EVALUATION OF RESIDUAL FEED INTAKE IN CENTRALLY-TESTED BULLS AND RELATED STEERS

by

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Abstract

Feed intake was measured on 1433 Angus, Simmental and composite Simmental-Angus bulls at the Auburn University Beef Evaluation Center (AUBEC) from 1977 to 2007. All bulls were housed at the AUBEC for a minimum of 70 days. Bulls were trained to individual Calan Gates® within 21 days of arriving. All bulls were consigned by individual Alabama producers. Bulls were measured for weight and height either biweekly or monthly depending on year. SC and ultrasound measurements for carcass traits were taken at yearling age (330 to 400 days). Feed intake and carcass trait data from 760 Angus and Simmental-composite steers were acquired courtesy of the American Simmental Association's (ASA) Carcass Merit Project. Residual feed intake (RFI) was determined by regressing metabolic mid-weight and ADG on intake by year of test for bulls and by contemporary group for steers. High percentage Angus bulls consumed more DM per day, had higher FCR and RFI than purebred Angus, halfbloods, high percentage Simmental and Simmental bulls. Angus steers consumed more DM per day had higher FCR and RFI than high percentage Angus steers and halfbloods. Heritability was estimated for RFI using MTDFREML in bulls (0.42±0.05) and in steers (0.20±0.05). Genetic correlations between steer and bull RFI ranged from -0.18 to 0.33 depending on covariate. Bulls and steers classified as low RFI consumed less DM per day and had more favorable FCR than medium and high RFI animals. Results indicate RFI is a moderately heritable trait and improvements within feed intake and FCR should be achievable when selection is made with RFI. However, selection of bulls based on their RFI in an attempt for them to sire more efficient steers may not be practical as the genetic relationships between steer RFI and bull RFI were variable.

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List of Abbreviations

ADG	Average daily gain
ASA	American Simmental Association
AUBEC	Auburn University Beef Evaluation Center
BCS	Body condition score
BF	12th rib fat thickness
BW	Body weight
CYG	Calculated yield grade
DFI	Daily feed intake
DM	Dry matter
EBV	Estimated breed value
EPD	Expected progeny difference
FCR	Feed conversion ratio
FGR	Fat gain rate
FI	Feed intake
G:F	Gain to feed ratio
HCW	Hot carcass weight
IGF-1	Insulin-like growth factor
KPH	Kidney, pelvic, heart fat percentage
LEA	Loin eye area

MMWT	Metabolic mid-weight (midtest weight$^{0.75}$)
MTDFREML	Multiple trait derivative free restricted maximum likelihood
PGR	Protein gain rate
REA	Longissimus dorsi area
REML	Restricted maximum likelihood
RFI	Residual feed intake
RFI_{ADJ}	Residual feed intake adjusted for fat thickness
$RFI_{Formula}$	Residual feed intake calculated using NRC equations
RFI_{g}	Residual feed intake adjusted for genetic merit
RFI_{II}	Residual feed intake adjusted for fat gain and empty body water weight
RFI_{III}	Residual feed intake adjusted for USIMF and ISBF gain
SC	Scrotal circumference
SD	Standard deviation
SE	Standard error
USBF	Ultrasound 12th rib fat thickness
USIMF	Ultrasound intramuscular fat
USREA	Ultrasound longissimus dorsi area
USRF	Ultrasound rump fat
YG	USDA yield grade
YWT	365 day adjusted yearling weight

INTRODUCTION

Feed cost represents the largest expense in beef production (Fan et al., 1995; Arthur et al., 2001a; Archer et al., 2002; Basarab et al., 2003). While the majority of feed consumed (60 to 75%) by beef animals is required for maintenance (Arthur et al., 2001a; Basarab et al., 2003), the remainder of intake is used for production traits such as growth, lactation and development. Output traits such as growth and carcass measurements have been characterized and used as the basis of selection by most performance minded cattle producers for many years. However, how efficiently a beef animal can convert its feedstuffs into a unit of production is a trait many want to be included into genetic evaluations. Producers, stockers and feeders desire cattle that produce the most outputs from the least amount of inputs possible. All stages of production could benefit from a genetic improvement in feed efficiency (Herd et al., 2003).

Questions arise from cow/calf producers when discussing efficiency. Can producers assume two cows of equal weight and milk production consume similar amount of feed? Factors including age, diet, temperature, breed, use of growth promoting implants and ionophores, along with other management and environmental variables influence the overall efficiency of the cow herd (Herring and Bertrand, 2002).

Feed efficiency is also important in the backgrounding stage. For every 0.06 decrease in the average feed conversion ratio (FCR) of a group of stocker calves, a producer could increase the stocking rate of the pasture by one head of cattle. A feeder perhaps can feel the effects of changes in feed efficiency more so than other sectors of beef production. Consider two pens of 100 steers each with statistically similar average daily gains (ADG) and final weights, with one pen having an as-fed FCR of 6 and the other pen having a FCR of 7. Over a period of 200 days, the feeder could realize thousands of dollars in savings for the more efficient pen. If selection for improvement in feed efficiency can be made, producers at all phases of the U.S. beef industry could experience dollars saved.

There are many measurements of feed efficiency described in the literature. Among those are FCR, gain to feed intake ratio (G:F), and residual feed intake (RFI). FCR is defined as the units of feed required for one unit of gain. The inverse of FCR is referred to as G:F, or in other words, units of gain per one unit of feed consumed. RFI is defined as the amount of feed an animal consumes over or under what is expected based on its weight and gain. An efficient animal would have a negative RFI and an inefficient animal would have a positive RFI. In order to acquire these measurements of feed efficiency, two primary types of data must be collected: serial weights of individual animals over a given time period and individual daily animal feed intake (FI). Feeding trials conducted by university researchers and progressive producers are currently the primary means of obtaining data for such traits.

When comparing beef cattle to other food producing livestock, cattle are the least efficient in converting feedstuffs to a source of protein. Pond-raised catfish have the most efficient FCR with a ratio 1.1:1.0. Broilers have a FCR equal to 2.0:1.0 and swine will consume 2.5 to 3.0 units of feed for every unit of gain. Conversely, the average growing beef animal exhibits a FCR of 6 to 7 units of feed on a dry matter basis (DM) for every unit of gain (Crews, 2005).

Literature suggests FCR is moderately heritable (Wolderhariat et al., 1978; Koots et al., 1994a; Arthur et al., 2001b). Genetic improvement should be possible in feed efficiency using FCR as a selection tool. However there are problems using ratios for selection (Gunnsett, 1984). Any change in the component traits of FCR (ADG or daily feed intake (DFI)) leads to changes in FCR. While FCR and ADG have favorable genetic and phenotypic correlations to one another, ADG tends to be correlated with increased weights in mature cows which are correlated with an increase in feed intake. Thus, savings realized in improvement in FCR may be offset by having larger cattle with higher energy requirements.

RFI was first proposed by Byerly (1941) in laying hens and in beef cattle by Koch and coworkers in 1963. RFI is calculated by subtracting predicted intake from actual, observed feed intake. RFI is the portion of feed intake not accounted for by measurable factors (Byerly, 1941; Koch et al., 1963, Crews, 2005). Predicted intake is derived from the regression equation of: $DFI = \beta_0 + \beta_1 (ADG) + \beta_2(WT) + RFI$, where DFI is the average daily feed intake, β_0 is the regression intercept, β_1 is the partial regression of daily intake on ADG and β_2 is the partial regression of daily intake on body weight. In almost all cases the weight variable used is the midweight on test raised to a power of 0.75 to equal its metabolic equivalent (MMWT). Statistical properties of RFI include the mean RFI within a group is equal to zero ($RFI \sim N(0,\sigma^2 RFI)$, and RFI is phenotypically uncorrelated to those measurable factors included in the base regression model (ADG and WT) (Kennedy et al., 1993).

There are many tools available for beef producers to use for bull selection. Producers can set threshold criteria for multiple traits and chose bulls with EPD values within the desired range. Opportunities exist for selection of a complete bull whose progeny have potential to be profitable. With the inclusion of a measure of feed intake, such as RFI, in a genetic evaluation, producers could evaluate differences in input costs instead of solely relying on output EPD values to predict profitability in future calf crops.

REVIEW OF LITERATURE

History of Central Feed Tests

In 1946, researchers at the U.S. Range Livestock Experiment Station in Miles City, Montana saw the need for characterization of performance and economically relevant traits in beef cattle (Knapp and Nordskog, 1946). Traits analyzed from 177 steer calves by 23 sires included birth weight, weaning weight, final weight, ADG and efficiency of gain. Heritabilities were determined by both half-sib correlations and sire-offspring regression. The authors estimated heritability for ADG to be 0.99 and 0.97, while those for efficiency of gain to be 0.54 and 0.48. The authors noted these estimates for ADG were unreasonably high, but left producers with encouragement that traits of ADG and FCR could be improved via selection.

The first recorded post-weaning full scale test for gain took place at Blue Bonnet Farm in McGregor, Texas, during 1949 and 1950 (Warwick and Cartwright, 1955). The authors noted in order for feeders to be profitable, cattle must have an ability to gain weight rapidly and hypothesized that gain of sires and dams in a feedlot type setting could be indicative of progeny gain. Eight hundred fifty three animals, both bulls and heifers either raised at the experiment station or consigned by local producers, were tested over a period of four years. It was determined placing bulls on performance tests would be preferred to traditional progeny testing since heritability for rate of gain was reasonably high. Producers could consign weaned bull calves to a test, have gain evaluated, and select bulls as sires based on ability to gain. Data generated from performance tests were used by producers both as a comparison and selection tool and, when contemporary groups were greater than 1, in the respective breed associations for genetic evaluations.

While the length of bull evaluations have varied over the years, in 1997, Archer and co-workers conducted a study to determine the optimal length of test for measuring feed intake and the interval needed between the collection of weights on 760 British-influenced bulls and heifers. Traits analyzed were ADG, DFI, FCR, and RFI. The range of test length varied from a minimum of 7 days to a maximum length of 119 days with 7 day intervals. These cattle had ad-libitum access to their diet. Feed intake was measured and cattle were weighed at intervals of 1, 2, 5 or 10 weeks. Additive genetic, environmental and phenotypic variances, genetic and phenotypic correlations and heritability estimates were calculated within and among traits. Although weekly weighing of the animals provided a greater efficiency of selection value and heritability estimate for RFI, bi-weekly weigh dates result in more favorable selection value and heritability estimates for ADG and FCR. The authors concluded a 35 d test was adequate for the measurement of DFI, but a 70 d test with bi-weekly weigh dates was necessary for the evaluation of ADG, FCR and RFI. Wang and coworkers (2006) argued the length of test could be shortened if measurements of DFI and body weights (BW) were repeated on each animal throughout the duration of the test. These authors found for the traits of ADG and RFI, test length could be shortened to 63 days and for DMI and FCR, the test duration could be cut to 35 and 42 days, respectively. Differences in recommended test length between the two studies could have occurred due to methods for collection of DFI.

The cattle Archer and coworkers (1997) used were fed using a system much like a Calan® system, where cattle have transponders within a collar around the animal's neck. However instead of manually weighing the feed, the feeding system is automatic and controlled by a small personal computer. The Wang study (2006) cattle were fed using a Growsafe® system, a system which uses radiofrequency identification to measure feed intake and several different feeding behaviors such as feeding frequency and meal duration. There are benefits to shortening the test length from 119 days to 63-70 days including decreased labor cost with each test and the possibility of having more than 2 tests in any given year. Shortening test length also decreases the chances of injury and sickness while on test.

Measures of Feed Efficiency:

Feed Conversion Ratio:

Feed conversion ratio is generally depicted as units of feed required for one unit of gain, or as its inverse, G:F, units of gain for every one unit of feed consumed. For FCR, a lower numerical value would identify a more efficient animal and for G:F, a larger number is indicative of greater efficiency. While FCR is moderately heritable (Arthur et al., 2001a; Arthur et al., 2001b; Arthur et al., 1997; Bishop et al., 1991b; Brown et al., 1988, Carter and Kincaid 1959a; Gengler et al., 1995; Koots et al., 1994a; Herring and Bertrand, 2002), it often has unfavorable genetic and phenotypic correlations associated with it that would offset any profitability a producer could gain from improvements in FCR, such as increases in mature BW and DFI.

Heritability of FCR:

While there has been a recent spark of interest in measuring feed efficiency, research has been conducted on this trait in beef animals since the mid 1940s (Knapp and Nordskog, 1946). Using data from 177 steer calves from 23 sires, Knapp and Nordskog (1946) determined heritability for FCR by both half-sib correlations and by a sire-offspring regression to be 0.54 and 0.48, respectively.

Shelby and coworkers (1955) used data from 635 Hereford steers by 88 sires and 9 inbred lines. They estimated heritability for efficiency (kg of gain/ 100 kg of TDN consumed) for individually fed steers to be 0.22. The authors noted G:F was the only trait analyzed in which dam lines were statistically significant, noting high efficiency lines could be developed (Shelby et al., 1955).

A heritability estimate for FCR of 0.38 ± 0.09 was published in 1955 by Warwick and Cartwright. Carter and Kincaid (1959a) determined heritability estimates for FCR using two methods: paternal half-sib correlation and regression of progeny average on sire's records from 424 calves and 38 sires. Half-sib heritability estimates for FCR were found to be 0.99 and 0.22. The authors noted the estimate of 0.99 was unrealistic but was only based on 18 degrees of freedom for the sires (Carter and Kincaid, 1959a).

Woldehawariat and coworkers (1978) published a summary of heritability estimates of various definitions of feed efficiency from published literature through 1977. The summary included 17 studies and reported 30 estimates of heritability. The authors averaged their findings and concluded FCR was moderately heritable with an overall weighted mean heritability of 0.47. In 1994, Koots and coworkers (1994a) also summarized heritability estimates in the literature for beef production traits from 1946 to

1991. They found mean heritability estimates (unweighted, weighted) for FCR to be 0.36 and 0.32 and G:F to be 0.42 and 0.37, respectively.

Using modern statistical techniques, such as restricted maximum likelihood (REML), and high technology feeding systems (Calan® and Growsafe®), heritability estimates for FCR continue to be reported in the range moderate to high. Archer and coworkers (1997) compared heritability estimates for several test durations. The 56 d test length measuring FCR was found to have the highest heritability estimate (0.48±0.13). Arthur and coworkers (2001a) found heritabilities of FCR in 15 month old and 19 month old Charolais bulls (n=510) of 0.46 ± 0.04 and 0.31 ± 0.06. These two traits were highly correlated both phenotypically and genetically (r_p=0.82, r_g=0.93 ±0.04) to one another (Arthur et al., 2001a). Using records from 1180 Angus bulls and heifers, a heritability of 0.29 ± 0.04 was estimated for FCR (Arthur et al., 2001b). A similar FCR heritability of 0.31 ± 0.09 was found in 966 bulls and heifers (Arthur et al., 1997). Schenkel and coworkers (2004) found a heritability of FCR in young beef bulls to be 0.37 ± 0.06.

Bishop and coworkers (1991b) reported a realized heritability for unadjusted FCR to be 0.26 and FCR adjusted for body weight to be 0.46. The authors noted differences in heritability estimates reflected variation accounted for by adjustment for body weight differences and thus maintenance requirements of individual progeny (Bishop et al., 1991b).

Lower heritability estimates for FCR have also been published on breeding animals (Brown et al., 1988; Fan et al., 1995; Gengler et al., 1995; Herd et al., 2000; Jensen et al., 1991). Using Angus and Hereford bulls, heritability estimates for FCR of 0.14 ± .07 and 0.13 ± .08, respectfully, were found by Brown and coworkers (1988). Fan and coworkers (1995) reported heritability estimates for FCR on 263 Angus and 271 Hereford bulls of 0.08 ± 0.09 and 0.35 ± 0.22, respectively with a pooled heritability of 0.16 ± 0.14. Gengler and coworkers (1995), using double-muscled Belgium Blue bulls, determined a heritability for FCR of 0.16 (1995). Using data from 540 British Hereford bulls, Herd and coworkers (2000) estimated the heritability of FCR to be 0.26 ± 0.09. In 1991, Jensen and coworkers published heritability estimates for FCR in dual purpose bulls to be 0.20 (from 28 days of age to 200 kg live weight) and 0.27 (from 200 kg to slaughter).

Heritability estimates for market animals tended to be more variable in the literature. Herring and Bertrand (2002) reported a heritability of FCR in 353 steers from the Angus Sire Alliance Project to be 0.15. Conversely, using data from 464 steers, a heritability estimate for FCR was found to be 0.41 ± 0.15 (Nkrumah et al., 2007b). On 1481 tropically adapted steers and heifers a heritability of 0.06 ± 0.04 was found for FCR (Robinson and Oddy, 2004).

In general, heritabilities for FCR are low to moderate in swine. Hermesch (1999) estimated the heritability of FCR to be 0.15 ± 0.04 in Australian pigs. Hoque and coworkers (2007) reported a heritability of FCR in Duroc pigs to be 0.27 ± 0.03. A heritability of 0.16 was found for FCR in large white swine (Johnson et al., 1999). Robison and Berruecos (1973) calculated FCR and G:F ratio on 321 barrows for three different intervals: age to age, weight to weight and age to weight. They found heritability estimates for FCR were higher than those for G:F (Robison and Berruecos, 1973). Cai and coworkers (2008) found of a heritability of G:F in 756 Yorkshire swine to be 0.17 ± 0.07.

Genetic and Phenotypic Correlations of FCR with Other Relevant Traits:

FCR with Feed intake:

Literature suggests FI can be improved (decreased) by selecting for lower FCR. Most reports find FI and FCR to have a phenotypic correlation between 0.30 and 0.72 (Arthur et al., 2001a,b; Baker et al., 2006; Herring and Bertrand, 2002; Liu et al., 2000; Nkrumah et al., 2004; Nkrumah et al., 2007c; Schenkel et al., 2004). Genetic correlations between FI and FCR most commonly fall within the rage 0.31 to 0.64 (Arthur et al., 2001a; Arthur et al., 2001b; Koots et al., 1994b). Koots (1994b) reported a mean genetic correlation between FCR and FI of 0.38 using published literature between 1946 and 1991.

Jensen and coworkers (1991) found much higher relationships between FCR and FI in 650 dual purpose bulls (r_p =0.90, r_g = 0.98). However, Castro Bulle and coworkers (2007), as well as Robinson and Oddy (2004) reported conflicting results. Castro Bulle and coworkers (2007) found G:F to be highly correlated phenotypically with DMI (r_p =0.744). Robinson and Oddy (2004) estimated negative relationships between FCR with FI (r_p = -0.14 ± 0.03 r_g = -0.49 ± 0.22). Carstens and Tedeschi (2006) reported FCR and FI to have a positive, but weak phenotypic relationship during both the growing (0.12) and finishing stages (0.25) of calves.

Hoque and coworkers (2007) reported genetic and phenotypic correlations using Duroc pigs between FCR and FI (r_p = 0.57 ± 0.08, r_g =0.46 ± 0.07). Cai and coworkers (2008) reported similar genetic and phenotypic correlations of G:F with DFI in Yorkshire swine (r_p = -0.26 ± 0.05, r_g = -0.26 ± 0.21).

FCR with ADG:

Most literature reports suggest FCR and ADG are negatively, but favorably related. Phenotypic correlations generally range from -0.50 to -0.74 (Authur et al., 2001a; Authur et al., 2001b; Baker et al., 2006; Carter and Kincaid, 1959b; Carstens et al., 2002; Lancaster et al., 2005; Liu et al., 2000; Nkrumah et al., 2004; Schenkel et al., 2004). Genetic correlations between FCR and ADG are normally found within the range of -0.32 to -0.62 (Authur et al., 2001a; Authur et al., 2001b; Carter and Kincaid, 1959b; Koots et al., 1994b; Schenkel et al., 2004). Gengler and coworkers (1995) estimated much higher genetic and phenotypic correlations between FCR and ADG in double muscled Belgian Blue bulls (r_p = -0.89; r_g = -0.66). These estimates suggest high performing/fast gaining cattle have a more efficient/lower FCR.

Conversely, Herring and Bertrand (2002) used 353 Angus steers from the Angus Sire Alliance Project to estimate genetic correlations between FCR and ADG (r_g= 0.01). The authors explained this low genetic correlation by stating that FCR was more driven by FI rather than ADG. Robinson and Oddy (2004) also had similar results. They found FCR to essentially lack a phenotypic correlation with ADG (r_p = -0.08 ± 0.03), but reported a very strong negative genetic correlation between the two traits (r_g = -0.86 ± 0.10). The authors defended their lack of a strong phenotypic correlation stating, there were inaccuracies in estimation of weight gain.

The relationship between FCR and ADG is important in both the growing and finishing stages of cattle and does not appear to change over time. Genetic and phenotypic correlations were found between FCR and ADG from 28 days of age to 200 kg live weight (r_p = -0.83, r_g = -0.89) and from 200 kg live weight to slaughter (r_p =-0.86,

r_g = -0.91) in 650 dual purpose bulls (Jensen et al., 1991). Carstens and Tedeschi (2006) reported FCR to be strongly correlated with ADG during both growing and finishing phases of production (-0.60 and -0.58).

In other studies where G:F was measured as an alternate to FCR, strong genetic and phenotypic correlations between ADG and G:F were reported (Castro Bulle et al., 2007; Fan et al., 1995). Castro Bulle and coworkers (2007) found G:F to be phenotypically correlated with ADG (0.966, $P<0.001$). Fan and coworkers (1995) found phenotypic and genetic relationships between G:F with ADG in Hereford and Angus cattle (Hereford r_p =0.42, r_g =0.62; Angus r_p = 0.73, r_g = 0.68).

Literature supports if a producer selects swine with improved ADG to harvest weight, an improvement in feed efficiency can be observed. Hoque and coworkers (2007) reported genetic and phenotypic correlations using Duroc pigs between FCR and ADG (r_g = -0.10 ± 0.07, r_p = -0.25 ± 0.09). Johnson and coworkers (1999) found stronger genetic and phenotypic and correlations between FCR and ADG (r_p =-0.39 and r_g = -0.32) in Large White Swine (Johnson et al., 1999).Cai and coworkers (2008) reported both genetic and phenotypic correlations of G:F with ADG in Yorkshire swine (r_p =0.46 ± 0.04, r_g = 0.30 ± 0.21).

FCR with body weight:

While there are many measurements of BW within the literature, FCR is generally positively correlated with all weaning and post-weaning BW such as yearling weight, on-test weight, mid-test weight, MMWT, final-test weight and mature BW. However, Arthur nd coworkers (2001a) reported a slightly different phenotypic correlation between FCR and 365 d body weight (r_p =-0.08; r_g =0.24 ± 0.09). Phenotypic correlations appear to be moderate while genetic correlations tend to be more variable. Koots and coworkers (1994b) reported a low genetic correlation between FCR and weaning weight from published literature (0.16). Most literature reports FCR to have a significant phenotypic correlation with initial test weight range from 0.28 to 0.46 (Baker et al., 2006; Carstens et al., 2002; Carstens and Tedeschi, 2006). Carstens and Tedeschi (2006) reported FCR during the growing and finishing phase of feeder cattle to be strongly correlated with initial weight (0.28 and 0.40).

Carter and Kincaid (1959b) used 195 steers by 36 sires to find phenotypic and genetic correlations between FCR and 182 d weight (r_p =0.26; r_g =0.43). Fan and coworkers (1995) found moderate phenotypic and genetic relationships between G:F with YWT (Hereford: r_p =0.27, r_g =0.47; Angus: r_p = 0.67, r_g = 0.61). Baker and coworkers (2006) found FCR to be phenotypically correlated with final weight after 70 days of test (0.34, P=0.01).

With mid-test weight and its metabolic equivalent (MMWT) being commonly used as regressors in the calculation of RFI, literature has shown FCR is related to both these traits. Lancaster and coworkers (2005) estimated a phenotypic correlation between FCR and MMWT (0.23) from 240 Angus and Brangus bulls. Phenotypic correlations of FCR with mid-test weight (0.60, P=0.0001) were found on 282 beef bulls of eight breeds by Liu and coworkers (2000). Arthur and coworkers (2001b) reported FCR to be lowly correlated with MMWT (r_p =0.16, r_g = -0.01 ±0.07). However, FCR is essentially uncorrelated with scrotal circumference (SC) (Arthur et al., 2001b; Hecht and Kriese-Anderson , 2007).

Hoque and coworkers (2007) reported genetic and phenotypic correlations using Duroc pigs between FCR and MMWT ($r_g = -0.36 \pm 0.14$, $r_p = -0.13 \pm 0.09$), suggesting as feed efficiency improves, swine get heavier.

FCR with carcass traits and other traits:

Most literature agrees about relationships between FCR and ADG, BW and FI. However, there is much variation among the relationship between FCR with other economically relevant traits such as ultrasound and carcass measurements of fat thickness, longissimus dorsi area and intramuscular fat.

An interesting note is the relationship between FCR with daily heat production. Nkrumah and coworkers (2007c) reported a significant phenotypic correlation between these two traits ($r_p = 0.37$, $P<0.05$). This suggests more efficient animals lost less energy in their body's biochemical processes to heat and most likely have lower maintenance energy levels.

There is much variation among literature reports on the relationship between FCR and ultrasound fat thickness. Arthur and coworkers (2001b) reported FCR was uncorrelated with ultrasound 12th rib fat thickness (USBF) and ultrasound rump fat. However, other significant phenotypic correlations between FCR and USBF were found by Schenkel and coworkers (2004) ($r_p = 0.14$; $P<0.05$) as well as Nkrumah and coworkers (2004) (0.21, $P<0.05$).

There is much dispute in the literature concerning the relationship between FCR and ultrasound longissimus dorsi area (USREA). Baker and coworkers (2006) found FCR to be phenotypically correlated with initial USREA (0.64, $P=0.001$) in 54 purebred

Angus steers. Schenkel and coworkers (2004) also found FCR to be significantly correlated with UREA (r_p = -0.07 r_g = -0.28; P<0.05) in young beef bulls, but in an opposite magnitude. USREA is commonly correlated with growth traits, thus a negative, low correlation between USREA and FCR is not uncommon (Arthur et al., 2001b).

When serial ultrasound measurements are taken throughout the duration of a test, traits such as protein gain rate (PGR) and fat gain rate (FGR) can be measured. PGR is determined by gain in size of the longissimus dorsi area divided by the number of days on test. FGR is calculated using USBF measurements. Castro Bulle and coworkers (2007), found G:F to be phenotypically correlated with PGR (0.447, P<0.05) and FGR (0.534, P<0.01). Nkrumah and coworkers (2004) reported conflicting results between FCR and FGR (0.20, P<0.05).

Like ultrasound measurements, carcass traits also vary in their relationship with FCR. Koots and coworkers (1994b) averaged genetic correlations from published literature of FCR with fat thickness (-0.24). Herring and Bertrand (2002) found similar genetic correlations of FCR with carcass fat (-0.09) and marbling score (0.14).Nkrumah and coworkers (2004) found FCR to be phenotypically related to carcass grade fat (0.19, P<0.05), lean meat yield (-0.18, P<0.05), and YG (0.24, P<0.05) on 150 hybrid cattle. Carter and Kincaid (1959b) used 195 steers by 36 sires to find phenotypic and genetic correlations between FCR with USDA feeder grade (r_p =0.11; r_g =-0.11), USDA slaughter grade (r_p =0.08; r_g =0.18) and USDA carcass grade (r_p =0.16; r_g =0.16). The relationships between FCR and carcass fat should not be taken lightly. While feeders could save money by improvements in FCR, perhaps they could also lose premiums if improvements in FCR caused a decrease in marbling.

Selection using FCR:

In a selection study designed by Bishop and others (1991a), 33 to 35 Angus bull calves were individually fed each year to acquire feed intake data for 5 years. The three highest and lowest bulls for FCR were selected to mate approximately 20 cows each. A different set of bulls were used each year for a total of 24 sires with 403 progeny.

Progeny were evaluated by sire groups for postweaning and carcass characteristics. After each 140 d test was completed, any animal with 8.9 mm of ultrasound backfat or more were harvested. Animals without the required backfat measurement of 8.9 mm were fed for additional 28 d periods until the desired minimum was reached. High FCR sires tended ($P< 0.10$) to sire calves with heavier adjusted 205 d weaning weights and on test weights. High FCR sires also sired calves with heavier final weights(379 kg vs. 360 kg; $P< 0.05$), more back fat (9.14 mm vs. 8.38 mm; $P< 0.05$), and better ADG (1.19 kg/d vs. 1.11 kg/d; $P< 0.01$) than the low FCR sires at the conclusion of the 140 d test.

There were no differences between the two sire groups for the traits of off test weight adjusted for a fat-constant endpoint or days on test. There were no statistically significant differences between low FCR and high FCR sired progeny for HCW, KPH, REA, YG, dressing percent, marbling or USDA quality grade. However, high FCR sired cattle had more backfat than cattle sired by the low FCR bulls (10.67 mm vs. 9.65 mm; $P< 0.05$). The author reported even though sires were divergently selected for FCR, there were no differences in the FCR of their progeny. (Bishop et al., 1991a).

Bishop and coworkers (1991b) estimated phenotypic correlations for FCR for the first 140 days on test, ADG for the first 140 days on test and FCR for the entire test with other traits (Bishop et al, 1991b). The authors defined a phenotypic correlation to be different from zero if it was greater than 0.39 or less than -0.39 (Bishop et al., 1991b). The traits of adjusted 205 d weaning weight, dressing percentage, 12th rib fat thickness, hip height, KPH, muscle color, muscle firmness, muscle texture, off-test weight, quality grade, REA, weight at the end of the 140 d test, and YG did not exhibit significant phenotypic relationships with FCR (Bishop et al, 1991b). Phenotypic correlations significantly different from 0 for FCR for the first 140 d included: FCR adjusted for the first 140 days (r_p = 0.89), average feed intake for the first 140 days (r_p = 0.49), feed intake for the entire test (r_p = 0.51), days on test (r_p = 0.44), FCR for the entire test (r_p = 0.63), and total gain (r_p = 0.60). The authors found no phenotypic relationships between the traits of ADG adjusted to a fat constant endpoint, ADG for the first 140 d, average BF at the end of the first 140 d and marbling (Bishop et al, 1991b). Phenotypic correlations significantly different from zero between adjusted FCR for the first 140 d were with the following traits: ADG to a fat constant endpoint (r_p = -0.40), ADG for the first 140 d (r_p = -0.54), feed intake for the entire test (r_p = 0.39), average BF at the end of the first 140 d (r_p = -0.44), days on test (r_p = 0.42), FCR for the entire test (r_p = 0.61), FCR for the first 140 d (r_p = 0.97), on-test age (r_p = -0.52) and total gain (r_p = 0.51). Phenotypic correlations significantly different from zero among adjusted FCR for the entire test were those with adjusted FCR for the first 140 d (r_p = 0.59), feed intake for the entire test (r_p = 0.58), and FCR for the first 140 d (r_p = 0.63) (Bishop et al, 1991b).

Problems associated with selecting for a ratio:

Many times genotypes with improved FCR will also have increased ADG, and therefore tend to have heavier mature cow weights, consequently requiring more feed inputs (Archer et al., 1999). Incorporating FCR into a selection index could cause problems. If one of its components was also used in the index (van der Werf, 2004). Gunsett (1984) suggested instead of making selection decisions on a ratio, one should use a linear index to increase selection responses. Direct selection on a ratio causes the pressure placed on the components to be a function of selection intensity. As the selection intensity increased, direct selection on the ratio causes the selection to be based primarily on the information in the numerator, regardless of the distributional properties of the components of the ratio. Selection on a ratio will change the selection pressure placed on the components in a non-linear fashion (Gunsett, 1984).

Residual Feed Intake:

Determination of RFI:

The literature has described several regression models to determine RFI (Arthur et al., 2003; Jensen et al., 1992; Hoque and Oikawa, 2004; Robinson and Oddy, 2004; Basarab et al., 2007). There is still much debate among the scientific community as to the correct regressors and whether the addition of regressors beyond MMWT and ADG are appropriate.

Arthur and coworkers (2003) analyzed traits of DFI, ADG, MMWT, USBF, change in USBF over a 70 d test, REA and change in USREA over a 70 d test. With the inclusion of the four preceding ultrasound carcass measurements in the regression model, the R^2 rose 4.8 percentage points in males and 2.3 percentage points in females. The authors found the correlation between the original model and the new model to be 0.94 and 0.97 for males and females, respectively, suggesting re-ranking among the animals would be small and insignificant. Therefore, the authors suggested using only the regressors of MMWT and ADG in determining RFI (Arthur et al., 2003). Research by Basarab and coworkers (2007) agreed. After calculating RFI using two methods, the traditional RFI model (using MMWT and ADG as regressors) and then adding a regressor of off-test back fat thickness (RFI_{ADJ}), the authors reported a simple correlation between the two RFI models was 0.96. This suggests they are essentially the same trait (Basarab et al., 2007).

Jensen and coworkers (1992) evaluated dairy bulls for two periods. Period 1 (P1) spanned from 28 days to 200 kg and period 2 (P2) spanned from 200 kg to slaughter. RFI was analyzed two ways. The first method adjusted RFI for body composition. The second method did not adjust for body composition. Carcass composition contributed very limited information in predicting total energy intake since both genetic and phenotypic correlations were high between the two calculations of RFI within each period ($R^2 > 0.94$) (Jensen et al., 1992).

Hoque and Oikawa (2004) analyzed RFI, using the standard regression equation, and genetic RFI (RFI_g) with the equation $FI=\beta W*MMWT + \beta G*ADG + RFI_g$, where genetic regression coefficient, $[\beta W / \beta G] = G^{-1}c$, where G=genetic covariance matrix of two production traits (MMWT and ADG) and c=vector of the genetic covariance of feed intake with production traits estimated using REML. The authors found a very high henotypic correlation between the two measurements of RFI (>0.95), and concluded RFI and RFI_g were, for all intents and purposes, the same trait.

Robinson and Oddy (2004) estimated heritability values for RFI (0.18 ± 0.06) and $RFI_{Formula}$ (0.13 ± 0.05) using standard regression equations and NRC predicted intake formula, respectively, on 1481 tropically adapted steers and heifers. RFI was highly correlated with $RFI_{Formula}$ ($r_p = 0.94 \pm 0.03$ $r_g = 0.98 \pm 0.03$).

Using 176 crossbred steers fed in a Growsafe® system, Basarab and coworkers (2007) calculated RFI three ways. RFI was estimated using ADG and MMWT (mid weight to the 0.75 power) as regressors (R^2=0.714 and 0.824 for year 1 and year 2, respectfully). RFI_{II} was estimated using ADG, MMWT, fat gain, and empty body H_2O weight (R^2=0.757, 0.853). RFI_{III} was estimated using ADG, MMWT, USBF gain, and ultrasound marbling gain (R^2=0.741, 0.846). The authors recommended RFI_{III} be used as the method for calculating RFI for central bull test station data so producers could select for RFI without any negative benefits from a carcass perspective.

Heritability of RFI:

Research suggests RFI is a moderately heritable trait and therefore selection can be successful. Koch and coworkers (1963) reported the first heritability estimate of RFI in beef cattle as 0.28 ± 0.11.

The resurging interest in beef cattle RFI was led by Australian researchers. When Archer and coworkers (1997) were determining optimum length for a performance test, they found heritability estimates for RFI ranged from 0.34 to 0.64. The authors concluded a 70 d test (h^2=0.62 ± 0.14) was sufficient for the calculation of RFI since at that point the efficiency of selection was 0.99. The researchers also reported that a 2 week interval between weigh dates was sufficient for the accurate calculation of RFI (Archer et al., 1997). Arthur and coworkers (1997) reported a similar heritability estimate of 0.44 ± 0.07 for RFI in 966 bulls and heifers.

Arthur and coworkers (2001a) determined heritability and correlation estimates for 2 ages of bulls (15 and 19 months). Fifteen month RFI heritability was found to be 0.46 ± 0.04 with a genetic variance of 0.255. The 19 month estimate of RFI heritability was lower at 0.31 ± 0.06 with a genetic variance of 0.147. The phenotypic and genetic correlations between the two measures of RFI were 0.93 ± 0.04 and 0.82, respectively (Arthur et al., 2001a). This suggests many of the same genes are being expressed at the 2 different ages in bulls. In a study using 1180 young Angus bulls, heritability of RFI was found to 0.39 ± 0.03 (Arthur et al., 2001b). Jensen and coworkers (1992) estimated heritability for RFI during different ages/weights. In contrast to Arthur and coworkers study, Jensen and coworkers reported a lower heritability estimate for both RFI and RFI_{ADJ} for the younger/lighter animals (0.077 ± 0.049 and 0.082 ± 0.059 vs. 0.275 ± 0.114 and 0.363 ± 0.171)(Jensen et al., 1992).

Lower estimates of RFI heritability in bulls have also been reported (Hecht and Kriese-Anderson, 2007; Herd and Bishop, 2000). Heritability estimates for RFI ranged from 0.08 to 0.16.

RFI heritability estimates for steers reported in literature seem to be lower and in a more consistent range than those estimates for breeding cattle. Schenkel and coworkers (2004) calculated RFI and RFI_{ADJ} and found heritabilities of them to be equal to 0.38 ±

0.07 and 0.39 ± 0.07, respectively. Nkrumah and coworkers reported a similar heritability of 0.21 ± 0.12 for RFI on steers (2007c).

Crews and coworkers (2003) estimated heritability for RFI on 410 Charolais sired crossbred steers for a 84 d growing phase and 112 d finishing phase. RFI heritability estimate for growing (high roughage) diet was 0.30 ± 0.07 and the RFI for finishing (high grain diet) to be 0.26 ± 0.06. The genetic correlation between these two traits was 0.55 ± 0.30, which indicates animals with the genetic potential for improved feed utilization on roughage-based diets may rank differently on a grain based diet.

Heritability of RFI in other livestock:

Heritability estimates of RFI in other mammals are lower than estimates from beef cattle. Cammack and coworkers (2005) estimated heritability of RFI in 1239 ram lambs to be 0.11 ± 0.05. Von Felde and coworkers (1996) found a heritability estimate for RFI in group-housed boars to be 0.18 ± 0.03. Heritability of RFI was found to be 0.23 ± 0.08 in Large White swine selected for growth (Nguyen et al., 2005). Gilbert and coworkers (2006) used ADG and BF to calculate RFI in swine (weight was not taken into account since the pigs were tested over a fixed BW range) and authors found that RFI had a heritability of 0.15 ± 0.03. Hoque and coworkers (2007) found RFI to have a heritability estimate in Duroc pigs to be 0.41 ± 0.14 (2007).

Johnson and coworkers (1999) calculated RFI in Large White swine four ways: RFI_1 (initial test age, initial test weight, and ADG), RFI_2 (initial test age, initial test weight, ADG, and BF), RFI_3 (initial test age, initial test weight, and LEA), and RFI_4

(initial test age, initial test weight, ADG, and LEA) and found heritabilities for those traits to be 0.17, 0.11, 0.15 and 0.10, respectively (1999).

Biological Basis for Differences in RFI

There are many factors that influence feed utilization in beef cattle. Factors include live weight to be maintained, ADG, maturity pattern, lactation status, stage of reproduction, metabolic rate, body composition, efficiency of nutrient absorption, energetic efficiency of tissue growth, disease status, activity, and environment (climate) (Arthur et al., 2004). Approximately one third of the variation in RFI can be explained by known processes including digestion (14%), heat increment of feeding (9%), body composition/energy retention (5%), and activity (5%) (Herd and Richardson, 2004). The remaining 67% of variation is believed to be caused by processes in the body including but not limited to protein turnover, ion pumping and protein leakage. Following divergent selection in beef cattle, there were six known biological mechanisms that accounted for 73% of the variation in RFI in beef cattle including: body composition (5%), feeding patterns (2%), protein turnover/metabolism/stress (37%), heat increment of fermentation (9%), digestibility (10%) and activity (10%) (Richardson and Herd, 2004).

Genetic and Phenotypic Correlations:

RFI phenotypic and genetic correlations with feed intake and FCR:

RFI is only useful as a selection tool if there is potential for improvement in FI and FCR. RFI most often has moderate to high correlations with FI. Phenotypic correlations between RFI and FI range from 0.52 to 0.72 (Arthur et al., 1997,2001a,b;

Baker et al., 2006, Carstens et al., 2002, Nkrumah et al., 2007c; Herd and Bishop, 2000; Lancaster, et al., 2005). Likewise, genetic correlations are strong as well. Genetic correlations between RFI and FI have been reported from 0.64 to 0.79 (Arthur et al., 2001a,b; Nkrumah et al., 2007c; Herd and Bishop, 2000). Jensen and coworkers (2002) reported stronger relationships between RFI and daily energy intake (r_p=0.78 ± 0.02 and r_g = 0.59 ± 0.12).

Neither the addition of regressors nor the time RFI is measured seems to affect the relationship between RFI and FI. Both RFI (RFI and RFI adjusted for off-test BF thickness) calculations were positively related to feed intake (r_p =0.51 to 0.53; $P<0.001$) (Basarab et al., 2007). RFI was estimated to have a strong phenotypic correlation with FI (0.65 and 0.67) in both growing and finishing cattle (Carstens and Tedeschi, 2006).

Cattle with low RFI should be the most efficient in terms of converting feedstuffs to a unit of gain. RFI appears to be moderately to strongly relate (both phenotypically and genetically) to FCR. Literature reports the phenotypic correlation between RFI and FCR to fall within the range of 0.42 to 0.76 (Arthur et al., 1997, 2001a,b, Baker et al., 2006; Basarab et al., 2007, Carstens et al., 2002; Lancaster, et al., 2005; Nkrumah, 2007c; Robinson and Oddy, 2004). RFI was estimated to have a strong phenotypic correlation with FCR (0.56 and 0.63) in both growing and finishing cattle (Carstens and Tedeschi, 2006). Genetic correlations between RFI and FCR range from 0.62 to 0.85 (Arthur et al., 2001a,b; Nkrumah, 2007c; Robinson and Oddy, 2004).

Wood and coworkers (2004) noted a significant genetic correlation (0.35) between postweaning RFI and plasma IGF-1 concentrations and concluded with further research there could be opportunities to use IGF-1 levels to screen bulls to test for RFI based on their plasma level of IGF-1. Therefore, if a producer had 500 bulls and the space to test 50, IGF-1 concentrations could be used to determine which 50 to test. Lancaster and coworkers (2008) reported a significant ($P<0.05$) phenotypic correlation between RFI and final serum IGF-1 concentrations (r_p =-0.49).

Gilbert and coworkers (2006) found RFI in swine to be genetically and phenotypically correlated with FI (r_g =0.38 ± 0.013 and r_p =0.70) and FCR (r_g =0.57 ± 0.013 and r_p =0.56). Hoque and coworkers (2007) found RFI to in Duroc pigs to be to be correlated with FCR (r_g =0.86 ± 0.13, r_p = 0.88 ± 0.11). Similar results were found by Von Felde et al. (1996) with RFI being phenotypically and genetically correlated with FI (r_p =0.98, r_g =0.97 ± 0.01) and FCR (r_p = 0.79, r_g =0.63 ± 0.13) in group housed boars.

RFI phenotypic and genetic correlations with ADG and weight:

Most literature agrees that RFI is phenotypically uncorrelated with its indicator traits weight and ADG since RFI is calculated using a regression model. However, there may be genetic relationships (Kennedy et al., 1993). Arthur and coworkers (2001a) found significant genetic relationships between RFI with BW (0.32 ±0.10) and ADG (-0.10 ± 0.08). This indicates that selecting for improved (lower) RFI could essentially result in decreased BW and ADG (Kennedy et al., 1993). However, RFI was found to be genetically independent from mature cow weight (r_g = -0.09 ± 0.26) (Herd and Bishop, 2000).

In another study by Arthur and coworkers (2001b), genetic correlations were observed between RFI and 200 day weight direct (r_g =-0.45 ± 0.17), 400 day weight direct (r_g =-0.26 ± 0.13), 200 day weight maternal (r_g =0.22 ± 0.20), and 400 day weight maternal (r_g =0.14 ± 0.25). However, RFI was not affected by pre-test rearing treatments (weaning at birth, 84 d or 168 d) (Herd and Bishop, 2000).

RFI correlations with postweaning measurements and carcass characteristics:

Most literature agrees traditionally calculated RFI (using ADG and MMWT as regressors) has low to moderate, positive correlations with measures of fat, including 12th rib fat thickness, rump fat and marbling. While some may argue, selecting for RFI should produce cattle with more favorable USDA Yield Grades (YG), the repercussions could include a decrease in USDA Quality Grades due to decreased marbling potential.

RFI is genetically and phenotypically related to USBF with correlations falling within the ranges of 0.14 to 0.19 and 0.17 to 0.48, respectively (Arthur et al., 1997; Arthur et al., 2001b; Robinson and Oddy, 2004). RFI is also related to ultrasound rump fat measurements (USRF). Arthur and coworkers (2001b) as well as Robinson and Oddy (2004) reported phenotypic correlations of 0.11 and 0.13 and genetic correlations of 0.72 and 0.48, respectively between RFI and URF. Carcass 12th rib fat thickness (BF) measurements are also correlated with RFI in the same manner as the ultrasound traits. Carstens and Tedeschi (2006) found RFI to have a slight significant phenotypic correlation with BF (0.11 and 0.33) in growing and finishing cattle (2006). However, Crews and coworkers (2003) found conflicting results of RFI in growing cattle being genetically correlated with BF (-0.24 ± 0.30). In finishing studies, cattle with high RFI (n=87) had more BF ($P< 0.01$) than cattle with low RFI (n=93) (Carstens and Tedeschi, 2006).

Before adjusting progeny RFI with off-test BF thickness, RFI was positively correlated with measures of body fat, including BCS, USBF, USBF gain per d, marbling score, marbling score gain per d, BF gain in 112 d, (r_p =0.21 to 0.27; $P<0.05$) (Basarab et al., 2003). In a 2007 study, Basarab and coworkers reported confirming results before adjusting RFI for fat thickness. Nkrumah and coworkers (2004, 2007) reported RFI to have significant phenotypic relationships with gain in BF (0.30), carcass BF (0.19), carcass grade fat (0.25, 0.23), lean muscle yield (-0.22, -0.21) and YG (0.28, 0.22).

RFI was shown to have a significant low positive phenotypic correlation with BF measured from three locations (top, middle and bottom), grade fat, fat class, marbling score and yield grade ($P<0.05$). However, after the adjustment the only trait showing a significant relationship was marbling score (r_p =0.14; $P=0.032$) (Basarab et al., 2007). Crews and coworkers (2003) also reported a weaker, but significant genetic relationship between RFI and marbling score (0.08 ± 0.32). Robinson and Oddy's (2004) research agreed by finding RFI to be correlated with ultrasound intramuscular fat (USIMF) (r_p = 0.12 ± 0.03; r_g =0.22 ± 0.17). This relationship between intramuscular fat and RFI was confirmed by Nkrumah and coworkers (2007) with a phenotypic correlation between the two traits of 0.17.

Since longissimus dorsi area is generally thought of as being highly related to BW, one might initially disregard its relationship to RFI. RFI has been found to have low genetic and phenotypic correlations with USREA, usually within the range of -0.20 to 0.20 (Arthur et al., 2001b; Basarab et al., 2007; Carstens and Tedeschi, 2006; Crews et al., 2003; Robinson and Oddy, 2004). However, Carstens and Tedeschi (2006) reported cattle with high RFI (n=87) had smaller REA ($P<0.05$) than cattle with low RFI (n=93).

After calculating RFI using MMWT and ADG, Basarab and coworkers (2003) adjusted RFI with regressors of USBF gain and USIMF gain (RFI_{III}). They found carcass lean (% of final weight) had a low negative correlation with RFI (r_p =-0.21, P=0.01) and RFI_{III} (r_p =-0.17,P=0.04). RFI for growing cattle was genetically correlated with carcass REA (0.15 ± 0.31). Herd and Bishop (2002) reported similar results as they found RFI to be phenotypically and genetically correlated with lean growth rate (r_p = -0.33 ± 0.04, r_g =-0.47 ± 0.17).

While RFI should be phenotypically uncorrelated with BW measurements, RFI has been found, in some cases, to be correlated with HCW. RFI for growing cattle was genetically correlated with HCW, 0.10 ± 0.30 (Crews et al., 2003), Nkrumah and coworkers (2007c.) found RFI to be phenotypically correlated with HCW (r_p =0.26; P<0.01).

Other unique findings in the literature describe the relationships of RFI with SC, heat production and serum leptin concentration. RFI was found to lack genetic and phenotypic correlations with SC (r_g = -0.03 ± 0.11, r_p =0.10) (Arthur et al., 2001b). Heat production had a moderate to strong positive correlations with all three calculations of RFI (0.56, 0.70, 0.54) (P<0.01), while retained energy only had positive significant correlations (r_p =0.28 and 0.25) with RFI_I and RFI_{III} (P<0.01) (Basarab et al., 2003). Nkrumah and coworkers found that animals with high concentrations of serum leptin had higher RFI than animals with medium and low concentrations (2007b), but the correlation of serum leptin and RFI was not significantly different from zero. Hegarty and coworkers (2007) found positive significant relationships between methane production rate.

Classification of RFI groups and differences across those groups:

While statistics across an entire group of animals is beneficial, sometimes it is useful to analyze traits within a group. In order for researchers to analyze quantitative traits within a group of animals, animals must first be classified. Common classifications reported in literature are high, medium and low. Animals are assigned a classification based on where their value for the given trait lies on the normal distribution graph. In RFI studies an animal classified as being in a high RFI group would possess a RFI >0.5 SD above mean. Animals with a medium classification would have a RFI ± 0.5 SD from the mean. Lastly, low RFI animals would have and RFI <0.5 SD below the mean.

Differences between dams of calves with different RFI classifications

In 2007, Basarab and coworkers analyzed 222 yearling calves and their dams to determine relationships between cow traits and RFI of their yearling offspring. Reproductive rates were measured in the dams. There were no significant differences among dams of high, medium or low RFI calves for pregnancy rate, calving rate, or weaning rate (Basarab et al., 2007). However, dams of high RFI progeny had more twins ($P<0.001$), and tended to have a higher death loss in their calves than dams of the medium and low RFI progeny.

Cow weights were measured after weaning of their first calf, pre-calving, pre-breeding, and weaning of their second calf. Weights of dams were statistically similar at each weighing. Cows were also ultrasounded on weigh dates. Dams of low RFI progeny had significantly more USBF than dams of medium and high RFI progeny at all four measuring dates .On the pre-breeding measurement day, dams of the high RFI progeny had higher BCS than dams of medium and low RFI progeny. One explanation is low RFI dams lost less weight since calving than dams of the other two groups (Basarab et al., 2007).

To test this finding, 116 dams were randomly selected over three trials for a feed test. Cows of similar age, pregnancy, body weight, BCS, USBF, rump fat thickness, and tailhead fat thickness were fed using the Growsafe® system and managed similarly to their progeny (Basarab et al., 2007). At the end of the trial, cow RFI was unrelated to cow weights, ADG, FCR, fat thicknesses and fat gains (Basarab et al., 2007). Cow RFI was phenotypically related ($P<0.001$) to feed intake ($r_p =0.83$), feeding duration ($r_p =0.36$), head down time ($r_p =0.62$), and feeding frequency ($r_p =0.50$) (Basarab et al., 2007).

Although not very strongly, cow RFI was also related ($r_p =0.30$; $P=0.025$) to calf RFI (Basarab et al., 2007). Dams of low RFI calves calved later in the season than dams of medium and high RFI progeny ($P=0.008$, <0.001) (Basarab et al., 2007). Dams of high RFI calves had higher FI and RFI values ($P=0.003$, 0.018) than the dams of the medium and low RFI calves (Basarab et al., 2007).

Differences between RFI classifications for FI and FCR

Cattle that have been classified as high or low RFI have significantly different FI and FCR. Baker and coworkers (2006) reported low RFI Angus steers consumed significantly less DM than high RFI steers (9.3 kg/d vs. 10.3 kg/d; $P<0.05$) and had better FCR (6.7 vs. 7.7; $P<0.05$) (Baker et al., 2006). In a similar study, Basarab and coworkers (2003) reported significant differences across the three RFI classifications for DM FCR (high: 5.95 vs. medium: 5.70 vs. low: 5.39). DMI also differed across the groups with the low RFI cattle having the most favorable values (8.00 kg/d) and the high RFI cattle having the most unfavorable values (8.93 kg/d) (Basarab et al, 2003). Carstens and coworkers (2002) reported high RFI steers consumed more feed ($P<0.001$) and had higher FCR ratios than the low RFI steers (Carstens et al., 2002). Nkrumah and coworkers (2004, 2007c) also found high RFI steers had higher FCR and consumed more DM than low RFI steers.

Kolath and coworkers (2006) compared 8 high RFI steers to 9 low RFI steers. The low RFI steers had higher G:F (0.20 vs. 0.16; $P<0.001$) and less average daily FI (7.40 vs. 8.94; $P<0.001$) than the high RFI steers (Kolath et al., 2006). Golden and coworkers (2008) findings agreed. Low RFI steers consumed less DM (6.99 kg vs. 10.30 kg; $P<0.001$) and had a greater G:F (0.200 vs. 0.146; $P<0.001$) then high RFI steers.

Differences between RFI classifications for growth and weights

When comparing RFI classified cattle, Basarab and coworkers (2003) found no significant differences among the groups for any growth traits (Basarab et al, 2003). Carstens and coworkers (2002) found ADG to be similar across three RFI groups. Kolath and coworker (2006) noted no significant differences between high and low RFI groups for initial body weight, final body weight, ADG, or HCW. Lancaster and coworkers (2005) found no significant differences between the groups for initial body weight, final body weight, ADG, or final SC. Golden and coworkers (2008) found no significant differences between the high and low RFI steers for the traits of initial body weight, final body weight, or ADG.

Differences between RFI classifications for carcass characteristics

Baker and coworkers (2006) analyzed carcass traits of HCW, REA, KPH, BF, YG, USDA marbling scores, USDA quality grade and found no significant differences between high RFI, medium RFI and low RFI groups. The authors did not detect any adverse relationship between RFI and meat quality or palatability (Baker et al., 2006).

Basarab and coworkers (2003) compared the weights of organs across the three RFI classifications. High and medium RFI steers had more kidney fat and more trim than low RFI steers (P=0.008, 0.002). High RFI steers had heavier stomachs, intestines, and livers than the medium and low RFI steers (P<0.05). When comparing carcass compositions of steers, there were no significant differences for lean, bone, subcutaneous fat, USIMF, or body cavity fat, nor were there differences among the distribution of fat (Basarab et al, 2003). There were also no differences found in the distribution of wholesale cuts across the three RFI groups (Basarab et al, 2003).

Initial USBF, final USBF, final USREA, final USIMF and final test weights were similar across RFI groups (Carstens et al., 2002). Low RFI steers had less rump fat than medium and high RFI steers (P=0.04) (Carstens et al., 2002). Nkrumah and coworkers (2004, 2007c) also reported high RFI steers to have more USBF gain per day, more USBF, more carcass grade fat, higher YG, and less lean meat yield than medium RFI and low RFI steers (Nkrumah et al., 2004). Kolath and coworkers' findings agreed as no significant differences were observed between high and low RFI groups for REA, BF, or YG (2006). Golden and coworkers (2008) conclusions were consistent, with no significant differences between high RFI and low RFI steers for the traits of HCW, REA, BF, or YG.

Other Differences between RFI classifications

Low RFI steers had lower retained energy (energy used for maintenance, growth or production, i.e. that energy consumed not used for heat production) than high and medium RFI steers ($P=0.002$) (Basarab et al, 2003). As RFI decreased across the groups so did heat production ($P<.0001$) (Basarab et al, 2003).

Nkrumah and coworkers (2006) found low RFI steers tended to have greater apparent digestibility for DM (H: 70.87 ± 1.97 vs. L: 75.33 ± 2.10; $P=0.10$) and crude protein (H: 69.76 ± 2.17 vs. L: 74.70 ± 2.29; $P=0.09$) when compared to high RFI steers. Low RFI steers lost less methane as a percent of gross energy (GE) intake than both the medium and high RFI steers (H: 4.28 ± 0.26 vs. M: 4.25 ± 0.35 vs. L: 3.19 ± 0.34; $P=0.04$) (Nkrumah et al., 2006). RFI was correlated with daily fecal output ($r_p=0.33$; $P<0.10$), daily methane production ($r_p=0.44$; $P<0.05$), daily heat production ($r_p=0.68$; $P<0.001$), daily retained energy ($r_p = -0.67$; $P<0.001$), apparent DM digestibility ($r_p = -0.33$; $P<0.10$), and crude protein digestibility ($r_p=-0.34$; $P<0.10$) (Nkrumah et al., 2006).

Mitochondria were isolated from the longissimus muscle of steers and respiratory control ratio (RCR) was measured. RCR of the low RFI steers was greater than the RCR of the high RFI steers ($P<0.05$) (Kolath et al., 2006). A greater RCR value results from a greater degree of coupling between respiration and oxidative phosphorylation and suggests an increase efficiency of electron phosphorylation. The authors also observed that high RFI steers had greater amounts ($P<0.05$) of plasma glucose than low RFI steers, which could be explained by their increased feed consumption (Kolath et al., 2006).

Experiments comparing RFI levels with feeding behavior

Golden and coworkers (2008) reported efficient animals ate fewer times per day than inefficient animals and found no significant differences in the daily eating rate in either experiment. However, the authors noted inefficient steers had a more variable eating pattern throughout the day (Golden et al., 2008).

Nkruhmah and others (2007a) found similar results. High RFI steers were at the feed bunk more minutes per day, ate more minutes per day, and ate more often than medium and low RFI steers (Nkrumah et al., 2007a). To access disposition, exit chute velocity was measured. No differences in exit chute velocity across the three RFI groups.

Lancaster and coworkers (2005) reported high RFI bulls ate more minutes per day (110.9 vs. 120.8 vs. 131.3) and more often (4.83 vs. 5.04 vs. 5.07) than the medium and low RFI bulls.

Van Eerden and coworkers (2004) investigated the possibility of phenotypically selecting pullets based on RFI. Three hundred fifty pullets were placed on a 72 day test and RFI was calculated after week 10. The top 50 efficient and the bottom 50 non-efficient RFI pullets were selected. Differences in RFI were significant throughout the trial. The realized difference in RFI was 8.6% of the mean FI of 77g/d (Van Eerden et al., 2004). No differences between the groups for traits of BW, age at first egg, total egg number, or total egg weight. Mean egg weight was found to be heavier in the low RFI group ($P<0.05$) (Van Eerden et al., 2004).

Divergent selection studies using RFI

Divergent selection studies are the best tool researchers have available to determine the efficacy of selection with RFI as criteria. After using bulls divergently selected for RFI over 5 years, Arthur and coworkers (2001c) found significant ($P<0.05$) divergence between the two selection lines for the trait of RFI, which translated into an annual realized direct selection response of 0.249 kg/day (Arthur et al., 2001c). Progeny from these two lines differed in their DFI LSMEANS as the low RFI line consumed an average of 9.4 ± 0.3 kg/d and the high RFI line consumed an average of 10.6 ± 0.3 kg/d (Arthur et al., 2001c). The authors concluded that based on this data, an average $27 per head was saved on animals in the low RFI line over the 100 d feeding period (Arthur et al., 2001c).

Angus, Hereford and Shorthorn females (n=284) were evaluated on a post-weaning test and were labeled as low RFI (negative RFI) or high RFI (positive RFI) based on their post-weaning RFI (Arthur et al., 1999). At approximately 42 months of age, after the weaning of their second calves, the open, non-lactating cows were subjected to a second 70 d feeding trial (Arthur et al., 1999). Although the authors found significant correlations between post-weaning RFI with cow RFI (r_p =0.36 $P<0.05$) and cow FI (r_p=0.30 $P<0.05$), there were not any other significant correlations between the post-weaning RFI with measures of production including ADG, liveweight, USBF, USREA and milk yield (Arthur et al., 1999). When comparing the two classifications of cows, the LS MEANS for FI and RFI were significantly different ($P<0.05$) (Arthur et al., 1999). High RFI cows had a feed intake of 1144 ± 16 kg and a RFI of 18.3 ± 11.4 kg while the low cows had a feed intake of 1093 ± 16 kg and a RFI of -29.0 ± 11.3 kg (Arthur et al., 1999). There were no other significant differences between the two groups of cows for live weight, ADG, USBF, USREA and Milk yield (Arthur et al., 1999).

Arthur and coworkers (2005) found after approximately 1.5 generations of divergent selection for post-weaning RFI, the difference in EBVs for RFI for the high efficient and low efficient cows was 0.8 kg/day, but there was no significant line difference for maternal productivity traits including: pregnancy rate, calving rate, weaning rate, calving day (low RFI cows tended to calve 5 days later in the season than high RFI cows P=0.07), milk yield, weight of calf born per cow exposed, weight of calf weaned per cow exposed, birth weight of calves, pre-weaning ADG and 220 d weight (Arthur et al, 2005).

Herd and co-workers (1998) measured pasture intake on 41 lactating Angus cows that had previously been ranked according to their RFI from a postweaning test. The two groups had similar rib and rump fat depths and reared calves of similar body weights. The pasture intakes were not different between the groups. Average mature cow weight differed between the groups with the low RFI cows being heavier (618 ± 16 kg vs. 577 ± 11 kg; P<0.05) and low RFI cows tended (P=0.07) to have a higher ratio of calf weaning weight to cow intake than the high RFI cows (Herd et al., 1998).

Herd and coworkers (2003b) used 144 low RFI steers and 165 high RFI steers to examine different characteristics of the two lines. Phenotypic correlations for RFI with ADG, o-test weight and final weight were not significant. However RFI was positively correlated with FI (r_p =0.50; P<0.001) and FCR (r_p =0.27; P<0.001). Low RFI steers tended (P<0.10) to have a higher, less favorable FCR than the high RFI steers (8.2 ± 0.2 vs. 7.6 ± 0.2). High RFI steers tended to have more USBF (11.6 ± 0.3 mm vs. 10.2 ± 0.3

mm), USRF (14.8 ± 0.4 mm vs. 13.1 ± 0.4 mm), and USREA (70.6 ± 0.9 cm2 vs. 66.9 ± 0.9 cm2) than low RFI steers. There were no differences between the lines for HCW or percent retail product, but high RFI steers did have a higher dressing percent (52.1 ± 0.3 vs. 52.9 ± 0.3) and more rump fat (14.9 ± 0.5 mm vs. 16.5 ± 0.5 mm) than the low RFI steers (Herd et al., 2003b).

271 and 250 steers were selected, after a single generation of divergent selection from a low and high RFI line, respectively, and measured for growth on pasture and body composition before feedlot entry (Herd et al., 2005). There were no differences between the LSMEANS for initial weight of backgrounding, but ADG throughout the backgrounding phase was higher for the low RFI steers (0.66 ± 0.1 kg/d vs. 0.64 ± 0.1 kg/d; $P<0.05$) (Herd et al., 2005). Low RFI steers tended ($P<0.10$) to weigh heavier at the end of the backgrounding phase (418 ± 3 kg vs. 409 ± 3 kg; $P<0.10$) and have smaller REA (52.1 ± 0.5 cm^2 vs. 52.6 ± 0.5 cm^2; $P<0.10$) (Herd et al., 2005). High RFI steers had more rib fat (3.2 ± 0.1 cm vs. 4.2 ± 0.1 cm; $P<0.05$) and rump fat than their low RFI contemporaries (4.4 ± 0.2 cm vs. 5.3 ± 0.2 cm; $P<0.05$) (Herd et al., 2005).

Selection for RFI, based on mid parent EBV for RFI, tended to improve FCR in steers on pasture with low RFI steers having a FCR on pasture equal to 6.36 ± 0.35 and high RFI steers FCR equal to 8.51 ± 0.74 ($P<0.10$) (Herd et al., 2002).

After a single generation of divergent selection on RFI, 91 Angus and Angus cross steers from the low RFI line and 98 Angus and Angus cross steers from the high RFI line were selected (McDonagh et al., 2001). There were no significant differences between the two groups of steers for final weight, REA, HCW, dressing percent or IMF. High RFI steers exhibited more rib fat (9.2 ± 0.3 mm vs. 10.1 ± 0.2 mm; $P<0.05$) and tended to have more rump fat than low RFI steers (11.5 ± 0.3 mm vs. 12.1 ± 0.3 mm; P=0.10) (McDonagh et al., 2001). The two lines were also similar for shear force and compression taken at 1 and 14 d postmortem. Low RFI steers had a lower myofibril fragmentation index on both day 1 (67.7 ± 1.8 vs. 72.5 ± 1.9; P<0.05) and day 14 (85.6 ± 1.2 vs. 89.5 ± 1.3; P<0.05) than the high RFI steers, however there was no significant difference between the two groups for myofibril fragmentation rate (McDonagh et al., 2001).

Meyer and coworkers (2008) concluded there were no significant differences between Hereford cows, with RFI values characterized as low or high from a postweaning test, for daily DMI on forage (n=2, 2 replicates of 7 cows each) (12.4 ± 0.9 vs. 15.6 ± 0.9; P=0.23), forage utilization (n=2, 2 replicates of 7 cows each) (75.5 ± 2.5 vs. 76.3 ± 2.5; P=0.84), or daily DMI per cow/calf pair (n=3, 3 replicates of 4 cow/calf pairs each)(12.5 ± 0.7 vs. 14.1 ± 0.7; P=0.12) (Meyer et al., 2008). The authors noted the number of animals used in this experiment was small (Meyer et al., 2008).

Yearling Angus steers, from dams and sires who had been tested and ranked as high RFI or low RFI, were subjected to a feed test and were labeled from the group in which they were born (Richardson et al., 2001). Steers from the high RFI group consumed more feed per day, had higher RFI, had more initial rump fat, tended to have more BF, had a smaller change in REA during the test, had more carcass fat, tended to have less beef yield from carcass, and tended to have more total dissected fat than the steers from the low RFI group (Richardson et al., 2001). The two groups of steers were similar for initial weight, ADG, and FCR (Richardson et al., 2001).

Pullets from a low RFI line consumed less gross energy (P=0.007) than pullets from the high line after 8 generations of divergent selection for RFI (Van Eerden et al., 2006). After 15 generations of divergent selection in laying chickens for low and high RFI in males and 18 generations in females, FCR was significantly lower in the low RFI lines for males (2.4 vs. 3.2, SE:0.25) and for females (2.9 vs. 3.3 SE=0.04) (Bordas and Minvielle, 1999).

Cai and coworkers (2008) found 34% of the phenotypic variation in DFI in swine could be accounted for by RFI with the remainder of variation being explained by ADG and backfat. Selection on RFI led to a significant reduction in DFI. After 4 generations of divergent selection for RFI, 92 gilts from the low RFI line had significantly lower RFI (P=0.002), lower DFI (P<0.0001), lower growth rates (P=0.022) and less BF (P=0.013) than 76 gilts from the control line (Cai et al., 2008).

Swennen and coworkers (2007) selected cockerels from high RFI (N=30) and low RFI (N=30) lines that had been divergently selected for either high or low RFI for 30 generations. Roosters were fed ad libitum from 24 weeks of age to 35 weeks of age. There were no differences in BW between the two lines, but daily FI was 50% higher in the high RFI group. The high RFI group had significantly (P<0.05) higher heat production per day. Liver weight of high RFI cockerels was significantly heavier than livers in the low RFI line. Estimated values of lean tissue mass, protein mass and water content was significantly higher in the high RFI group (Swennen et al., 2007). Fat tissue mass was significantly (P<0.0001) greater in the low RFI line (Swennen et al., 2007).

Conclusion:

With all the traits and tools available for purebred beef producers, many opportunities exist for multi-trait selection. The inclusion of a measure of feed intake in a National Cattle Evaluation would allow producers to evaluate differences between measures of input among their cattle. Reducing feed costs would be a benefit to the entire beef industry from the cow/calf producers to the packer.

Objectives of this research are:

1) Observe breed composition differences for feed intake, growth and carcass traits
2) Observe trait differences of low, medium and high RFI in centrally tested bulls and Simmental sired steers
3) Estimate heritability for RFI in central tested bulls and steers
4) Compare RFI in bull and steers

AN EVALUATION OF RESIDUAL FEED INTAKE IN CENTRALLY-TESTED BULLS AND STEER RELATIVES

INTRODUCTION

Feed costs represent the largest expense in beef production (Fan et al., 1995; Arthur et al., 2001a: Archer et al., 2002; Basarab et al., 2003) While the majority of feed consumed (60-75%) by beef animals is required for maintenance, the remainder is used for production traits such as growth, lactation and development (Arthur et al., 2001a; Basarab et al., 2003). How efficiently a beef animal can convert its feedstuffs into a unit of production is a trait many desire to be included into genetic evaluations. All stages of production could benefit from a genetic improvement in feed efficiency (Herd et al., 2003).

To select for improved feed efficiency, producers must have inexpensive tools at their disposal. There are many measurements of feed efficiency described in literature. Among those is residual feed intake (RFI). RFI is defined as the amount of feed an animal consumes over or under what is expected based on its weight and gain. In order to determine RFI, weights of animals over a period of time and daily feed intake (DFI) must be collected.

RFI was first proposed in laying hens by Byerly (1941) and later in beef cattle (Koch et al., 1963). RFI is the portion of feed intake not accounted for by measureable factors (Byerly, 1941; Koch et al., 1963; Crews, 2005). Predicted feed intake is derived from the regression equation of

$$\text{daily DMI} = \beta_0 + \beta_1(\text{ADG}) + \beta_2(\text{WT}) + \text{RFI}$$

where β_0 is the regression intercept, β_1 is the partial regression of daily DMI on ADG and β_2 is the partial regression of daily DMI on body weight.

With the inclusion of a measure of feed intake, such as RFI, in a genetic evaluation, producers could evaluate differences in input costs instead of solely relying on output EPD values to predict profitability of future calf crops.

The objectives of this research are: 1) observe trait differences in bulls and steers of varying breed compositions, 2) observe trait differences between low, medium and high RFI bulls and steers, 3) estimate heritability of RFI centrally-tested bulls and steer relatives, 4) compare RFI in bulls and steers.

MATERIALS AND METHODS

Animal Care and Use

Experimental protocols were approved for bulls by the Auburn University Institutional Animal Care and Use Committee through the Standard Operating Procedure 0404-P-0068.

Description of Data

Centrally-tested bulls

Data were collected on Angus and Simmental bulls consigned to the Auburn University Bull Test from 1977 to 2007. All bulls (N=1433) were housed at the Auburn University Beef Evaluation Center (AUBEC) throughout the duration of each test.

Additionally, in 2007, a group of progressive Alabama Simmental producers leased the facility to conduct a feeding trial on large contemporary groups of yearling bulls (n=96).

Upon arrival, bulls were grouped by breed and weight then assigned to one of 8 pens. For the 2007 test group, bulls were grouped by contemporary group then by weight upon arrival. Each pen had a maximum capacity of 12 head. During a 21 d warm-up period, bulls were trained to the Calan Gate® system (American Calan, Northwood, NH), diet and to pens. Each pen had an indoor and outside component. Inside dimensions were 9.1 m wide by 10.2 m long. In this enclosed area, feed bunks and an automatic water trough shared between two pens were located. The outside pen dimensions were 18.6 m at their widest point by 92.7 meters long. Each outside pen was divided into three 6.2 m wide strips. Bulls had access to one strip of their respective pen at a time and were rotated across the three strips weekly. Bulls had ad libitum access to a total mixed ration (TMR) balanced for energy (TDN= ~70%), protein (not < 12.5%) and fiber content (not > 20%). Exact composition of the TMR varied over years due to availability and cost of ingredients. Bulls were fed by hand, twice daily, an amount initially determined by 2.5% of their BW and from then on fed based on an amount they could eat with 0.45 to 2.27 kg of orts remaining in the bunk. For the 2007 test, orts were weighed back daily, but for previous tests orts were only weighed back on days the bulls were weighed. Between the years of 1977 and 1989 the length of the test was 140 d. Test length shortened with the tests of 1990, 2000 and 2007 to 112 d, 84 d and 70 d, respectfully. Bull weight and hip heights were recorded bi-weekly for the 2007 test. For previous tests, bull weights and hip height were measured every 28 d.

Simmental-sired steers

Many bulls tested at AUBEC shared common ancestors with steers fed at the University of Illinois, Urbana, IL as part of the American Simmental Association's (ASA) Carcass Merit Program. Data from steers were courtesy of Dr. Wade Schaffer and the American Simmental Association (Bozeman, MT). The Carcass Merit Program was designed to allow Simmental/Simbrah producers to progeny test herd sires for both carcass merit and feed efficiency. For a fee and donation of 30 to 60 straws of semen, producers could test any bull of their choosing. Semen was used on an Angus based cowherd to emulate the genetics of the present day U.S. cowherd. Within each calf crop of the carcass merit program, a producer could expect 10 to 30 slaughter progeny out of each sire (acquired from www.7070Beef.com, November 16, 2009).

After calving, steers were reared and managed in adherence with a typical beef cattle operation in the Midwestern United States. Steers were born in the months of January through March then weaned when the average age of the calf crop was 205 d. Approximately two weeks after weaning, steers were divided into pens, each equipped with a Growsafe® feeding system (GrowSafe Systems Ltd., Airdrie, Alberta, Canada). DMI was measured on each steer. BW measurements were taken for in-weight, mid-test weight, and final weight. Steers harvested in 2007 were measured initially for 12th rib fat thickness (Initial_USBF), longissimus doris area (Initial_USREA), and intramuscular fat percentage (Initial_USIMF) using real-time ultrasound. Steers harvested in 2006 were not measured for Initial_USREA, but had Initial_USBF and Initial_USIMF measurements recorded. When yearling weights were taken on the steers harvested in 2007, ultrasound measurements were taken for 12th rib fat thickness (USBF), longissimus doris area

(USREA), and intramuscular fat percentage (USIMF). Steers harvested in 2006 were only measured as yearlings for USIMF.

Calculation and Classification of RFI

RFI for bulls and steers were calculated from the regression equation of:

$$\text{daily DMI} = \beta_0 + \beta_1 (\text{ADG}) + \beta_2(\text{WT}) + \text{RFI},$$

where daily DMI is the average daily feed intake, β_0 is the regression intercept, β_1 is the partial regression coefficient of daily intake on ADG and β_2 is the partial regression coefficient of daily intake on body weight. ADG and $\text{MidWt}^{0.75}$ were used as regressors on daily DMI (SAS Inst., Inc., Cary, NC, 2003).

RFI values were calculated by year in which bulls were on test. In most instances, producers only consigned 1 or 2 elite bulls from their calf crop. Thus, determining RFI values using weaning contemporary group would not have yielded meaningful results.

RFI for steers was calculated within contemporary group (CG). Each steer was assigned to its respective CG based on birth farm, year and pen. Steers born in 2005 and 2006 were from one of four farms. Pen in which the steers were fed was also an important fixed effect since diets differed across the pens.

Bulls and steers were assigned to one of three RFI classifications (low, medium or high) based on their individual RFI and the standard deviation of the sample population. High RFI classified animals were those with an RFI greater than 0.5σ from 0. Animals with a medium RFI classification were those with RFI were equal to or between -0.5σ and 0.5σ. Low RFI classified animal had RFI less than 0.5σ from 0.

Bulls and steers used in this study belonged to one of five breed compositions (BC): Angus, high percentage Angus, Angus-Simmental halfbloods, high percentage Simmental or Simmental. Differences among least squares means for breed compositions were separated using the pdiff option GLM procedure in SAS (SAS Inst., Inc., Cary, NC, 2003). Differences were considered significant if $P<0.05$.

In an additional analysis, composite animals were compared to their purebred Angus and Simmental counterparts, by replacing BC in the general linear model for a breed type fixed effect. Three breed types were used in the analysis: Angus, composites and Simmentals. Differences among least squares means for breed types were separated using the pdiff option in the GLM procedure in SAS (SAS Inst., Inc., Cary, NC, 2003). Differences were considered to be significant for all models when $P<0.05$.

The general linear model used was:

$$Y_{ijk} = CG_i + BC_j + e_{ijk}$$

Where:

Y_{ijk} = observed value for the dependant variable of the kth animal of the ith CG with the jth breed composition. (Dependant traits included body weight traits, gain, feed intake traits, ultrasound carcass traits for bulls and additionally, carcass traits for steers.)

i = contemporary group fixed effect

j = breed composition fixed effect

and covariates of age, final weight, or frame score of bull and steers were used.

Relationships between RFI and Other Traits

Simple means for steer and bull traits adjusted for age, weight and frame were calculated using PROC GLM in SAS (SAS Inst., Inc., Cary, NC, 2003). Phenotypic correlations using PROC CORR in SAS (SAS Inst., Inc., Cary, NC, 2003) were estimated among RFI and birth weight, weaning weight, on-test performance traits and ultrasound carcass traits for bulls and steers. Additionally, phenotypic correlations were estimated among RFI and carcass traits for steers.

Bulls and steers were assigned a RFI classification based on where their value for the given trait lay on the normal distribution graph. In this study an animal classified as being in a high RFI group possessed a RFI >0.5 SD above mean. Animals with a medium classification had RFI ± 0.5 SD from the mean. Lastly, low RFI animals had RFI <0.5 SD below the mean.

The general linear model used was:

$$Y_{ijkl} = CG_i + BC_j + RFIclass_k + e_{ijkl}$$

Where:

Y_{ijkm} = observed RFI value of the l^{th} animal of the i^{th} CG with the j^{th} breed composition, k^{th} RFI classification

i = contemporary group fixed effect

j = breed composition fixed effect

k = RFI classification fixed effect

and covariates of age, final weight, or frame score of bull and steers were used.

Estimation of Genetic Parameters for RFI

A bivariate, two-trait sire-maternal grandsire (sire-mgs) model was used to estimate (co)variances of bull and steer RFI using MTDFREML (Boldman et al., 1993). In a bivariate model, traits are assumed to be different from one another. The environmental covariance between bull and steer RFI is assumed to be zero.

The bivariate sire-mgs model used was:

$$Y_{ijklm} = CG_i + BC_j + s_k + mgs_l + e_{ijklm}$$

Where:

Y_{ijkl} = observed RFI value of the mth animal of the ith CG with the jth breed composition, kth sire and lth maternal grandsire

i = contemporary group fixed effect

j = breed composition fixed effect

k = random sire effect

l = random maternal grandsire effect

and covariates of age, final weight, or frame score of bull and steers were used.

To begin the (co)variance analysis, the initial simplex entered was 1 x 10^{-6} and was iterated only one round in order to establish priors. Restart analyses were completed when the variance of function values (-2 log L) in the simplex were equal to 1 X 10^{-9}. Each analysis was then restarted using the previous estimates of parameters to verify the function values (-2 log L) was reached and were iterated to a maximum of 10,000. When the -2 Log L number reached its minimum, analysis were converged (Boldman et al., 1993). Heritability was estimated for both bulls and steers by the equation $4*\sigma_S^2 / \sigma_P^2$, with each covariate. Genetic correlations were estimated between the two traits by dividing the covariance by the square root of the product of the additive variances.

RESULTS AND DISCUSSION

Simple means for traits of bulls and steers adjusted for each covariate are found in Tables 1 and 2. Overall, all bulls tested from 1977 to 2007 averaged 405 d of age and 595 kg off-test. Similar to the bulls, steers averaged 419 d of age and 597 kg at harvest. Yearling frame scores averaged 6.6 and 6.0 for bulls and steer, respectively. All traits in the analysis had similar means for all three covariates used.

Table 3 describes the breed composition of each dataset. Most bulls were purebred Angus or Simmental, whereas most steers were composite type animals. This suggests most Simmental breeders nominated primarily purebred Simmental bulls for the steer progeny test. Additionally, only recently, the use of composite bulls have been promoted by and suggested for use by purebred breeders in commercial herds.

Table 4 describes the amount of pedigree links between and within the two datasets. There were 643 total sires with an average of 3.4 progeny with 310 sires having more than one progeny in the dataset. Additionally, 219 of the sires with progeny were also paternal grandsires, indicating several animals were half-siblings to sires. There were also 145 maternal grandsires in the A^{-1} relationship matrix that also served as sires. Table 5 contains the number of sires with feed intake data from the AUBEC. Twenty eight sires in A^{-1} had individual FI records and a total of 41 bulls had at least one descendant with feed intake data in. Individual feed intake records for 1433 bulls and 769 steers were used in the analysis when covariates of final test weight and age at the end of test were analyzed. Five less records were in the dataset when frame score was used as a covariate. The pedigree file contained 2,689 unique pedigrees.

Analysis of breed composition fixed effect

Central tested bulls

Breed composition differences are shown by covariate for central tested bulls in Tables 6-8. In general, as the amount of Simmental increased in the cattle, weights and frames scores also increased. As percent Angus increased in the bulls and steers, likewise did intramuscular fat percentages and backfat measurements.

When traits were adjusted to an off-test age for central tested bulls (Table 6), breed composition differences were seen in the traits of off-test final weight, frame score, birth weight, weaning weight, initial weight, yearling weight, WDA, daily DMI, FCR, USREA, USIMF, SC and RFI. As expected, age adjusted Simmental and high percentage Simmental bulls were heavier at all stages of life when compared to their Angus contemporaries. Angus bulls had lighter birth weights than half-blood, high percentage Simmental and Simmental bulls. When adjusted to an age constant, Angus bulls remained lighter at weaning, the beginning of test, at yearling and at the conclusion of test than their high percentage Simmental and purebred Simmental counterparts. These results agree with those published in literature over the past several decades (Adams et al.,1973; Lawlor et al., 1984; Cain and Wilson, 1983; Urick et al., 1991). Van Vleck and Cundiff compiled data from decades of research at the Meat Animal Research Center to develop across-breed EPD adjustment factors. Producers must add an adjustment factor to

Simmental birth weight, weaning weight and yearling weight EPD values in order directly to compare to an Angus EPD (Van Vleck and Cundiff, 2006).

Larger frame scores and scrotal circumferences are often associated with heavier weights. In this analysis, Angus bulls had the smallest frame score and SC of the 5 breed compositions when they were adjusted to an age constant.

Although no trend was observed, feed intake traits of daily DMI, FCR and RFI also differed across the breed compositions when adjusted to an age constant. High percentage Angus composite bulls consumed more DM, and had higher, less favorable FCR and RFI than bulls of the other 4 breed compositions. However, these data could be misleading as there were only 5 bulls belonging in this category. The lack of significance of heterosis for feed intake traits is has been established in the literature (Ellersieck et al., 1977; Elzo et al., 2009). Ellersieck and coworkers (1977) found a lack of significant interactions between sire breed and dam breed for feed efficiency, unless feed efficiency was adjusted to a weight-constant basis. Elzo and coworkers (2009) reported that heterosis was insignificant for RFI, FCR, gain, but increased DFI in Angus, Brahman, and Angus/Brahman composites.

When adjusted to an age-constant, Angus bulls had significantly smaller USREA than bulls of the other 4 breed compositions. In general, as Simmental influence increased in central-tested bulls, USIMF and USBF decreased linearly ($P<0.05$). These results agree with those published by Johnson and coworkers (1988) and Hassen and coworkers (1998). When analyzing data to compile across-breed EPD adjustment factors, producers must subtract an adjustment factor from Simmental marbling and fat EPD values to directly to compare to an Angus EPD (Van Vleck, et al., 2007).

Nearly identical results were seen when traits were adjusted to an off-test final weight constant (Table 7). While Angus bulls in this dataset were significantly older than Simmental bulls, the differences in those ages, is not sufficient to explain differences within other traits.

As expected, when frame score was used as a covariate (Table 8) opposite results were obtained for growth traits, but similar results were maintained for ultrasound carcass traits, feed intake traits and SC. Unlike results from the analyses using the covariates of off-test age and off-test final weight, significant difference across breed compositions for total gain and ADG arose when frame score was used as a covariate. Since Angus cattle are generally smaller framed and earlier maturing than Simmental cattle, the two breeds were at different points on their respective growth curves at the beginning of test. Therefore, when traits were all adjusted to a common frame score, Simmental bulls were most likely still increasing in overall skeletal size while the Angus bulls were beginning to deposit fat.

Steers of the Carcass Merit Program:

Differences in breed compositions for steers of the carcass merit program are presented in Tables 9-11. Since there are only 3 steers in the dataset with more than 50% Simmental influence, and standard errors for these steers prevent any significant difference from being observed, those results will not be further discussed.

When traits were adjusted to an age-constant basis, similar results to the centrally tested bulls were discovered for birth weight and weaning weight. No differences were observed across the three breed types for yearling weight, WDA, harvest weight or frame score. Steers composed of 50% Simmental and 50% Angus breeding exhibited more gain over the test than the high percentage Angus steers. However, Angus steers had higher ADG than both 50% and high percentage Angus steers ($P<0.05$).

When feed intake traits were adjusted to age at harvest, Angus steers consumed more DM per day, and exhibited higher, less favorable FCR and RFI than 50% Angus steers. As Simmental influence decreased in the steers of the carcass merit program, RFI linearly increased significantly across the three breed compositions. These findings support results from the Germplasm Evaluation project. Cundiff and coworkers (1981) reported that purebred Herefords and Angus steers had higher, less favorable FCR than their F_1 counterparts.

Angus and Angus-based steers had a higher percentage of intramuscular fat, higher yield grades and smaller REA than the half-bloods. Similarly, Urick and coworkers (1991) reported that Simmental-sired steers had heavier HCW, less 12th rib fat thickness (BF) and a lower marbling score than Angus-sired steers.

Breed- type analysis:

Bulls and steers were grouped into one of three breed types based on their breed composition: Angus, Composites, or Simmental to look more closely at feed intake traits. FCR and RFI for bulls were similar for each of the three breed types when adjusted for age. However, when adjusted for final weight and frame, daily DMI differed across the three breed types. In contrast to bull findings, Angus steers had higher, less favorable RFI, DMI and FCR than composite steers with all three adjustments.

Heritability estimates and the genetic correlation between bull and steer RFI

Heritability estimates for bull and steer RFI are shown on Table 12. This table also contains the genetic correlation estimated between bull and steer RFI. Heritability was estimated to be between 0.41 and 0.43 for bulls and 0.17 and 0.23 in steers, depending on the covariate (off-test age, frame score, or weight) used in the analysis.

RFI heritability estimates for central-tested bulls are within the range of those published in the literature. Arthur and coworkers (1997) reported a similar heritability estimate of 0.44 ± 0.07 for RFI in 966 bulls and heifers. In 2001, Arthur and coworkers (2001a) determined heritability for bulls at 15 and 19 months of age to be 0.46 ± 0.04 and 0.31 ± 0.06, respectfully. In a study using 1180 young Angus bulls, heritability of RFI was found to be 0.39 ± 0.03 (Arthur et al., 2001b).

RFI heritability estimates for steers in this dataset were slightly lower than those in reported literature. Schenkel and coworkers (2004) calculated RFI and $RFI_{ADJ\ for\ BF}$ and estimated heritabilities of 0.38 ± 0.07 and 0.39 ± 0.07, respectively. Crews and coworkers (2003) estimated heritability for RFI on 410 Charolais sired crossbred steers for a 84 d growing phase and 112 d finishing phase. RFI heritability estimate for growing (high roughage) diet was 0.30 ± 0.07 and the RFI for finishing (high grain diet) to be 0.26 ± 0.06. However, Nkrumah and coworkers reported a heritability of 0.21 ± 0.12 for RFI with steers (2007c), which is similar to results found in this study.

Heritability estimates from this study and literature reports indicate RFI should be a moderately heritable trait. Thus genetic improvement could be achieved if selection was based on RFI. However, it is unclear whether RFI in bulls is the same trait as RFI in steer progeny. Depending on the covariate used in the (co) variance analysis, all estimated genetic correlations were significantly less than 1.0 (range -0.18 to 0.33). MacNeil and Northcutt (2008) suggest genetic correlation estimates of greater than 0.8 indicate alternative measures of the same trait or an absence of a genetic by environmental interaction. Sex of the animal may play an important role in RFI and efficiency in general. Nkrumah and coworkers (2004) found bulls to be more efficient than steers in crossbred cattle. More research is needed to determine the relationship between bull and steer RFI.

Phenotypic correlations between RFI and other economically relevant traits

Phenotypic correlations between RFI and the other traits are recorded on Table 13. RFI was found to have significant phenotypic correlations with age, weaning weight, WDA, FCR, USBF, USIMF, and DMI in centrally-tested bulls. In addition to FCR, DMI, and USBF, RFI was also found to be phenotypically correlated with total gain, initial USBF and initial USIMF in steers of the carcass merit program.

While the correlations between RFI and age, weaning weight, and WDA in centrally-tested bulls were relatively weak, correlations with other traits were more moderate. The moderate phenotypic correlations of RFI with FCR and DMI agreed with published literature (Arthur et al., 1997,2001a,b; Baker et al., 2006, Carstens et al., 2002, Nkrumah et al., 2007c; Herd and Bishop, 2000; Lancaster, et al., 2005). These moderate, positive correlations show that animals with favorable RFI values generally also have favorable FCR and DMI values.

Published literature reports phenotypic correlations between RFI and UBF to fall within the range of 0.17 to 0.48 (Arthur et al., 1997; Arthur et al., 2001b; Robinson and

Oddy, 2004). However, the observed phenotypic correlation between the two traits in this dataset of central tested bulls was lower than published range (0.11). This could be a function of lean bulls with little variation in ultrasound 12th rib back fat measurements. Bull IMF and RFI also had a low phenotypic correlation (0.15) that agrees with reports by Basarab and coworkers (2007), Crews and coworkers (2003), Robinson and Oddy (2004), and Nkrumah and coworkers (2007).

Correlation results were similar for steers of the carcass merit project for feed intake traits. Phenotypic correlations of RFI with daily DMI and FCR were positive and high, agreeing with those of published literature (Arthur et al., 1997,2001a,b; Baker et al., 2006, Carstens et al., 2002, Nkrumah et al., 2007c; Herd and Bishop, 2000; Lancaster, et al., 2005).

A low to moderate positive phenotypic correlation between RFI and all three measurements of 12th rib fat thickness was observed in steers. This result indicates animals with lower, more favorable RFI have less fat. As expected, positive, low to moderate relationships were also observed between RFI with calculated yield grade (CYG) and USDA YG. While a very weak correlation was observed between RFI and initial USIMF, there was no evidence of this correlation being present at harvest, meaning selecting for favorable RFI most likely would not affect USDA quality grades.

Comparison of RFI classifications

When comparing the three classes of RFI for central tested bulls (Tables 14-16) for each of the three covariates, there were no differences between RFI classifications for the traits of initial weight, final weight, gain, ADG, IMF, SC or UREA. The lack of differences among growth traits and gain agreed with results published by Basarab and coworkers (2003), Carstens and coworkers (2002), Kolath and coworkers (2006), Lancaster and coworkers (2005) and Golden and coworkers (2008).

When adjusting for age, bulls within the intermediate RFI class had significantly heavier birth weights than bulls in the other two classes. No other significant differences were found for birth weight among the RFI classifications when adjusting for final weight or frame score. Arthur and coworkers (2005) reported no significant differences between two lines of cattle divergently selected for RFI for birth weight.

For each of the three covariates, significant differences between the three RFI classes were found for weaning weight. Low RFI bulls were significantly heavier at weaning than bulls of the other two classes. Bishop and coworkers (1991a) noted that high FCR sires tended ($P< 0.10$) to sire calves with heavier adjusted 205 d weaning weights and on test weights, but weaning weight lacked a phenotypic correlation with FCR in Angus bulls (Bishop et al., 1991a).

When adjusting for final weight on test, yearling weight was significantly different between high and low RFI classes. Bulls with favorable (low) RFI values had heavier adjusted yearling weights than bulls within the high RFI class. Differences also were observed for WDA when using covariates of final weight and frame score. Bulls within the low RFI class had higher WDA ratios than bulls in the high or unfavorable RFI class.

As expected, each of the three RFI classes differed significantly for the traits of daily DMI, and total DMI (Baker et al., 2006; Basarab et al, 2003; Carstens et al., 2002; Kolath et al., 2006; Golden et al., 2008). High RFI bulls consumed more daily DM, thus more feed over the length of the test and had higher, less favorable FCR than medium and low RFI bulls. Low RFI bulls consumed less DM and had lower FCR than bulls in the medium RFI class.

When adjusted for all three covariates, low RFI bulls exhibited less UBF than bulls in the medium and high RFI classes. When adjusting for frame score, medium RFI bulls had less UBF than bulls in the High RFI class. There is much conflict in the literature about differences between RFI classes for UBF. Carstens and coworkers (2002) reported low RFI steers had less rump fat than medium and high RFI steers. Nkrumah and coworkers (2004, 2007c) reported high RFI steers to have more BF gain per day, more BF, more carcass grade fat, higher YG, and less lean meat yield than medium RFI and low RFI steers. However, Kolath and coworkers reported no significant differences between high and low RFI groups for REA, BF, or YG (2006). Golden and coworkers (2008) conclusions were consistent with the Kolath study, with no significant differences between high RFI and low RFI steers for the traits of HCW, REA, BF, or YG.

Differences across steer RFI classifications are presented in Tables 17-19. Results were similar between the three covariates and three RFI measurements for the traits of USDA YG, total gain, total DMI, daily DMI, FCR, calculated YG, BF and UBF.

In general, steers with high and medium RFI exhibited higher YG (both calculated and plant YG) than their low RFI contemporaries. Nkrumah and coworkers (2004, 2007c) also reported high RFI steers to have higher YG, and less lean meat yield than medium RFI and low RFI steers. Kolath and coworkers’ (2006) and Golden and coworkers (2008) findings disagreed as neither found significant differences between high and low RFI groups for YG.

As expected, there were differences between the three RFI classes for the feed intake traits. Results agreed with published literature as High RFI steers consumed more feed than medium and low RFI steers. Low RFI steers ate less than the steers of the other two RFI classes. Likewise, steers differed in their abilities to covert feed to gain. Steers in the low RFI category had more favorable FCR than steers of the other two RFI classes. These results agree with those published by Baker and coworkers (2006), Basarab and coworkers (2003) Carstens and coworkers (2002), Nkrumah and coworkers (2004, 2007c), Kolath and coworkers (2006) and Golden and coworkers (2008).

ADG was similar across the three RFI classifications for each calculation and each covariate. Published literature agrees with these findings (Basarab et al, 2003; Carstens et al., 2002; Kolath et al., 2006; Lancaster et al., 2005). However, there were significant differences among the three RFI classes for total gain on test. Low RFI steers gained more over the entire test than high RFI steers.

Differences across the groups for measurements of 12th rib fat thickness, whether it be via ultrasound (UBF) or on the carcass (BF) agreed with the findings of Carstens and coworkers (2002), Nkrumah and coworkers (2004, 2007c) Kolath and coworkers (2006) and Golden and coworkers (2008). Steers in the low RFI classes had significantly less back fat at yearling and harvest than steers in the high and medium categories.

When adjusting traits for final weight and frame score, differences with REA were observed. Steers in the low RFI class exhibited significantly larger REA than their contemporaries within the other two RFI classes. Published literature does not report of any differences across groups for this trait (Carstens et al., 2002; Kolath et al., 2006).

When adjusting for final weight differences were observed across the three RFI classes for WDA, birth weight and initial UBF. Low RFI steers, generally had lower mid-test weights, thus lower MMWT and WDA, than their medium and high RFI contemporaries. However, Low RFI steers were heavier at birth than other steers. The steers within high and medium RFI classes had more UBF at the beginning of the test than low RFI steers. This agrees with the findings of Nkrumah and coworkers (2004, 2007c).

IMPLICATIONS

The trait of RFI is a moderately heritable trait and should be able to be incorporated into a genetic evaluation. However, with low and negative genetic correlations between bull and steer RFI, selection of low RFI bulls may not be result in efficient steer progeny. Within each sex, animals with low RFI exhibited lower FCR and daily DMI. There were no differences between the RFI classes for ADG and final test weights. More research needs to be completed on the relationships between parent RFI as an indicator trait for steer RFI.

Table 1: Simple means ± SE of performance and ultrasound carcass traits of central-tested bulls adjusted for each covariate

Trait[a]	N	Covariate		
		Age	Final wt	Frame score
Age, d			405 ± 26	405 ± 27
Final wt, kg	1434	595 ± 53		595 ± 49
Frame score	1430	6.6 ± 1.2	6.6 ± 1.1	
Birth wt, kg	1041	37.5 ± 4.52	37.5 ± 4.32	37.5 ± 4.29
Weaning wt, kg	1357	306 ± 37	306 ± 32	306 ± 30
Initial wt, kg	1434	399 ± 55	399 ± 30	399 ± 49
Yearling wt, kg	1427	549 ± 49	549 ± 35	549 ± 37
WDA, kg·d^{-1}	1434	1.47 ± 0.13	1.47 ± 0.10	1.47 ± 0.11
Total gain, kg	1434	196 ± 41	196 ± 30	196 ± 32
ADG, kg·d^{-1}	1434	1.74 ± 0.27	1.74 ± 0.22	1.74 ± 0.23
Daily DMI, kg·d^{-1}	1434	11.7 ± 1.4	11.7 ± 1.1	11.7 ± 1.2
FCR	1434	6.83 ± 1.01	6.83 ± 1.00	6.83 ± 1.03
USREA, cm^2	861	93.2 ± 9.1	93.3 ± 8.7	93.3 ± 8.8
USBF, mm	1316	8.5 ± 3.5	8.5 ± 3.4	8.5 ± 3.7
USIMF, %	501	3.39 ± 0.81	3.39 ± 0.91	3.39 ± 0.98
SC, cm	1183	36.7 ± 2.6	36.7 ± 2.6	36.7 ± 2.4
RFI, kg	1434	0.00 ± 0.78	0.00 ± 0.74	0.00 ± 0.74

[a] Trait definitions: Age: age in days at the end of the test period
Final wt: final weight at the end of the test period
Frame score: frame score at the end of test
Birth wt: birth weight recorded within 24 hours of birth
Weaning wt: adjusted 205 day weaning weight
Initial wt: weight at the beginning of the test period
Yearling wt: 365 day adjusted yearling weight
WDA: weight per day of age
Total gain: total gain on test
ADG: average daily gain
Daily DMI: average amount of dry matter consumed per day
FCR: feed conversion ratio, amount of feed consumed per one kg of gain
USREA: ultrasound longissimus dorsi area taken near the end of the test period
USBF: ultrasound fat thickness taken at the 12th and 13th rib taken near the end of test period
USIMF: ultrasound percent intramuscular fat taken near the end of the test period
SC: scrotal circumference measured near the end of the test period
RFI: residual feed intake calculated by year of test

Table 2: Simple means ± SE of performance, ultrasound and carcass traits steers adjusted for each covariate

Trait[a]	N	Covariate		
		Age	Final wt	Frame score
Age, d	769		419 ± 23	419 ± 15
Final wt, kg	769	597 ± 43		597 ± 34
Frame score	769	6.0 ± 1.5	6.0 ± 1.5	
Birth wt, kg	507	41.6 ± 5.6	41.6 ± 5.1	41.6 ± 4.4
Weaning wt, kg	757	293 ± 30	293 ± 34	293 ± 31
Yearling wt, kg	756	529 ± 34	529 ± 30	529 ± 34
WDA, kg·d^{-1}	769	1.42 ± 0.10	1.43 ± 0.08	1.43 ± 0.10
Total gain, kg	769	291 ± 32	291 ± 20	291 ± 34
ADG, kg·d^{-1}	769	1.61 ± 0.19	1.61 ± 0.11	1.61 ± 0.18
Daily DMI, kg·d^{-1}	769	9.9 ± 1.2	9.9 ± 0.8	9.9 ± 1.1
FCR	769	6.18 ± 0.65	6.18 ± 0.57	6.18 ± 0.70
USREA, cm^2	390	66.6 ± 4.3	66.6 ± 4.3	66.6 ± 4.6
USBF, mm	390	0.79 ± 0.23	0.79 ± 0.18	0.79 ± 0.26
USIMF, %	758	4.90 ± 0.72	4.90 ± 0.80	4.90 ± 0.70
Initial_USREA, cm^2	388	50.5 ± 4.4	50.5 ± 4.0	50.5 ± 4.7
Initial_USBF, mm	748	0.21 ± 0.15	0.21 ± 0.12	0.21 ± 0.14
Initial_USIMF, %	750	3.75 ± 0.55	3.75 ± 0.54	3.75 ± 0.53
HCW, kg	769	382 ± 27	382 ± 27	382 ± 22
REA, cm^2	757	92 ± 9.9	92 ± 8.4	92 ± 9.9
BF, mm	769	12.7 ± 3.7	12.7 ± 3.4	12.7 ± 3.5
CYG	757	2.84 ± 0.68	2.84 ± 0.62	2.84 ± 0.65
USDA_YG	769	2.6 ± 0.6	2.6 ± 0.5	2.6 ± 0.6
Marbling score	769	544 ± 70	544 ± 75	544 ± 73
RFI, kg	769	0.00 ± 0.64	0.00 ± 0.62	0.00 ± 0.66

[a] See Table 1 for abbreviations

Initial_USREA: ultrasound longissimus dorsi area taken prior to the start of the test period
Initial_USBF: ultrasound fat thickness taken at the 12th and 13th rib taken prior to the test period
Initial_USIMF: ultrasound percent intramuscular fat taken prior to the start of the test period
REA: longissimus dorsi area
BF: 12th rib fat thickness
CYG: calculated yield grade
USDA_YG: USDA yield grade
MARBLING: marbling score
RFI: RFI calculated by year of test and contemporary group

Table 3: Breed composition and frequency of centrally tested bulls and carcass merit project steers

Breed Composition	Frequency and Percentage	
	Bulls	Steers
100% Angus	917 (63.95%)	104 (13.52%)
More than 50% Angus (>50 AN)	5 (0.35%)	199 (25.88%)
50% Angus 50% Simmental (50 AN: 50 SM)	43 (3.0%)	463 (60%)
More than 50% Simmental (>50 SM)	57 (3.97%)	3 (0.39%)
100% Simmental	412 (28.73%)	0 (0%)
Total	1434	769

Table 4: Frequency of sires, paternal grandsires and maternal grandsires of central tested bulls and steer relatives

Frequency of Progeny	Sire	Paternal Grandsires	Maternal Grandsires
1	333	-	-
2-9	263	-	-
>10	47	-	-
Total	643	219	145

Table 5: Frequency of sires with individual recorded feed intake data

Frequency of Progeny	Sire*
1	17
2-10	10
>10	1
Total	28

* Some sires described in the above table also served as paternal and maternal grandsires.

* There were 13 bulls fed at AUBEC that were maternal or paternal grandsires of centrally tested bulls or steers.

Table 6: Least squares means for performance traits of centrally tested bulls adjusted for off-test age

		Breed Composition				
Trait[e]	Model R^{2}	Angus	> 50% Angus	50 AN: 50 SM	>50% SM	Simmental
Final wt, kg	42.1%	585±2^{a}	596±21^{ab}	591±9^{ab}	605±7^{b}	597±2^{b}
Frame score	66.5%	6.1 ± 0.0^{a}	6.8 ± 0.3^{b}	7.0 ± 0.1^{b}	7.2 ± 0.1^{b}	7.1 ± 0.0^{b}
Birth wt, kg	26.0%	35.9 ± 0.2^{a}	39.3 ± 1.8^{abc}	39.1 ± 0.8^{b}	41.6 ± 0.9^{c}	40.0 ± 0.2^{bc}
Weaning wt, kg	32.4%	300 ± 1^{a}	294 ± 15^{ab}	303 ± 6^{ab}	314 ± 5^{b}	311 ± 2^{b}
Initial wt, kg	57.6%	391 ± 1^{a}	390 ± 17^{ab}	391 ± 7^{ab}	401 ± 6^{ab}	399 ± 2^{b}
Yearling wt, kg	37.2%	542 ± 1^{a}	542 ± 19^{abc}	536 ± 8^{ab}	556 ± 7^{c}	552 ± 2^{bc}
WDA, kg·d^{-1}	36.8%	1.45 ± 0.00^{a}	1.48 ± 0.05^{ab}	1.46 ± 0.02^{ab}	1.50 ± 0.02^{b}	1.48 ± 0.01^{b}
Total gain, kg	68.8%	197 ± 1	207 ± 11	200 ± 5	204 ± 4	198 ± 1
ADG, kg·d^{-1}	39.9%	1.72 ± 0.01	1.81 ± 0.10	1.74 ± 0.04	1.79 ± 0.03	1.72 ± 0.01
Daily DMI, kg·d^{-1}	39.7%	11.5 ± 0.0^{a}	13.2 ± 0.5^{b}	11.4 ± 0.2^{a}	11.7 ± 0.2^{a}	11.5 ± 0.1^{a}
FCR	36.5%	6.80 ± 0.03^{a}	7.80 ± 0.39^{b}	6.70 ± 0.16^{a}	6.63 ± 0.14^{a}	6.81 ± 0.05^{a}
USREA, cm^{2}	37.0%	90.6 ± 0.4^{a}	92.2 ± 3.5^{b}	94.7 ± 1.5^{b}	96.4 ± 1.7^{b}	96.7 ± 0.5^{b}
USBF, mm	52.3%	9.77 ± 0.09^{a}	8.53 ± 1.13^{ab}	7.32 ± 0.47^{b}	6.08 ± 0.40^{c}	5.36 ± 0.13^{c}
USIMF, %	37.4%	3.68 ± 0.04^{ab}	4.21 ± 0.32^{a}	3.43 ± 0.14^{bc}	3.34 ± 0.16^{c}	2.91 ± 0.07^{d}
SC, cm	27.3%	36.3 ± 0.1^{a}	37.0 ± 1.1^{abc}	36.6 ± 0.5^{ab}	37.4 ± 0.5^{bc}	37.8 ± 0.1^{c}
RFI, kg	2.5%	0.02 ± 0.03^{a}	1.65 ± 0.40^{b}	-0.12 ± 0.15^{a}	-0.04 ± 0.12^{a}	-0.06 ± 0.04^{a}

[a-d] Columns with different subscripts differ at $P<0.05$

[e] See Table 1 for trait abbreviations

Table 7: Least squares means for performance traits of centrally tested bulls adjusted for off-test final weight

Trait[e]	Model R^2	Breed Composition				
		Angus	> 50% Angus	50 AN: 50 SM	>50% SM	Simmental
Age, d	44.8%	408 ± 1^{b}	408 ± 10^{ab}	410 ± 4^{ab}	404 ± 3^{ab}	404 ± 1^{a}
Frame score	73.5%	6.1 ± 0.0^{a}	6.7 ± 0.3^{b}	7.0 ± 0.1^{b}	7.1 ± 0.1^{b}	7.1 ± 0.00^{b}
Birth wt, kg	26.5%	35.9 ± 0.2^{a}	39.2 ± 1.8^{abc}	39.1 ± 0.8^{b}	41.6 ± 0.9^{c}	40.0 ± 0.2^{bc}
Weaning wt, kg	48.2%	301 ± 1^{a}	292 ± 13^{ab}	302 ± 6^{ab}	309 ± 4^{ab}	311 ± 2^{b}
Initial wt, kg	86.7%	396 ± 1	390 ± 10	395 ± 4	393 ± 3	397 ± 1
Yearling wt, kg	70.6%	544 ± 1^{a}	537 ± 13^{ab}	534 ± 5^{a}	548 ± 5^{ab}	551 ± 2^{b}
WDA, $kg \cdot d^{-1}$	67.4%	1.46 ± 0.00^{a}	1.46 ± 0.04^{ab}	1.45 ± 0.02^{ab}	1.47 ± 0.01^{ab}	1.48 ± 0.00^{b}
Total gain, kg	77.0%	199 ± 1	205 ± 10	200 ± 4	201 ± 3	198 ± 1
ADG, $kg \cdot d^{-1}$	55.2%	1.73 ± 0.01	1.80 ± 0.09	1.74 ± 0.03	1.76 ± 0.03	1.72 ± 0.01
Daily DMI, $kg \cdot d^{-1}$	59.5%	11.6 ± 0.0^{a}	13.2 ± 0.4^{b}	11.4 ± 0.02^{a}	11.5 ± 0.01^{a}	11.5 ± 0.0^{a}
FCR	32.9%	6.82 ± 0.03^{a}	7.83 ± 0.40^{b}	6.74 ± 0.17^{a}	6.65 ± 0.14^{a}	6.80 ± 0.05^{a}
USREA, cm^2	47.0%	90.6 ± 0.3^{a}	92.0 ± 3.2^{ab}	95.0 ± 1.4^{b}	96.1 ± 1.6^{b}	96.4 ± 0.5^{b}
USBF, mm	56.5%	9.84 ± 0.08^{c}	8.47 ± 1.08^{bc}	7.33 ± 0.45^{b}	5.90 ± 0.39^{a}	5.29 ± 0.13^{a}
USIMF, %	37.4%	3.68 ± 0.04^{bc}	4.21 ± 0.32^{c}	3.44 ± 0.14^{b}	3.34 ± 0.16^{b}	2.91 ± 0.07^{a}
SC, cm	34.2%	36.4 ± 0.1^{a}	37.0 ± 1.0^{abc}	36.7 ± 0.4^{ab}	37.4 ± 0.4^{bc}	37.8 ± 0.1^{c}
RFI, kg	1.9%	0.02 ± 0.03^{a}	1.67 ± 0.36^{b}	-0.11 ± 0.15^{a}	-0.03 ± 0.13^{a}	-0.07 ± 0.04^{a}

[a-d] Columns with different subscripts differ at P<0.05

[e] See Table 1 for trait abbreviations

Table 8: Least squares means for performance traits of centrally tested bulls adjusted for off-test frame score

		Breed Composition				
Trait[e]	Model R^{2}	Angus	> 50% Angus	50 AN: 50 SM	>50% SM	Simmental
Age, d	26.3%	406 ± 1	410 ± 12	411 ± 5	408 ± 4	405 ± 1
Final wt, kg	38.7%	605 ± 2^{a}	594 ± 21^{ab}	584 ± 9^{b}	586 ± 7^{b}	578 ± 3^{b}
Birth wt, kg	27.0%	36.1 ±0.2 ^{a}	39.2 ± 1.9^{abc}	38.9 ± 0.8^{b}	41.4 ± 0.9^{c}	39.7 ± 0.2^{b}
Weaning wt, kg	43.2%	308 ± 1^{b}	289 ± 13^{ab}	294 ± 6^{ab}	301 ± 5^{ab}	301 ± 2^{b}
Initial wt, kg	48.1%	404 ± 2^{a}	389 ± 19^{ab}	387 ± 8^{b}	387 ± 7^{b}	385 ± 2^{b}
Yearling wt, kg	54.6%	556 ± 1^{b}	534 ± 16^{ab}	523 ± 7^{b}	536 ± 6^{b}	535 ± 2^{b}
WDA, kg·d^{-1}	53.4%	1.49 ± 0.00^{a}	1.45 ± 0.04^{ab}	1.42 ± 0.02^{b}	1.44 ± 0.02^{b}	1.43 ± 0.01^{b}
Total gain, kg	70.7%	201 ± 1^{a}	205 ± 11^{ab}	197 ± 5^{ab}	199 ± 4^{ab}	193 ± 1^{b}
ADG, kg·d^{-1}	43.2%	1.75 ± 0.01^{b}	1.80 ± 0.10^{ab}	1.72 ± 0.04^{ab}	1.74 ± 0.03^{ab}	1.68 ± 0.01^{a}
Daily DMI, kg·d^{-1}	37.1%	11.8 ± 0.0^{b}	13.2 ± 0.5^{c}	11.3 ± 0.2^{a}	11.4 ± 0.2^{ab}	11.3 ± 0.1^{a}
FCR	32.9%	6.81 ± 0.03^{ab}	7.84 ± 0.40^{b}	6.75 ± 0.17^{a}	6.67 ± 0.14^{a}	6.81 ± 0.05^{a}
USREA, cm^{2}	35.1%	91.1 ± 0.4^{a}	91.9 ± 3.5^{ab}	94.3 ± 1.5^{b}	95.4 ± 1.7^{b}	95.7 ± 0.5^{b}
USBF, mm	51.1%	9.80 ± 0.10^{c}	8.58 ± 1.14^{bc}	7.37 ± 0.48^{b}	6.07 ± 0.41^{a}	5.32 ± 0.15^{a}
USIMF, %	37.6%	3.67 ± 0.04^{c}	4.21 ± 0.32^{c}	3.45 ± 0.14^{b}	3.36 ± 0.16^{b}	2.93 ± 0.07^{a}
SC, cm	26.4%	36.6 ± 0.1^{a}	36.9 ± 1.1^{ab}	36.4 ± 0.5^{a}	37.0 ± 0.5^{ab}	37.4 ± 0.1^{b}
RFI, kg	2.0%	0.01 ± 0.03^{a}	1.67 ± 0.36^{b}	-0.10 ± 0.15^{a}	-0.01 ± 0.12^{a}	-0.05 ± 0.04^{a}

[a-d] Columns with different subscripts differ at $P<0.05$

[e] See Table 1 for trait abbreviations

Table 9: Least squares means for carcass merit project steers adjusted for off-test age

Trait[e]	Model R^{2}	Breed Composition Angus	 > 50% Angus	 50 AN: 50 SM	 >50% SM
Final wt, kg	31.0%	595 ± 4	592 ± 3	598 ± 2	614 ± 24
Frame score	12.7%	6.0 ± 0.1	5.8 ± 0.1	6.1 ± 0.1	6.3 ± 0.9
Birth wt, kg	43.2%	37.2 ± 0.7^{a}	40.1 ± 0.4^{b}	42.6 ± 0.4^{c}	48.2 ± 2.9^{c}
Weaning wt, kg	58.3%	286 ± 3^{a}	290 ± 2^{b}	296 ± 2^{c}	315 ± 16^{abc}
Yearling wt, kg	52.4%	533 ± 4	530 ± 3	534 ± 2	567 ± 19
WDA, kg·d^{-1}	49.0%	1.42 ± 0.01	1.41 ± 0.01	1.43 ± 0.01	1.47 ± 0.06
Total gain, kg	33.6%	286 ± 3^{ab}	286 ± 3^{a}	293 ± 2^{b}	301 ± 18^{ab}
ADG, kg·d^{-1}	32.0%	1.67 ± 0.02^{b}	1.61 ± 0.01^{a}	1.62 ± 0.01^{a}	1.71 ± 0.10^{ab}
Daily DMI, kg·d^{-1}	39.5%	10.55 ± 0.1^{b}	9.95 ± 0.1^{a}	9.90 ± 0.1^{a}	10.45 ± 0.6^{ab}
FCR	28.8%	6.32 ± 0.07^{b}	6.23 ± 0.05^{ab}	6.13 ± 0.04^{a}	6.05 ± 0.37^{ab}
USREA, cm^{2}	13.6%	66.1 ± 1.6	66.7 ± 0.4	66.0 ± 0.3	63.0 ± 2.5
USBF, mm	38.2%	10.8 ± 0.8^{cb}	8.3 ± 0.2^{b}	7.3 ± 0.2^{a}	8.8 ± 1.3^{abc}
USIMF, %	30.2%	5.26 ± 0.08^{c}	4.94 ± 0.06^{b}	4.71 ± 0.04^{a}	5.04 ± 0.42^{abc}
Initial_USREA, cm^{2}	24.7%	46.4 ± 1.5^{a}	51.7 ± 0.4^{c}	49.9 ± 0.3^{b}	48.8 ± 2.5^{abc}
Initial_USBF, mm	45.3%	3.0 ± 0.1	2.3 ± 0.1	2.2 ± 0.1	2.5 ± 0.7
Initial_USIMF, %	28.4%	3.96 ± 0.06^{b}	3.89 ± 0.04^{b}	3.67 ± 0.03^{a}	3.45 ± 0.29^{ab}
HCW, kg	32.3%	381 ± 3	379 ± 2	383 ± 1	392 ± 15
REA, cm^{2}	33.1%	84.2 ± 1.0^{a}	90.8 ± 0.8^{b}	93.0 ± 0.5^{b}	88.4 ± 5.4^{ab}
BF, mm	22.9%	15.6 ± 0.4^{c}	13.2 ± 0.3^{b}	11.7 ± 0.2^{a}	13.7 ± 2.1^{abc}
CYG	25.4%	3.49 ± 0.07^{c}	2.92 ± 0.05^{b}	2.77 ± 0.04^{a}	3.23 ± 0.37^{abc}
USDA_YG	20.6%	3.13 ± 0.06^{c}	2.59 ± 0.05^{b}	2.48 ± 0.03^{a}	2.35 ± 0.35^{ab}
Marbling score	23.9%	585 ± 7^{c}	556 ± 6^{b}	534 ± 4^{a}	534 ± 41^{abc}
RFI, kg	4.1%	0.30 ± 0.08^{c}	0.06 ± 0.06^{b}	-0.07 ± 0.04^{a}	0.10 ± 0.41^{abc}

[a-d] Columns with different subscripts differ at P<0.05

[e] See Tables 1 and 2 for trait abbreviations

Table 10: Least squares means for carcass merit project steers adjusted for off-test final weight

		Breed Composition			
Trait[e]	Model R^2	Angus	> 50% Angus	50 AN: 50 SM	>50 SM
Age, d	70.0%	436 ± 2[c]	426 ± 1[b]	422 ± 1[a]	455 ± 10[d]
Frame score	16.0%	5.8 ± 0.1[a]	5.8 ± 0.1[a]	6.1 ± 0.1[b]	5.6 ± 0.9[ab]
Birth wt, kg	37.3%	36.7 ± 0.7[a]	40.5 ± 0.5[b]	43.2 ± 0.4[c]	45.0 ± 3.0[bc]
Weaning wt, kg	55.2%	274 ± 3[a]	286 ± 2[b]	294 ± 2[c]	282 ± 17[abc]
Yearling wt, kg	68.1%	516 ± 3[a]	536 ± 2[c]	530 ± 2[b]	512 ± 16[abc]
WDA, kg·d^{-1}	83.6%	1.37 ± 0.01[a]	1.41 ± 0.00[b]	1.42 ± 0.00[c]	1.31 ± 0.03[a]
Total gain, kg	68.4%	295 ± 2	292 ± 2	293 ± 1	307 ± 12
ADG, kg·d^{-1}	68.4%	1.63 ± 0.01	1.61 ± 0.01	1.61 ± 0.01	1.54 ± 0.07
Daily DMI, kg·d^{-1}	56.9%	10.3 ± 0.08[b]	9.9 ± 0.07[b]	9.8 ± 0.05[a]	9.5 ± 0.49[ab]
FCR	34.3%	6.34 ± 0.06	6.22 ± 0.05	6.14 ± 0.03	6.18 ± 0.35
USREA, cm^2	20.3%	66.2 ± 1.5[ab]	67.0 ± 0.4[b]	65.9 ± 0.3[a]	63.2 ± 2.4[ab]
USBF, mm	12.6%	8.3 ±0.9[ab]	8.1 ± 0.2[b]	7.5 ± 0.1[a]	6.5 ± 1.5[ab]
USIMF, %	31.2%	5.29 ±0.07[c]	4.95 ± 0.06[b]	4.71 ± 0.04[a]	5.05 ± 0.41[abc]
Initial_USREA, cm^2	31.9%	47.1 ± 1.4[a]	52.0 ± 0.4[c]	50.0 ± 0.3[b]	48.4 ± 2.3[abc]
Initial_USBF, mm	41.4%	26.9 ± 0.1[b]	21.9 ± 0.1[a]	21.8 ± 0.1[a]	17.6 ± 0.7[ab]
Initial_USIMF, %	28.0%	4.00 ± 0.05[b]	3.96 ± 0.04[ab]	3.67 ± 0.03[a]	3.55 ± 0.29[ab]
HCW, kg	99.8%	382.3 ± 0.1[b]	381.9 ± 0.1[a]	381.9 ± 0.1[a]	382.3 ± 0.7[ab]
REA, cm^2	35.5%	87.2 ± 0.9[a]	92.4 ± 0.7[b]	91.5 ± 0.5[b]	93.3 ± 5.2[ab]
BF, mm	22.8%	15.0 ± 0.3[c]	13.1 ± 0.2[b]	11.6 ± 0.2[a]	12.2 ± 2.1[abc]
CYG	19.7%	3.30 ± 0.07[c]	2.85 ± 0.05[b]	2.73 ± 0.04[a]	2.74 ± 0.38[abc]
USDA_YG	18.4%	3.01 ± 0.06[b]	2.55 ± 0.04[a]	2.46 ± 0.03[a]	2.06 ± 0.35[a]
Marbling score	20.2%	602 ± 7[c]	563 ± 6[b]	536 ± 4[a]	567 ± 41[abc]
RFI, kg	1.7%	0.18 ± 0.07[b]	0.01 ± 0.06[b]	-0.08 ± 0.04[a]	-0.14 ± 0.41[ab]

[a-d] Columns with different subscripts differ at $P<0.05$

[e] See Tables 1 and 2 for trait abbreviations

Table 11: Least squares means for carcass merit project steers adjusted for off-test frame score

Trait^{e}	Model R^2	Breed Composition			
		Angus	> 50% Angus	50 AN: 50 SM	>50 SM
Age, d	70.3%	436 ± 2^{c}	426 ± 1^{b}	422 ± 1^{a}	454 ± 9^{c}
Final wt, kg	34.4%	591 ± 4	592 ± 3	597 ± 2	603 ± 22
Birth wt, kg	36.8%	36.5 ± 0.7^{a}	40.4 ± 0.5^{b}	43.1 ± 0.4^{c}	45.3 ± 3.0^{bc}
Weaning wt, kg	49.1%	274 ± 2^{a}	286 ± 3^{b}	295 ± 2^{c}	286 ± 18^{abc}
Yearling wt, kg	34.0%	513 ± 4^{a}	524 ± 3^{b}	530 ± 2^{b}	519 ± 22^{ab}
WDA, kg·d^{-1}	29.7%	1.36 ± 0.01^{a}	1.39 ± 0.01^{b}	1.42 ± 0.01^{c}	1.33 ± 0.07^{abc}
Total gain, kg	33.7%	291 ± 3^{ab}	289 ± 3^{a}	294 ± 2^{b}	311 ± 18^{ab}
ADG, kg·d^{-1}	23.9%	1.61 ± 0.02	1.59 ± 0.01	1.61 ± 0.01	1.57 ± 0.11
Daily DMI, kg·d^{-1}	32.8%	10.20 ± 0.11^{b}	9.84 ± 0.09^{a}	9.84 ± 0.06^{a}	9.65 ± 0.61^{ab}
FCR	28.3%	6.37 ± 0.06^{b}	6.25 ± 0.05^{b}	6.14 ± 0.04^{a}	6.16 ± 0.36^{ab}
USREA, cm^{2}	14.1%	65.1 ± 1.5	66.7 ± 0.4	66.0 ± 0.3	63.2 ± 2.5
USBF, mm	12.8%	8.4 ± 0.9^{ab}	8.1 ± 0.2^{b}	7.4 ± 0.2^{a}	6.5 ± 1.5^{ab}
USIMF, %	30.2%	5.27 ± 0.07^{c}	4.94 ± 0.06^{b}	4.71 ± 0.04^{a}	5.06 ± 0.41^{abc}
Initial_USREA, cm^{2}	24.6%	46.2 ± 1.5^{a}	51.7 ± 0.4^{c}	50.0 ± 0.3^{b}	48.5 ± 2.5^{abc}
Initial_USBF, mm	41.0%	2.7 ± 0.1^{b}	2.2 ± 0.1^{a}	2.2 ± 0.1^{a}	1.8 ± 0.7^{ab}
Initial_USIMF, %	27.8%	4.00 ± 0.05^{b}	3.91 ± 0.04^{b}	3.67 ± 0.03^{a}	3.55 ± 0.29^{ab}
HCW, kg	35.8%	379 ± 3	379 ± 2	382 ± 1	386 ± 15
REA, cm^{2}	28.3%	86.6 ± 1.0^{a}	91.8 ± 0.8^{b}	91.6 ± 0.6^{b}	93.4 ± 5.5^{ab}
BF, mm	20.3%	14.9 ± 0.4^{c}	13.0 ± 0.3^{b}	11.6 ± 0.2^{a}	12.3 ± 2.1^{abc}
CYG	17.1%	3.29 ± 0.07^{b}	2.85 ± 0.05^{a}	2.73 ± 0.04^{a}	2.78 ± 0.38^{ab}
USDA_YG	17.0%	3.01 ± 0.06^{b}	2.55 ± 0.05^{a}	2.46 ± 0.03^{a}	2.08 ± 0.35^{a}
Marbling score	19.8%	601 ± 7^{c}	562 ± 6^{b}	535 ± 4^{a}	567 ± 41^{abc}
RFI, kg	1.5%	0.19 ± 0.07^{b}	0.02 ± 0.06^{ab}	-0.08 ± 0.04^{a}	-0.14 ± 0.41^{ab}

$^{a-d}$ Columns with different subscripts differ at $P<0.05$

^{e} See Tables 1 and 2 for trait abbreviations

Table 12: Heritability estimates ± SE for RFI among bulls and steers and genetic correlation ± SE between bull RFI and steer RFI with each covariate

Covariate	Bull RFI h^2	Steer RFI h^2	Genetic Correlation
Age, d	0.43 ± 0.05	0.23 ± 0.07	0.33 ± 0.04
Final Weight, kg	0.41 ± 0.05	0.17 ± 0.07	-0.18 ± 0.04
Frame Score	0.42 ± 0.05	0.18 ± 0.07	-0.00 ± 0.04

*SE was calculated 2/√N (Falconer and Mackay, 1989)

Table 13: Phenotypic correlations between RFI and other traits in central-tested bulls and steers of the Carcass Merit Program

	Bulls				Steers		
Trait[a]	N	R_p	Pvalue		N	R_p	Pvalue
Age, d	1434	0.07	0.0060		769	-0.07	0.0616
Final wt, kg	1434	0.00	0.9800		769	-0.04	0.2658
Frame score	1431	-0.03	0.2137		769	0.02	0.5908
Birth wt, kg	1041	0.00	0.9925		507	0.02	0.615
Weaning wt, kg	1357	-0.07	0.0120		757	0.03	0.4027
Initial wt, kg	1434	0.00	0.9793		-	-	-
Yearling wt, kg	1427	-0.03	0.1958		756	0.08	0.0345
WDA, $kg \cdot d^{-1}$	1434	-0.06	0.0285		769	0.02	0.6485
Total gain, kg	1434	0.00	1.0000		796	-0.1	0.0039
ADG, $kg \cdot d^{-1}$	1434	0.00	1.0000		769	0.00	1.0000
Daily DMI, $kg \cdot d^{-1}$	1434	0.55	<.0001		769	0.56	<.0001
FCR	1434	0.44	<.0001		769	0.62	<.0001
USREA, cm^2	861	-0.06	0.0659		390	-0.05	0.3161
USBF, mm	1316	0.11	<.0001		390	0.31	<.0001
USIMF, %	501	0.15	0.0006		758	0.06	0.1285
SC, cm	1183	-0.01	0.8635		-	-	-
Initial_USREA, cm^2	-	-	-		388	-0.06	0.2095
Initial_USBF, mm	-	-	-		748	10	0.0069
Initial_USIMF, %	-	-	-		750	0.08	0.0251
HCW, kg	-	-	-		769	-0.04	0.2809
REA, cm^2	-	-	-		757	-0.2	<.0001
BF, mm	-	-	-		769	0.18	<.0001
CYG	-	-	-		757	0.25	<.0001
USDA_YG	-	-	-		769	0.24	<.0001
Marbling score	-	-	-		769	0.01	0.7613

[a] See Tables 1 and 2 for trait abbreviations

Table 14: Least squares means for production traits of centrally tested bulls classified by RFI and adjusted for off-test age

Trait[e]	Model R^{2}	RFI Classification		
		Low	Medium	High
Final wt, kg	42.2%	599 ± 5	594 ± 6	595 ± 5
Frame score	66.6%	6.9 ± 0.1[b]	6.8 ± 0.1[a]	6.9 ± 0.1[b]
Birth wt, kg	26.2%	39.1 ± 0.5[a]	39.9 ± 0.5[b]	39.5 ± 0.5[a]
Weaning wt, kg	32.8%	308 ± 4[b]	303 ± 4[a]	303 ± 4[a]
Initial wt, kg	57.7%	397.8 ± 5	393.4 ± 5	393.7 ± 4
Yearling wt, kg	37.3%	548 ± 5	544 ± 5	546 ± 5
WDA, kg·d^{-1}	37.0%	1.48 ± 0.01	1.47 ± 0.01	1.47 ± 0.01
Total gain, kg	68.8%	201 ± 3	201 ± 3	202 ± 3
ADG, kg·d^{-1}	39.9%	1.76 ± 0.02	1.76 ± 0.02	1.76 ± 0.02
Daily DMI, kg·d^{-1}	61.6%	11.0 ± 0.1[a]	11.8 ± 0.1[b]	12.7 ± 0.1[c]
FCR	50.0%	6.41 ± 0.1[a]	6.90 ± 0.1[b]	7.43 ± 0.1[c]
USREA, cm^{2}	37.3%	94.8 ± 1.0	94.1 ± 1.0	93.5 ± 1.0
USBF, mm	52.9%	7.03 ± 0.3[a]	7.41 ± 0.3[b]	7.74 ± 0.3[b]
USIMF, %	37.8%	3.45 ± 0.1	3.51 ± 0.1	3.61 ± 0.1
SC, cm	27.5%	37.2 ± 0.3	37.0 ± 0.3	37.0 ± 0.3
RFI, kg	77.6%	-0.66 ± 0.05[a]	0.21 ± 0.05[b]	1.13 ± 0.04[c]

[a-c] Columns with different subscripts differ at P<0.05

[e] See Table 1 for trait abbreviations

Table 15: Least squares means for production traits of centrally tested bulls classified by RFI and adjusted for off-test final weight

Trait[e]	Model R^{2}	RFI Classification		
		Low	Medium	High
Age, d	45.2%	404 ± 3[a]	406 ± 3[ab]	409 ± 3[b]
Frame score	73.5%	6.9 ± 0.1	6.8 ± 0.1	6.8 ± 0.1
Birth wt, kg	26.7%	39.1 ± 0.5	38.9 ± 0.5	39.5 ± 0.5
Weaning wt, kg	48.8%	307 ± 3[b]	302 ± 3[a]	300 ± 3[a]
Initial wt, kg	86.7%	394 ± 3	394 ± 3	394 ± 2
Yearling wt, kg	70.8%	546 ± 3[b]	543 ± 3[ab]	541 ± 3[a]
WDA, kg·d^{-1}	67.7%	1.48 ± 0.0[b]	1.47 ± 0.0[b]	1.46 ± 0.0[a]
Total gain, kg	77.0%	200 ± 3	201 ± 3	200 ± 2
ADG, kg·d^{-1}	55.3%	1.75 ± 0.02	1.75 ± 0.02	1.75 ± 0.02
Daily DMI, kg·d^{-1}	82.7%	10.9 ± 0.07[a]	11.8 ± 0.07[b]	12.7 ± 0.07[c]
FCR	47.5%	6.41 ± 0.10[a]	6.91 ± 0.10[b]	7.47 ± 0.09[c]
USREA, cm^{2}	47.4%	94.6 ± 1.0	94.0 ± 1.0	93.5 ± 0.8
USBF, mm	57.1%	6.97 ± 0.29[a]	7.39 ± 0.28[b]	7.68 ± 0.29[b]
USIMF, %	37.9%	3.46 ± 0.10	3.51 ± 0.10	3.61 ± 0.10
SC, cm	34.3%	37 ± 0.3	37 ± 0.3	37 ± 0.3
RFI, kg	77.6%	-0.66 ± 0.05[a]	0.21 ± 0.05[b]	1.13 ± 0.04[c]

[a-c] Columns with different subscripts differ at $P<0.05$

[e] See Table 1 for trait abbreviations

Table 16: Least squares means for production traits of centrally tested bulls classified by RFI and adjusted for off-test frame score

Trait[e]	Model R^2	RFI Classification		
		Low	Medium	High
Age, d	26.9%	406 ± 3[a]	407 ± 3[a]	412 ± 3[b]
Final wt, kg	38.7%	589 ± 6	588 ± 6	592 ± 6
Birth wt, kg	27.3%	39.0 ± 0.5	38.8 ± 0.5	39.4 ± 0.5
Weaning wt, kg	43.6%	302 ± 4[b]	299 ± 4[a]	296 ± 4[a]
Initial wt, kg	48.1%	390 ± 5	389 ± 5	392 ± 5
Yearling wt, kg	54.6%	539 ± 4	537 ± 4	536 ± 4
WDA, kg·d^{-1}	53.6%	1.45 ± 0.01[b]	1.45 ± 0.01[ab]	1.44 ± 0.01[a]
Total gain, kg	70.7%	199 ± 3	199 ± 3	200 ± 3
ADG, kg·d^{-1}	43.2%	1.74 ± 0.03	1.74 ± 0.03	1.74 ± 0.03
Daily DMI, kg·d^{-1}	61.5%	10.8 ± 0.1[a]	11.7 ± 0.1[b]	12.6 ± 0.1[c]
FCR	47.5%	6.41 ± 0.10[a]	6.91 ± 0.09[b]	7.48 ± 0.10[c]
USREA, cm^2	35.2%	94.1 ± 1.1	93.7 ± 1.0	93.3 ± 1.1
USBF, mm	51.9%	7.02 ± 0.3[a]	7.42 ± 0.3[b]	7.80 ± 0.3[c]
USIMF, %	38.0%	3.47 ± 0.10	3.51 ± 0.10	3.61 ± 0.10
SC, cm	26.5%	37 ± 0.3	37 ± 0.3	37 ± 0.3
RFI, kg	77.7%	-0.65 ± 0.05[a]	0.22 ± 0.04[b]	1.14 ± 0.05[c]

[a-c] Columns with different subscripts differ at P<0.05
[e] See Table 1 for trait abbreviations

Table 17: Least squares means of performance, ultrasound and carcass traits of Carcass Merit Project steers classified by RFI and adjusted for age

Trait[e]	Model R^2	RFI Classification		
		Low	Medium	High
Final wt, kg	31.3%	602 ± 7	601 ± 6	596 ± 7
Frame score	12.7%	6.1 ± 0.2	6.0 ± 0.2	6.1 ± 0.2
Birth wt, kg	44.0%	41.4 ± 0.8^{a}	42.6 ± 0.8^{b}	41.4 ± 0.8^{a}
Weaning wt, kg	58.3%	297 ± 5	297 ± 4	296 ± 5
Yearling wt, kg	52.4%	541 ± 5	541 ± 5	541 ± 5
WDA, kg·d^{-1}	49.2%	1.44 ± 0.02	1.44 ± 0.02	1.42 ± 0.02
Total gain, kg	34.2%	295 ± 5^{b}	292 ± 5^{ab}	288 ± 5^{a}
ADG, kg·d^{-1}	32.2%	1.67 ± 0.03	1.66 ± 0.03	1.64 ± 0.03
Daily DMI, kg·d^{-1}	59.0%	9.5 ± 0.1^{a}	10.2 ± 0.1^{b}	10.9 ± 0.1^{c}
FCR	58.7%	5.69 ± 0.08^{a}	6.15 ± 0.08^{b}	6.71 ± 0.08^{c}
USREA, cm^2	14.7%	65.9 ± 0.8^{b}	64.8 ± 0.8^{a}	65.1 ± 0.8^{ab}
USBF, mm	42.1%	8.4 ± 0.4^{a}	8.6 ± 0.4^{a}	9.7 ± 0.4^{b}
USIMF, %	30.3%	4.95 ± 0.12	4.99 ± 0.11	5.02 ± 0.12
Initial_USREA, cm^2	25.0%	49.6 ± 0.8	49.1 ± 0.8	48.9 ± 0.8
Initial_USBF, mm	45.8%	2.4 ± 0.2^{a}	2.5 ± 0.2^{ab}	2.7 ± 0.2^{b}
Initial_USIMF, %	28.8%	3.69 ± 0.08	3.75 ± 0.08	3.78 ± 0.08
HCW, kg	32.5%	385 ± 4	385 ± 4	382 ± 4
REA, cm^2	35.4%	90.7 ± 1.5^{c}	88.8 ± 1.4^{b}	86.5 ± 1.5^{a}
BF, mm	24.4%	13.0 ± 0.6^{a}	13.4 ± 0.6^{b}	14.3 ± 0.6^{c}
CYG	28.5%	2.95 ± 0.10^{a}	3.09 ± 0.10^{b}	3.28 ± 0.10^{c}
USDA_YG	24.1%	2.48 ± 0.10^{a}	2.64 ± 0.10^{b}	2.79 ± 0.09^{c}
Marbling score	24.3%	545 ± 11	556 ± 11	551 ± 11
RFI, kg	76.7%	-0.66 ± 0.06^{a}	0.06 ± 0.05^{b}	0.88 ± 0.06^{c}

[a-c] Columns with different subscripts differ at P<0.05

[e] See Tables 1 and 2 for trait abbreviations

Table 18: Least squares means of performance, ultrasound and carcass traits of Carcass Merit Project steers classified by RFI and adjusted for final weight

		RFI Classification		
Trait[e]	Model R^{2}	Low	Medium	High
Age, d	70.7%	438 ± 3^{b}	434 ± 3^{a}	432 ± 3^{a}
Frame score	16.1%	5.8 ± 0.2	5.8 ± 0.2	5.9 ± 0.2
Birth wt, kg	38.4%	40.4 ± 0.9^{a}	42.0 ± 0.8^{b}	41.1 ± 0.9^{ab}
Weaning wt, kg	55.4%	282 ± 5	285 ± 4	287 ± 5
Yearling wt, kg	69.1%	515 ± 4^{a}	521 ± 4^{b}	528 ± 4^{c}
WDA, kg·d^{-1}	83.9%	1.37 ± 0.01^{a}	1.38 ± 0.01^{b}	1.39 ± 0.01^{b}
Total gain, kg	69.0%	301 ± 3^{b}	296 ± 3^{a}	293 ± 3^{a}
ADG, kg·d^{-1}	68.4%	1.59 ± 0.02	1.60 ± 0.02	1.60 ± 0.02
Daily DMI, kg·d^{-1}	81.8%	9.18 ± 0.09^{a}	9.93 ± 0.08^{b}	10.77 ± 0.09^{c}
FCR	61.7%	5.80 ± 0.07^{a}	6.23 ± 0.07^{b}	6.77 ± 0.08^{c}
USREA, cm^{2}	21.4%	66. 2 ± 0.8^{b}	65.1 ± 0.7^{a}	65.6 ± 0.8^{ab}
USBF, mm	22.1%	6.9 ± 0.5^{a}	7.6 ± 0.4^{b}	9.0 ± 0.5^{c}
USIMF, %	31.3%	4.97 ± 0.11	5.01 ± 0.11	5.04 ± 0.11
Initial_USREA, cm^{2}	32.0%	49.6 ± 0.7	49.2 ± 0.7	49.3 ± 0.7
Initial_USBF, mm	42.5%	2.0 ± 0.2^{a}	2.2 ± 0.2^{b}	2.4 ± 0.2^{b}
Initial_USIMF, %	28.2%	3.75 ± 0.08	3.79 ± 0.08	3.81 ± 0.08
HCW, kg	99.8%	382 ± 0.2	382 ± 0.2	382 ± 0.2
REA, cm^{2}	38.5%	93.3 ± 1.4^{c}	90.8 ± 1.4^{b}	88.6 ± 1.4^{a}
BF, mm	25.0%	12.4 ± 0.6^{a}	12.9 ± 0.5^{a}	13.9 ± 0.6^{b}
CYG	24.8%	2.74 ± 0.10^{a}	2.92 ± 0.10^{b}	3.14 ± 0.10^{c}
USDA_YG	23.1%	2.35 ± 0.09^{a}	2.54 ± 0.09^{b}	2.71 ± 0.10^{c}
Marbling score	20.4%	563 ± 11	571 ± 11	564 ± 12
RFI, kg	76.6%	-0.70 ± 0.06^{a}	0.03 ± 0.05^{b}	0.85 ± 0.06^{c}

[a-c] Columns with different subscripts differ at P<0.05

[e] See Tables 1 and 2 for trait abbreviations

Table 19: Least squares means of performance, ultrasound and carcass traits of Carcass Merit Project steers classified by RFI and adjusted for frame score

		RFI Classification		
Trait	Model R^{2}	Low	Medium	High
Age, d	70.9%	438 ± 3^{b}	434 ±2^{a}	431 ± 3^{a}
Final wt, kg	34.6%	596 ± 6	597 ± 6	592 ± 6
Birth wt, kg	37.7%	40.4 ± 0.9^{a}	41.9 ± 0.8^{b}	40.9 ± 0.9^{ab}
Weaning wt, kg	49.3%	283 ± 5	286 ± 5	286 ± 5
Yearling wt, kg	34.4%	518 ± 6^{a}	522 ± 6^{ab}	525 ± 6^{b}
WDA, kg·d^{-1}	29.9%	1.37 ± 0.02	1.38 ± 0.02	1.38 ± 0.02
Total gain, kg	34.6%	300 ± 5^{b}	296 ± 5^{ab}	291 ± 5^{a}
ADG, kg·d^{-1}	23.9%	1.59 ± 0.03	1.60 ± 0.03	1.59 ± 0.03
Daily DMI, kg·d^{-1}	55.6%	9.2 ± 0.14^{a}	9.9 ± 0.13^{b}	10.7 ± 0.14^{c}
FCR	56.7%	5.81 ± 0.08^{a}	6.23 ± 0.08^{b}	6.79 ± 0.08^{c}
USREA, cm^{2}	15.2%	65.9 ± 0.8^{b}	64.8 ± 0.8^{a}	65.1 ± 0.8^{ab}
USBF, mm	22.0%	6.9 ± 0.5^{a}	7.6 ± 0.4^{b}	9.0 ± 0.5^{c}
USIMF, %	30.3%	4.96 ± 0.11	5.00 ± 0.11	5.03 ± 0.11
Initial_USREA, cm^{2}	24.8%	49.3 ± 0.8	49.0 ± 0.8	48.8 ± 0.8
Initial_USBF, mm	42.0%	2.0 ± 0.2^{a}	2.2 ± 0.2^{b}	2.4 ± 0.2^{b}
Initial_USIMF, %	28.0%	3.75 ± 0.08	3.79 ± 0.08	3.82 ± 0.08
HCW, kg	36.0%	382 ± 4	382 ± 4	379 ± 4
REA, cm^{2}	31.5%	93.2 ± 1.5^{c}	90.7 ± 1.4^{b}	88.2 ± 1.5^{a}
BF, mm	22.3%	12.4 ± 0.06^{a}	12.9 ± 0.06^{ab}	13.8 ± 0.06^{b}
CYG	21.8%	2.74 ± 0.10^{a}	2.92 ± 0.10^{b}	3.13 ± 0.11^{c}
USDA_YG	21.5%	2.36 ± 0.09^{a}	2.54 ± 0.09^{b}	2.71 ± 0.10^{c}
Marbling score	20.1%	563 ± 11	570 ± 11	563 ± 11
RFI, kg	76.6%	-0.69 ± 0.06^{a}	0.04 ± 0.05^{b}	0.86 ± 0.06^{c}

[a-c] Columns with different subscripts differ at $P<0.05$

[e] See Tables 1 and 2 for trait abbreviations

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