire et le modèle RFI de groupe. Il n'y avait pas de corrélation ($P > 0,05$) entre les mesures corporelles linéaires et les niveaux de métabolites circulants (à l'exception de l'urée) et les caractéristiques d'importance économique. La mesure du RFI comme indicateur d'efficience alimentaire est difficile chez les vaches de boucherie en gestation. De grandes variations d'efficacité entre les vaches demeurent et pourraient être reliées aux mécanismes qui influencent l'entretien et la dépense énergétique.

Mots clés: Vache, efficience alimentaire, alimentation résiduelle, métabolites, dimensions corporelles

Winter feed costs represent the greatest costs of production for cow/calf producers (Kaliel and Kotowich 2002). In conventional cow/calf production systems this period also coincides with mid- to late-gestation. Although adequate nutrition is needed for growth, pregnancy and reproduction and maintenance of bodily functions, there may be large differences between animals in how energy and nutrients are utilized, which may enable producers to select for more feed efficient breeding females.

Traditionally, feed efficiency measures are expressed as a ratio of input (feed) to output (performance). These feed conversion ratios are mutually exclusive and may not reflect true feed efficiency. The concept of net feed efficiency or residual feed intake (RFI) was initially characterized for use in beef cattle by Koch et al. (1963) and represents the difference between the actual feed intake and the predicted feed intake based upon the regression of body weight and performance, usually growth, in terms of average daily gain (ADG). Negative RFI represents efficient animals and positive RFI, inefficient animals (Montanholi et al. 2009; Kelly et al. 2010).

Although measures of RFI have gained increased interest in the research community in growing animals, very little research has been conducted evaluating the measurement of RFI in the pregnant beef cow. Measuring feed efficiency in cows in this phase of the production cycle may pose several challenges, as output measures, such as body weight gain or loss, changes in body composition, or growth of the conceptus are difficult to quantify. During this period, cows may also maintain body weight, having body weight gains close to zero, or actually lose weight. This poses challenges to using RFI in the mature beef cow. As well, little information is available analyzing measures of RFI in mature pregnant beef cows fed forage-based diets, since the majority of RFI research has been conducted in a feedlot setting where primarily concentrate or pelleted feeds were used. It is hypothesized that including body composition and body parameter measures in prediction models would improve the fit of RFI models and that serum metabolites and phenotypic body measurements may be associated with differences in RFI of mature pregnant cows.

The objectives of this experiment were: (1) to investigate variables that may reduce variability in the measurement of RFI in the pregnant beef cow, (2) to investigate relationships between measures of feed efficiency and circulating serum metabolites or phenotypic body measurements in mature pregnant beef cows.

MATERIALS AND METHODS

Animals and Experiment Design

All experiments followed the recommendations of the Canadian Council on Animal Care (1993) and met the approval of the University of Guelph Animal Care Committee. Data from five experiments involving different treatments and/or replications were combined to accomplish the objectives of this study. The combined dataset contained 321 feed and performance records. A summary of all experiments can be found in Table 1. All experiments utilized non-lactating pregnant (mid-to-late gestation) multiparous beef cows fed over the winter, leading up to parturition. All animals were primarily of Angus and Simmental crossbreeding and were housed at the Elora Beef Research Station (EBRC) or at the New Liskeard Agriculture Research Station (NLARS). Cows were all individually fed for ad libitum intake, and dry matter intake was measured using Calan gates (American Calan Inc., Northwood, NH). Animals included in this dataset were all fed over the winter and remained on their respective diets until approximately 1 wk prior to the earliest parturition date. In all trials, cows were weighed on 2 consecutive days at the start and at the end of the trial period, and at 28-d intervals during the trials. All cows were weighed every 28 d and ultrasound measures obtained at the start and end of the trial for rib fat (between the 12th and 13th rib) and rump fat depth measurements (between the coxal and ischiatic tuber), using an Aloka SSD-500 ultrasound unit (Corometrics Medical Systems, Wallingford, CT). Cattle were removed from the dataset for: carrying twins, premature births, aborting fetuses, or mastitis.

A brief description of each experiment is as follows. The first experiment, containing groups 1 and 2, examined the effect of including different crop residues in a haylage-based total mixed ration (TMR) in wintering rations fed to pregnant cows leading up to parturition (Wood et al. 2010a,b). Cows were fed for 82 d leading up to the earliest day of parturition. Group 1 was the control group from this experiment, where cows were fed haylage

Table 1. Summary of treatment group mature cow experiments included in the combined dataset

No.	Trial	Treatment (if applicable)	Research Station[z]	n	Days on feed
1	The effect of the inclusion of crop residues as a winter feed source in haylage-based rations on the performance of pregnant beef cows	Control – full haylage	EBRC	23	82
2	The effect of the inclusion of crop residues as a winter feed source in haylage-based rations on the performance of pregnant beef cows	Wheat straw	EBRC	21	82
3	The effects of restrictive feeding over the winter on the performance of prepartum crossbred beef cows	Control – full haylage replicate 1	NLARS	12	105
4	The effects of restrictive feeding over the winter on the performance of prepartum crossbred beef cows	Control – full haylage replicate 2	NLARS	12	105
5	Relationships between RFI and body parameters and circulating metabolites	–	NLARS	54	112
6	Relationships between RFI and body parameters and circulating metabolites	–	EBRC	63	105
7	The effect of moderate dietary restriction on visceral organ weight, hepatic oxygen consumption, and metabolic proteins associated with energy balance in mature pregnant beef cows.	High-intake group	EBRC	23	105
8	Relationships between RFI and circulating metabolites	–	EBRC	64	98
9	Relationships between RFI and circulating metabolites	–	NLARS	52	112

[z]EBRC, Elora Beef Research Station; NLARS, New Liskeard Agriculture Research Station.

for ad libitum intake. Group 2 was fed a TMR consisting of haylage and 40% wheat straw [dry matter (DM) basis].

Cows from the second experiment included those assigned to the control treatment (2 yearly replicates) and were fed grass and alfalfa haylage for ad libitum intake for 105 d leading up to parturition. The cows on the restricted-intake treatments were not used in the current data set.

The third and fourth experiments were conducted to investigate relationships between circulating metabolites (for groups 5, 6, 7 and 9) and cow body parameter measurements (linear measures of hip height and width, length, and body circumference at three points; groups 5 and 6 only) with RFI and other measures of performance and efficiency. Cows were randomly assigned to pen and fed a TMR containing 79.5% grass haylage, 30% wheat straw, and 0.5% commercially available beef cow trace mineral supplement (DM basis) for ad libitum intake. Experiments utilizing groups 5 and 9 were conducted at NLARS and groups 6 and 8 conducted at EBRC.

The fifth experiment investigated the effects of moderate feed restriction on visceral organ mass and protein expression within tissues associated with energy balance in pregnant beef cows (Wood et al. 2013). The data included in this analysis as group 7, came from cows from the non-restricted fed group that were not selected for slaughter. Cows were fed a TMR containing 79.5% haylage and 20% wheat straw, and 0.5% commercially available beef cow trace mineral supplement (DM basis) for 105 d leading up to parturition.

Diets and Feed Sample Analysis

Weekly TMR samples were collected from each experiment and frozen at $-20°C$ for future analysis. Samples were later dried at 55°C for 96 h to determine DM concentration and then ground to pass through a 1-mm screen. All feed analysis was carried out at Agri-Food Laboratories Inc. (Guelph, ON). Dry matter analysis was done in accordance with the Association of Official Analytical Chemists guidelines (1990, Method 930.15.). Acid detergent fibre (ADF) and neutral detergent fibre (NDF) were determined using the methods of Robertson and Van Soest (1981) using an Ankom fibre analyzer (Ankom Technology Corp., Fairport, NY). Percent crude protein (CP) was determined by multiplying 6.25 by percent dietary nitrogen as determined by the Leco Nitrogen analyzer (Leco Corporation, St. Joseph, MI). Dietary analysis for each group is reported in Table 2.

Serum Collection and Analysis

To investigate relationships between common circulating serum metabolites and measures of feed efficiency and performance in cows, serum samples were obtained from cows from groups 5, 6, 8, and 9. Blood samples were obtained prior to feeding at approximately 0900 via jugular veinipuncture into non-heparinized tubes and allowed to stand at room temperature for at least 30 min to allow for clotting before being stored on ice. Samples were centrifuged for 25 min at $3000 \times g$ and serum separated and frozen at $-20°C$ until further analysis. Serum samples were analyzed at the University of Guelph Animal Health Laboratory (Guelph, ON) for serum urea, glucose, non-esterified fatty acid (NEFA), beta-hydroxybutyrate (BHBA) and total cholesterol using Roche cobas c311 and Immulite 1000 analyzers (Hoffmann- La Roche Ltd., Mississauga, ON).

Table 2. Dietary analysis of rations fed to each treatment group

	Treatment group								
Analysis[z]	1	2	3	4	5	6	7	8	9
DM (%)	36.7	47.6	41.8	34.4	45.7	45.4	36.8	45.4	44.7
CP (% DM)	18.3	11.7	15.4	14.9	9.7	12.1	12.2	10.3	9.6
NDF (% DM)	49.5	64.5	47.9	50.8	61.1	53.2	58.2	62.0	59.6
ADF (% DM)	42.2	50.6	39.6	42.9	41.1	39.0	39.4	44.2	40.8
NEm[y] (Mcal kg^{-1})	1.5	1.4	1.4	1.3	1.4	1.4	1.5	1.1	1.3

[z]Average of weekly samples. DM, dry matter; CP, crude protein; NDF, neutral detergent fibre; ADF, acid detergent fibre.
[y]Net energy for maintenance. Calculated according to Weiss et al. (1992) and National Research Council (1996).

Body Parameter Measures

To investigate relationships between measures of feed efficiency and objective measures of cow body phenotype, cows from groups 5 and 6 were measured at the start and end of the feeding period and the average measurement used. Measures included: body length (from the point of shoulder to end of the rump), hip height (from ground to base of tail head), hip width (parallel to ground across pin bones), heart girth (circumference around the midsection caudal to shoulder), mid-girth (circumference around middle over navel), and girth at flank (circumference around the middle at the flank and cranial to the udder). Body length was measured using a metal tape measure and girth measures were obtained using a fabric measuring tape. Hip height was measured using a livestock height measuring stick and hip width measures obtained using calipers. All measurements were taken by the same individual at each research station.

Determination of Traits, Residual Feed Intake, and Statistical Analysis

Average daily gain and mid-point body weight (BW) for the test period were calculated from monthly BW measurements using regression over time using Proc GLM in SAS software (SAS Institute, Inc. 2008). Average R^2 for these models was $>95\%$. Metabolic mid-point BW was calculated as mid-point $BW^{0.75}$ (Kleiber 1961). In order to attempt to remove the effects of conceptus growth, pregnancy-corrected mid-point body weight (pCBW) and pregnancy-corrected ADG (pcADG) were calculated by subtracting calculated conceptus weight from actual BW at each corresponding stage of gestation and then applying regression as above. Conceptus weight was calculated using the equations outlined by Silvey and Haydock (1978) to estimate conceptus weight based on measured calf birth weight and day of gestation back-calculated from actual date of parturition.

Residual feed intake was calculated for each cow by subtracting actual dry matter intake (DMI) from predicted DMI as previously described (Koch et al. 1963). Model parameters for predicted DMI were determined by linear regression using PROC GLM in SAS software (SAS Institute, Inc. 2008), the R^2, coefficient of variation and RMSE were recorded for each model. The basic model for RFI contained only mid-point BW and ADG (Koch et al. 1963). Other models tested included: metabolic BW, ultrasound measures of fatness, cow age/parity, and pregnancy corrections. In addition, models examined over the whole dataset included effect of research station, and treatment/replicate group. To express the effects of treatment group as a continuous function, dietary parameters were included as covariates in the model The Bayesian information criterian (BIC) was determined for each DMI model using PROC MIXED in SAS software (SAS Institute, Inc. 2008) to assess the fit of the RFI model.

Pearson correlations were conducted to investigate the relationships between measures of feed efficiency and performance within applicable treatment groups. Models of RFI used for correlations were calculated as previously described above, and included basic RFI (mpBW and ADG) calculated within each treatment/replicate group and group RFI (mpBW, ADG and treatment group as covariates). Correlations included mid-point BW, DMI, ADG, pcADG, F:G, G:F, basic RFI, and group RFI. Benjamini and Hochberg (1995) adjustment for false discovery rate was applied using PROC MULTTEST (SAS Institute, Inc. 2008). Traits found significantly correlated to basic RFI or group RFI were added as covariates to predicted DMI equations.

RESULTS AND DISCUSSION

Descriptive statistics for traits in the whole combined dataset can be found in Table 3. Table 4 reports the goodness of fit (R^2, CV, RMSE) for regression models used to predict DMI for RFI calculations. The basic model for RFI (Koch et al. 1963), including only BW and ADG, had a much lower R^2 than observed by other reports in growing animals (48 and 60%, Koch et al. 1963; 70%, Arthur et al. 2003; 71 and 72%, Basarab et al. 2003; 68%, Schenkel et al. 2004; 58%, Montanholi et al. 2009; 77%, Kelly et al. 2010; 72–82%, Kelly et al. 2011). Lawrence et al. (2011, 2013) reported that in second parity pregnant Simmental heifers second parity cows, the RFI model (containing $BW^{0.75}$, ADG) accounted for 24–29% of the variation observed in DMI, which is

Table 3. Mean, standard deviation and number of data points for mature beef cows used in assessing measures of RFI

Item[z]	*n*	Mean	SD	Min	Max
Age (yr)	321	5.24	2.5	2	15
Day of gestation at trial start (d)	321	151	18.3	98	193
Initial BW (kg)	321	703	92.8	508	964
Final BW (kg)	321	793	92.9	603	1075
Mid-point BW (kg)	321	708	92.5	507	979
DMI (kg d^{-1})	321	12.97	2.05	6.39	22.45
ADG (kg d^{-1})	321	0.86	0.315	−0.13	1.68
pcADG (kg d^{-1})	321	0.44	0.33	−0.69	1.38
G:F (kg kg^{-1})	321	0.067	0.024	−0.009	0.148

[z]BW, body weight; DMI, dry matter intake; ADG, average daily gain; pcADG, pregnancy corrected ADG (Silvey and Haydock 1978); G:F, gain to feed ratio.

similar to the variation observed in the present experiment. Meyer et al. (2008) measured RFI in growing heifers fed a high-forage diet and found a larger range in RFI than previously reported in the literature. They suggested that increased variability is introduced when measuring RFI with high-forage diets, due to feed sorting, spillage and wasting feed, which is less prevalent in pelleted or high-grain rations. Since all animals were fed forage diets, feed wastage and spillage may contribute to variability observed in the models (Table 4).

A large variation amongst the cows themselves may also be contributing to lower R^2 observed in the present study. It is suggested that controlling as many factors as possible is important in measuring RFI (Arthur and Herd 2008). Variation in age, type, size, etc. among groups of cows may be considerably greater than among groups of growing steers, bulls or heifers. Basarab et al. (2007) also measured RFI in mid-gestation beef cows fed forage and also observed much larger CV and SD in cows vs. RFI measures in their growing progeny. It may be more difficult to control for variation in cow type, when measuring RFI in mature cows.

There was no improvement in R^2 for the feed intake prediction model when metabolic BW was used versus actual mid-point BW (Table 4). Montanholi et al. (2009) also did not find any improvements of using metabolic BW over actual midpoint BW. One of the critiques of the Kleiber (1961) ratio ($BW^{0.75}$) for metabolic BW is that although it may be accurate across species, it may not accurately reflect metabolic differences within each species that are minimally different in BW (Schmidt-Nielson 1970). Relatively small differences in BW may not accurately reflect true variation in maintenance between cows.

As BW gain in the pregnant cow is confounded with growth of the conceptus, pregnancy-corrected BW was calculated and then used to calculate pcADG. However, pregnancy-corrected BW or pcADG did not improve the overall fit (increased R^2, or major reduction of BIC) of the model (Table 4). This may in part be due to the fact that the model described by Silvey and Haydock (1978) is an estimate of conceptus growth and would have error associated with such a model, and may add variability rather than reduce variability in predicted DMI model used to calculate RFI. Accurately assessing conceptus growth in the live animal may yield greater improvements in RFI.

Table 4. Model fit statistics for residual feed intake (DMI models) with differing covariates over the entire dataset of mature pregnant beef cows

	Across all treatment/replicate groups				
Model covariates[z]	*N*	R^2	CV	R MSE	BIC
mpBW ADG	321	0.236	13.85	1.796	1304.6
BW_75 ADG	321	0.236	13.86	1.795	1300.6
pcBW ADG	321	0.237	13.84	1.794	1304.1
mpBW pcADG	321	0.222	13.99	1.813	1310.7
BW_75 pcADG	321	0.222	13.98	1.812	1306.6
mpBW fBF ADG	321	0.240	13.81	1.791	1307.9
mpBW cBF ADG	321	0.242	13.81	1.791	1309.7
mpBW iBF cBF ADG	321	0.265	13.63	1.768	1302.7
mpBW fRF ADG	277[y]	0.207	13.48	1.769	1125.0
mpBW cRF ADG	277[y]	0.269	12.95	1.700	1101.7
mpBW iRF cRF ADG	277[y]	0.278	12.89	1.691	1103.6
mpBW iRF cRF iBF cBF ADG	277[y]	0.309	12.65	1.660	1101.1
mpBW AGE ADG	321	0.254	13.71	1.777	1301.3
mpBW Station ADG	321	0.467	11.58	1.502	1191.7
mpBW Station iRF cRF iBF cBF ADG	277	0.471	11.10	1.456	1030.6
mpBW TRMT ADG	321	0.538	10.91	1.414	1148.5

[z]mpBW, mid-point BW; BW_75, mid-point $BW^{0.75}$; pcBW, pregnancy corrected BW (Silvey and Haydock 1978); pcADG, pregnancy corrected ADG; fBF, final d of trial ultrasound backfat, cBF, change in ultrasound backfat; iBF, initial ultrasound backfat; fRF, final ultrasound rump fat; cRF, change in ultrasound rump fat; iRF, initial ultrasound rump fat; age, cow age in years; station, research station (class variable); TRMT, treatment/replicate group.
[y]Ribfat measurements were not obtained on cows from groups 1 and 2.

Ultrasound measures of backfat and rump fat, as well as change in rump fat or rib fat over the feeding period, had variable impact on predicted DMI model fit (Table 4). The model for DMI, which contained both initial backfat and rump fat as well as change in backfat and rump fat, increased the R^2 by 7.3% over the basic model for predicted DMI, while BIC decreased. Black et al. (2013) reported that RFI models containing the covariates ADG, energy-corrected milk production and change in BF accounted for the greatest amount of variation in DMI models for mature lactating beef cows. Others have shown that the addition of measures of fatness have shown modest improvement in model fit [> 5% improvement (Richardson et al. 2001), and 3.9%; (Basarab et al. 2003)]. Mader et al. (2009) also reported positive correlations between RFI and backfat measures, in addition to internal fat (kidney fat weight proportion). Perhaps the addition of internal fatness measures will increase accuracy of RFI measures in pregnant cows. There were minimal differences between measures of backfat or ultrasound measures of rump fat when included separately.

When research station was added to the model as a class variable, R^2 of the predicted DMI model increased 23.1 percentage units over the basic predicted DMI model and BIC decreased (Table 4). This indicates that controlling for environment and management plays an import role in accurately determining RFI. However, when the basic model for DMI was investigated within each research station, the R^2 was very similar. This may indicate that although management and environmental differences exist between research stations, experimental design, diets, etc., overall variation within each research premises is consistent. When treatment/replicate group was included as a class variable, which accounts for both research station differences as well as dietary treatment or replicate (if applicable), the greatest R^2 of the models was achieved. The R^2 for this model was increased by 30.2 percentage units over the basic model and the BIC was reduced. When ultrasound measures of fat were added to the model containing only research station, the R^2 did not greatly improve, although BIC decreased.

When dietary composition factors were included as continuous variables in the model (CP, NDF, and NEm together) for predicted DMI, R^2 was increased 25.4 percentage units over the basic model (data not shown). This suggests that the nutritional aspects of management group may play a significant role in modeling RFI in mature pregnant beef cows. Individually, CP, NDF, or net energy for maintenance did not greatly improve R^2 (24 to 29 percentage units; data not shown) when added to the basic model of RFI. Herd et al. (2004) suggested that differences in digestion account for 14% of variation in RFI and heat increment of feeding accounts for 9% of variation between animals in RFI. In addition, poorer fitting RFI models were observed with animals fed lower-quality diets (those containing $\geq$30% DM of wheat straw). This may be due to greater ADF and dietary bulk, which may limit ad libitum intake due to increased gut fill. Additionally, cows that were fed high-quality rations (lower ADF) (groups 1, 3, 4, and 7) had higher base RFI R^2 (55.5 vs. 23.0 percentage units on average; data not shown). As in this study, Meyer et al. (2009) also observed greater variation in feed intake when measuring RFI on heifers fed a forage diet. However, Retallick and Faulkner (2012) found that there was a strong correlation between RFI rank when heifers were fed a forage-based diet and when they were fed a grain-based diet, which suggests that overall major underlying mechanisms (e.g., metabolic factors) influencing feed efficiency may be partially independent of diet type. Perhaps feed value and digestion kinetics may play a more important role in differences between cow RFI, when cows are fed a high-forage diet.

Relationships between Measures of Feed Efficiency and Circulating Serum Metabolites

Descriptive statistics and relationships between circulating metabolites on the final day of the feeding period and cow age, performance measures and measures of feed efficiency are found in Tables 5 and 6, respectively. Circulating urea concentration was positively correlated ($P \leq 0.05$) with DMI, ADG, pcADG, G:F and the group RFI model. Furthermore when urea was added as a covariate to the basic RFI model, an increase in model R^2 was observed (Table 7). This suggests that protein metabolism may play a role in regulating feed efficiency in the pregnant beef cow. Circulating urea has been used as an indicator of protein status in the animal, and largely represents the degradation of protein sources, either endogenous (muscle catabolism) or exogenous (from feed) (Sniffen et al. 1992). Kelly et al. (2010, 2011) also found positive correlations between serum urea and DMI in growing heifers and bulls and feed conversion ratio in growing heifers, but not with RFI. However, Richardson et al. (2004) found that while RFI was positively correlated with circulating urea

Table 5. Descriptive statistics for circulating serum metabolites and linear body measures for combined dataset of mature pregnant beef cows

Item[z]	n	Mean	SD
Glucose (mmol L^{-1})	227	3.39	0.385
Urea (mmol L^{-1})	227	3.28	0.63
NEFA (mmol L^{-1})	227	0.66	0.456
BHBA (μmol L^{-1})	227	306	128.1
Total cholesterol (mmol L^{-1})	227	2.71	0.432
Hip height (cm)	114	143.9	57.13
Hip width (cm)	114	58.4	25.97
Body length (cm)	114	156.1	8.15
Heart girth (cm)	114	212.6	11.17
Mid-girth (cm)	114	258.9	13.68
Girth at flank (cm)	114	229.6	12.82

[z]NEFA = non-esterified fatty acid; BHBA = β-hydroxybutyrate.

Table 6. Corrected Pearson partial correlations between performance and feed efficiency measures and circulating serum metabolites measured at the end of test in mature pregnant beef cows[z]

Item	Glucose	Urea	NEFA[y]	BHBA[y]	Total cholesterol
Age	0.13	−0.10	0.02	0.004	**−0.35**
Mid-point BW	**0.30**	**−0.20**	0.11	−0.009	**−0.26**
DMI	0.04	**0.40**	**−0.30**	**−0.23**	**−0.15**
ADG	0.02	**0.36**	**−0.21**	**−0.19**	0.05
pcADG[x]	0.04	**0.34**	**−0.24**	**−0.23**	0.07
G to F[w]	0.002	**0.22**	−0.10	−0.09	0.13
Basic RFI[v]	0.03	−0.02	0.13	−0.02	−0.12
Group RFI[u]	−0.05	**0.29**	**−0.17**	−0.06	−0.06

[z]Treatments groups 5, 6, 8, and 9. Values in bold font indicate significance ($P \leq 0.05$).
[y]NEFA = non-esterified fatty acid; BHBA = β-hydroxybutyrate.
[x]pcADG, pregnancy corrected average daily gain calculated using estimates for conceptus growth from the equation described by Silvey and Haydock (1978).
[w]Gain to feed.
[v]Within each contemporary group calculated residual feed intake using the regression of average daily gain and midpoint body weight (Koch et al. 1963).
[u]Residual feed intak calculated over whole dataset, with treatment/replicate group included as a covariate. See last equation in Table 4.

in young animals (post-weaning), this relationship disappeared as the animal matured. Research from the same research group found that efficient (low RFI) steers were leaner both entering and exiting the feedlot (Richardson et al. 1998, 2001) indicating that greater body protein accretion is a desirable efficient phenotype. Lawrence et al. (2013) did not find any significant correlation with circulating urea in pregnant cows (2013), or heifers, but did find significant negative correlation with creatine (2011), indicating that muscle/protein degradation may be an important metabolic process in feed efficiency. Pigs divergently selected for RFI have reduced activity of pathways regulating protein turnover rate (calpain activity and 20S proteasome activity) in muscle (Cruzen et al. 2012). Protein synthesis and degradation are known to be energy demanding processes (Gill et al. 1989; Kelly et al. 1991). Further research into understanding protein metabolism in the mature cow may be beneficial to understanding feed efficiency.

Circulating NEFA concentrations were negatively correlated ($P \leq 0.01$) with DMI, ADG, pcADG and group RFI, while BHBA was negatively correlated ($P \leq 0.01$) with DMI, ADG and pcADG. In growing heifers, Kelly et al. (2010) reported negative correlations between NEFA and DMI, feed conversion and their base model of RFI, while BHBA showed positive relationships between DMI, feed conversion ratio and basic and complex models of RFI. In addition, Lawrence et al. (2011) reported a tendency ($P = 0.07$) for a correlation between NEFA and RFI classification in pregnant beef heifers, but no significant relationship between NEFA or BHBA in cows (Lawrence et al. 2013). In bulls, no relationships were found between BHBA and NEFA with DMI, ADG, F:G or RFI (Kelly et al. 2011). Since circulating NEFA and BHBA concentration represent catabolism of body fat and ketone production, respectively (Wathes et al. 2007), the ability of the pregnant cows to mobilize fat may play an important role in feed efficiency in mature pregnant beef cows.

Serum glucose was not correlated ($P \geq 0.05$) with age, DMI, ADG or pcADG or measures of feed efficiency. Similar to our results, Kelly et al. (2010) also found no relationships between feed efficiency measures and glucose concentration. Glucose was positively correlated with mpBW. Total circulating cholesterol concentrations were negatively correlated ($P \leq 0.04$) with cow age, mpBW and DMI. Conversely, a positive relationship ($P = 0.02$) between total cholesterol concentration and R^2 RFI model was observed.

When final urea and/or NEFA concentrations were added as covariates to the model for predicted DMI,

Table 7. Model fit statistics for RFI (DMI models) with differing covariates over the entire dataset of mature pregnant beef cows using serum urea and non-esterified fatty acid measures as covariables

	Across all treatment/replicate groups				
Model covariates[z]	N	R^2	CV	R MSE	BIC[x]
mpBW TRMT ADG	321	0.538	10.91	1.414	1148.5
mpBW TRMT UREA ADG	227[y]	0.462	10.83	1.423	818.4
mpBW TRMT NEFA ADG	227[y]	0.435	11.10	1.458	828.4
mpBW TRMT UREA NEFA ADG	227[y]	0.464	10.84	1.424	818.6
mpBW ADG	321	0.236	13.85	1.796	1304.6
mpBW UREA ADG	227[y]	0.356	11.78	1.547	856.2
mpBW NEFA ADG	227[y]	0.322	12.08	1.587	867.1
mpBW UREA NEFA ADG	227[y]	0.400	11.489	1.509	845.2

[z]mpBW, midpoint body weight; TRMT, treatment andéor replicate group; ADG, average daily gain; UREA, final trial d serum urea concentration; NEFA, final trial d serum non-esterified fatty acid concentration.
[y]Serum metabolites were obtained from groups 5, 6, 8, and 9.
[x]Bayesian information criteria.

more variation in DMI was accounted for over the basic (mpBW + ADG) model (Table 7). The addition of circulating urea concentration made the single most reduction in DMI variation over the traits investigated (with the exception of research station/ treatment group) over the basic model containing only mpBW and ADG. However, no additional improvement was observed when treatment/replicate group was also included in the model for DMI. In summary, the serum metabolite data suggest that metabolic pathways involved with protein metabolism and lipid metabolism may play roles in regulating feed efficiency in pregnant beef cows. Future research is needed to identify key regulatory steps in these metabolic pathways, which may be used to improve efficiency in pregnant beef cows.

Relationships between Measures of Feed Efficiency and Body Parameter Measures

Linear measurements of body dimensions may provide insight into changes in maintenance energy requirements and surface area and gut capacity (Kleiber 1961). Descriptive statistics of linear body measures can be found in Table 5 and correlations between linear body parameter measurements and measures of performance and feed efficiency in Table 8. Hip height was not ($P \geq 0.05$) correlated with any measure of age, performance or efficiency measurement. This may indicate that frame size does not play a role in measures of efficiency in the mature pregnant cow. In growing animals, Basarab et al. (2003) and Kelly et al. (2010) found no correlations between hip height or wither height, respectively, and RFI. Hip width was positively correlated ($P \leq 0.05$) with DMI and mid-point BW. Hip width may reflect differences between animals in muscularity in addition to pelvic area.

Body length was positively correlated ($P < 0.001$) with mid-point BW and DMI and also was positively correlated ($P = 0.003$) with cow age. Body length was negatively correlated ($P \leq 0.03$) with basic RFI. This differs from results in growing heifers, where no relationships between ADG or RFI and body length were observed (Kelly et al. 2010); however, relationships to DMI were similar to what was observed in the present experiment.

Measures of the animal's girth, particularly the heart girth have been shown to have strong correlations with BW (Heinrichs et al. 1992). As expected, all three girth measures were strongly positively correlated ($P < 0.001$) with mid-point BW.

Feed intake was positively correlated ($P < 0.001$) with heart and mid-girth measurements but not the flank measurement of girth circumference ($P = 0.15$). Since this measurement is taken caudal to the stomach complex, it may not be as greatly influenced by gut fill, where heart and mid-girth measurements may reflect increased rumen fill with increased DMI.

Measures of ADG and pcADG were not correlated ($P \geq 0.05$) with hip height or width, body length or heart or mid-girth circumference. Girth at the flank was negatively correlated ($P \leq 0.05$) with ADG and pcADG. All three girth measures were negatively correlated ($P \leq 0.05$) with G:F. This may be in part driven by intake in the case of heart and mid-girth and ADG in flank girth. Basic RFI was positively correlated ($P = 0.03$) with girth at flank. With the exception of body length and girth at flank, there were no correlations with the RFI models investigated. When body length or circumference around the body at the flank were included in the model, a moderate reduction in model variation was observed ($R^2 = 31$ and 27%, respectively; data not shown) and did not improve variation beyond the inclusion of treatment group as a covariate. Similar to the results of the present study, Kelly et al. (2010) did not find any correlations with linear measures of body characteristics and models of RFI in growing heifers.

The results of the current study indicate that the use of RFI models to determine feed efficiency have variable results when used in mature pregnant beef cows. In the most fundamental form, Koch's model of RFI measures "outputs", while holding "inputs" constant.

Table 8. Corrected Pearson partial correlations between performance measures and linear body parameter measures in mature pregnant beef cows[z]

	Hip height	Hip width	Body length	Heart girth	Mid-girth	Girth at flank
Age	0.03	0.05	**0.30**	**0.45**	**0.37**	**0.56**
Mid-point BW	0.11	**0.23**	**0.62**	**0.85**	**0.82**	**0.89**
DMI	0.13	**0.21**	**0.43**	**0.39**	**0.46**	0.16
ADG	−0.04	0.06	0.09	−0.15	−0.006	**−0.35**
pcADG[y]	−0.05	0.07	0.06	−0.19	−0.04	**−0.36**
G to F[x]	−0.08	−0.02	−0.09	**−0.33**	**−0.20**	**−0.44**
basic RFI[w]	0.04	−0.17	**−0.29**	−0.03	0.09	**0.22**
Group RFI[v]	0.04	0.007	−0.01	−0.10	0.03	−0.16

[z]Treatments groups 5 and 6. Values in bold font indicate significance ($P \leq 0.05$).
[y]Pregnancy corrected average daily gain calculated using estimates for conceptus growth from the equation described by Silvey and Haydock (1978).
[x]Gain to feed.
[w]Within each contemporary group calculated residual feed intake using the regression of average daily gain and midpoint body weight (Koch et al. 1963).
[v]Residual feed intake calculated over whole dataset, with treatment/replicate group included as a covariate. See last equation in Table 4.

In the mature, non-lactating beef cow, measuring inputs may pose a greater challenge as cows are primarily fed forage or are on pasture and intake may not be able to be as precisely measured as with pelleted or high-grain rations (Meyer et al. 2008). Similarly, measuring outputs in beef cows may pose similar challenges. In growing animals, output is often characterized as growth or body weight gain. As cows have reached their mature size, they have nominal body growth, and weight changes more likely reflect changes in body composition, differences in gut fill, and growth of the conceptus. As it is more difficult to measure these parameters accurately in the live animal, fitting RFI models poses greater challenges. In general, measures of body fat did moderately improve model fit. Low nutrition and resulting minimal body weight gain (or loss) may result in lower model predictability.

Herd et al. (2004) suggested that approximately two-thirds of variation between animals that are efficient and those that are inefficient relate to basal metabolic rate, cellular maintenance requirements, and related energy lost as heat. As maintenance energy costs represent approximately 70 to 75% of the total annual energy requirements for the mature beef cow (Ferrell and Jenkins 1985), understanding animal differences in maintenance requirements is of particular importance. Although heat production was not measured in any of these experiments, it has been shown to improve accuracy in RFI models (Montanholi et al. 2009; Colyn et al. 2010) and may prove beneficial to measures of RFI in mature, pregnant cows.

Further investigations into correlations between feed efficiency measures and metabolic measurements are warranted. Correlations between circulating metabolites and feed efficiency traits suggest that protein metabolism may play a role in maintenance energy metabolism, as circulating urea was correlated with G to F and RFI models examined. Measures of girth at the flank may be of interest as a potential linear body measure as they was correlated with BW and feed conversion ratio, but not related to DMI. However, remaining body parameter measures were not correlated with RFI models tested and likely do not contribute to animal variation in RFI measures of feed efficiency in mature pregnant cows.

Measuring feed efficiency in mature, pregnant beef cows is complex. A large proportion of variation between animals in RFI measures of feed efficiency remains unknown and may not be an appropriate measure of efficiency in the gestating beef cow. Models including circulating urea concentration may be beneficial in the reduction of variation in models for prediction of DMI in mature cows. Further investigation into other factors and potential molecular mechanisms influencing maintenance energy and protein costs and expenditures is warranted.

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