Defining Feed Efficiency in Beef Cattle

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Introduction

Most breeding programs have focused on improving economically relevant output traits such as growth, carcass quality and fertility to enhance the economic viability of beef production systems. Generally absent from current breeding programs in the U.S. are avenues for exploiting genetic variation in feed efficiency, even though reductions in feed inputs would substantially improve profitability of beef operations. While the expense of measuring feed intake has no doubt curtailed the implementation of genetic strategies focused on feed efficiency in the past, emerging commercialization of technologies to more cost effectively measure intake has helped to renew interest in this area. The National Beef Cattle Evaluation Consortium recently formed a working group to assess current knowledge regarding genetic and phenotypic variation of various feed efficiency traits, and to consider alternative methods to advance industry adoption of breeding programs that seek to improve genetic merit for efficient utilization of feed resources. The purpose of this paper is to characterize various feed efficiency traits for post-weaning beef cattle, focusing phenotypic relationships with performance and carcass traits.

Feed Efficiency Traits

It is not feasible to measure the efficiency of beef production from an integrated system, as this would require measurements of multiple outputs and inputs of breeding and replacement females as well as their slaughter progeny. Thus, for genetic evaluation purposes, we are forced to measure feed inputs and outputs in targeted stages of the production cycle. Given that the vast majority of feed inputs are used by the breeding herd compared to slaughter progeny, and that substantial animal variation exist in maintenance energy requirements (Johnson et al., 2003), it would seem logical to directly target reductions in feed inputs of breeding females to improve the efficiency of integrated production systems. Unfortunately, large-scale measurement of forage intake by mature cows is not practical, which necessitates the need to focus on feed inputs of growing animals. Expectations are that appropriate use of a feed efficiency trait in growing cattle, which accounts for genetic variation in efficiency of feed utilization to support maintenance and growth requirements, will generate progeny that are efficient in all segments of the industry. With the exception of Archer et al. (2002), few studies have examined genetic relationships between efficiency of growing and mature beef cattle to validate this expectation—more studies are clearly warranted.

The term *efficiency* implies a ratio of outputs to inputs. Liveweight gain and daily dry matter feed intake are typically used to measure ratiobased feed efficiency traits like gross feed efficiency (or its inverse feed conversion ratio; FCR), although output traits can also be expressed as carcass or lean product, and input traits as digestible or metabolizable energy intake. While FCR (feed/gain ratio) is useful to evaluate the effects of diet quality, environment, and management practices (e.g., implants, ionophores) on production efficiency in growing and finishing cattle, FCR has limited value as an efficiency trait for genetic improvement, even though FCR is moderately heritable (Crews, 2005). Firstly, FCR is strongly correlated (r_g > 0.50) with growth traits (Arthur et al., 2001a, Schenkel et al., 2004), such that selection to

reduce post-weaning FCR (improved efficiency) would increase genetic merit for growth and mature size of breeding females (Herd and Bishop, 2000). Secondly, FCR is a gross measure of feed efficiency in that it does not attempt to partition feed intake between maintenance and growth requirements. Because FCR is a gross measure of efficiency that is strongly associated with growth traits, postweaning selection for FCR will not necessarily lead to improvements in feed efficiency of breeding females. In fact, Archer et al. (2002) found that the genetic correlation between FCR measured in post-weaning heifers and mature cows was only 0.20, even though feed intake and average daily gain (ADG) of heifers was strongly correlated to feed intake ($r_g = 0.94$) and ADG ($r_g = 0.72$) of mature cows. Thirdly, as discussed by Crews (2005), selection based on ratio traits like FCR can result in divergent and unpredictable genetic responses of component traits (growth and intake) if the genetic variances of the component traits are different. For example, Bishop et al. (1991) found that feed intake was not reduced, but that ADG was higher in progeny from Angus sires selected for low compared to high FCR. Collectively, these studies suggest that selection to reduce post-weaning FCR will increase cow mature size and have minimal affects on feed inputs, and thus efficiency of feed utilization in integrated beef production systems.

Alternative approaches to defining feed efficiency traits involve partitioning of feed portions needed to support inputs into maintenance and growth requirements. include maintenance efficiency, Examples which is defined as a ratio of feed intake used for maintenance (actual feed intake minus predicted feed for growth) per unit of metabolic body size (BW^{0.75}), and partial efficiency of growth (**PEG**), which is the ratio of ADG per unit of feed used for growth (actual feed intake minus predicted feed for maintenance; see Table 1). For both traits, the predictions of feed inputs for maintenance or growth are derived from feeding standards (e.g., NRC, 1994). For PEG,

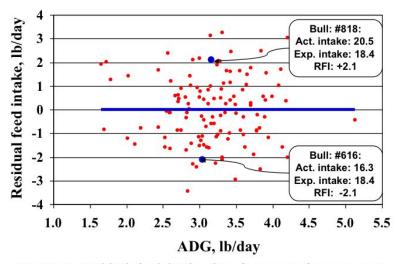


Figure 1. Residual feed intake data from a performance test conducted at the Beef Development Center (Test 1; 115 Angus and Brangus bulls; Lancaster et al., 2005).

feed input for maintenance is derived from a population estimate of maintenance energy requirements in beef cattle, and this amount subtracted from actual feed intake to estimate feed available for growth. Therefore, PEG will not capture inherent animal variation in energetic efficiencies associated with maintenance. Despite this shortcoming, PEG has an apparent advantage over FCR as a feed efficiency trait, as genetic (Arthur et al., 2001b) and phenotypic correlations (Nkrumah et al., 2004; Lancaster et al., 2005) between ADG and PEG are substantially lower compared to those between ADG and FCR. Moreover, feed intake is more strongly associated with PEG in a favorable direction compared to FCR (see section below).

Residual Feed Intake

A third approach to defining feed efficiency involves using an animal's weight and growth rate to partition feed inputs into maintenance and growth components. A phenotypic linear regression equation, computed using intake and performance data from a contemporary set of animals, is used to determine an animal's expected feed intake based on its weight and growth rate over a given test period. The animal's actual feed intake net (more or less) its expected feed intake is referred to as residual

feed intake (**RFI**). Efficient animals are those that consume less feed then expected based on their size and growth rate, thus efficient animals will have negative RFI. Conversely, inefficient animals will consume more feed than expected and have positive RFI.

A notable feature that distinguishes RFI from other feed efficiency traits is that it is phenotypically independent of the production traits used to compute expected intake. This is demonstrated in Figure 1 using data from 115 Angus and Brangus bulls. Despite considerable variation in ADG of bulls on this test, there was (as expected) an equal number of slow and fast gaining bulls with low (efficient) and high (inefficient) RFI. The two bulls (#616 vs #818) highlighted in Figure 1 had divergent RFI (-2.1 vs +2.1 lb/d) even though expected feed intakes were similar (18.4 lb/d), because bull #818 consume 4.2 lb more feed per day than bull #616. Expected feed intakes were similar because the two bulls had similar ADG (3.04 vs 3.16 lb/d) and final BW (1102 and 1077 lb) at the end of the test. Bull #616 was also more efficient than bull #818 as determined by FCR (5.37 vs 6.49). In fact, RFI is highly correlated phenotypically with FCR (Nkrumah et al., 2004; Lancaster et al., 2005; see section below), even though FCR is negatively correlated with grow traits. These results demonstrate that RFI is a more suitable trait to use in comparing animals during post-weaning tests that differ in production.

As with other feed efficiency traits, RFI has been shown to be moderately heritable (see Crews, 2006; this proceedings). Australian

research has demonstrated that progeny from parents selected for low RFI after almost two generations were similar in yearling weight (845 vs 838 lb) and ADG (3.17 vs 3.08 lb/d), but consumed less feed (20.7 vs 23.3 lb/d) and had lower FCR (6.6 vs 7.8) compared to progeny from parents selected for high RFI (Arthur et al., 2001a). Additionally, Archer et al. (2002) reported that RFI in post-weaning heifers was strongly correlated ($r_g > 0.90$) to RFI measured in the same females as mature cows. These results suggest that selection for improved post-weaning RFI has the potential to produce progeny that are efficient in all segments of the industry.

Further Merits of Residual Feed Intake

Based on Australian research, Herd et al. (2004) estimated that approximately one third of the biological variation in RFI could be explained by differences in digestion, heat increment of feeding and activity, and that the other two thirds was likely due to differences in heat production (mechanisms unknown). Nkrumah et al. (2006) recently reported that RFI was correlated with methane (0.44) and heat production (0.68) in growing calves. Moreover, we have found that digestibility was negatively correlated with RFI (-0.33), but not FCR in growing steers (Brown, unpublished), and that feeding duration was positively correlated with RFI (0.43), but not FCR in growing bulls (Lancaster et al., 2005). Collectively, these studies indicate that RFI is a trait that appears to reflect inherent variation in biologically relevant processes that are related to feed efficiency, but not growth.

Table 1. Traits used to assess efficiency of feed utilization in growing beef cattle

	- m	_	Favorable
Trait	Definition	Formula	phenotype
	Actual DMI per unit weight		
FCR	gain	DMI ÷ ADG	low
	Metabolizable energy intake		
Maintenance	(MEI) for maintenance per	MEI - (fat gain \div k_f) -	
efficiency	MBW	(protein gain \div k _p) \div MBW†	low
•		ADG ÷ (DMI - DMIm);	
Partial		DMIm = expected DMI	
efficiency of	ADG per unit of DMI	required for maintenance	
growth; PEG	available for growth	(NRC, 1984)	high
	•	Expected DMI from	
Residual feed	Actual DMI net expected DMI	regression of ADG on MBW	
intake; RFI	based on MBW and ADG	and DMI	low
RFI adjusted		Expected DMI from	
for	Actual DMI net expected DMI	regression of DMI on MBW,	
composition;	based on MBW, ADG and	ADG and carcass	
RFIc	carcass composition traits	composition traits	Low
Model-		DMR computed from	
predicted Feed		growth, composition &	
conversion	DMI required (DMR) from	environmental traits (CVDS	
ratio; R:G	CVDS model per unit gain	model) ÷ ADG	low

 $[\]dagger k_f$ and k_p are standard partial efficiencies of ME use for fat and protein deposition, respectively.

Model Assisted Selection

A fourth approach to identifying efficient animals is through the use of mathematical models. The Cornell/Cattle Value Discovery System (CVDS) was developed to allocate feed inputs to individual animals fed in group pens (Fox et al., 2001). An enhanced, dynamic version of the CVDS model was developed (Tedeschi et al., 2004) to improve accuracy of prediction of individual dry matter feed required (DMR) and FCR of group-fed cattle. Fox et al. (2004) evaluated the use of CVDS to compute individual DMR of group-fed bulls. Results from a three-year test conducted in New York demonstrated that the sum of model-predicted DMR for individual bulls was within 2% of the actual pen feed intakes. Jorgensen Angus (Ideal, SD) has used the CVDS to predict feed efficiency in 867 bulls from 56 sires over the past 5 years—the sum of model-predicted DMR has been within 3 to 5% of actual pen feed

intakes. Tedeschi et al. (2006) recently reported phenotypic correlations between DMR, and DMI and ADG of 0.75 and 0.65, respectively, in steers fed high-grain diets.

Additional studies have been conducted to determine heritability estimates of modelpredicted DMR, and genetic correlations with actual feed intakes. Williams et al. (2005) used the Decision Evaluator for the Cattle Industry (DECI) and the CVDS models to compare model-predicted DMR with actual feed intakes in 504 steers and 52 sires. Heritability estimates of DMR were about 0.33 for both models, and genetic correlations between DMI and DMR were greater than 0.95. Similarly, Kirschten et al. (2006) reported heritability estimates of 0.35 for CVDS-predicted DMR, and strong genetic correlations of 0.98 between DMI and DMR. These authors suggested that model-predicted DMR may be useful in genetic evaluations with

minimal differences between DECI and CVDS models in predicting DMR.

Despite the strong genetic correlations found between model-predicted DMR and actual feed intakes (Williams et al., 2005, Kirschten et al., 2006), phenotypic correlations are lower and indicate that about 50 to 70% of the variation in actual intakes can be explained by these models. Predictions of DMR for individual animals are based on diet (chemical analysis), environment, and individual animal data (weight, ADG, maturity, composition). Thus, DMR predictions are similar to feed intake predictions derived from phenotypic linear regression models that use weight and ADG to calculate RFI. Therefore, current models used to predict DMR have limited capability to account for individual animal variation in actual feed intake associated with inherent animal differences in efficiency, as defined by RFI.

It is envisioned that future models can be developed to more accurately quantify individual animal variation in feed intake associated with biological processes (e.g., feeding behavior, heat production, digestibility) that are linked to animal variation in feed Successful parameterization of efficiency. models that incorporate the input of easilymeasured biologically relevant traits (e.g., feeding behavior) or genetic markers linked to RFI, should be more accurate and useful in identifying individuals with improved feed efficiency.

Phenotypic Relationships Among Feed Efficiency Traits in Growing and Finishing Calves

We recently performed a Meta analysis of eight studies to characterize the feed efficiency traits defined in Table 1, and to examine their correlations with performance and carcass traits in growing and finishing calves. An additional objective was to evaluate the effectiveness of the CVDS (Tedeschi et al., 2004) to predict DMR and DMR:ADG ratio (**R:G**) in growing

and finishing calves. Two databases were assembled and analyzed separately. The first database consisted of four studies that included growing steers and heifers (N = 514) fed highroughage diets (0.93 to 0.97 Mcal ME/lb), with initial body weights averaging 604 lb. The second database consisted of four studies that included finishing steers (N = 320) fed highgrain diets (1.24 to 1.36 Mcal ME/lb), with initial body weights of 789 lb. Within studies, cattle were individually fed and managed in a similar manner. For CVDS-model predictions, carcass traits were used to compute adjusted final weights at 28% empty body fat (AFBW) in the finishing studies, whereas, in the growing studies ultrasound measurements at the end of the test were used to compute AFBW.

The model R² of the multiple regression equations used to compute RFI were 0.68 and 0.67 for growing and finishing studies, respectively, indicating that about two thirds of the variation in feed intake was explained by variation in weight and ADG in both studies. In both growing and finishing studies, FCR was strongly correlated with ADG (-0.60 and -0.58) and initial weight (0.28 and 0.40), but weakly correlated with feed intake (0.12 and 0.25), demonstrating that favorable FCR phenotypes had substantially lighter initial weights and higher ADG, and consumed slightly less feed. In contrast, RFI was strongly correlated with intake (≈ 0.65) in growing and finishing calves, but as expected, RFI was not correlated phenotypically with initial weights or ADG. In both growing and finishing calves, PEG was weakly correlated with ADG (0.20 and 0.11) and initial weights (0.14 and 0.10), but strongly correlated with feed intake (-0.57 and -0.64). showing that favorable PEG phenotypes ate substantially less feed and had slightly higher ADG and initial weights. The phenotypic correlations between these three feed efficiency traits and their component traits (growth and intake) were comparable to those reported in previous studies (Arthur et al., 2001a,b; Nkrumah et al., 2004; Lancaster et al., 2005).

All feed efficiency traits were strongly correlated to each other (± 0.50) in favorable directions. In general, phenotypic correlations between efficiency, intake and growth traits in growing calves were remarkably similar to those found in finishing calves. Phenotypic correlations between all three of the feed efficiency traits and final rib fat thickness were

weak (± 0.11 to 0.15) for growing calves and moderate (± 0.21 to 0.38) for finishing calves, such that the favorable phenotypes tended to be leaner. In general, correlations between feed efficiency traits and final ribeye area were either weak or not different from zero.

Table 2. Pearson correlation of adjusted traits for growing (above diagonal) and finishing (below diagonal) calves

		Growing studies									
	Trait	ADG	iBW	DMI	RFI	PEG	FCR	DMR	R:G	BF	REA
	ADG		0.14	0.61	0.00	0.20	-0.60	0.93	-0.71	0.06	0.08
	iBW	0.10		0.53	0.00	-0.25	0.28	0.65	0.29	0.28	0.45
	DMI	0.62	0.51		0.65	-0.57	0.12	0.73	-0.14	0.24	0.25
udies	RFI	0.03	0.06	0.67		-0.87	0.56	0.54 ₁	0.04	0.11	0.00
ing st	PEG	0.11	-0.38	-0.64	-0.84		-0.77	0.27	-0.52	-0.15	-0.10
Finishing studies	FCR	-0.58	0.40	0.25	0.63	-0.79		-0.29	0.81	0.11	0.11
	DMR	0.84	0.64	0.71	0.04	0.27	-0.51		-0.43	0.22	0.25
	R:G	-0.52	0.32	-0.04	0.06	-0.52	0.61	0.01		0.19	0.14
	BF	0.20	0.22	0.44	0.33	-0.38	0.21	0.47	0.26		0.22
	REA	0.24	0.32	0.19	-0.14	0.02	-0.11	0.20	-0.09	-0.20	

^a Correlations in bold are significantly greater then zero; P < 0.05. ADG is average daily gain, iBW is initial body weight, DMI is dry matter intake, RFI is residual feed intake, DMR is dry matter required (model predicted), PEG is partial efficiency for gain, FCR is feed conversion ratio, R:G is DMR to ADG ratio (model predicted), BF is back fat, and REA is ribeye area.

Model-predicted DMR were highly correlated with ADG (> 0.80) and actual intake (\approx 0.70) in both growing and finishing calves. In addition, DMR were negatively correlated with actual FCR in both growing (-0.29) and finishing (-0.51) calves, and positively correlated with RFI (0.54) in growing calves. However, model-predicted DMR were not correlated with RFI in finishing (0.04) calves, and were negatively correlated with R:G in growing (0.43), but not

finishing (0.01) ealves. These results demonstrate that phenotypic correlations with model predictions of DMR and R:G were at times inconsistent across growing and finishing calves in this study.

To illustrate the phenotypic variation in RFI and relationships with other component traits, calves within growing and finishing studies were separated into low and high RFI groups (Table 3); low RFI calves being those that ranked less

than 0.5 SD from the mean RFI of 0.0 ± 1.80 and 0.0 ± 1.96 lb/d for growing and finishing calves, respectively. For growing studies, calves with low RFI consumed 18% less feed and had 18% lower FCR and 44% higher PEG compared to calves with high RFI. In the finishing studies, low RFI calves consumed 20% less feed and had 21% lower FCR and 48% higher PEG than high RFI calves. Initial and final body weights and ADG were similar for low and high RFI phenotypes in both the growing and finishing calves. Thus, similar phenotypic variations in RFI were observed in growing and finishing calves. In economic terms, the difference in feed costs between finishing calves with low and high RFI equates to \$0.32/day or \$38.00 during a 120-day feeding period, assuming ration costs of \$0.07/lb (dry matter basis).

There were no differences in ultrasound estimates of carcass composition (rib fat thickness or ribeye area) between calves with low and high RFI in the growing studies,

however, in the finishing studies calves with low RFI had less carcass fat and larger REA than calves with high RFI. Clearly, there was larger differential in carcass fatness between low and high RFI phenotypes in finishing vs growing studies, which likely reflects greater expression of genetic potential for fat tissue deposition, due to the fact that these calves were fed a high-grain diet and were older during the RFI measurement period. These results suggests that selection for improved RFI may potentially impact carcass quality traits (e.g., marbling) in an antagonistic manner, especially if selection for RFI were applied to earlier maturing cattle on moderate- to high-energy diets. A number of studies have reported weak to moderate genetic correlations between RFI and carcass fat (Arthur et al., 2001a,b; Schenkel et al., 2004). The inclusion of carcass fat traits along with ADG and weight to compute RFI may be warranted to minimize unfavorable responses in carcass quality traits (see Crews, 2006; this proceedings).

Table 3. Characterization of performance, ultrasound composition, and feeding efficiency traits in growing and finishing animals with low and high residual feed intake ^a

	Growing Studies			Finishing Studies				
Traits	Low RFI	High RFI	SE	<i>P</i> -value	Low RFI	High RFI	SE	<i>P</i> -value
Number of calves	155	156			93	87		
Growth traits								
Initial BW, lb	611	611	7.12	0.99	721	734	12.8	0.56
Final BW, lb	780	780	8.35	0.98	1142	1150	15.9	0.32
Daily gain, lb/d	2.34	2.34	0.04	0.90	3.11	3.13	0.09	0.38
Feed efficiency traits								
Dry matter intake, lb/d	19.2	23.4	0.26	< 0.01	18.6	23.4	0.37	< 0.01
Residual feed intake,	-2.03	2.09	0.11	< 0.01	-2.25	2.36	0.18	< 0.01
Partial eff. of growth ^b	0.26	0.18	.004	< 0.01	0.31	0.21	0.01	< 0.01
Feed conversion ratio	8.44	10.28	0.15	< 0.01	6.05	7.63	0.13	< 0.01
Ultrasound/carcass traits								
12 th rib fat, in	0.20	0.21	0.01	0.20	0.40	0.56	0.02	< 0.01
Ribeye area, in ²	10.17	10.20	0.12	0.65	12.25	11.84	0.15	< 0.05

^a Animals with low and high RFI were < 0.50 and > 0.50 SD from average RFI, respectively (RFI SD was 1.80 and 1.96 lb/d for growing and finishing studies, respectively).

^b ADG/DMI for growth.

Measuring Feed Efficiency in Commercial Bull-Test Facilities—Case Study

A feed-intake and feeding behavior system (GrowSafe System Ltd.) was recently installed at the Beef Development Center (Millican, TX), in partnership with the Animal Science Department at Texas A&M University. This was the first installation of a GrowSafe® feedintake system in a U.S. commercial bull-test facility. The protocol used to measure performance and feed intake of bulls at the Beef Development Center is similar to that established by Archer et al. (1997). Bulls are assigned to one of two pens each equipped with nine GrowSafe® feed bunks, and adapted to the test diet (30% silage-based ration) for 28 d prior to measuring feed intake and feeding behavior traits (feeding duration, meal frequency) for 70 d. During the 70-d test period, bulls are weighed at 14-d intervals, and linear regression of weights on day of test used to compute growth rates. Scrotal circumference and ultrasound measurements of rib fat thickness, ribeye area and marbling are obtained at the start and end of the tests. To date, feed intake, growth and ultrasound carcass data have been successfully measured, and producer reports generated for almost 500 bulls and heifers. Our results demonstrate that this feed-intake measurement technology is robust and accurate enough to function in a commercial cattle-feeding operation.

As biological efficiency, however defined, does not always equate to profitability it will be critical to develop selection tools that also incorporate economic inputs to facilitate industry adoption. Crews et al. (2006) developed a three-trait selection index with the objective to improve feedlot profitability of market progeny from bulls tested for feed efficiency. Economic weights were derived from net revenue projections of Charolais crossbred steers individually fed a high-grain diet, and an index generated to compute weighting factors for bull RFI, ADG and yearling weight. Index values typically range

from 80 to 120. We have recently started providing this index data to producers along with performance and feed efficiency data. Shown in Figure 2 are RFI data from a test involving 125 Angus and Brangus bulls. For this test, bulls with index values greater than 105 (n = 38) had 17% higher ADG, consumed 9% less feed, and had 22% lower FCR compared to bulls with index values less than 95 (n = 37). The high-index bulls had lower RFI (-1.7 vs + 1.6 lb/d), but similar yearling weights (1035 vs 1045 lb) compared to the low-index bulls.

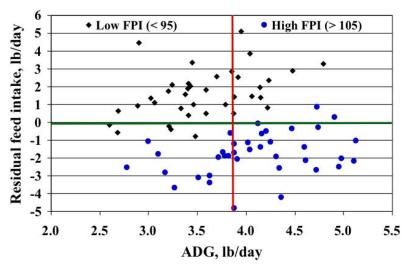


Figure 2. Residual feed intake data from a performance test conducted at the Beef Development Center (Test 2; 125 Angus and Brangus bulls; Lancaster et al., 2005). Only data for low (< 95) and high (> 105) feedlot profit index (FPI) bulls are plotted.

Summary

Considerable genetic variation exists in beef cattle for feed intake unaccounted for by differences in weight and growth rate—residual feed intake, thereby providing opportunities to improve profitability of beef production systems through reductions in feed inputs, with minimal influences on growth or mature size. To facilitate industry adoption, it will be critical to establish BIF guidelines for the collection of data (intake, growth, ultrasound) required to appropriately measure feed efficiency traits, and to develop selection tools that incorporate both

biological and economic parameters to support profit-driven breeding programs.

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