Variation in Feed Efficiency of Growing Heifers and Implications for Intensified Cow-Calf Production

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Introduction

Global demand for food has been projected to increase 70% by 2050 in order to support a growing population that is becoming more urbanized and affluent. As disposable incomes increase in developing countries, people will elect to include more animal-protein foods in their diet. This rising demand for animal protein will require a concomitant increase in the supply of cereal grains as well as protein and forage feedstuffs to support livestock production systems. Unfortunately, the increase in demand for livestock feed has coincided with a reallocation of cropland resources to support the production of biofuels from cereal grains, which has created higher and more volatile costs of feed inputs in recent years (*Figure 1*). As ruminant animals are capable of utilizing low-quality feedstuffs not directly usable by humans or non-ruminant animals, beef producers are poised to play a key role in meeting future global demands for animal-based protein foods. However, the biological efficiency of converting feed to meat is much lower in ruminant animals compared to pork and poultry, due primarily to inherent disadvantages in reproductive rates that greatly increase the cost of maintaining the cow herd. In fact, the cow herd consumes 82% of total feed inputs in calf-fed production systems, and 64% of total feed inputs in yearling-fed systems (Basarab et al., 2012). Thus, since 70 to 75% of total energy requirements for beef production are used for maintenance, more then half of total feed energy inputs needed to produce beef is associated with the energetic costs of supporting maintenance energy requirements of cows. Numerous studies have reported breed differences in cow maintenance energy requirements, and there is evidence to demonstrate that substantial genetic variation in maintenance requirements exist within breeds (Taylor et al., 1986; Hotovy et al., 1991). However, the opportunity to select for lower maintenance requirements is limited by our inability to easily measure this trait. Moreover, numerous studies have demonstrated that positive genetic relationships exist between maintenance requirements and genetic merit for productive traits like milk production and growth (Taylor et al., 1986; Frisch and Vercoe, 1981). Thus, the necessity to focus our efforts on selection for efficiency of feed utilization in postweaning animals, with the expectation that appropriate selection for feed efficiency in growing cattle will generate progeny that are efficient in all sectors of the industry. While feed efficiency traits have been fairly well characterized in growing cattle, there is a critical need to better understand the associations between genetic merit for feed efficiency in postweaning animals and life-cycle efficiency of the cow herd.

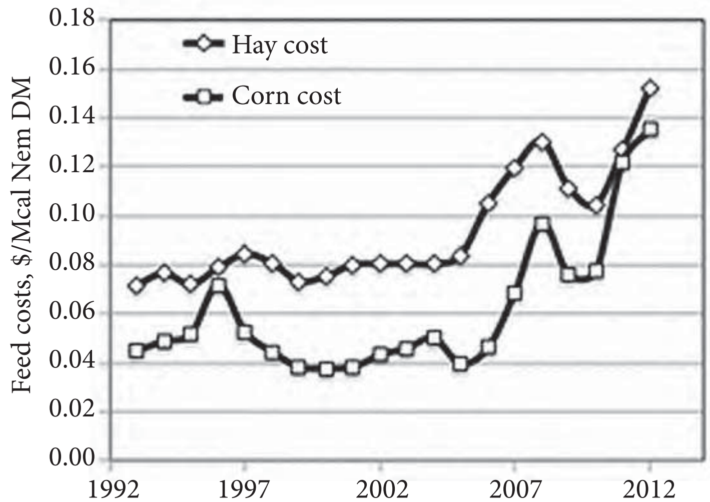

Figure 1. Costs of grass hay and corn grain based on 1.12 and 2.16 Mcal NEm/kg DM, respectively (Livestock Marketing Information Center).

Genetics of Efficiency in Beef Cattle

Regulation of feed intake and efficiency of feed utilization by animals involves a complex set of biological processes and metabolic pathways that are influenced by an animal's genotype as well as numerous management and environmental factors. Feed intake is associated with animal size and productivity in positive manner, such that single-trait selection for enhanced growth potential will increase energy requirements and appetite resulting in minimal favorable change in efficiency of feed utilization (Castilhos et al., 2010). Conversely, selection for lower feed intake will reduce genetic merit for growth resulting in undesirable affects on productivity. Most of the early research on the genetics of efficiency focused on ratio-based traits like feed:gain ratio (**F:G**). Because F:G is strongly correlated (r_g > -0.50) with growth traits in a negative manner, favorable postweaning selection for F:G will increase genetic merit for growth and mature size of breeding females (Herd and Bishop, 2000). Although selection for F:G would be expected to improve efficiency of feedlot progeny, there would be minimal effects on efficiency of progeny destined to become replacement females. Archer et al. (2002) reported that F:G measured in postweaning Angus heifers was highly correlated with mature weight (r_g = -0.54), but weakly correlated with feed intake (r_g = 0.15) in mature cows. These studies demonstrate that selection to improve F:G in growing cattle will lead to indirect selection for increased cow mature size and feed costs, with minimal affects on efficiency of feed utilization in mature cows.

An alternative approach to measuring feed efficiency involves partitioning feed energy inputs into maintenance and production components. Linear regression methods are used to compute expected feed intake based on an individual animal's BW and performance, with residual feed intake (**RFI**) defined as the difference between actual and expected feed intake. In growing animals, RFI quantifies inter-animal variation in feed intake that is unexplained by differences in BW and growth rate — efficient animals are those that consume less feed than expected for a given BW and growth rate. Residual feed intake has been shown to be moderately heritable and genetically independent of BW and level of production in poultry, pigs and beef and dairy cattle. In selection studies with poultry, pigs and beef cattle, progeny from parents divergently selected for RFI had substantial differences in feed intake, while maintaining similar body size and productivity. Because RFI is independent of body size and level of production, RFI better reflects inherent variation in metabolic processes associated with efficiency of feed utilization than ratio-based feed efficiency traits. In growing beef cattle, variation in RFI has been linked to differences in heat production, methane production, composition of gain and digestibility demonstrating that numerous biological processes are responsible for genetic variation in RFI. Herd and Arthur (2009) estimated that approximately one-third of the biological variation in RFI could be explained by inter-animal differences in digestion, heat increment, composition of gain and activity, with the remaining two-thirds of variation in RFI linked to differences in energy expenditures associated with biological processes like protein turnover, ion pumping and mitochondrial function. Moreover, in beef cattle the energetic costs associated with eating, chewing and ruminating can account for 10 to 33% of the total metabolizable energy derived from forages (Susenbeth et al., 1998). Multiple studies have shown that duration and frequency of feeding events were positively correlated with RFI, but minimally associated with F:G (Nkrumah et al., 2007; Lancaster et al., 2009b). Using slaughter-balance technique, Basarab et al. (2003) found that heat production was 10% higher in steers with high compared to low RFI phenotypes. Nkrumah et al. (2006) reported that steers with low RFI produced 21% less heat than steers with high RFI. Collectively, these studies demonstrate that inter-animal variation in whole-animal energy expenditure represents a substantial proportion of the observed differences in RFI, and indicate that this trait is highly associated with maintenance energy requirements.

Differences in body composition may also contribute to variation in RFI as lean tissue requires less energy per unit of gain than fat. In Angus bulls fed moderate-energy diets, Lancaster et al. (2009ab) found weak positive correlations between RFI and final ultrasound backfat depth, such that more efficient bulls and heifers were leaner. Slightly higher positive correlations between RFI and carcass fat traits have been reported in finishing steers (Basarab et al., 2003; Nkrumah et al., 2004), suggesting that differences in carcass composition may account for more of the variation in RFI of cattle that are fed high-energy diets then cattle fed low-energy diets. Differences in energy expenditures associated with growth of visceral organs such as liver, gastrointestinal tract and heart can also contribute to observed differences in RFI, as the metabolic activity of these tissues is much higher than carcass tissues. Basarab et al. (2003) found that steers with low RFI had 8% lower liver and total gastrointestinal tract weights compared to steers with high RFI phenotypes. In steers fed a high-grain diet, Nkrumah et al. (2006) found that steers with low RFI phenotypes had 28% lower methane energy losses and 6% higher apparent digestibilities compared to steers with high RFI phenotypes. Krueger et al. (2009) found that low-RFI Brangus heifers fed a roughage-based diet had 3% higher apparent digestibilities than heifers with high RFI. Based on observed differences in feed intake and apparent digestibilities for nitrogen and phosphorus between heifers with divergent phenotypes for RFI, Krueger et al. (2009) estimated that fecal excretion rates for nitrogen and phosphorus were 36 and 32% lower, respectively, in heifers with low compared to high RFI. Thus, improvements in feed efficiency will help mitigate the environmental impact of livestock production systems through reductions in nutrient excretions and methane-gas emissions (Basarab et al., 2013).

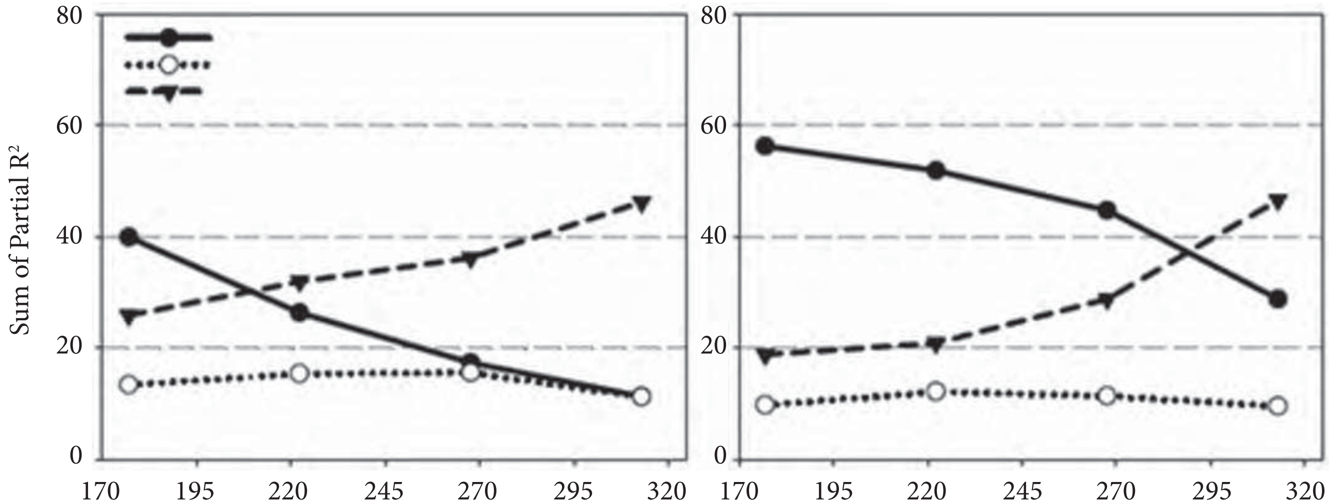

Figure 2. Comparison of variation in net revenue explained by productivity, feed efficiency and carcass quality related traits at various ration and base carcass price ($142 and $172/cwt for panels A and B, respectively) scenarios.

Responses to Postweaning RFI Selection

Feedlot Performance and Feed Efficiency. Few studies to date have examined direct and correlated responses to selection for RFI on performance and profitability of feedlot cattle. In an Australian study, Angus cattle were divergently selected for postweaning RFI for approximately 2 generations (Arthur et al., 2001). Significant divergence between selection lines was reported with direct selection responses in RFI equating to 0.55 lb DM/d per year. Progeny from parents selected for low RFI were similar in yearling BW and ADG, but consumed 11% less feed and had 15% lower F:G than progeny from high-RFI parents. Walter et al. (2012) examined phenotypic variation in performance, feed efficiency and carcass traits in Angus-based composite steers (N = 508) fed a high-grain diet. Steers classified as having low phenotypes for RFI (± 0.50 SD from mean RFI) consumed 16% less feed and had 18% lower F:G ratio then high-RFI steers. As expected, ADG and hot carcass weight were not affected by RFI. Steers with low RFI had significantly greater ribeye area and less backfat depth resulting in lower USDA yield grades (3.08 vs 3.25) compared to high-RFI steers. However, USDA quality grades (386 vs 398) were also lower for steers with low RFI. Despite the reduction in QG, carcass value based on grid-formula adjustments for carcass weight, YG and QG were not affected by RFI classification. Compared with high-RFI steers, net revenue favored the low-RFI steers by almost $64/head.

In this same study, Hafla et al. (2012b) evaluated interrelationships among productivity, feed efficiency and carcass traits to determine their relative contributions in explaining inter-animal variation in net revenue (**NR**). Using 3-year average prices for ration ($222/ton), carcass ($142/cwt), carcass premiums/discounts (e.g., choice-select spread; $6.25/cwt) and feeder calves obtained at the time of study, NR was found to be positively correlated with initial BW, ADG, carcass weight and QG (r_p = 0.28, 0.34, 0.49 and 0.27), and negatively correlated with DMI, F:G, RFI and YG (r_p = -0.18, -0.56, -0.53 and -0.29, respectively). Stepwise regression analysis revealed that nearly 74% of variation in NR was explained by these variables, with productivity (initial BW, ADG, carcass weight), feed efficiency (DMI, RFI) and carcass quality (YG, QG) related traits accounting for 26.4, 32.0, and 15.4% of NR variation, respectively.

To determine the sensitivity of input-output prices on factors affecting variation in NR, various ration ($177, $222, $267 and $312/ton), and carcass price scenarios ($142 and $172/cwt) were evaluated (Figure 2). As ration costs increased, the proportion of NR variation attributed to feed efficiency traits increased, while that attributed to productivity traits decreased.

At the higher carcass price scenarios, the proportion of explained variation in NR attributed to productivity-related traits increased relative to variation explained by the feed efficiency traits. With the choice-select spread of $6.25/cwt (average of 3-year study) held constant for these price scenarios, the variation in NR explained by carcass quality traits was minimally affected by change in ration price, and was slightly reduced when carcass price increased. Increases in choice-select spread would be expected to increase the proportion of NR variation explained by carcass quality traits relative to productivity and feed efficiency related

Table 1. Effects of heifer residual feed intake (RFI) classification on performance and forage intake in pregnant Bonsmara females

Trait	*Heifer RFI Classification*		
	Low RFI	*High RFI*	*SE*
Performance and forage intake[†]			
Initial BW, lb	1,069	1,056	18
BW gain, lb/d	0.64	0.81	0.13
Forage DMI, lb/d	24.2[a]	29.3[b]	1.21
Forage DMI, % mid-test BW	2.14[a]	2.61[b]	0.10
Change in BCS during study	-0.16	-0.09	0.08
Rump fat depth, in	0.46	0.44	0.04
Other traits			
Bunk visit frequency, bouts/d	116	119	7
Bunk visit duration, min/d	149[a]	198[b]	13
Heart rate, beats/min	66.1[a]	71.1[b]	1.7
Lying bout frequency, bouts/d	10.4	10.1	0.3
Step count, steps/d	105	98	6

[†]BW and BW gain were corrected for conceptus weight.

[a,b]Means without common superscripts differ at $P < 0.05$.

traits. These results demonstrate the relative importance of genetic merit for performance, feed efficiency and carcass quality in contributing to profitability of feedlot progeny of similar breed type and management background, which can be dynamically altered by changing input-output price scenarios.

Cow Efficiency and Productivity. Few studies have been conducted to determine if favorable selection for postweaning RFI will improve life-cycle efficiency of mature beef cows. Archer et al. (2002) measured postweaning RFI in Angus, Hereford and Shorthorn heifers and again in the same females following the birth of their 2nd calf. During this study, the mature cows were open and nonlactating, and were fed the same diet provided to heifers during the postweaning tests. Strong genetic correlations were observed between postweaning RFI of heifers, and feed intake and RFI (r_g = 0.64 and 0.98) of mature open cows, although the corresponding phenotypic correlations were lower (r_p = 0.34 and 0.40, respectively). A low negative genetic correlation between heifer RFI and mature cow weight (r_g = -0.22) was observed, indicating that favorable selection based on postweaning RFI will improve efficiency of feed utilization in cows with minimal affects on mature size. In a more recent study, Herd et al. (2011) reported a positive phenotypic correlation (r_p = 0.38) between postweaning RFI in heifers and RFI in open, dry cows that were fed *ad libitum*.

Basarab et al. (2007) examined the phenotypic relationships between RFI of progeny that were fed a high-grain diet and the efficiency of their dams while fed a high-roughage diet. Cows that produced calves with low RFI phenotypes consumed 11% less feed (23.8 vs 26.8 lb/d) than cows that produced calves with high RFI phenotypes. The RFI of cows were positively correlated (r_p = 0.30) with RFI of calves, but the low magnitude of this association suggests that RFI measured in cows fed a roughage diet may be a different trait than RFI measured in finishing calves. In this study, mature BW were similar between cows that produced progeny with divergent RFI phenotypes. Arthur et al. (2005) examined the effects of divergent selection for RFI over about 1.5 generations on maternal productivity of Angus cows. As expected, mature cow weights were similar for cows divergently selected for RFI, although cows selected for low RFI had lesser rump-fat depth at the start of the breeding season. No differences in calf birth or weaning weights were observed between the two RFI selection lines.

To determine if RFI classification of growing heifers was associated with efficiency of forage utilization in productive cows, Hafla et al. (2013) measured postweaning RFI in Bonsmara heifers for 2 consecutive years (N = 115), with the most and least efficient (N = 48) heifers retained for breeding. During the postweaning tests, heifers with low RFI consumed 20% less feed than high-RFI heifers, while maintaining similar body size and gain. Pregnant 1st and 2nd parity females were subsequently fed chopped hay in pens equipped with electronic feeders to measure forage intake. Pregnant females that were efficient (low RFI) as heifers subsequently consumed 17% less forage and spent 25% less time consuming forage (duration of bunk visit events) then their contemporaries that were inefficient (high RFI) as heifers (*Table 1*). Postweaning RFI classification did not affect gain in BW, gain in body condition score or ultrasound measurements during the study. Physical activity as assessed by lying-bout frequency and duration, and daily step counts was not affected by heifer RFI classification, although heart rates were 7% lower in pregnant females with low RFI as heifers. Significant interactions between parity and heifer RFI classification were not observed in this study. In a study involving 6 *Bos indicus* and *Bos tarus* breed types, Black et al. (2013) measured feed intake of 74 3-year-old females during first lactation that were previously determined to have divergent RFI phenotypes as heifers. Heifers with low RFI consumed 21% less feed then high-RFI heifers, with no differences in BW or daily gains observed. Lactating females with low RFI as heifers consumed 10% less feed (87% bermudagrass silage based diet) than females that were inefficient as heifers. Remarkably, heifer RFI classification had no effect on milk production, change in BW gain or body fat reserves during the 70-d study. In both studies, age at first or second calving was not affected by RFI classification as heifers. Results from these studies indicate that postweaning RFI in heifers is favorably associated phenotypically with efficient utilization of feed by gestating and lactating cows, with minimal affects on productivity or reproductive performance.

Associated Responses to Postweaning RFI Selection

Cow Reproductive Traits. Australian researchers were the first to examine the associations between selection for RFI and reproductive performance in beef cattle (Arthur et al., 2005). In Angus cattle, the effects of divergent selection for RFI on reproductive traits were examined across 3 breeding seasons. While differences in pregnancy, calving and weaning rates were not observed between selection lines, low-RFI cows calved 5 d later than cows selected for high RFI. However, the delay in calving date did not affect weaning weight, or weaning weight per cow exposed to breeding. Retrospectively, Basarab et al. (2007) examined the reproductive performance of crossbred cows (10 breeding seasons) that had produced progeny with divergent RFI phenotypes. Pregnancy, calving and weaning rates was similar between cows that produced progeny with divergent RFI phenotypes, but cows that produced low-RFI progeny calved 5 days later than cows that produced high-RFI progeny. In agreement with the previous studies, Donoghue et al. (2011) found that Angus females selected for low-RFI calved 8 days later then those selected for high RFI even though pregnancy and calving rates were similar. In all 3 studies, significant interactions between RFI line and mating year were not detected, indicating that observed differences in calving date in favor of high-RFI cows were likely due to delays in onset of puberty rather then to delays in return to estrus during the post-partum interval. In support of these findings, Crowley et al. (2011) reported that RFI of performance-tested bulls was genetically correlated in a negative manner (r_g = -0.29) with age at first calving, but not with calving to first service (r_g = -0.03) or calving intervals (r_g = 0.01). Thus, it appears that favorable selection for RFI may delay the onset of puberty in heifers, thereby increasing age at first conception without negatively affecting subsequent reproductive performance.

It has been well established that adequate body fat reserves are critical to hasten the onset of puberty in developing heifers. Given that numerous studies have demonstrated that low-RFI steers, bulls and heifers typically have less fat reserves compared to their high-RFI contemporaries, it would not be surprising to find negative associations between RFI and age of puberty. Lancaster et al. (2009a) reported that gain in rib-fat depth was 21% less in Brangus heifers with low RFI compared to those with high RFI. However, age of puberty, the proportion cycling by the end of the test, and pregnancy rate were not affected by RFI group in this study (Lancaster et al., 2008). In British-breed type heifers, Shaffer et al. (2011) found that RFI was positively correlated with rib-fat depth (r_p = 0.27), and negatively associated with age at puberty, such that for each unit reduction in RFI the onset of puberty was delayed by 7.5 d. Despite the negative relationship between RFI and age at puberty, pregnancy rates were similar between heifers with divergent phenotypes for RFI in this study. Donoghue et al. (2011) used serial ultrasonography to measure onset of puberty in heifers divergently selected for RFI. While not significant, the proportion of heifers that attained puberty was numerically lower in low-RFI heifers. Rump-fat depth was greater in heifers with high RFI, and irrespective of selection line, those heifers determined to have reached puberty had greater rump-fat depth than heifers that had not cycled. The lower fat reserves in heifers selected for low RFI likely contributed to the 8-day delay in age at first calving observed in this study.

In contrast to these studies, Basarab et al. (2011) found that crossbred heifers with low postweaning RFI had lower conception rates from day 12 to 37, and tended ($P = 0.09$) to have lower overall pregnancy rates (76.8 vs 86.3%) than high-RFI heifers. To determine if variation in body fat reserves contributed to the negative relationship between RFI and pregnancy outcome, postweaning RFI was adjusted for rib-fat depth. Heifers with low fat-adjusted RFI still had significantly lower conception rates from day 22 to 32 of the breeding season, but overall pregnancy rates (79.6 vs 83.7%) were no longer significantly different from heifers with high fat-adjusted RFI. Basarab et al. (2011) further surmised that test protocols designed to measure RFI in heifers from 8 to 12 mo of age may favor the selection of slightly later maturing animals based on the premise that heifers reaching puberty by the start of the test have increased energy expenditures associated with sexual development compared to their contemporaries that reach puberty at the end of the test. When RFI was adjusted for variation in both rib-fat depth and feeding behavior (frequency of feed bunk events), significant differences in overall pregnancy rate (80.8 vs 83.3%) were no longer observed. Collectively, these results imply that inter-animal variances in body fat reserves and activity associated with stage of sexual development may need to be considered when measuring RFI in breeding animals to ensure that favorable selection for RFI does not negatively affect long-term reproductive performance of beef cows.

Bull Reproductive Traits. The effects of favorable selection for postweaning RFI on bull fertility have yet to be extensively investigated. Hafla et al. (2012a) examined the relationships between RFI in bulls, and sperm motility and morphology of fresh semen. Bulls with low RFI phenotypes had similar sperm motility compared to bulls with high RFI. However, sperm morphology was weakly correlated with RFI, such that bulls with low RFI tended to have a lower proportion of normal sperm (74.0 vs 77.2%). Although Wang et al. (2012) found that sperm morphology was not affected by RFI classification of bulls, the proportion of bulls not meeting the minimum requirement for sperm motility tended ($P = 0.07$) to be greater in bulls with low RFI than those with high RFI. In this same study, bull fertility was also evaluated using a multi-sire natural-mating system involving bulls with divergent RFI. Despite finding decreased sperm motility in the low-RFI bulls, the number of progeny produced per sire was actually higher for low-RFI bulls (18.3 vs 11.8), as 2 of the high-RFI bulls failed to sire any progeny. In the studies cited above, RFI was not phenotypically correlated with scrotal circumference, which is known to be positively associated with sperm-producing ability and age of puberty of heifer progeny. Likewise, several Australian and Canadian studies have found that scrotal circumference was genetically independent of RFI in growing bulls. These results suggest the possibility that the low-RFI bulls may have been slower to reach puberty resulting in lower sperm quality at the time semen samples were collected. As with developing heifers, postweaning RFI in bulls may need to be adjusted for variation in backfat depth to prevent indirect selection for later maturing bulls.

Implications and Conclusions

There is substantial genetic variation in feed intake unrelated to variances in body size and productivity in beef cattle, which can be quantified by RFI. Adoption of multi-trait selection indexes to identify cattle with superior genetic merit for RFI will improve life-cycle efficiency and profitability of production systems through reductions in maintenance energy requirements and the costs of feed inputs with minimal effects on other economically relevant traits. To minimize the risk of indirect selection for later maturity in replacement heifers or reductions in quality grade of slaughter progeny, RFI should be adjusted for ultrasound backfat depth. While numerous seedstock operations and commercial bull test centers now have electronic measurement systems to collect individual feed intake data, this infrastructure capacity will need to be expanded to provide greater access to sires with accurate breeding values for feed efficiency. Advances in genomic technologies will continue to improve the accuracy and reduce the cost of identifying feed-efficient sires across multiple breeds and production environments. Development of decision-support tools that integrate these technologies with individual-animal phenotype data on feed efficiency and other economically important traits will improve profit margins of beef cattle production systems. Moreover, substantial reductions in manure nitrogen and phosphorus excretion, and greenhouse gas (e.g., methane) emissions are achievable through implementation of these selection indices (Basarab et al., 2013). Finally, more research is needed to examine effects of selection for postweaning RFI on life-cycle efficiency under more restrictive environmental conditions (e.g., low forage quality), and with *Bos indicus* breed types to more fully understand potential genotype by environmental interactions that most likely exist.

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