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Assessing feed efficiency in beef steers through feeding behavior, infrared thermography and glucocorticoids*

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A better understanding of the factors regulating feed efficiency and their potential as predictors of feed efficiency in cattle is needed. Therefore, the potential of three classes of traits, namely, feeding behavior characteristics: daily time at feeder (TF; min/day), time per meal (TM; min), meal size (MS; g DM), eating rate (ER; g DM/min), number of daily meals (NM) and daily visits to the feeder (VF); infrared (IR) thermography traits (°C): eye (EY), cheek (CK), snout (SN), ribs (RB) and hind area (HA); and glucocorticoid levels: fecal cortisol metabolites (FCM; ng/g) and plasma cortisol (PC; ng/ml) as predictors of efficiency were evaluated in 91 steers (436 ± 37 kg) over 2 years (Y1 = 46; Y2 = 45). Additionally, the individual traits of each of these three classes were combined to define three single traits. Individual daily feed intake of a corn silage and high-moisture corn-based diet was measured using an automated feeding system. Body weight and thermographs were taken every 28 days over a period of 140 days. Four productive performance traits were calculated: daily dry matter intake (DMI), average daily gain (ADG), feed to gain ratio (F : G) and residual feed intake (RFI). Steers were also classified into three RFI categories (low-, medium- and high-RFI). Among the feeding behavior characteristics, MS and ER were correlated with all efficiency traits (range: 0.26 to 0.75). Low-RFI (more efficient steers) had smaller MS, lower ER and fewer VF in comparison to high-RFI steers. Less efficient steers (high-RFI) performed more VF during the nocturnal period than more efficient steers. More efficient steers had lower CK and SN temperatures than less efficient steers (28.1°C v. *29.2°C and 30.0°C* v. *31.2°C), indicating greater energetic efficiency for low-RFI steers. In terms of glucocorticoids, PC was not correlated with efficiency traits. In contrast, more efficient steers had higher FCM in comparison to less efficient steers (51.1* v. *31.2 ng/g), indicating that a higher cortisol baseline is related to better feed efficiency. The overall evaluation of the three classes of traits revealed that feeding behavior, IR thermography and glucocorticoids accounted for 18%, 59% and 7% of the total variation associated with RFI, respectively. These classes of traits have usefulness in the indirect assessment of feed efficiency in cattle. Among them, IR thermography was the most promising alternative to screen cattle for this feed efficiency. These findings might have application in selection programs and in the better understanding of the biological basis associated with productive performance.*

Keywords: beef cattle, cortisol, fecal cortisol metabolites, residual feed intake, skin temperature

Implications

Predictors for feed efficiency such as feeding behavior patterns, thermographs of the animals' body surface and levels of glucocorticoids can have economical and environmental benefits for the beef cattle industry. The possibility of selecting cattle using these predictors could alleviate the need of obtaining the expensive individual feed intake records, also making the selection for feed efficiency more accessible in the beef industry. Moreover, efficient cattle have a lower environmental footprint. An efficient steer can consume over 400 kg less during the feedlot phase, resulting in less pollution in comparison to a less efficient steer for the same productive performance.

Introduction

An alternative to improve the profitability and the environmental sustainability of the beef industry is through the

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improvement of feed efficiency. There are several productive performance traits described for livestock species, which include conventional measures such as daily dry matter intake (DMI), average daily gain (ADG) and feed to gain ratio (F : G). During the last decade, feed efficiency in beef cattle has been intensely investigated through the concept of residual feed intake (RFI). Residual feed intake was first defined for beef cattle by Koch *et al.* (1963). In contrast to other efficiency traits discussed by Archer *et al.* (1999), RFI is the only trait that is phenotypically independent from production traits (e.g. growth rate). Therefore, RFI likely reflects more variation in basic metabolic processes (Richardson *et al.*, 2001; Nkrumah *et al.*, 2006; Castro Bulle *et al.*, 2007) than variation due to differences in level of production. Several studies applying the concept of RFI (e.g. Herd *et al.*, 2004; Richardson *et al.*, 2004; Kolath *et al.*, 2006) have revealed important metabolic differences between more and less efficient cattle. However, there is a shortage of indicator traits that can be effectively used for nutritional manipulation or genetic selection for feed efficiency.

Variation in feed efficiency can occur as a result of differences in energy expenditure associated with certain behaviors. For instance, more efficient bulls took 6% less steps than less efficient bulls, which accounted for 10% of RFI variation (Richardson *et al.*, 2000). There is also an evidence (Richardson and Herd, 2004; Nkrumah *et al.*, 2006; Golden *et al.*, 2008) that beef cattle with distinct feed efficiencies may have different feeding behaviors. In a study with sheep, Webster (1978) observed that heat production increased by 40% to 80% as the animals begin to eat and this change persisted until the animal stopped eating. Furthermore, Adam *et al.* (1984) reported that feeding behaviors are potential factors to determine the energetic costs of feeding in cattle. Thus, feeding behavior characteristics are potentially associated with the energetic costs of feeding, which influence the animals' productive performance.

Infrared (IR) thermography can be used to measure the body surface temperature patterns of cattle. These measurements have several of applications in the cattle industry. Researchers have been able to detect early infection (Hurnik *et al.*, 1984), meat quality (Tong *et al.*, 1995), fear-related responses (Stewart *et al.*, 2008). In addition, preliminary studies have shown the possibility of using IR thermography for assessing RFI (Schaefer *et al.*, 2005; Montanholi *et al.*, 2007), which were followed by a more comprehensive study on the assessment of productive performance traits with this same technology (Montanholi *et al.*, 2009). This later application is rooted in the fact that more efficient animals have a lower basal energy requirement (Richardson *et al.*, 2001; Nkrumah *et al.*, 2006; Castro Bulle *et al.*, 2007) and, therefore, a lower amount of heat to be dissipated through the body surface (Kleiber, 1961). Moreover, Montanholi *et al.* (2008) demonstrated that IR thermography can be applied in the prediction of heat production in cattle.

Glucocorticoids play a key role in energy metabolism, influencing the animals' performance (Sapolsky, 2002). Cortisol is released in the blood stream as a response to the activation of the hypothalamic-pituitary-adrenocortical axis (Moberg, 2000), which exhibits a circadian rhythm (Thun and Eggenberger, 1996) and is also increased under stressful situations (Möstl and Palme, 2002). Cortisol and its metabolites can be assessed in several matrices. Blood plasma cortisol (PC) and fecal cortisol metabolites (FCM) were chosen to represent a relatively stressful sampling and a minimum stress sampling procedure, respectively (Möstl and Palme, 2002). In addition, PC represents the immediate response of the adrenal gland and FCM reflect the long-term response (baseline), representing the cortisol that was released into the blood stream about 12 h before sampling (Palme *et al.*, 1999 and 2005).

The objectives of this study were to: 1. evaluate the relationships between productive performance traits and feeding behavior, IR thermography traits and glucorticoid levels; 2. assess the contribution of each of these three classes of traits to the total variation observed for RFI.

Material and methods

Animals and management

The experiment followed recommendations as outlined by the Canadian Council of Animal Care guidelines (1993) and was approved by the University of Guelph animal care committee. Animals and management have been described previously (Mader *et al.*, 2009). Briefly, 91 (46 in year 1; 45 in year 2) steers (average initial weight = 313 ± 6.2 kg) from Angus and Simmental crossbred cows sired by maternal (Angus, Simmental or Angus and Simmental crossbred), Charolais, or Piedmontese bulls were used. Steers originated from the University of Guelph Elora Beef Research Center, New Liskeard Agriculture Research Station and also from commercial herds. Steers were housed in indoor pens bedded with wood shavings with breed groups evenly distributed among pens of 12 to 15 animals. Pens were equipped with four automated feeding stations each (Insentec, BV, Marknesse, The Netherlands). The feeding stations were similar to those described by Tolkamp and Kyriazakis (1997) and Chapinal *et al.* (2007). Radio frequency identification tags were placed in the right ear of each steer prior to the start of the experiment. The automated feeding system recorded the time and weight of the feeder at the beginning and at the end of each feeding event for each steer 24 h a day. These measures were used to define the feeding behavior characteristics and to obtain DMI.

Steers had a period of approximately 2 weeks to adjust to the facilities and feeding system. They were offered a corn-silage based diet (CP: 13.3% and 16.0%, NDF: 44.4% and 34.9% for years 1 and 2, respectively) *ad libitum* during the adaptation phase and through the first 56 days of the experiment (growing period). After the 56-day grower period, steers were adapted to a high moisture corn-based diet (CP: 13.8% and 14.7%, NDF: 23.6% and 17.9% for years 1 and 2, respectively) over 28 day and fed for a further 56 day (finishing period). Feeders were filled twice a day during the first 84 days and once a day during the finishing phase. The ingredients of the diets are presented

Table 1 *Ingredients of growing and finishing diets*

	% of DM
Ingredients (growing)	
Corn silage	86.1
Soybean meal	12.0
Premix A[a]	1.9
Ingredients (finishing)	
High moisture corn	80.0
Haylage	10.0
Soybean meal	4.7
Corn gluten meal	1.8
Premix B[b]	3.5

DM = dry matter.

[a] Contains 50% of limestone, and 50% of a mineral and vitamin premix (7% Ca, 7% P, 2.5% Na, 2% Mg, 0.5% K, 0.6% S, 25 mg/kg Co, 55 mg/kg I, 1,350 mg/kg Cu, 1,300 mg/kg Fe, 2,600 mg/kg Mn, 3,850 mg/kg, 600,000 IU/kg vitamin A, 200,000 IU/kg vitamin D and 1,000 IU/kg vitamin E).

[b] Contains 62.0% soybean meal, 27.1% limestone, 5.4% salt, 0.4% monensin, 1.4% trace minerals (153,013 mg/kg Zn, 122,445 mg/kg Mn, 30,598 mg/kg Cu, 27,100 mg/kg Fe, 368 mg/kg Co, 1,531 mg/kg I), 3.7% vitamin premix (4,400,000 IU/kg vitamin A, 1,100,000 IU/kg vitamin D and 7,700 IU/kg vitamin E).

in Table 1. Steers were weighed on two consecutive days at the beginning and at the end of the 140-day experiment, and every 28 days during the experimental period. IR images were taken every 28-day concomitantly to the body weight (BW) assessment. Blood and fecal samples were collected only in the second year on days 84 and 140 of the experimental period. Blood samples were harvested by jugular venipuncture using a 10 ml blood collection tube (Vacuntainer®; BD Inc., Franklin Lakes, NJ, USA) containing sodium heparin mounted with a 20 ga needle. Blood samples were immediately stored on ice until centrifugation (3,000 × **g** for 20 min) to separate the blood plasma, which was stored at −80°C until further analysis for PC levels. Fecal samples were obtained through rectal palpation and stored at −20°C and processed as described by Palme *et al.* (2000) for further analysis for FCM levels.

Productive performance and feeding behavior traits

The dataset collected by the automated feeding system was first filtered, to exclude outlier records or days where mechanical problems had occurred, as described by Mader *et al.* (2009). The DMI over the testing period was calculated from the remaining records. Residual feed intake was calculated using the general linear model procedure of SAS (Statistical Analysis System, 2003), as described by Koch *et al.* (1963):

$$DMI = \beta_0 + \beta_1(ADG) + \beta_2(BW) + RFI,$$

where β_0 is the regression intercept, β_1 and β_2 are the coefficients of the multiple linear regression of DMI on ADG and on mid-trial BW and the residual of the model represents the RFI. The R^2 observed for this regression was 0.59 and 0.72 for year 1 and 2, respectively. The ADG was determined by a regression of BW on days on trial, with six observations per animal. Mid-trial BW was calculated by computing the animals' intercept plus the ADG times 70 (half of the experimental period). F : G was also determined as a ratio of DMI : ADG.

Six feeding behavior characteristics were defined, including: time spent at feeder per day (TF; min/day), time per meal (TM; min/meal), meal size (MS; kg DM/meal), eating rate (ER; g DM/min), number of meals per day (NM; events/day) and daily visits to the feeder (VF; events/day). These traits represent the average of experimental period per animal. The number of visits to the feeder was computed at 60 min interval throughout the day, and diurnal patterns between RFI phenotypes were examined between night (20:01 to 8:00 h) and day periods (8:01 to 20:00 h). Moreover, meal was considered as distinct eating periods that might include short breaks but which are separated by intervals of no longer than 7 min (Forbes, 1986).

IR thermography

IR thermography was performed using an IR portable camera (ThermaCam™ SC2000; FLIR Systems Inc., Wilsonville, OR, USA; Montanholi *et al.*, 2008) equipped with a built-in lense (24°) and calibrated with an emissivity value of 0.98. IR images were taken of multiple body locations, including eye (EY), cheek (CK), snout (SN), ribs (RB) and hind area (HA) (Figure 1), while the animal was restrained in a squeeze chute. All IR were taken approximately 1.5 m from each of the body locations studied. The IR thermographs were interpreted using the ThermaCam™ Researcher 2001 software (FLIR Systems AB, Danderyd, Sweden). For each of the locations photographed, a specific shape was considered in order to keep a constant sub-area (Figure 1) and the average temperature (°C) of each body location was computed.

Determination of glucorticoids (or their metabolites)

Plasma cortisol (ng/ml) was measured directly using a commercially available radioimmunoassay kit (Coat-A-Count, Diagnostic products Corporation, Los Angeles, CA, USA). The intra- and interassay coefficients of variation were 5.1% and 10.8%, respectively. The determination of FCM (ng/g) was performed with a group-specific 11-oxoetiocholanolone enzyme immunoassay (EIA), measuring 11,17-dioxoandrostanes (Palme and Möstl, 1997). Its intra- and interassay coefficients of variation were 10.1% and 11.9%, respectively. This EIA has previously been validated in cattle (Palme *et al.*, 1999) and successfully applied in this species (Palme *et al.*, 2000; Pesenhofer *et al.*, 2006).

Statistical analysis

Data were analyzed using the SAS software. The general linear models procedure was used to obtain the adjusted values for year and sire breed effects, according to the following model:

$$Y_{ijk} = \mu + Year_i + SB_j + e_{ijk},$$

where Y_{ijk} is the *k*-th trait measured on the *j*-th sire breed and evaluated on the *i*-th year; μ is the overall mean for the

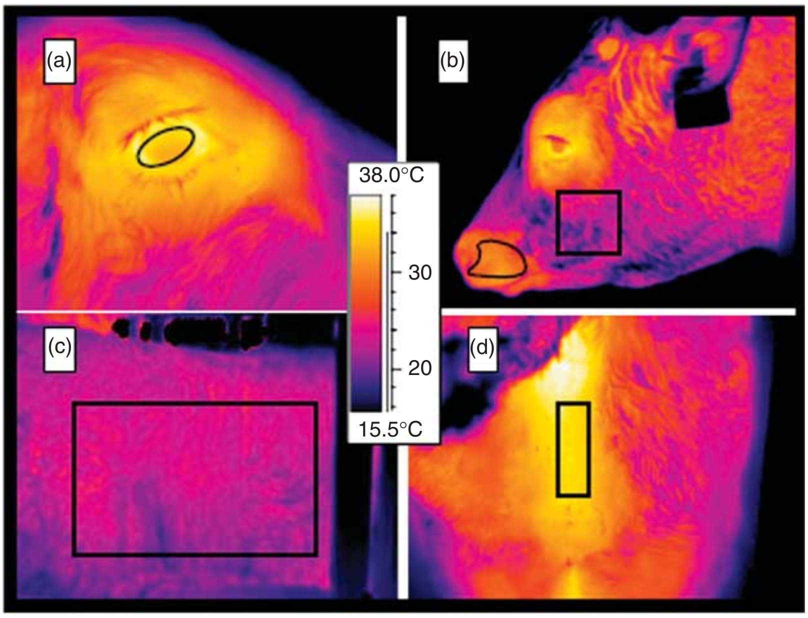

Figure 1 Illustrative infrared images of the eye surface (a), cheek (b) snout (b), ribs (c) and hind area (d). Note the shapes used to define each body location for image interpretation.

trait; *Year* is the fixed effect of the *i*-th year; *SB* is the fixed effect of the *j*-th sire breed (maternal, Charolais and Piedmontese); and e_{ijk} is the residual random effect associated with the *k*-th measure. The adjusted trait measures were then calculated as: $Y^{*}_{ijk} = Y_{ijk} - \widehat{Year}_j - \widehat{SB}_j$. In the case of glucocorticoids a similar model was used without the year effect, because they were only measured in the second year. The five sets of IR data were averaged prior adjusting with the model above. In addition, the need of adjusting FCM concentration for DMI was also verified by including DMI as a covariate, as one could argue that potential differences could be resulted from the intestinal passage rate and not of actual levels of FCM. Pearson correlations between productive performance traits, feeding behavior characteristics, IR thermography traits, and glucocorticoid levels were also calculated using the correlation procedure. Due to the great number of correlations calculated, false discovery rate (Benjamini and Hochberg, 1995) was controlled at a 5% level. Steers were also classified into three RFI-categories with similar number of steers in each group: low-RFI (-0.5 ± 0.1 kg/day, more efficient), medium-RFI (-0.1 ± 0.2) and high-RFI (0.6 ± 0.2). Means of productive performance traits (DMI, ADG and F : G), feeding behavior, IR thermography traits and glucocorticoid levels were tested across the three RFI categories, using the general linear model procedure applying Scheffé's multi comparison test.

In addition, using the SAS partial least squares procedure, all the feeding behavior traits were summarized into a single new variable, such as that strength of the relation of the new variable and the RFI was maximized. The same was also done individually for the IR thermography traits and the glucocorticoid traits were summarized as three single variables. Then these three new variables were analyzed by multiple regression analysis to assess their individual simultaneous contribution (based on R^2) to the total RFI variation.

The SAS mixed procedure was used to analyze and describe the pattern of visits to the feeder by hour of the day. The model utilized in this procedure included time of the day (24 h/day) on the model described above; and the covariance structure that best fit the variance was heterogeneous compound symmetry. For all analyses data were considered statistically significant when $P \leqslant 0.05$ and were considered a trend towards significance when $0.10 \geqslant P > 0.05$.

Results

The descriptive statistics of all traits studied are presented in Table 2. The correlations between feeding behavior, IR thermography and glucocorticoid levels with productive performance traits are shown in Table 3. In comparison to the other feeding behavior traits, MS and ER had the strongest positive correlation with RFI. These two traits also had the strongest positive correlation with RFI in comparison to the remaining feeding behavior traits. Time spent at the feeder and VF was positively correlated with RFI. Time spent at the feeder and TM was moderately associated with ADG, and TM had a positive correlation with DMI. In general, IR traits were more closely associated with RFI in comparison to the other productive performance traits, with the exception of RB that was not correlated to any of the efficiency traits. In addition, the non-core body locations (SN and CK) were correlated with all feed efficiency traits. Residual feed intake had correlations up to 48% greater with IR thermography traits in comparison to other productive performance traits. In relation to glucocorticoids, FCM exhibited a positive correlation with ADG and negative correlations with F : G and RFI. Conversely, PC was not

Table 2 *Descriptive statistics*

Traits (abbreviation; unit)	Mean	s.d.	Minimum	Maximum
Productive performance traits				
Dry matter intake (DMI; kg DM/day)	8.97	0.97	6.35	11.63
Average daily gain (ADG; kg/day)	1.64	0.19	1.02	2.10
Feed to gain ratio (F : G; DMI/ADG)	5.47	0.61	4.25	6.92
Residual feed intake (RFI; kg/day)	0.00	0.55	−1.15	1.92
Average body weight (kg)	435.8	37.4	338.5	527.4
Feeding behavior				
Time at feeder (TF; min/day)	155.39	23.36	99.79	210.58
Time per meal (TM; min)	15.06	2.42	10.01	22.70
Meal size (MS; g DM)	1,000	211.2	653.2	1,680.2
Eating rate (ER; g DM/min)	67.00	12.35	44.12	101.72
Number of meals (NM; per day)	9.21	1.21	6.62	12.37
Visits to the feeder (VF; per day)	53.00	13.55	23.66	85.04
Infrared thermography				
Eye (EY; °C)	33.60	1.27	26.60	35.60
Cheek (CK; °C)	26.93	1.88	22.50	30.80
Snout (SN; °C)	28.61	1.68	25.90	33.80
Ribs (RB; °C)	27.43	2.84	22.30	31.70
Hind area (HA; °C)	34.05	1.02	31.20	36.70
Glucocorticoids				
Fecal cortisol metabolites (FCM; ng/g)	43.51	21.36	12.79	97.97
Plasma cortisol (PL; ng/ml)	37.37	11.12	15.61	63.46

Table 3 *Correlations between productive performance traits (DMI, ADG, F : G and RFI) and feeding behavior, infrared thermography traits and glucocorticoid levels*

Traits (abbreviation; unit)	DMI	ADG	F : G	RFI
Feeding behavior				
Time at feeder (TF; min/day)	0.13^a	0.32**▲	−0.18^a	0.24*▲
Time per meal (TM; min)	0.22*▲	0.32**▲	−0.12^a	−0.15^a
Meal size (MS; g DM)	0.75**▲	0.38**▲	0.34**▲	0.41**▲
Eating rate (ER; g DM/min)	0.63**▲	0.26*▲	0.46**▲	0.44**▲
Number of meals (NM; per day)	0.16^a	0.06^a	0.10^a	0.15^a
Visits to the feeder (VF; per day)	−0.16^a	−0.12^a	−0.02^a	0.35**▲
Infrared thermography				
Eye (EY; °C)	0.18^a	0.29*▲	0.12^a	0.27*▲
Cheek (CK; °C)	0.28*▲	0.20*▲	0.25*▲	0.37**▲
Snout (SN; °C)	0.24*▲	0.38*▲	0.28*▲	0.41**▲
Ribs (RB; °C)	0.17*	0.10^a	0.06^a	0.13^a
Hind area (HA; °C)	0.13^a	0.16*	0.09^a	0.26*▲
Glucocorticoids				
Fecal cortisol metabolites (FCM; ng/g)	0.07^a	0.39**▲	−0.35*▲	−0.45**▲
Plasma cortisol (PL; ng/ml)	−0.04^a	0.10^a	−0.13^a	0.03^a

DMI = dry matter intake; ADG = average daily gain; F : G = feed to gain ratio; RFI = residual feed intake.
^{a}$P > 0.05$; * $P < 0.05$; ** $P < 0.01$.
▲Experimentwise significant correlations for a 5% false discovery rate (Benjamini and Hochberg, 1995).

correlated with any of the productive performance traits. In addition, FCM adjusted for DMI had the same relationships as observed for FCM (results not shown), and in fact DMI explained < 0.5% of the FCM variation.

The effects of RFI group on productive performance, feeding behavior, IR thermography traits and glucocorticoid levels are presented in Table 4. Low RFI (more efficient) steers had lower DMI, F : G and RFI (1.12 kg/day lower daily feed intake) than the less efficient steers ($P < 0.05$) with no difference in ADG. In relation to feeding behavior traits, it was observed that low-RFI steers had smaller MS, slower ER and less often VF ($P < 0.05$) than high-RFI steers. Figure 2 shows the 24 h pattern for VF from low- and high-RFI groups. High-RFI steers numerically ($P < 0.10$) visited the feeder more often than low-RFI steers over the day. In addition, high-RFI steers visited the bunk 15% more often

Table 4 *Residual feed intake group means for productive efficiency, feeding behavior, infrared thermography traits and glucocorticoid levels*

Traits (abbreviation; unit)	Low-RFI	Medium-RFI	High-RFI	s.e.m.*	*P*-value
Productive efficiency traits					
Dry matter intake (DMI; kg DM/day)	8.1^{b}	8.1^{b}	9.0^{a}	0.16	< 0.001
Average daily gain (ADG; kg/day)	1.6	1.5	1.5	0.03	0.211
Feed to gain ratio (F : G; DMI/ADG)	5.2^{b}	5.5^{b}	6.0^{a}	0.10	< 0.001
Residual feed intake (RFI; kg/day)	-0.52^{c}	-0.08^{b}	0.60^{a}	0.05	<0.001
Average body weight (kg)	424.0	440.1	434.3	29.32	0.189
Feeding behavior					
Time at feeder (TF; min/day)	156.4	158.4	167.6	4.30	0.354
Time per meal (TM; min)	14.5	13.9	13.8	0.44	0.383
Meal size (MS; g DM)	840.3^{b}	820.2^{b}	970.5^{a}	37.38	0.046
Eating rate (ER; g DM/min)	59.7^{b}	60.1^{b}	68.4^{a}	2.18	0.009
Number of meals (NM; per day)	9.1	9.5	9.6	0.22	0.343
Visits to the feeder (VF; day)	48.4^{b}	53.5^{b}	58.7^{a}	2.42	0.037
Infrared thermography					
Eye (EY; °C)	32.6	33.3	33.5	0.34	0.102
Cheek (CK; °C)	28.1^{b}	27.7^{b}	29.2^{a}	0.34	0.042
Snout (SN; °C)	30.0^{b}	30.9^{a}	31.2^{a}	0.39	0.033
Ribs (RB; °C)	30.5	30.4	30.7	0.52	0.382
Hind area (HA; °C)	33.7	34.2	34.6	0.19	0.082
Glucocorticoids					
Fecal cortisol metabolites (FCM; ng/g)	51.1^{a}	42.8^{b}	31.2^{b}	5.42	0.040
Plasma cortisol (PL; ng/ml)	40.9	40.0	41.3	3.04	0.944

RFI = residual feed intake.
^{a,b}means within a row having a different superscript letter differ ($P < 0.05$).
*Highest value for standard error of the mean (s.e.m.) between RFI groups means.

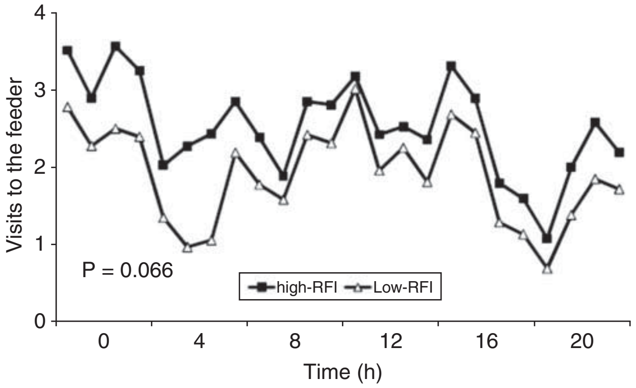

Figure 2 Number of visits to the feeder over the circadian cycle in steers with high and low residual feed intake (RFI; average pooled s.e.m. = 0.15, range = 0.08 to 0.21, with minor differences between groups and time of the day).

($P < 0.05$) than low-RFI steers between 20:01 and 08:00 h. Regarding the IR traits, more efficient steers had lower temperatures in the non-core body locations ($P < 0.05$) in comparison to less efficient steers, but similar temperatures in the other body locations. In addition, low-RFI steers had higher levels of FCM ($P < 0.05$) but similar PC ($P > 0.10$) in comparison to high-RFI steers.

The relative explanation of the RFI variation by IR thermography, feeding behavior and glucocorticoids differed greatly. IR thermography accounted for most of the explained RFI variation (59%). Additionally, feeding behavior and glucocorticoid levels accounted for 18% and 7% of the RFI explained variation. Furthermore, 16% of the RFI variation was not explained by the three groups of traits studied.

Discussion

Feeding behavior, IR thermography and glucocorticoid levels are relatively uncommon traits in beef cattle, requiring a comparison with the available literature. The majority of the means observed for feeding behavior traits (Table 2) are similar to values observed in other studies. Time spent at the feeder per day, MS, ER and NM were comparable with the observations of Romney *et al*. (2000) and Gomez *et al*. (2007), who used an automated feeding system similar to the system used in this study. Time per meal was lower in comparison to the values found by Deswysen *et al*. (1993) and Romney *et al*. (2000). This probably was due to the distinct definitions of meal used in each of these studies. The value for VF was greater than the average value reported by Nkrumah *et al*. (2006) for feedlot beef steers. However, our VF value without considering the visits where zero intake was observed was 44.98 ± 12.75, which is closer to the observation made by Nkrumah *et al*. (2006). Means of the IR thermography traits followed the pattern observed elsewhere (Whittow, 1962; Montanholi *et al*., 2008 and 2009) with warmer temperatures at the core body locations, and extremities around 7°C cooler. Fecal cortisol metabolites concentration had a similar range and wide variation as observed by Palme *et al*. (2000) and Pesenhofer *et al*. (2006) in dairy cows, under the same determination technique and laboratory. Similarly, the PC was within the range observed by other authors, with values ranging from 18.7 ng/ml in beef steers (Colditz *et al*., 2007) to 38.0 ng/ml in beef heifers (Curley *et al*., 2008), also using radioimmuno assays.

Feeding behavior and productive performance

Except for NM, all feeding behavior characteristics had moderate correlations with some of the productive performance traits, indicating that feeding behavior characteristics may be used in the assessment of animal performance. The stronger association of MS and ER with DMI in comparison to the other feeding behavior characteristics is an indication of the important role these traits can play in the assessment of DMI. In a study with dairy cows from different breeds, MS and ER were also the main factors to explain DMI capacity (Senn *et al*., 1995). As a result of the correlations of MS and ER with DMI, a corresponding response was also found for the other productive performance traits. Differently from our results, Lancaster *et al*. (2005) did not find significant correlations between F : G and ER. The correlation between ADG and TF was comparable to the findings of Schwartzkopf-Genwein *et al*. (2002) and Lancaster *et al*. (2005).

In relation to RFI (Tables 3 and 4), steers that consumed larger meals (MS) and in a shorter period of time (ER) had a less desirable RFI, which was also found by Gomez *et al*. 2007, but not by Lancaster *et al*. (2005) and Golden *et al*. (2008). The relationship between ER and RFI is supported by the association between RFI and basal energy requirements (Richardson *et al*., 2001; Castro Bulle *et al*., 2007) and the findings from Adam *et al*. (1984), where ER was a key factor in determining the energy cost of eating in cattle. Time spent at the feeder was correlated with RFI in our study and also in the study conducted by Lancaster *et al*. (2005). Additionally, Nkrumah *et al*. (2006) observed that high-RFI steers spent 50% more time feeding in comparison to low-RFI steers. According to Adam *et al*. (1984), TF is another major factor for comprising the energetic costs of feeding. Robinson and Oddy (2004) and Golden *et al*. (2008) found that low-RFI steers consume fewer meals per day (NM), which is in contrast to Basarab *et al*. (2003), Gomez *et al*. (2007), and the current results. These differences are probably not only due to the experimental differences but also to the diversity of definitions for meal across these studies. The positive correlation of VF with RFI was also found by Lancaster *et al*. (2005) in growing beef bulls. VF was different across the RFI-groups (Table 4), with low-RFI steers having fewer VF, which is similar to the pattern observed by Nkrumah *et al*. (2006). Moreover, together with TF, VF do not require the actual measurement of individual feed intake, which might represent an advantage in comparison to the other feeding behavior traits investigated.

The 24 h pattern for VF (Figure 2) revealed a numerically higher frequency ($P < 0.10$) of VF for high-RFI steers through the day, with less efficient steers having more VF during the nocturnal period ($P < 0.05$). Golden *et al*. (2008) evaluated ER across 3-h time periods for efficient and inefficient animals and did not observe differences between the two groups, but they suggested that less efficient cattle have more variability in feed intake throughout the periods of the day. Unfortunately, there is limited other research exploring feeding patterns across the day in animals with distinct feed efficiencies, other than investigations on different feedstuffs demonstrating effects of time of the day on feed preferences (Deswysen *et al*., 1993; Senn *et al*., 1995).

IR thermography and productive performance

The fact that IR readings from the non-core body locations (CK and SN) were correlated with all productive performance measures agrees with previous results (Montanholi *et al*., 2009) with the observation that IR thermographs of the body extremities are better predictors of heat production than core body locations in cattle (Montanholi *et al*., 2008), and also with the key role of extremities for body heat dissipation (Whittow, 1962; van den Heuvel *et al*., 2004). In response to feed consumption all animals have the heat increment of feeding (Baldwin *et al*., 1980). Similarly, in response to storage or growth of body tissues (ADG), energy will be required and also heat will be produced (Birkett and de Lange, 2001). Moreover, RFI reflects more the basal energy requirements (Richardson *et al*., 2001; Castro Bulle *et al*., 2007) and the caloric input used to supply these requirements results in heat production as an outcome of the metabolic functions (Blaxter, 1962). The heat produced by the animal is greatly dissipated through the skin in the form of radiation (Kleiber, 1961), which can be captured using IR thermography. Therefore, lower temperatures of extremities may be expected for low-RFI steers, in comparison to less efficient steers (Table 4). Moreover, the temperatures of extremities are also potential indicators of other productive performance traits discussed above.

Interestingly, EY did not exhibit a considerable association with efficiency traits, even though EYs are not part of the core body. There are two potential explanations for this finding. First, EYs have no major function as a heat dissipating organ and their surface temperature is heavily influenced by the time since the last blink episode (Fujishima *et al*., 1996). Second, EY follows the rectal temperature very closely (Schaefer *et al*., 2004), suggesting a better application of EY as an indicator of core body temperature. The other two IR traits, RB and HA, were not important indicators of efficiency. Ribs area temperature is not only a core body trait, but also influenced by the hair length that is quite variable in beef cattle having different influences on heat dissipation (Arkin *et al*., 1991). The fact that HA was correlated to RFI and had numerically lower temperature in the low-RFI group probably has to do with the minimum and more uniform hair coverage of this body location across different animals. However, this body location temperature was 52% less correlated with heat production than non-core body locations (Montanholi *et al*., 2008).

Glucocorticoids and productive performance

PC was not associated with any productive performance trait in this study. In contrast, Richardson *et al*. (2004) reported correlations ($P < 0.05$) of −0.58 and −0.40 with PC and DMI and RFI, respectively. A trend of higher levels of PC in less efficient steers and a trend for a positive relationship between blood PC concentration of steers and their sire's estimated breeding value for RFI were also observed (Richardson *et al*., 2004). Curley *et al*. (2008) provided evidence that fearfulness traits are directly associated with PC. In another study similar traits were associated with inferior performance (Voisinet *et al*., 1997). Thus, rapid and greater responses of the adrenal gland for cortisol release (PC) are apparently associated with lower efficiency, but this study did not support this association.

In contrast to PC, FCM had considerable correlations with most of the productive performance traits. The FCM results suggest that more efficient animals have higher long term basal cortisol levels, which is also independent of the DMI that influences the intestinal passage rate (Van Soest, 1994). Geverink *et al*. (2002) found that calmer gilts have greater baseline cortisol levels. In another study Geverink *et al*. (2004) found that calmer gilts have improved energetic efficiency. Similarly, Voisinet *et al*. (1997) demonstrated that calmer feedlot cattle have improved performance. According to the extensive review by Koolhaas *et al*. (1999) on coping styles, shy animals have greater cortisol baseline and when exposed to stress situations have a predominantly parasympathetic response causing a conservation-withdrawal response that is associated to energy conservation. On the other hand, bold animals have a lower cortisol baseline and under stress have a sympathetic response causing a fight and flight response that increases the energy expenditures. Based on these facts, we have evidence to suggest that more efficient cattle have shy coping style, which is associated with a greater cortisol baseline (FCM) and the respective superior feed efficiency.

Furthermore, the distinct results for FCM and PC are not surprising because PC can change by a factor of 10 or more within minutes and is influenced by regular periodicities and also by the sampling procedure (von Holst, 1998). Therefore, interpretation of cortisol levels based on a single blood sample might be imprecise. Conversely, the FCM exhibit substantial individual variation and better reflects adrenocortical activity than PC (Palme *et al*., 1999). In addition, FCM better reflect the biologically active proportion of cortisol because only the free cortisol from the blood is available for metabolism and excretion (Palme *et al*., 2005).

Overall explanation of RFI variation

The relative importance of each of the groups of traits to explain the total variation observed for RFI was not the same. Body surface temperature (IR thermography traits) accounted for the greatest portion of the RFI variation (59%). Similarly, Montanholi *et al*. (2009) also observed a major role of IR thermography in the explanation of RFI variation and the application of this technology to detect heat production (Montanholi *et al*., 2008). In addition, Richardson and Herd (2004) observed that a variation component partially representing the maintenance requirements (energy production) accounted for 37% of the RFI variation. Therefore, these similarities may suggest that the IR thermographs are capable to detect differences in heat production associated with feed efficiency. Feeding behavior and glucocorticoids had a lower, but still relevant, impact on the explanation of RFI variation. All the biological differences between more and less efficient steers found in this study and elsewhere (e.g. Richardson *et al*., 2004; Kolath *et al*., 2006; Nkrumah *et al*., 2006) may be useful to select the most efficient animals and also to monitor potential undesirable side effects of selection for improved efficiency in cattle (Rauw *et al*., 1998).

Conclusions

Feeding behavior, IR thermography and fecal cortisol metabolites are correlated with feed efficiency traits and thus there may be the potential for application of some of these measurements in the assessment of efficiency traits in beef cattle. Based on this study, a more efficient steer (low RFI) would consume smaller meals, eat slower, visit the feeder less often, have cooler body extremities and also have greater baseline cortisol levels in comparison to a less efficient steer. In addition, the body surface temperature (IR thermography) accounted for more than 70% of the RFI variation explained by the three groups of traits evaluated together, which indicates an important application of IR technology. Moreover, these findings open the possibility of considering alternative technologies (less expensive) to assess feeding behavior traits (e.g. time at the feeder or visits to the feeder), and suggest the possibility of using fecal cortisol metabolites as an indicator of efficiency in beef cattle.

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