EVALUATION OF FEED EFFICIENCY TRAITS WITH POST-WEANING GROWTH AND ULTRASOUND TRAITS IN CENTRAL TEST BULLS

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VITA

Genevieve Sue (Davis) Hecht, daughter of James Vernon Davis and Colleen Leslie (Graham) Davis, was born February 10, 1981 in Big Rapids, Michigan. Genevieve grew up on a small beef farm where she was involved in 4-H and FFA. In 1999, she graduated from Chippewa Hills High School in Remus, Michigan. She received her Bachelor of Science Degree in Animal Science from Michigan State University in East Lansing, Michigan in 2003. While there, she was employed at the Michigan State University Purebred Beef Barn and was active in the MSU Block and Bridle Club. After graduation from Michigan State University she received a Graduate Assistantship to attend Auburn University in Auburn, Alabama where she is currently pursuing her Master of Science degree in Animal Breeding and Genetics under the guidance of Dr. Lisa A. Kriese-Anderson. She will graduate in December 2007. In 2005, Genevieve was married to Christopher Adam Hecht and they reside in Reese, Michigan on the family farm.

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Since 1978, individual feed intake has been measured on bulls (n = 2,180) consigned to the Auburn University Bull Test along with weights, heights, scrotal circumference and ultrasound carcass traits. Test length since 1977 was reduced from 140 d to 112 d to 84 d. Eight breeds were analyzed using MTDFREML to estimate heritabilities of and genetic correlations between residual feed intake (RFI) and ADG, scrotal circumference (SC), ultrasound 12th rib fat thickness (USFAT), ultrasound *longissimus* muscle area (USREA) and percent intramuscular fat (USIMF). Breeds included were Angus (n = 857), Brangus (n = 41), Charolais (n = 380), Gelbvieh (n = 103), Hereford (n= 192), Limousin (n = 106), Santa Gertrudis (n = 106) and Simmental (n = 395). Traits were analyzed using three-trait analyses and a sire-maternal grandsire model with either age or weight as covariates. Fixed effects included length of test, breed and year. (Co)variance estimates were averaged across analyses to arrive at a final estimate.

Heritability Estimates of Traits Across Breeds

Covariate	RFI	ADG	SC	USFAT	USREA	USIMF	FCR
Age	0.10	0.17	0.16	0.16	0.09	0.14	0.13
Weight	0.09	0.16	0.17	0.15	0.13	0.13	0.12

Estimates of Genetic Correlations between RFI and Associated Traits Across Breeds

Covariate	ADG	SC	USFAT	USREA	USIMF	FCR
Age	-0.08	0.12	-0.13	-0.77	0.77	0.49
Weight	0.08	0.17	-0.02	-0.70	0.73	0.46

Heritability and genetic correlation estimates of all traits were on the lower end of reported literature estimates. These results may be due to consignment of elite bulls to a central test station. Results also suggest selection of animals with a lower residual feed intake should not increase individual size and should improve feed efficiency.

Key Words: Beef Cattle, Feed Efficiency, Genetic Parameters, Ultrasound

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INTRODUCTION

Providing feed to animals is the largest cost input in most animal production systems (Fan et al., 1995; Arthur et al., 2001a; Archer et al., 2002; Basarab et al., 2002; Herd et al., 2003), with 60 to 75% of total feed requirements utilized by the beef animal for maintenance (Arthur et al., 2001a; Basarab et al., 2002). Individual cattle vary in their ability to efficiently utilize feed (Fan et al., 1995; Arthur et al., 2001a). Currently, beef cattle are the least efficient converters of feedstuffs to unit gain among major protein providers. Farm raised fish are most efficient (1.1 pounds of feed to 1.0 pound of gain) followed by poultry (2 pounds of feed to 1.0 pound of gain) and swine (2.5 or 3 pounds of feed to 1.0 pound of gain). Cattle are a distant fourth with a feed conversion ratio (FCR) of 7.5 or 8 pounds of feed to 1.0 pound of gain. Any improvement of the output of beef per unit of feed used over the entire production system would be of significant economic benefit (Herd et al., 2003).

Many different facets contribute to the overall efficiency of a beef production system for both the breeding herd and feeder cattle. Growth traits and other production traits (reproductive rate, mature cow size, feed intake, and milk production) must be considered when determining the overall efficiency of the cow herd. Herring and Bertrand (2002) discussed factors influencing overall efficiency of the cow herd. Those factors included age, diet, temperature, breed, growth promoting implants, use of ionophores, and many other management and environmental variables. All of these factors need to be considered when evaluating the overall efficiency of a herd.

Cattle able to maintain body condition helps defer input cost, which is the primary feed cost of most cow/calf operations. Cattle able to maintain body condition with the same amount of feed can be defined as cattle with a better feed efficiency. In a feedlot, feed efficiency is one of the primary factors in profit or loss in a pen of cattle.

There are several methods to examine and define feed efficiency in cattle. Feed efficiency is most commonly expressed as a ratio of G:F or its inverse feed conversion ratio (FCR). This ratio can also be adjusted to a common body weight to account for differences in size. However, Koch et al. (1963) discussed selection for a trait defined by a ratio may lead to erroneous or unexpected results. Twenty years later, Gunsett (1984) argued that direct selection on FCR may not be the best way to improve efficiency, because: (i) the statistical properties of ratios are poor and selection response can be erratic; (ii) the use of a ratio as a selection criterion results in different responses in the component traits; and (iii) ratios may produce fallacious indications of economic efficiency. Crews (2006) concluded ratios and other measures of efficiency generally suffer from similar limitations in that they are too related to other economically important traits. Both beef cattle (Koch et al., 1963) and poultry (Byerly, 1941) results suggest using net feed efficiency (NFE) or residual feed intake (RFI) as the appropriate measure for examining feed efficiency in livestock species. Residual Feed Intake (RFI) is defined as the difference between the actual feed intake and the expected feed intake requirements for maintenance of body weight and production (Byerly, 1941; Koch et al., 1963).

Many studies have examined at least one definition of feed efficiency in beef cattle (Dawson et al., 1955; Shelby et al., 1955; Koch et al., 1963; Fan et al., 1995; Arthur et al., 1999, 2001a,b; McDonagh et al., 2001; Richardson et al., 2001; Archer et al., 2002). In general, most studies utilizing a ratio definition of FCR have suggested FCR is moderately heritable (0.22 to 0.80) with a moderate to high genetic correlation with post-weaning average daily gain (-0.32 to -0.69) and feed consumption (0.71 to 0.79) (Koots et al., 1994a; Archer et al., 1997; Richardson et al., 1998; Herd and Bishop, 2000; Arthur et al., 2001a,b; Herring and Bertrand, 2002; Herd et al, 2003). Many researchers and extension specialists instructed producers to select high average daily gain individuals to improve feed efficiency. This selection strategy probably favored larger framed individuals with excellent appetites. Currently researchers are focusing on RFI as a more appropriate selection tool for improving feed efficiency without increasing mature cow size.

One way researchers can collect data on postweaning growth traits is the use of central bull test stations. Central bull test stations are used in many parts of the country to evaluate post-weaning performance of bulls under uniform conditions. The first test stations were used to demonstrate performance concepts and improve growth rate in many breeds of beef cattle. The first full scale evaluation test for gain was conducted with bulls and heifers in 1949-1950 in Texas (Warwick and Cartwright, 1955).

With the development of national cattle evaluations conducted by many breeds today, central test stations are now used by seedstock breeders as an additional source of performance records on their bulls. Also, central test stations may serve as a demonstration of how to conduct an on-farm performance test (Dolezal and Silcox, 2004).

Central test stations document post-weaning gain performance and provide educational opportunities for prospective bull buyers. The stations also serve as a good source of bulls for commercial and seedstock herds. Test stations not only provide a seedstock producer with a place to market individual bulls, but it also gives the producer an opportunity to advertise their breeding program.

It is difficult to obtain measures of individual feed intake on the farm. A few central test stations in America have measured individual feed intake for considerable time. The purpose of this study was to examine feed efficiency traits with post-weaning growth and carcass ultrasound traits in central test bulls in Alabama.

REVIEW OF LITERATURE

Measures of Feed Efficiency

Feed Conversion Ratio. One definition of feed efficiency is the ratio of G:F or its inverse feed conversion ratio (FCR). FCR is defined as the units of feed consumed by an animal divided by the units of gain over a specific time period.

Heritability estimates for average daily gain (ADG), FCR, and residual feed intake (RFI) were examined in a study to determine optimum test length for measuring feed intake and FCR (Archer et al., 1997). Variance components, heritability estimates, phenotypic and genetic correlations, and the efficiency of selection using shortened tests compared with a 119 d test were used as criteria to assess the optimum test length. Data consisted of feed intake and weight records from 760 animals from 78 different sires originating from both research and industry herds. All cattle were given ad-libitum access to feed and individual intake of each animal was recorded. Archer and coworkers (1997) found a 70 d test was required to get an accurate measure of growth rate, FCR, and RFI. In another study, Wang and coworkers (2006) determined ADG, DMI, FCR, and RFI test duration could be shortened to 63, 35, 42, and 63 days, respectively. Measuring traits with a shortened test will defer some costs associated with having a traditional 119 d test, without compromising the accuracy of data being collected on traits being studied. This would also allow for conducting more than two tests a year to collect information on bulls.

Heritability estimates for FCR reported by Archer and coworkers (1997) ranged from 0.18 at 28 d to 0.42 at 70 d to 0.36 at 119 d. These heritability estimates were all measured with data collection occurring every two weeks. Heritability estimates reported for FCR also indicated there was little improvement in accuracy past 70 d.

Archer et al. (2002) conducted a post-weaning performance test using heifers. Upon completion of the test, heifers entered the cow herd. After the birth of their second calf, cows were not rebred. Approximately ten weeks after the calves were weaned, cows re-entered the test facility to examine FCR on mature cows. Archer and coworkers (2002) reported a moderately heritable estimate (0.26) on mature cows for FCR with a strong genetic correlation (-0.87) with ADG, suggesting selection to improve FCR may affect cow size.

Approximately 30 years ago, Woldehawariat et al. (1977) summarized heritability estimates concerning feed efficiency of beef cattle. Various heritability estimates of FCR were reported ranging from 0.26 to 0.80. A heritability estimate of 0.36 was reported for G:F. More recent studies agree FCR is moderately heritable (Koots et al., 1994a and Arthur et al., 2001a). However, Herd and Bishop (2000) reported a smaller heritability estimate for FCR of 0.17 on Hereford bulls.

Many literature reports suggest single trait selection for lower feed conversion should result in higher degrees of growth with less feed intake. Koots et al. (1994b) reported genetic correlations in beef cattle between FCR and post-weaning gain (Total Gain, TG), fat thickness and feed intake (FI) were -0.53, -0.24 and 0.38, respectively, suggesting they are moderately related to each other. Arthur et al. (2001a,b) reported similar genetic correlations between FCR and average daily gain (ADG) (-0.62 and -0.46) and FCR and FI (0.31 and 0.64) for Angus and Charolais breeds, respectively.

Herd et al. (2003) concluded strong genetic relationships exist between feed intake and FCR measured postweaning. Other genetic correlations reported in the literature vary. Koch et al. (1963) and Woldehawariat et al. (1977) reported positive genetic correlations of 0.79 and 0.23, respectively, between post-weaning ADG and FCR. Arthur et al. (2001a) reported a negative genetic correlation of -0.74, between post-weaning ADG and FCR. However, these recent studies continue to confirm strong genetic relationships between FI and FCR. FCR and ADG were related in a favorable direction in these recent studies.

Woldehawariat et al. (1977) also summarized genetic and phenotypic correlation estimates between post-weaning feed efficiency and other traits from literature. Genetic correlation estimates between FCR and ADG ranged from -0.41 to 0.31, suggesting there is a moderate correlation between ADG and FCR. However, the direction of the correlation is unclear. Genetic correlations of -0.34 between FCR and TG on test and 0.23 between FCR and post-weaning ADG were reported by Woldehawariat et al., (1977).

The phenotypic correlation between FCR and ADG ranged from -0.26 to 0.55, suggesting there is a moderate correlation between ADG and FCR (Woldehawariat et al., 1977). Again, the direction of the phenotypic correlation is unclear. This uncertainty could be a result of analyzing a ratio trait.

Bishop et al. (1991a,b) conducted a divergent selection experiment for FCR using Angus cattle. Angus bull calves were individually fed in a 140 d post-weaning test. The three highest for and three lowest FCR bulls were selected each year and randomly mated to approximately 20 Angus cows. A total of 403 progeny were evaluated in post-weaning trials from 1983 to 1986.

Two measures of FCR were used in this study. They were group FCR (unadjusted) for the first 140 d on test and FCR adjusted for maintenance as recommended by BIF (2002). Bishop et al. (1991b) reported heritability estimates of 0.26 for unadjusted group FCR and 0.46 for FCR adjusted for maintenance. Both estimates are similar to previous estimates reported and are moderately heritable.

Other heritability estimates for FCR in beef cattle reported in the literature include those of Knapp and Nordskog (1946) of 0.48, Dawson et al. (1955) of 0.32, Carter and Kincaid (1959a) of 0.99, Brown and Gifford (1962) of 0.80, and Brown et al. (1988) of 0.14. Realized heritability estimates for FCR in swine were reported by Dickerson and Grimes (1947) of 0.24, Bernard and Fahmy (1970) of 0.11, Jungst et al. (1981) of 0.09, Webb and King (1983) of 0.007, and Bereskin (1986) of 0.061. In poultry, Wilson (1969) reported a realized heritability estimate for FCR of 0.34 and Pym and Nichols (1979) reported an estimate of 0.44. Once again all of these heritability estimates indicate FCR among species is moderately heritable.

Residual Feed Intake. Measuring RFI was first described by Byerly (1941) when examining net efficiency of laying hens. Koch and coworkers (1963) recognized in growing beef cattle that differences exist in weight maintained and weight gain and has an effect on feed requirements. Koch et al. (1963) suggested feed intake could be adjusted for BW and weight gain by dividing feed intake into two different components. Those components are expected and residual portions of feed intake for the given level of production. The residual portion of feed intake describes the amount individuals deviate from the expected level of feed intake. Koch and coworkers (1963) initially found RFI was a heritable trait in beef cattle (0.28 ± 0.11), with efficient animals having a lower or negative value for RFI. Since maintenance and growth requirements are not accounted for by G:F or its inverse FCR, RFI comparisons between animals may be a better measure of efficiency (Kolath et al., 2006).

Several heritability estimates of RFI are in the literature. RFI appears to be moderately heritable. Pitchford (2004) provided a summary of RFI heritability estimates. Heritability estimates include 0.27 on dual purpose cattle, a range of 0.08 to 0.36 on growing dairy males, 0.22 for growing dairy females, 0.19 for lactating heifers and a range of 0.0 to 0.16 for lactating cows. Herd and Bishop (2000) reported a similar heritability of 0.16 for Hereford bulls. Archer et al. (1997) reported a RFI heritability estimate of 0.41 on Angus, Hereford, Polled Hereford and Shorthorn heifer and Angus bull progeny. Arthur et al. (2001a,b) reported similar heritability estimates for RFI of 0.39 for Charolais bulls and for Angus bulls and heifers.

Archer and coworkers (1997) showed environmental variance estimates for RFI decreased from 0.57 $(kg/d)^2$ at 7 d to 0.13 $(kg/d)^2$ at 70 d. After 70 d results show only a small decrease in environmental variance estimates for RFI, suggesting the extra measurement time did not improve accuracy of measurements (Archer et al., 1997). Heritability estimates for RFI reported by Archer and coworkers (1997) ranged from 0.34 at 7 d to 0.62 at 70 d to 0.60 at 119 d. The genetic correlation of RFI between 70 d and 119 d was 0.98. This suggests the same measure of RFI was measured at 70 d and 119 d. Thus, measuring RFI for 70 d is adequate to find genetic differences.

Heritability estimates for RFI have been reported in several other species. Mrode and Kennedy (1993) reported heritability estimates ranging from 0.30 to 0.38 in growing boars. Von Felde et al. (1996) reported a smaller RFI heritability estimate of 0.18 also in growing boars. Heritability estimates for RFI of laying hens were reported by Luiting and Urff (1991a,b), Bordas et al. (1992), and Tixier-Boichard et al. (1995) ranging from 0.12 to 0.62. Tixier-Boichard et al. (1995) also reported a heritability estimate for RFI of 0.33 for cockerels, which is within the range of laying hens. Pitchford (2004) also summarized heritability estimates for RFI ranging from 0.16 to 0.28 in mice, 0.28 to 0.33 in sheep and 0.32 in Tribolium.

There appears to be sufficient genetic variation to select for RFI (Herring and Bertrand, 2002). Since RFI appears to be a moderately heritable trait, and is similar to estimates for traditional growth traits (Crews, 2006) selecting animals that are naturally efficient may improve overall efficiency of a herd.

Genetic correlations between RFI postweaning and maturity. To improve herd efficiency, genetic relationships between feed efficiency traits with mature cow performance traits must be known and understood. Herd et al. (2003) reported no genetic correlation estimate between post-weaning RFI and mature cow size. This correlation suggests selection of cattle with lower post-weaning RFI values will not increase cow size. Conversely, a strong positive genetic correlation between post-weaning FCR with cow size was found suggesting selecting for reduced post-weaning FCR may cause a change in cow size. If cow size increases, nutritional requirements also increase, therefore, FCR may not improve. If cow size decreases, FCR may improve, but decreasing cow size may not be the best method to improve FCR.

Mice were allotted to a high or low RFI line (Archer et al., 1998). Mice were housed individually for measurement of post-weaning ad-libitum feed intake and weight measurement. Eight males were retained for sires and every female was retained for the breeding colony at the conclusion of the post-weaning test. Mature measurements were taken on female mice after litters were weaned. Post-weaning and mature traits measured were ADG, mid-weight and daily feed intake. Heritability of RFI postweaning was estimated at 0.27 and 0.29 at maturity. In mice, this suggests genetic variation exists for RFI at post-weaning and maturity. A genetic correlation between RFI post-weaning and RFI maturity was 0.60. Animals ranked for RFI measurements taken post-weaning should remain ranked in a similar fashion at maturity. A correlated improvement in efficiency of mature mice (at maintenance) was noted based on selection for post-weaning low RFI of mature animals. These results suggest post-weaning RFI may be a suitable selection criterion for use in livestock to improve efficiency of young animals and decrease feed costs in the breeding herd (Archer et al., 1998).

RFI differences appear to continue into maturity. Herd and coworkers (2003) conducted a comprehensive study examining the response to selection of post-weaning RFI on cow traits and steers that were finished on pasture or a feedlot. Parents were selected and assigned to a low or a high RFI line based on their post-weaning RFI data. At maturity, low RFI cows finished on pasture were 7% heavier, had similar rib fat and rump fat depths, and reared calves of similar BW to the high RFI cows, but consumed no more feed than high RFI cows. The advantage in efficiency of the low RFI cows, when expressed as a ratio of calf BW to cow feed intake, was 15%, suggesting a phenotypic association between post-weaning RFI of the young female and her later efficiency as a cow/calf unit on pasture (Herd et al., 2003).

In a feedlot setting, mature cow RFI and feed intake were the only traits that differed over the 70 d test period between the low and high RFI line. There were no significant differences in BW, rib fat depth, or ADG throughout the test period between the low and high RFI lines. Milk yield was measured once using the calf weigh-suckle-weigh method over the test period on cows. There was no difference in milk production between the high and low RFI lines. Herd et al. (2003) suggested females more efficient as weanlings required less feed as mature cows, with no compromise in performance.

Parents were selected based on their RFI measurement from a post-weaning test conducted at eight to twelve months of age. Their bull and heifer progeny were then evaluated for post-weaning RFI under the same test regimen used to test their parents (Herd et al., 2003). After five years of selecting animals on post-weaning RFI, the direct response for RFI was -0.54 ± 0.18 kg/day in the low RFI line and 0.70 ± 0.17 kg/day in the high RFI line. Herd et al., (2003) also reported a reduction in daily feed intake with a reduced or improved FCR in the low RFI line as compared to the high RFI line. Yearling weight and post-weaning ADG were not affected by selection on post-weaning RFI.

Steer progeny were evaluated for post-weaning RFI following a single generation of divergent selection for post-weaning RFI (Herd et al., 2003). The response to selection of post-weaning traits was examined utilizing steers finished on pasture and in the feedlot. Steer progeny finished on pasture from the low RFI line tended to gain faster than progeny from the high RFI line. Herd et al. (2003) reported no significant difference in daily pasture intake between the selection lines. FCR was 6.4 ± 0.4 kg/kg for the low

RFI line and 8.5 ± 0.8 kg/kg for the high RFI line ($P < 0.1$). A positive regression coefficient of FCR with mid-parent estimated breeding value (EBV) for RFI (2.9±1.5, $P < 0.1$) provided evidence for low RFI in the parents being genetically associated with superior efficiency of FCR on pasture by their steer progeny (Herd et al., 2003).

Angus and crossbred Angus steers were evaluated for growth, feed intake, FCR, and some carcass characteristics in the feedlot phase. This study concluded that steer progeny of low RFI parents grew as fast as or faster than steers of high RFI parents, but ate less feed per unit of gain. The steer progeny also produced carcasses of acceptable fat finish with no compromise in retail meat yield, and as a consequence, should be more profitable to feed in a feedlot (Herd et al., 2003).

Some studies reported strong positive genetic correlations between RFI and FCR in beef cattle. Herd and Bishop (2000) reported a genetic correlation of 0.70 and Arthur et al., (2001a,b) reported estimates of 0.85 and 0.66, respectively. Finally Schenkel et al. (2004) reported a genetic correlation between RFI and FCR of 0.69.

Similar estimates have been reported for RFI and feed intake: 0.64 (Herd and Bishop, 2000); 0.69 and 0.79 (Arthur et al., 2001a,b) and 0.81 (Schenkel et al., 2004). Phenotypically, RFI was positively correlated with DMI (0.54) and FCR (0.42) but was not phenotypically correlated with BW measurements or ADG (Baker et al., 2006). ADG and BW measurements were similar among RFI groups. High RFI steers had greater DMI ($P < 0.004$) and FCR ($P < 0.002$) than did the low RFI steers (Baker et al., 2006). These results suggest that selection for improved (lower) RFI will result in a declining genetic trend for feed intake (Crews, 2006).

Residual Feed Intake Effects on Meat Quality and Palatability

Baker et al. (2006) studied the effects RFI could have on meat quality and palatability. Data were collected on purebred Angus steers (n = 54). Initial (d 28 of test) ultrasound *longissmus* muscle area (USREA) showed a positive phenotypic correlation with FCR (0.64) but was not correlated with RFI. Baker et al. (2006) found no differences between high, mid, or low RFI steers for initial (d 28 of test) ultrasound fat thickness (USFAT), 71 d USFAT, initial (d 28 of test) USREA, and 71 d USREA. The study also suggested meat quality and palatability were not different between high and low RFI Angus steers.

Biological Basis for Variation in Residual Feed Intake in Beef Cattle

Biological mechanisms underlying the variation in feed efficiency in animals with similar body weight and growth weight are not well understood. At least five major processes were identified by Herd et al. (2004) in which variation in efficiency can arise (Figure 1). The existence of genetic variation in RFI offers potential that selection for low RFI will produce progeny that eat less, with no compromise in growth performance. However, the biological basis of such variation is largely unknown.

Richardson and Herd (2004) reported results following a single generation of divergent selection for RFI on Angus steer progeny and identified seven major processes contributing to variation in RFI (Figure 2). These authors suggest it was important to identify the biological basis for RFI in beef cattle. Knowing this may lead to a more efficient method of selection for RFI (such as molecular markers) and help ensure selection against RFI will not have unexpected detrimental effects on progeny.

Synthesis of Potential Mechanisms. Herd and coworkers (2004) provided percentage breakdowns of mechanisms contributing to phenotypic variation for RFI in beef cattle. Mechanisms (Figure 1) include 9% for heat increment of feeding (HIF); 14% for digestion; 5% for body composition; 5% for activity. The remaining 67% were other factors responsible for variation in RFI.

Richardson and Herd (2004) also reported similar estimates of what is currently known about mechanisms contributing to variation in RFI (Figure 2). Richardson and Herd (2004) reported biological variation in RFI may be attributed to body composition (5%), animal feeding patterns (2%), protein turnover, tissue metabolism and stress (37%), heat increment of fermentation (9%), animal digestion (10%), animal activity (10%) and other biological mechanisms that are not fully understood (27%).

Johnson and coworkers (2003) would add to the list of traits that receive more attention by researchers and cattle producers. These traits include rate of gain, BW and prolificacy. These authors would also separate metabolism into two components, maintenance and growth metabolism. Including these traits in gain and metabolism will help to ensure minimal or no negative consequences for selection of improved RFI.

Feed Intake. Variation in feed intake is associated with variation in maintenance requirements. As feed intake increases, the amount of energy needed to digest feed increases (Herd et al., 2004). The amount of energy expended by the tissues themselves also increases per unit weight of the animal. This is known as heat increment of feeding (HIF). Given that selection for RFI is associated with variation in intake, animals that eat less, at the same level of performance, could be expected to have less energy expended as HIF.

Digestion. Increases in level of feed intake relative to maintenance usually decreases digestion of feed, as measured by total tract disappearance. Genetic variation appears to influence total tract digestion of feed (Herd et al., 2004). Young bulls and heifers, phenotypically ranked as low or high for RFI, tended to differ in their ability to digest dry matter by approximately 1% (Richardson et al., 1996). This difference in dry matter digestibility accounted for 14% of the difference in intake between the two groups of cattle.

Variation in the supply of amino acids is due in part to variation in efficiency of microbial protein production in the rumen and appearance in the portal vein (Herd et al., 2004). In dairy cows, there is evidence that selection for high milk yield is accompanied by improvement in digestion and/or absorption of dietary energy and protein (Adams and Belyea, 1987). Results summarized by Herd and coworkers (2004) suggest differences in the processes of digestion and substrate availability, at least in portal blood, do occur. Herd and coworkers (2004) concluded these results provide a possible mechanism to explain variation in efficiency of feed utilization, without the need to invoke variation in nutrient utilization.

Dry matter digestibility was phenotypically correlated with RFI (-0.44). This determined differences in digestibility that accounted for 19% of the phenotypic variation in RFI (Richardson and Herd, 2004). The direction of the correlation suggests lower RFI values were associated with higher digestibility. Richardson and Herd (2004) suggest some of the differences in digestibility may be associated with differences in rate of passage.

Body Composition and Metabolism. According to Herd et al. (2004), the deposition of the same weight of lean tissue and fat has different energy costs. There is more variation in the efficiency of depositing lean gain than fat gain. There have been few studies in which contribution of body composition to genetic variation in heat production or feed efficiency has been studied (mice, Archer and Pitchford, 1996; beef cattle, Richardson et al., 1999). These authors found variation in composition was small, relative to variation in heat production.

It is useful to consider possible causes of variation in metabolism which impact heat production. Many of these processes contribute to the maintenance energy requirement of an animal (Herd et al., 2004). Some of these processes include demonstrated differences in energy efficiency used for maintenance between animals (Archer et al., 1999). Also, there is evidence that maintenance energy requirement per unit metabolic weight was closely associated with genetic variation in RFI (Herd and Bishop, 2000). Another process includes protein turnover. Protein turnover in living animals is an energetically expensive process and variation in protein metabolism has been shown to accompany genetic selection for growth and other traits in domestic animals (Herd et al., 2004).

All together, evidence supports many possible mechanisms of variation in metabolism. Variations in metabolism are principally regulated at the tissue level (Herd et al., 2004). If there are differences in nutrient supply due to variation in digestion and absorption of feed, there may also be associated changes in hormone release and thus tissue responsiveness, over and above the availability of substrate (Herd et al., 2004).

Herd and coworkers (2004) suggest the challenge remains in identifying the possible contributors to variation in efficiency associated with other desirable traits.

Results show from the RFI selected steer group that chemical composition was correlated with genetic variation in RFI. Steer progeny of low RFI parents have less whole body chemical fat and more whole body chemical protein, as compared to progeny of high RFI parents (Richardson and Herd, 2004). It was estimated these differences contributed 5% of the genetic variation in RFI.

Measurements taken on steers following divergent selection for RFI support the hypothesis that rates of protein degradation and protein accretion in the whole body are correlated with variation in RFI in beef cattle. From these measurements Richardson and Herd (2004) concluded more efficient steers possess a more efficient mechanism for protein deposition. Less efficient steers have a greater rate of protein degradation and higher levels of protein catabolism in the liver. With all these factors taken into consideration, Richardson and Herd (2004) concluded it is likely there is genetic association between protein turnover and RFI.

Activity. Variation in heat production and energy available for maintenance and growth also occurs as a result of differences in energy expenditure associated with activity (Herd et al., 2004). Activity also contributes to substantial proportions of the variation in RFI in chickens (Braastad and Katle, 1989; Katle, 1991; Luiting et al., 1991). Luiting and coworkers (1991) concluded 79% of the genetic difference in RFI of lines of chickens divergent for RFI could be related to a difference in physical activity. In mice selected for and against RFI post-weaning, there were marked differences in activity pattern, such that more efficient mice were less active than less efficient mice (Herd et al., 2004).

Differences in activity can also be associated with variation in RFI in cattle. Herd et al. (2004) reported a phenotypic correlation of 0.32 between RFI, based on activity as measured with a daily pedometer count. Approximately 10% of observed variation in RFI was explained by this measure of activity. Mechanisms associated with variation in activity include work involved in feeding, ruminating and walking at various speeds (Herd et al., 2004).

Thermoregulation. The principal route for energy loss in ruminants is evaporative heat loss. To a large extent this is regulated by rate of respiration. No studies to date have examined the relationship between respiration rate and RFI. Postural change and other adaptations such as seeking shelter and huddling do not, by themselves, constitute a large proportion of variation in heat loss, except in extreme situations (Herd et al., 2004).

Feeding Patterns. Richardson and Herd (2004) examined feeding patterns in steers bred for high or low RFI values. High RFI steers tended to have a faster decline in the length of average daily feeding sessions, and the high RFI steers had longer eating sessions early in the test as compared to low RFI steers. This, along with the observed difference in profiles for the total time spent on daily feeding, suggest that high RFI steers were standing and feeding longer than low RFI steers. This contributes 2% of the variation associated with RFI (Richardson and Herd, 2004).

Studies on monogastric species reveal the potential importance of differences in activity to variation in RFI. DeHaer et al. (1993) found in a study with pigs that total daily feeding time and number of visits to a feeding station showed a positive phenotypic correlation with RFI (0.64 and 0.51, respectively). On a daily basis these results indicate animals ranked by improved RFI spent less time feeding when visiting the feeding station.

Stress. Fraser et al. (1975) defined stress as an abnormal or extreme adjustment in the physiology of an animal to cope with adverse effects of its environment and management. Cattle in an intensive husbandry system, such as a feedlot, are potentially subjected to an increased abundance of stressors, such as sudden noise, dust, transportation, mixing, and close proximity to others. Using results for red and white blood cell parameters of steers selected for RFI, high RFI steers may be more susceptible to stress than low RFI steers (Richardson and Herd, 2004).

Richardson and Herd (2004) concluded there are many mechanisms contributing to variation of RFI (Figure 2). Further research is required to understand these and other possible biological mechanisms that contribute to RFI.

Nkrumah and coworkers (2006) studied the relationship of feedlot FCR, performance, and feeding behavior with metabolic rate, digestion, and energy partitioning in beef cattle ranked by RFI. Differences among the groups of RFI selected steers were found to include efficiency in energy of ADG, FCR, DMI, but not in metabolic BW or ADG. There were no significant differences observed among RFI groups for heat increment of feeding, even though the low RFI steers had 32.6% lower heat increment of feeding. Nkrumah et al. (2006) reported a negative association between RFI and digestibility of dietary crude protein (-0.34) and dry matter (-0.33).

There were also no significant results reported for NDF and ADF analyses of diets on RFI levels. The analyses did indicate NDF digestibility was less in high RFI steers than low RFI steers (Nkrumah et al., 2006). Feedlot FCR of steers was also unrelated to any of the metabolic rate and energy partitioning traits. Nkrumah and coworkers (2006) concluded differences in metabolism; mainly digestibility and methane production, heat production, and energy retention are responsible for a major part of the variation among animals in RFI.

Other Important Post-Weaning Traits

There are many traits that are important for producers to consider when selecting bulls for their breeding program. Traits easily measured include average daily gain (ADG) and scrotal circumference (SC). Improved gains result in heavier market weights, while larger yearling SC measurements may improve heifer fertility. Yearling SC measurements are genetically correlated to age at puberty in subsequent daughters (Moser et al., 1996 and Vargas et al., 1998).

Average Daily Gain (ADG). ADG is another way to measure post-weaning growth in livestock. ADG is moderately to highly heritable in beef cattle with estimates ranging from 0.13 to 0.47 (Bishop et al., 1991b; MacNeil et al., 1991; Veseth et al., 1993; Archer et al., 1997; Evans et al., 1999; and Jakobsen et al., 2000), and 0.26 in ram lambs (Cammack et al., 2005).

ADG shows a negative genetic correlation with fat thickness (FT) and FCR (-0.20 and -0.43, respectively). This negative correlation indicates that selection for improved ADG may result in lower subcutaneous FT measurements and an improved FCR (MacNeil et al., 1991).

Scrotal Circumference. Bull selection for increased scrotal circumference is considered to be a fast way to genetically improve fertility traits in beef cattle (Keeton et al., 1996). Scrotal circumference is found to be highly heritable with estimates reported ranging from 0.16 to 0.78 (Coulter and Foote, 1979; Neely et al., 1982; Knights et al., 1984; Bourdon and Brinks, 1986; Nelson et al., 1986; Lunstra et al., 1988; Smith et al., 1989; Meyer et al., 1990; Kriese et al., 1991a; Meyer et al., 1991; Keeton et al., 1996; Evans et al., 1999; Eler et al., 2004). More importantly, yearling SC is genetically related to more traits of female reproduction.

Real-Time Ultrasound

Ultrasound is used for live animal carcass prediction. Carcass composition can be determined on all species of livestock using real-time ultrasound technology (Perkins et al., 1997). The first animal evaluation using the application of ultrasound was in 1956 in the United States (Stouffer, 2004). Ultrasound is a non-destructive, humane method to provide quantitative identification of muscle and fatty tissue of the live animal (Perkins et al., 1997). Backfat thickness over the 12th rib was the first trait evaluated in beef cattle. Currently, cattle evaluated by carcass ultrasound utilize real-time ultrasound technology. Today, the most common carcass traits evaluated with ultrasound include back fat thickness (USFAT) and *longissimus* muscle area (USREA), rump fat thickness (USRF) and percent intramuscular fat (USIMF) at yearling age.

Genetic evaluations for carcass traits based on ultrasound measurements have the potential to increase the rate of genetic progress and reduce the expenses involved in progeny testing. However, it is important to obtain reliable heritability and genetic correlation estimates between carcass measurements on finished steers and ultrasound measurements on yearling bulls (Devitt and Wilton, 2001). Heritability estimates for ultrasound carcass traits have been well published in a variety of research studies (Arnold et al., 1991; Moser et al., 1998; Crews et al., 2003; Carstens and Tedeschi, 2006). Additionally, genetic correlations between progeny carcass traits and yearling ultrasound traits have been published and suggest genetic progress can be made in actual carcass traits with ultrasound-based selection.

Heritability Estimates and Genetic Correlations for Ultrasound Measurements. It is industry standard for ultrasound measurements to be taken at yearling age for carcass traits (BIF, 2002). Level of diet and environment can affect the variation seen in populations measured and thus heritability estimates. In general, heritability estimates USFAT, USREA and USIMF are moderately heritable. However, a wide range of estimates can be found in the literature.

An early literature report estimated heritability for USFAT at 0.04 and USREA at 0.12 on 385 Hereford bulls (Turner et al., 1990). Using a larger sample size, Arnold and coworkers (1991) reported heritability estimates for USFAT and USREA of 0.26 and 0.25, respectively. These estimates were on a constant weight basis utilizing both Hereford bull (n = 3,089) and heifer (n = 393) data. Devitt and Wilton (2001) reported heritability estimates for yearling ultrasound bull measurements to a constant weight basis also. These estimates were 0.44 for USREA, 0.24 for USIMF, and 0.55 for USFAT. In later literature estimates, Hassen et al. (1998a) reported heritability estimates of 0.05 for USFAT and 0.21 for USREA. Crews and Kemp (2002) reported heritability estimates for bull USREA, heifer USREA, bull USFAT, and heifer USFAT (0.61, 0.49, 0.50, and 0.44, respectively).

The literature provides few studies where heritability estimates are adjusted to a common age. Some of the first heritability estimates reported for ultrasound measured traits were moderately heritable. Arnold and coworkers (1991) reported age constant heritability estimates for USFAT (0.26) and USREA (0.28). Earlier literature reports heritability estimates adjusted to a common age for USFAT (0.14) and USREA (0.40) on Brangus cattle (Johnson et al., 1993). Moser and coworkers (1998) reported age constant heritability estimates of 0.11 for USFAT and 0.29 for USREA. More recent literature reports age constant heritability estimates of 0.48 for USREA, 0.23 for USIMF, and 0.52 for USFAT on yearling bull ultrasound data (Devitt and Wilton, 2001). Stelzleni et al., (2002) reported similar ultrasound heritability estimates for USREA, USFAT, and USIMF (0.31, 0.26, and 0.16, respectively) on Brangus bulls and heifers. Ultrasound measured traits adjusted to a common age are all moderately to highly heritable.

One article in the literature reported heritability estimates for ultrasound measured traits with backfat thickness held constant. Devitt and Wilton (2001) reported a heritability estimate of 0.48 for USREA and 0.23 for USIMF. These estimates taken on yearling bull ultrasound measurements were moderately to highly heritable.

Crews et al. (2003) examined genetic parameters and their live animal indicators in Simmental cattle and found that replacement bull and heifer USFAT resulted in heritabilities of 0.53 and 0.69, respectively. Low heritability estimates were reported earlier in Brangus cattle by Johnson et al. (1993) and Moser et al. (1998) for yearling USFAT when bull and heifer data were combined. Shepard et al. (1996), however, estimated a heritability estimate of 0.56 for yearling USFAT in Angus cattle. Heritability estimates of 0.37 and 0.51 for replacement bull and heifer USREA (Crews et al., 2003) were also reported. These are also similar to previously reported heritability estimates indicating the potential to improve carcass characteristics in the breeding herd's offspring.

Correlations between Real-Time Ultrasound and Carcass Traits. Literature reports genetic correlations between real-time ultrasound measured traits (USFAT, USREA and USIMF) and their corresponding carcass traits (12th rib fat thickness, *longissimus* muscle area and marbling score) are highly correlated to one another. This suggests yearling bull ultrasound measured traits can be used to improve progeny carcass characteristics for the feedlot phase.

Research shows few reports of genetic correlations between postweaning growth traits and ultrasound measured traits adjusted to live weight. One study reports genetic correlations between ADG and USFAT and USREA (-0.02 and 0.06 respectively) were small because the data were adjusted for live weight (Arnold et al., 1991). When adjusted for age, genetic correlations revealed consistently positive relationships among USFAT with ADG and USREA with ADG (0.23 and 0.33, respectively). The genetic correlation between age constant USFAT with USREA was greater in magnitude (0.48) than weight constant analysis (0.39). When examined to either a weight constant or an age constant basis, backfat measurements in these yearling Hereford cattle were positively correlated with growth rate and size (Arnold et al., 1991). These estimates suggest ultrasound and carcass traits are moderately heritable and selection based on ultrasound measurements could improve progeny carcass measurements.

Crews and coworkers (2002) collected real-time ultrasound images on composite bulls (n = 224), steers (n = 116), and heifers (n = 257) three times, including 60 d post-weaning, near one year of age and three to seven days prior to harvest. Real-time ultrasound images were collected by one technician and interpreted by a second technician.

The residual correlation between USREA and *longissimus* muscle area was 0.87 (Crews et al., 2002). Indicating USREA measurements taken post-weaning accurately reflect variability in *longissimus* muscle area measured at older ages or harvest. These results compare favorably with those of previous studies showing moderate to high correlations between USREA and *longissimus* muscle area. Smith et al. (1992) reported simple correlations of 0.43 and 0.63 between USREA and *longissimus* muscle area measurements in two studies. Hassen et al. (1998b) reported correlations of 0.48 and 0.44, respectively, between USREA and *longissimus* muscle area. Higher correlations of 0.60 (Perkins et al., 1992) and 0.52 to 0.72 for multiple technicians (Herring et al., 1994) have also been reported between USREA and *longissimus* muscle area.

Yearling and USFAT measures resulted in residual correlations of 0.78 and 0.86 with carcass fat thickness, respectively (Crews et al., 2002). A similar correlation (0.89) between USFAT and carcass fat thickness in steers and heifers was reported by Faulkner et al. (1990). High similar correlations (0.70 to 0.82) between USFAT and carcass fat thickness have also been reported in several studies (Perkins et al., 1992; Smith et al., 1992; Herring et al., 1994; Hassen et al., 1998b).

Devitt and Wilton (2001) utilized crossbred steer carcass data (n = 843) and yearling bull ultrasound measurements (n = 5,654) to estimate genetic parameters of carcass traits from two different sources and to determine the genetic correlations between steer carcass measurements and bull ultrasound measurements.

Age constant genetic correlations between crossbred steer carcass data and yearling bull ultrasound measurements were also reported by Stelzleni et al. (2002). These genetic correlations were between steer *longissimus* muscle area and USREA (0.66), steer marbling score and USIMF (0.80), steer backfat and USFAT (0.88), and steer ADG and bull ADG (0.72). Similar genetic correlations were reported by Moser et al. (1998) between carcass *longissimus* muscle area and USREA (0.66) and carcass backfat with USFAT (0.69) with age held constant.

Devitt and Wilton (2001) also reported genetic correlation estimates with backfat held constant. Genetic correlations between steer carcass traits and yearling bull ultrasound measurements with backfat held constant were steer REA with USREA (0.57), steer marbling with USIMF (0.68) and steer ADG with bull ADG (0.87) (Devitt and Wilton, 2001).

Finally, Devitt and Wilton (2001) looked at genetic correlation estimates with weight held constant. Genetic correlations between steer carcass traits and yearling bull ultrasound traits adjusted to a common weight were 0.75 between steer REA and USREA, 0.68 between steer marbling score and USIMF, and 0.91 between steer BF and USFAT (Devitt and Wilton, 2001). All moderate to high genetic correlations reported by Devitt and Wilton (2001), regardless of which trait was held constant, were similar overall in sign and magnitude.

A year later, Crews and Kemp (2002) reported similar positive genetic correlations between ultrasound measured traits and steer carcass traits. The genetic correlations reported between bull USREA and carcass REA, heifer USREA and carcass

REA, bull USFAT and carcass fat thickness, and heifer USFAT and carcass fat thickness were 0.71, 0.67, 0.23, and 0.66, respectively.

Most literature concludes USREA and USFAT measurements taken near weaning and yearling ages could be used to predict corresponding carcass measurements in beef steers, bulls, and heifers. Predictions based on yearling measurements were more accurate for fat thickness; however, predictions based on weaning vs. yearling measurements were similar for muscle area (Crews et al., 2002). All literature reported indicates genetic progress can be made in actual carcass traits with ultrasound-based selection (Devitt and Wilton, 2001). Ultrasound measured traits in the breeding herd were consistent with carcass measured traits in the finishing herd (Crews and Kemp, 2002).

Variation in Ultrasound Measurements Among Breeds. Breed differences have been shown by many studies for reproduction, growth and carcass traits. One study detected ultrasound trait differences (Bergen et al., 1997) among breeds. Measurements were taken on British (Angus, Hereford and Shorthorn) and Continental (Charolais and Simmental) breeds of cattle during a post-weaning performance test. Breed differences were detected ($P < 0.05$) for end of test ultrasound measurements. Charolais and Simmental bulls had less fat than British breed bulls, but did not differ from each other at the end of test. Among the British breed bulls, Angus and Shorthorn bulls were fatter than Hereford bulls. Continental breeds had larger USREA than British breeds but did not differ from each other. Within the British breeds, Angus and Shorthorn bulls did not differ from each other but had larger USREA than Hereford bulls (Bergen et al., 1997). Bergen and coworkers (1997) concluded the moderate heritability of these traits, combined with their high degree of within-breed phenotypic variation, indicates that ultrasound may make a valuable addition to genetic improvement programs for carcass traits.

Conclusion

There are many definitions of feed efficiency that are used in the beef cattle industry. The most popular definition used is the ratio of G:F or its inverse FCR. G:F and FCR were reported to be moderately heritable throughout the literature. However, there has been increasing interest in RFI recently. RFI is defined as the difference between an animal's actual feed intake and expected feed intake for their level of production. Heritability estimates of RFI were also reported to be moderately heritable throughout the literature. RFI may be a better efficiency comparison tool among individuals because it takes into consideration size of the animal where G:F or FCR does not.

Many underlying biological mechanisms occur in individual animals that cause certain animals to have better efficiency than others. Digestion of feed, metabolism and animal activity level are some of the biological mechanisms that can differ in individuals. These underlying biological mechanisms are not fully understood and further research is needed.

ADG was also reported to be moderately heritable, while SC was reported to be highly heritable throughout the literature suggesting that genetic improvement can be made with these traits. Post-weaning ultrasound measured traits were moderately to highly heritable. Post-weaning ultrasound measurements (USFAT, USREA, and USIMF) were found to be genetically correlated to carcass trait (12th rib fat thickness, *longissimus* muscle area, and marbling score) estimates taken on individuals post-harvest. This suggests that genetic progress can be made in actual carcass traits with ultrasound-based selection.

Individual performance records collected on bulls in a central test can be added to National Cattle Evaluation (NCE) models to predict EPD's. Producers can then use their respective breed's EPD's to select a total package herd sire for their breeding program.

Research Objectives

The purpose of this research is to:

1. Determine heritability estimate of RFI in bulls measured at a central test.
2. Determine genetic correlations of RFI in central test bulls with other postweaning measures of growth, efficiency and product end point.
3. Determine phenotypic and genetic trends for RFI in central test bulls.
4. Determine relationships of traits in low and high RFI bulls.

EVALUATION OF FEED EFFICIENCY TRAITS WITH POST-WEANING GROWTH AND ULTRASOUND TRAITS IN CENTRAL TEST BULLS

Introduction

Central bull test stations are used in many parts of the country to evaluate post-weaning performance of bulls under uniform conditions. The first test stations were used to demonstrate performance concepts and improve growth rate in many breeds of beef cattle. The first full scale evaluation test for gain was conducted with bulls and heifers in 1949 in Texas (Warwick and Cartwright, 1955). With the development of national cattle evaluations conducted by many breeds today, central test stations are now used by seedstock breeders as an additional source of performance records on their bulls.

There are several ways to examine and define feed efficiency in cattle; many times being expressed as a ratio of G:F or its inverse feed conversion ratio (FCR). Another measure of efficiency, residual feed intake (RFI) is defined as the difference between the actual feed intake and the expected feed intake requirements for maintenance of body weight and production (Koch et al., 1963). Since maintenance and growth requirements are not accounted for by G:F, RFI comparisons between animals may be a better measure of efficiency (Kolath et al., 2006).

Many studies have examined at least one of the definitions of feed efficiency in beef cattle (Dawson et al., 1955; Koch et al., 1963; Arthur et al., 1999, 2001a,b). In general, studies utilizing a ratio definition of feed efficiency and RFI have suggested feed efficiency and RFI are moderately heritable (0.22 to 0.80 and 0.14 to 0.62, respectively). With RFI being moderately heritable, genetic change can be achieved based on selection of low RFI bulls.

The objective of this study was to determine heritability estimates of and phenotypic and genetic correlations between post-weaning growth and ultrasound carcass measurements of bulls consigned in a full feed bull test. Also, bulls were ranked for RFI to determine relationships of traits measured between low RFI bulls and high RFI bulls.

MATERIALS AND METHODS

Experimental Data

Data were collected on bulls consigned to the Auburn University Bull Test from 1977 to 2004. All bulls were consigned by individual breeders located primarily in the Southeastern United States. Guidelines for full-feed central bull test programs were followed as outlined by the Beef Improvement Federation (BIF, 2002).

A total of 2,277 bulls from 26 breeds were evaluated at the test station since 1977. For this analysis 2,180 records on eight breeds were utilized. The eight breeds included in the analyses were Angus, Brangus, Charolais, Gelbvieh, Hereford, Limousin, Santa Gertrudis, and Simmental.

Bulls were housed at the Beef Cattle Evaluation facility on the Auburn University campus. The facility, constructed in 1976, consists of 8 pens with 12 Calan-Gates installed in each pen. Individual feed intake was measured for a maximum of 96 bulls per evaluation. One evaluation was held each year. Bulls were delivered in late July to early August each year. After a 21 day acclimation period, bulls were weighed on test.

Bulls remained at the test facility until sale day. Depending on year, bulls were sold via auction from January through March.

Bulls had inside and outside access with inside pen dimensions of 6.096 meters wide by 9.144 meters long. Water was provided using automatic water troughs with one trough supplying water to two pens. Outside pen dimensions have changed over the years to maximize bull health and minimize environmental impact. Until 2002, outside pens consisted of a dirt and stone foundation. In 2002, common bermudagrass (*Cynodon dactylon*) was planted to minimize nutrient runoff, rock upheaval and increase foot health of bulls. Currently, outside pens are 54.864 meters wide by 92.6592 meters long and divided into three 18.288 meter strips. Bulls were allowed access to one strip per pen weekly. This allowed grass coverage to be maintained for the duration of the test.

From 1977 to 1989 length of test was 140 d. In 1990, length of test was shortened to 112 d. In 2000, test length was shortened to 84 d.

Bulls were fed twice daily with access to ad-libitum amounts of the diet. Enough feed was placed in each bunk to ensure 0.45 to 2.27 kg remained in each bunk prior to the next feeding. Feed weights were recorded at each feeding. Orts were taken as necessary between weigh days. Orts were always measured each weigh day.

Throughout the years, the composition of the feed has remained fairly consistent. Diet ingredients changed due to availability and cost. All diets were formulated for a constant level of total digestible nutrients (TDN) and protein (CP). Table 1 describes TDN, CF, and CP levels of the diet since 1977.

Data Collection

At bull delivery, initial weight, hip height and scrotal circumference were measured. A general health exam was also performed by Auburn University College of Veterinary Medicine personnel. Bulls were allotted into one of the eight pens by breed, hip height and weight. Bulls not meeting entry requirements for weight (2.5 pounds weight per day of age), scrotal circumference and health were excused from the test.

Appropriate BIF guidelines for full feed bull evaluations were followed throughout the years. Bulls had an adjustment period of 21 d to become accustomed to the facility, calan gate and diet. Bulls unable to adjust to calan gates by d 21 were excused from the test. At the end of 21 d, bulls were weighed and measured for hip height on two consecutive days. The weights and heights were averaged for an on test weight and height. Subsequent measurements were taken every 28 d until the end of the evaluation. Bulls were again measured on subsequent days at the end of the evaluation. Final scrotal circumference was also taken at this time.

At each weigh period, daily feed intakes, weight and hip height were used to determine FCR, average daily gain (ADG), weight per day of age (WDA) and frame score.

Feed intake data was used to determine residual feed intake (RFI). RFI values for this study were estimated as outlined by Okine et al., (2004) and Archer (Personal Communication, 2005, 2007) and detailed in Appendix A.

At the end of the feeding evaluation, adjusted yearling weight was also calculated (BIF, 2002). From 1985 to 1991, fat thickness measurements were taken on bulls. These estimates were obtained ultrasonically or by using a probe at the 12th rib. Beginning in

1992, real time ultrasound measurements of carcass composition were taken. From 1992 to 1998, measures of 12th rib fat thickness (USFAT) and *longissimus* muscle area (USREA) were routinely taken. Beginning in 1998, measures of percent intramuscular fat (USIMF) were added. In general, ultrasound measures were taken between 56 d and 84 d of the feed evaluation using an Aloka 210 real-time ultrasound machine in the beginning (1985 - 1993) and an Aloka 500 real-time ultrasound machine (Corometrics Medical Systems, Wallingford, CT, 17.2 cm transducer) after 1993. Dates were adjusted yearly to ensure bulls fit required age windows of appropriate national breed associations. All ultrasound information has been collected by the same technician, since 1992.

Data Analysis

Data were edited using SAS (SAS Institute Inc., Cary, NC) to check means, minimum numbers and maximum numbers for errors. Prior to editing, there were 2,277 bulls in the dataset. Edits reduced the number of records available for analysis to 2,180. Breeds to analyze were determined by the total number of each breed and the representation of each breed across years.

Eight breeds were included in the final dataset. They included Angus, Brangus, Charolais, Gelbvieh, Hereford, Limousin, Santa Gertrudis, and Simmental. Further editing of the data set eliminated bulls with incomplete or unknown pedigrees or data. Data were analyzed using age of bull at sale date and final test weight as a covariate. Bulls with missing birth dates were removed from the final data set when age was used as a covariate. When final weight was used as a covariate, those bulls that did not have an age were included because they had a final weight.

Model

A sire-maternal grandsire (sire-mgs) model was used to estimate (co)variance components of the data using MTDFREML (Boldman et al., 1993). A series of three-trait multiple trait analyses were used to estimate all (co)variance components. (Co)variance components were used to form estimates of heritability and genetic correlations. The basic sire-mgs model used was:

Y_{ijklm} = length of test_i +year_j + breed_k + s_l + mgs_m + e_{ijklm}

Where:

i = length of test fixed effect

j = year of test fixed effect

k = breed of bull on test fixed effect

l = random sire effect

m = random maternal grandsire effect

and covariates of final test weight or age of bull at sale date were used.

The general form of the mixed model matrix equations for the sire-mgs model was:

$$\begin{bmatrix} X'X & \begin{matrix} X'Z_1 & X'Z_2 \end{matrix} \\ \begin{matrix} Z'_1X \\ Z'_2X \end{matrix} & \begin{bmatrix} Z'_1Z'_1 & Z'_1Z'_2 \\ Z'_2Z'_1 & Z'_2Z'_2 \end{bmatrix} + G^{-1} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{s}_1 \\ \widehat{mgs}_1 \end{bmatrix} = \begin{bmatrix} X'\underline{y} \\ Z'_1\underline{y} \\ Z'_2\underline{y} \end{bmatrix}$$

Where

X = Incidence matrix that relates fixed effects to vector of observations y

Z_1 = Incidence matrix that relates random effects of sire to the model

Z_2 = Incidence matrix that relates random effects of maternal grandsire effects to the model

G^{-1} = Inverse of numerator relationship matrix including (co)variance components

$\hat{\beta}$ = Fixed effects of breed, year and length of test

$\hat{s}_1$ = Random effects of sire

$\widehat{mgs}_1$ = Random effects of maternal grandsire

$\underline{y}$ = Vector of observations

The (co)variance matrix for random effects was:

$$V\begin{bmatrix} s \\ mgs \\ e \end{bmatrix} = \begin{bmatrix} A\sigma^2_s & A\sigma_{s,MGS} & 0 \\ A\sigma_{s,MGS} & A\sigma^2_{MGS} & 0 \\ 0 & 0 & I\sigma^2_e \end{bmatrix}$$

Where

A = Numerator relationship matrix for all sires and mgs in the analysis

I = Identity matrix for residual effects

σ^2_s = The variance of sire effects

$\sigma_{s,mgs}$ = The covariance between sire effects and MGS effects

σ^2_{mgs} = The variance of MGS effects

σ^2_e = The variance of residual effects

Analyses were stopped when the variance of function values (-2 log L) in the simplex were equal to 1×10^{-9}. Each analysis was then restarted using the estimates of parameters as new priors to verify a local minimum was not reached. All models converged to a global minimum when there was no change in function values (-2 log L) (Boldman et al., 1993).

A maximum of 3,739 animals were contained in the inverse of the numerator relationship matrix (A^{-1}), with final weight as a covariate. Fewer animals were included in A^{-1} when ultrasound traits were analyzed. There were 2,962 animals included in USFAT analyses. USREA analyses included 2,045 animals and USIMF analyses contained 1,100 animals were in A^{-1}.

A maximum of 3,725 animals were included in A^{-1} with age as covariate. Once again, fewer animals were included in A^{-1} when ultrasound traits were analyzed. There were 2,957 animals included in USFAT analyses. USREA analyses included 2,045 animals and USIMF analyses included 1,100 animals in A^{-1}.

With age as covariate a total of 958 sires and 1,111 MGS were in the final data set. There were 398 sires and 378 MGS with more than one progeny. With final weight as a covariate a total of 962 sires and 1,115 MGS were in the final data set. There were 400 sires and 379 MGS with more than one progeny.

Traits analyzed included total gain on test (TG), FCR, RFI, ADG, USFAT, USREA, USIMF and scrotal circumference (SC). (Co)variances were converted from σ^2_s, σ^2_m, and σ_{sm} to σ^2_a and σ_{a1a2} values. (Co)variance components were averaged across analyses for each trait to determine final estimates which can be seen in Tables 2, 3, 4, and 5. These values were used to estimate heritabilities and correlations.

Residual Feed Intake Analyses

Bulls were classified as high RFI (RFI ≥ 0) or low RFI (RFI < 0) individuals. Because of the inherent nature of RFI, half of the bulls were classified into each category. To evaluate differences of other measured traits in high and low RFI bulls, GLM models in SAS (SAS Institute Inc., Cary, NC) were run to examine TG, ADG, adjusted 365 d weight (YW), initial weight (IW), USFAT, USREA, USIMF, frame score (FS), feed intake (FI), scrotal circumference (SC), FCR and RFI. Fixed effects were year, breed, length of test, and RFI classification. Covariates were again age at sale date or final weight. The LSMEANS procedure of SAS (SAS Institute Inc., Cary, NC) was used to separate means.

RESULTS AND DISCUSSION

Raw means of performance data for each covariate are contained in Table 6 and Table 7. On average bulls were 405 d of age when sold and had an average final weight of 586 kg. Bulls had similar means for FCR, ADG, SC, USIMF, YWT, USREA, USFAT and RFI for age and weight adjusted analyses.

Raw means of performance data by breed for each covariate are in Table 8 and Table 9. From these simple means, Charolais, Gelbvieh, Limousin, Hereford, and Santa Gertrudis breeds had lower RFI values than other breeds. British breeds (Angus and Hereford) on average were fatter than Continental breeds (Charolais, Gelbvieh, Limousin and Simmental) and had smaller *longissimus* muscle areas.

Heritability Estimates and Correlations

Heritability estimates and phenotypic and genetic correlations among traits are found in Tables 10 and 11. Heritability estimates adjusted to a common age or weight were similar in magnitude, except for USREA. In all cases, except TG, heritability estimates were lower than published literature reports.

Heritability estimates for efficiency based traits adjusted to a common age were 0.13 for FCR and 0.10 for RFI (Table 10). Heritability estimates adjusted to a common weight were 0.12 for FCR and 0.09 for RFI (Table 11). Most heritability estimates for FCR and RFI are moderate (Koch et al., 1963; Woldehawariat et al., 1977; Herd and Bishop, 2000; and Pitchford, 2004). However, Brown and coworkers (1988) reported a smaller heritability estimate of 0.14 for FCR. Pitchford (2004) also reported a smaller heritability estimate for RFI in growing dairy males of 0.08.

Heritability estimates reported in the literature for FCR range from 0.14 to 0.80 (Woldehariat et al., 1977; Brown et al., 1988; Herd and Bishop, 2000 and Arthur et al., 2001a). Arthur and coworkers (2001b) reported heritability estimates for FCR on Charolais bulls at 15 and 19 months of age (0.46 and 0.31, respectively). Age and weight adjusted heritability estimates reported in this study were comparable to earlier, smaller heritability estimates of 0.14 by Brown et al. (1988) and 0.15 by Herring and Bertrand (2002).

Heritability estimates reported in the literature for beef cattle RFI range from 0.16 to 0.41 (Koch et al., 1963; Archer et al., 1997; Herd and Bishop, 2000; Arthur et al., 2001a). Pitchford (2004) reported a range of heritability estimates for RFI on growing dairy males from 0.08 to 0.36. Estimates found in this study fall into the lower range of these values.

One explanation for these low heritability estimates is the data structure. Although bulls were reared together post-weaning, initial contemporary group (CG) structure was lost. Pre-weaning differences in management and selection strategies were not accounted for in the model. Also, field data heritability estimates are generally lower than heritability estimates from designed studies because there are more people involved (beef unit manager, bull test supervisor and student employees) with data collection throughout the years. With a designed study, usually the same person(s) is collecting the data so there should be less room for error.

Heritability estimates for postweaning growth traits adjusted to a common age or weight were low for ADG, TG and SC. Literature estimates for ADG range from 0.13 to 0.47 (Bishop et al., 1991b; MacNeil et al., 1991; Fan et al., 1995; Archer et al., 1997; Jakobsen et al., 2000) with most being moderate in size. Using Hereford and Angus cattle Fan et al. (1995) reported ADG estimates of 0.16 and 0.43 for heritability. Herring and Bertrand (2002) also reported a lower heritability estimate of 0.28 for ADG.

The same trends were seen for TG adjusted for either covariate (Table 10 and 11). Low heritability estimates for TG have been reported previously especially when breed association field data were analyzed (Kriese et al., 1991a,b). However, with designed studies TG is generally found to be moderately heritable (Koch et al. 1963, 2004; Woldehawariat, 1977).

Most literature reports heritability estimates of SC to be moderate to highly heritable ranging from 0.36 to 0.78 (Coulter and Foote, 1979; Bourdon and Brinks, 1986; Meyer et al., 1991; Evans et al., 1999; and Eler et al., 2004). However, this study found low heritability estimates for SC. Kriese and coworkers (1991a) reported SC heritability estimates on Brangus and Hereford cattle field data (0.16 and 0.53, respectively). The low heritability estimates could be a function of the type of bulls consigned to central test stations. Breeders generally consign only their best bulls, thus decreasing additive genetic variation. Additionally, since eight breeds were present in the data, the fixed effect of breed in the model could be accounting for significant amounts of the variation present.

USFAT, USREA and USIMF heritability estimates were also low in magnitude adjusted for either covariate (Table 10 and 11). Arnold and coworkers (1991) reported age and weight adjusted heritability estimates on Hereford bulls and heifers for USFAT (0.23 and 0.26) and USREA (0.33 and 0.25).

In 1990, Turner and coworkers reported heritability estimates for USFAT (0.04) and USREA (0.12) on yearling Hereford bulls. However, Arthur et al. (2001a) reported much larger heritability estimates for USFAT (0.35) and USREA (0.27). The estimates reported in this study, adjusted to a common age or weight, were lower than most heritability estimates reported throughout the literature involving ultrasound measured traits.

Phenotypic Correlations Between RFI and Associated Traits. Phenotypic correlations between RFI and postweaning growth traits (ADG and TG) were small or zero when adjusted to a common age or weight (Table 10 and 11). These results are in agreement with previously reported literature (Koch et al., 1963; Jenson et al., 1992a; Arthur et al., 2001a,b; Basarab et al., 2003; and Carstens and Tedeschi, 2006). This suggests RFI as a measure of efficiency is independent of gain in growing bulls. Phenotypic selection of individual bulls with improved RFI should not affect the size of animal.

RFI had a strong positive phenotypic correlation with FCR (0.61 and 0.60) when adjusted to a common age and weight, respectively. Herd and Bishop (2000) reported a phenotypic correlation between RFI and FCR of 0.61 on Hereford cattle while Arthur et al. (2001a) reported a correlation of 0.53. Carstens and Tedeschi (2006) reported a similar phenotypic correlation between RFI and FCR of 0.56, while Baker et al. (2006) reported a phenotypic correlation of 0.42. These phenotypic correlations are related in a favorable direction, indicating that phenotypic selection for improved RFI will result in improved FCR.

RFI was phenotypically uncorrelated with SC for both age and weight adjusted analyses (0.02 and 0.04, respectively). Arthur et al. (2001a) also reported a low phenotypic correlation of 0.10 between RFI and SC. RFI does not appear to phenotypically influence SC size.

Most phenotypic correlations between RFI and ultrasound measured traits adjusted to a common age or weight were similar in sign and magnitude, except USFAT. RFI had a positive phenotypic correlation with USFAT (0.12) and USIMF (0.13) and a negative phenotypic correlation with USREA (-0.17), when adjusted to a common age. When adjusted to a common weight, RFI had a positive phenotypic correlation with USFAT (0.35) and USIMF (0.13) and a negative phenotypic correlation with USREA (-0.16).

Literature reports of phenotypic correlations between RFI and USFAT and USREA are variable. Arthur et al. (2001a) reported a low phenotypic correlation between RFI and USFAT (0.14). Carstens and Tedeschi (2006) reported a smaller correlation of 0.11. Baker et al. (2006) reported a phenotypic correlation of 0.00 between RFI and USFAT, while Crews and coworkers (2003) reported a negative phenotypic correlation between RFI and USFAT. Phenotypic correlations reported in this study between RFI and USFAT (0.12 and 0.35) were positive, indicating cattle with improved RFI will tend to be leaner at the 12th and 13th rib.

Arthur et al. (2001a) reported a low phenotypic correlation between RFI and USREA (0.06). Carstens and Tedeschi (2006) reported RFI was not phenotypically correlated to USREA (0.00), while Baker et al. (2006) reported a small negative phenotypic correlation between RFI and USREA (-0.09). The correlations reported in this study for age and weight adjusted analyses between RFI and USREA is similar in sign to that of Baker et al. (2006), but is greater in scale (-0.17 and -0.16, respectively). These results indicate cattle with improved phenotypic RFI tended to produce a larger *longissimus* muscle area.

Basarab et al. (2003) reported a phenotypic correlation between RFI and USIMF of 0.13, which was reported in this study when adjusted to a common age or weight. These results indicate as RFI improves in cattle their intramuscular fat will increase. This seems to suggest that cattle with improved RFI values marbled better, which mean these cattle have an opportunity to improve their quality grade.

Genetic Correlations Between RFI and Associated Traits. Literature suggests RFI is independent of size reporting genetic correlations of zero or close to zero (Herd and Bishop, 2000; Arthur et al., 2001a,b). Genetic correlations between RFI and ADG and TG adjusted to a common age or weight reported in this study are similar to other estimates (-0.08 and -0.06 or 0.08 and 0.10, respectively). Arthur et al. (2001a,b) reported genetic correlations between RFI and ADG of -0.04 and -0.10, respectively, while Herd and Bishop (2000) reported a slight positive genetic correlation of 0.09. This study, along with most literature, suggests selection for improved RFI should not affect animal size.

RFI had a positive genetic correlation with FCR for both age and weight adjusted analyses (0.49 and 0.46, respectively). Most literature reports strong positive genetic correlations between RFI and FCR (Fan et al., 1995; Herd and Bishop, 2000; Arthur et al., 2001a,b). Arthur et al. (2001a,b) reported a genetic correlation between RFI and FCR of 0.66 involving Angus cattle and 0.85 involving Charolais cattle. Herd and Bishop (2000) reported a similar genetic correlation (0.70) between RFI and FCR. Schenkel et al. (2004) reported a correlation of 0.69, while Fan et al. (1995) reported much larger genetic correlations of 0.90 involving Angus cattle and 1.00 involving Hereford cattle. This favorable strong genetic correlation is indicative that both traits are measures of efficiency.

RFI had a positive genetic correlation with SC when adjusted to a common age or weight (0.12 and 0.17, respectively). Studies indicate that RFI is independent of SC. Arthur et al. (2001a) reported a negative genetic correlation between RFI and SC (-0.03). These findings are not surprising. Since SC is genetically correlated to growth (Kriese et al., 1991a,b), and RFI is not related to growth, no strong genetic correlations should be present between RFI and SC.

RFI had a strong positive genetic correlation with USIMF (0.77 for age adjusted analysis and 0.73 for weight adjusted analysis). However RFI was negatively correlated genetically to USFAT (-0.13 for age adjusted analysis and -0.02 for weight adjusted analysis) and USREA (-0.77 for age adjusted analysis and -0.70 for weight adjusted analysis).

Nkrumah et al. (2007) reported genetic correlations between two different calculations of RFI and USIMF. RFI was calculated using a phenotypic regression and genetic regression. Genetic correlations between phenotypic RFI and USIMF (0.32) and genetic RFI and USIMF (0.44) were reported (Nkrumah et al., 2007). The results reported in this study were much greater in magnitude (0.77 and 0.73) than those reported in literature, indicating a strong genetic relationship between RFI and USIMF. This could be a result of low numbers of USIMF measurements. Cattle with an improved RFI have the potential genes to reduce their intramuscular fat. This may cause slaughter cattle to not marble as well, and could potentially affect quality grade.

Arthur et al. (2001a) reported a genetic correlation between RFI and USFAT (0.l7). Schenkel et al. (2004) reported a similar correlation of 0.16 between RFI and USFAT, while Basarab et al. (2004) reported a negative genetic correlation of -0.24. Nkrumah et al. (2007) reported genetic correlations between phenotypic RFI and USFAT and genetic RFI and USFAT to be 0.35 and -0.04, respectively. The correlations reported in this study for age or weight adjusted analysis (-0.13 and -0.02, respectively) were similar to what Basarab et al. (2004) reported. Results indicate selection for improved RFI may be genetically associated with an increased potential for subcutaneous fat deposition at the 12th and 13th rib.

Arthur et al. (2001a) reported a genetic correlation between RFI and USREA of 0.09, while Schenkel et al. (2004) reported a negative genetic correlation of -0.17. Nkrumah et al. (2007) reported genetic correlations between phenotypic RFI and USREA and genetic RFI and USREA (-0.52 and -0.65, respectively). Results published in this study are similar in sign and magnitude (-0.77 and -0.70) to those reported in the literature. These genetic correlations indicate that selection for improved RFI may increase *longissimus* muscle area.

Phenotypic Correlations Between FCR and Associated Traits. Phenotypic correlations between FCR and ADG and TG of -0.50 and -0.63, respectively, adjusted to a common age were reported in this study. Phenotypic correlations between FCR and

ADG and TG, -0.70 and -0.74, respectively, adjusted to a common weight were also reported. Woldehawariat et al. (1977) reported a range of phenotypic correlations between FCR and ADG (-0.26 to 0.55). Arthur et al. (2001a,b) reported phenotypic correlations on Angus and Charolais cattle between FCR and ADG (-0.74 and -0.54, respectively). Baker et al. (2006) and Carstens and Tedeschi (2006) reported similar phenotypic correlations between FCR and ADG (-0.65 and -0.60, respectively), while Nkrumah et al. (2004 and 2007) reported correlations of -0.63 and -0.69 between FCR and ADG. These high negative phenotypic correlations suggest that selection for favorable phenotype (improved FCR) will increase gain in growing bulls.

There were no phenotypic correlations reported in the literature between FCR and TG. The phenotypic correlation between FCR and TG was -0.63 when adjusted to a common age and -0.74 when adjusted to a common weight. However, TG and ADG are the same trait. One would expect phenotypic correlations between FCR and ADG or TG to be very similar.

The phenotypic correlation between FCR and SC, adjusted to a common age and weight, was 0.01. Arthur et al. (2001a) reported a phenotypic correlation between FCR and SC of 0.00. The results reported in this study are similar to that reported by Arthur et al. (2001a) indicating bulls ranked for favorable phenotype (improved FCR) had no effect on SC size.

Phenotypic correlations adjusted to a common age between FCR and USFAT (0.11), USREA (-0.09) and USIMF (0.11) were reported in this study. Phenotypic correlations adjusted to a common weight between FCR and USFAT, USREA and USIMF were 0.10, -0.06 and 0.12, respectively.

Arthur et al. (2001a) reported a phenotypic correlation between FCR and USFAT of 0.08, while Nkrumah and coworkers (2004) reported a much larger correlation between FCR and USFAT (0.21). Carstens and Tedeschi (2006) reported a phenotypic correlation between FCR and USFAT of 0.11, while Baker et al. (2006) reported a correlation of 0.13, which is similar to what was reported in this study for age and weight adjusted analyses (0.11 and 0.10, respectively). These results indicate there is little to no phenotypic correlation between FCR and ultrasound measured traits.

Arthur et al. (2001a) reported a phenotypic correlation between FCR and USREA of 0.03. Baker et al. (2006) reported a correlation of 0.12, while Carstens and Tedeschi (2006) reported a correlation of 0.11 between FCR and USREA. Meanwhile, Nkrumah et al. (2004) reported a slight negative phenotypic correlation between FCR and USREA (-0.08), which is similar to what was reported in this study for age or weight adjusted analyses (-0.09 and -0.06, respectively). These results suggest there is no phenotypic correlation between FCR and USREA.

There were no papers that reported phenotypic correlations between FCR and USIMF. However, Nkrumah et al. (2004) reported a phenotypic correlation between FCR and ultrasound marbling (USMAR) of 0.10, indicating FCR was independent of USMAR. The correlations reported from this study between FCR and USIMF, adjusted to a common age or weight was 0.11 and 0.12, respectively which was similar to what Nkrumah et al. (2004) reported.

Genetic Correlations Between FCR and Associated Traits. Overall genetic correlations between FCR and postweaning growth traits were similar in sign and magnitude when adjusted to a common age or weight. However, genetic correlations between FCR and ultrasound measured traits varied in sign and magnitude.

Genetic correlations between FCR and ADG and TG, adjusted to a common age were -0.60 and -0.76, respectively. Correlations between FCR and ADG and TG, adjusted to a common weight were -0.82 for both. Arthur et al. (2001a,b) reported a genetic correlation between FCR and ADG on Angus and Charolais cattle (-0.62 and -0.46, respectively). Herd and Bishop (2000) reported a similar genetic correlation between FCR and ADG (-0.62) and MacNeil et al. (1991) reported a correlation of -0.43. Koch et al. (1963) reported a correlation of 0.79, while Woldehawariat et al. (1977) reported genetic correlations ranging from -0.41 to 0.31. These estimates were similar in sign and magnitude with most estimates reported throughout the literature.

Woldehawariat et al. (1977) also reported a genetic correlation between FCR and TG of -0.34. Koots et al. (1994b) reported a slightly higher correlation of -0.53 between FCR and TG. The correlations reported in this study for age and weight adjusted analyses were similar in sign and slightly higher (-0.76 and -0.82, respectively) than those reported throughout the literature. However these results, coupled with correlations between FCR and ADG do show gain traits are highly related with FCR.

The genetic correlation between FCR and SC adjusted to a common age was -0.04. This study also reported a genetic correlation adjusted to a common weight of 0.15. Genetic correlations reported throughout the literature were inconsistent also. Arthur et al. (2001a) reported a genetic correlation of -0.10 between FCR and SC, while

Woldehawariat et al. (1977) reported a larger correlation of 0.48. The genetic correlations reported in this study indicate SC was independent of FCR. Since SC and growth are genetically correlated (Kriese et al. 1991a) and FCR is correlated with growth we would expect to see a genetic correlation between FCR and SC.

Genetic correlations between FCR and ultrasound measured traits (USFAT, USREA and USIMF), adjusted to a common age were -0.05, -0.47 and 0.22, respectively. Weight adjusted genetic correlations between FCR and USFAT (0.01) and USREA (-0.39) and USIMF (0.19) were also reported in this study.

Arthur et al. (2001a) reported genetic correlations between FCR and USFAT of 0.03, while Koots et al. (1994b) reported a correlation of -0.24. Correlations reported in this study for age and weight adjusted analyses were -0.05 and 0.01 between FCR and USFAT. These genetic correlations suggest selection for improved FCR should be independent of subcutaneous fat deposition at the 12th and 13th rib.

Arthur et al. (2001a) reported a genetic correlation between FCR and USREA of -0.12. The estimates reported in this study for age and weight adjusted traits were -0.47 and -0.39, respectively. These results suggest selection for improved FCR may increase *longissimus* muscle area.

There were no genetic correlations between FCR and USIMF reported in the literature. However, the results reported in this study were 0.19 and 0.22 for age and weight adjusted analyses, respectively. These results indicate selection for improved FCR may reduce the amount of fat deposited within the *longissimus* muscle area.

Other Phenotypic Correlations. In general, phenotypic correlations between postweaning growth traits (TG and ADG) and ultrasound measured traits (USFAT and USREA) differed in sign and magnitude except USIMF when adjusted to a common age or weight. Phenotypic correlations adjusted to a common age between TG and USFAT (0.11), USREA (0.21) and USIMF (-0.06) were reported in this study. Johnson et al. (1993) reported an age constant phenotypic correlation between TG and USFAT (0.07). There were no other papers reporting age-adjusted phenotypic correlations. TG and USFAT were slightly correlated (0.11) in this study and similar to what Johnson et al. (1993) reported. This low result indicates little relationship between gain on test and subcutaneous fat depostition.

Johnson et al. (1993) also reported an age constant phenotypic correlation between TG and USREA (0.07). The correlation from this study between TG and USREA (0.21) was much greater in magnitude than what was reported in the literature. This estimate indicates that as growing bulls gained weight on test their *longissimus* muscle areas increased in size.

There were no reports of phenotypic correlations between TG and USIMF in the literature. The correlation between TG and USIMF adjusted to a common age in this study was weak (-0.06) indicating intramuscular fat was phenotypically independent of gain in young growing bulls.

This study also reported a phenotypic correlation between TG and SC adjusted to a common age (0.22). Johnson et al. (1993) reported a correlation between TG and SC of 0.18, which is similar in sign and magnitude to what was reported in this study. These results indicate that SC size is phenotypically correlated in a favorable way with gain in centrally tested bulls at a common age.

There were no phenotypic correlations adjusted to a common weight reported throughout the literature. Phenotypic correlations between TG and USFAT, USREA and USIMF were -0.06, -0.04 and -0.07, respectively. All of these phenotypic correlations reported between TG and ultrasound measured traits were low and indicate gain on test was phenotypically independent of ultrasound measured traits.

Phenotypic correlations between ADG and ultrasound measured traits (USFAT and USREA) differed in sign and magnitude except for USIMF for age or weight adjusted analyses. Age adjusted phenotypic correlations between ADG and USFAT, USREA and USIMF were 0.08, 0.21 and -0.07, respectively. Weight adjusted phenotypic correlations between ADG and USFAT, USREA and USIMF were -0.06, -0.05 and -0.16, respectively.

Carstens and Tedeschi (2006) reported a phenotypic correlation between ADG and USFAT of 0.06. The age adjusted correlation reported in this study was similar to what Carstens and Tedeschi (2006) reported and indicates ADG was independent of subcutaneous fat deposition. The weight adjusted correlation reported in this study was similar in magnitude but differed in sign compared to Carstens and Tedeschi's (2006) estimate.

Phenotypic correlations for age and weight adjusted analyses between ADG and USREA were 0.21 and -0.05, respectively in this study. Carstens and Tedeschi (2006) reported a phenotypic correlation between ADG and USREA of 0.08. Age adjusted phenotypic correlation between ADG and USREA (0.21) reported in this study indicates as bulls gain more per day on test their *longissimus* muscle area will also increase in size. However, the weight adjusted correlation indicates that *longissimus* muscle area size was phenotypically independent of how much weight the bull gained on an average daily basis.

The phenotypic correlations reported in this study between ADG and USIMF for age and weight adjusted analyses was -0.07 and -0.16, respectively. There were no phenotypic correlations between ADG and USIMF reported throughout the literature. Phenotypic correlations from this study between ADG and USIMF indicate post-weaning ADG was phenotypically independent of USIMF.

The age adjusted phenotypic correlation reported in this study between ADG and SC was 0.21, while the weight adjusted phenotypic correlation was 0.05. Age adjusted phenotypic correlation between ADG and SC indicates bulls ranked for the best ADG tended to phenotypically have larger SC. However, weight adjusted phenotypic correlation between ADG and SC indicated ADG was phenotypically independent of SC. This is understandable since at heavier weights, SC is not going to get much larger.

Phenotypic correlations between ultrasound traits were similar in sign and magnitude for age and weight adjusted analyses, except the correlation between USFAT and USREA. Phenotypic correlations adjusted to a common age between USFAT and USREA and USIMF were 0.11 and 0.35, respectively. Phenotypic correlations adjusted to a common weight between USFAT and USREA and USIMF were -0.01 and 0.36, respectively. The phenotypic correlation between USREA and USIMF was -0.10 when adjusted to a common age or a common weight.

Stelzleni et al. (2002) reported a phenotypic correlation between USFAT and USREA and USIMF of 0.16 and 0.17, respectively. The phenotypic correlation between USFAT and USREA adjusted to a common age or weight in this study was small and indicates no phenotypic relationship between USREA and USFAT. However, the results reported in this study between USFAT and USIMF were greater in magnitude than what Stelzleni et al. (2002) reported. Indicating subcutaneous fat deposition increases in growing bulls, intramuscular fat in the *longissimus* muscle area will also tend to phenotypically increase. Stelzleni et al. (2002) reported a phenotypic correlation between USREA and USIMF of -0.08. The results reported in this study between USREA and USIMF were similar in sign and magnitude to those reported in the literature indicating there was little or no relationship between performances of these traits.

Phenotypic correlations between ultrasound measured traits and SC were similar for both age and weight adjusted analyses. There were no phenotypic correlations reported in the literature between ultrasound measured traits and SC. The correlations reported in this study were small and close to zero, regardless of sign, indicating SC size was phenotypically independent of ultrasound measured traits.

Other Genetic Correlations. TG in this study was slightly to moderately genetically correlated to the ultrasound measured traits. Genetic correlations between TG and USFAT, USREA and USIMF were 0.20, 0.10 and 0.04, respectively when adjusted to a common age.

Johnson et al. (1993) reported age adjusted genetic correlations between TG and USFAT (0.44) and USREA (0.43). These estimates were higher than what was found in this study. Results reported in this study indicate selection for increased weight gain will result in slightly fatter animals and larger *longissimus* muscle areas. There were no genetic correlations between TG and USIMF reported throughout the literature. The genetic correlation (0.04) in this study between TG and USIMF was small suggesting that intramuscular fat was independent of gain in growing bulls.

TG was genetically correlated to SC (0.19) when adjusted to a common age. Johnson et al. (1993) reported an age constant genetic correlation between TG and SC of 0.38. This estimate is larger than what was reported in this study, but indicates that selection for increased SC size would result in growing bulls with larger gains. These results were not unexpected because SC tends to be correlated with growth in bulls.

Weight adjusted genetic correlations between TG on test and ultrasound measured traits indicate TG had no genetic impact on ultrasound measured traits. Genetic correlations between TG and USFAT (-0.01), USREA (0.04) and USIMF (0.11) were estimated in this study. There were no weight adjusted genetic correlations between TG and ultrasound measured traits reported in literature.

The genetic correlation between TG and SC was 0.01 when adjusted to a common weight. This estimate was much lower than the age adjusted estimate reported earlier (0.19). Literature reports that gain and SC size is correlated, however the correlation reported here indicates SC size is independent of gain.

Age adjusted genetic correlations between ADG and USFAT, USREA and USIMF were 0.23, 0.07 and 0.05, respectively. Arnold et al. (1991) reported age adjusted genetic correlations between ADG and USFAT (0.23) and USREA (0.33). The genetic correlation between ADG and USFAT indicate subcutaneous fat deposition is positively correlated to average daily weight gain in young growing bulls. However, the genetic correlation between ADG and USREA (0.07) reported in this study adjusted to a common age was lower than the estimate (0.33) reported by Arnold et al. (1991). The small positive genetic correlation between ADG and USREA in this study may indicate yearling bulls gaining more weight on a daily basis was genetically independent of *longissimus* muscle area size.

There were no genetic correlations reported in literature between ADG and USIMF. The small positive correlation between ADG and USIMF (0.05) adjusted to a common age indicates bulls gaining more weight on a daily basis were genetically independent to the amount of intramuscular fat deposited in their *longissimus* muscle area.

The genetic correlation between ADG and SC, adjusted to a common age, was related in a favorable direction (0.21). This moderate correlation between ADG and SC suggests that as bulls on test gain more weight on a daily basis their SC measurement will also increase. This was not unexpected since SC has been reported to be correlated with postweaning growth traits in growing bulls.

The genetic correlations between ADG and ultrasound measured traits were small and positive when adjusted to a common weight. The correlations between ADG and USFAT, USREA and USIMF were 0.03, 0.08, and 0.17, respectively in this study. Arnold et al. (1991) reported genetic correlations adjusted to a common weight between ADG and USFAT (-0.02) and USREA (0.06). Arnold and coworkers (1991) estimates were similar to estimates reported in this study. This suggests post-weaning growth was independent of ultrasound measured traits when adjusted to a weight basis.

There were no genetic correlations between ADG and USIMF adjusted to a common weight reported in literature. There was a slight genetic correlation between ADG and USIMF in this study (0.17). This correlation implies that as a bull's ADG increases on test, the bull has the genetic potential to increase the amount of intramuscular fat deposited in their *longissimus* muscle.

The genetic correlation between ADG and SC adjusted to a common weight was 0.04. This correlation is small and indicates that SC size was independent of ADG of centrally tested bulls. This was surprising to find since growth traits and SC size has been found to be genetically correlated to each other in the literature.

Genetic correlations were also reported in this study between the ultrasound measured traits for age and weight adjusted analyses. Once again the genetic correlations adjusted to a common weight were lower but similar in sign than those adjusted to a common age. Genetic correlations adjusted to a common age between USFAT and USREA and USIMF were 0.18 and 0.34, respectively. Genetic correlations adjusted to a common weight between USFAT and USREA and USIMF were 0.07 and 0.45, respectively. The genetic correlation adjusted to a common age between USREA and USIMF was -0.24. The genetic correlation adjusted to a common weight between USREA and USIMF was -0.07.

Stelzleni and coworkers (2002) reported a genetic correlation between USFAT and USREA of -0.09. This correlation was lower than what was found in this study for both age and weight adjusted analyses (0.18 and 0.07, respectively). The correlations from this study indicate that as *longissimus* muscle area increases in size the bull tends to deposit more subcutaneous fat. The low negative correlation reported by Stelzleni and coworkers (2002) implies no correlation between USFAT and USREA.

Stelzleni et al. (2002) also reported a genetic correlation between USFAT and USIMF of 0.36. This correlation was similar in sign and magnitude to what was reported in this study for both age and weight adjusted analyses (0.34 and 0.45, respectively). These genetic correlations imply that as bulls deposit more subcutaneous fat they have the genetic potential to deposit more intramuscular fat in their *longissimus* muscle also.

Stelzleni et al. (2002) reported a genetic correlation between USREA and USIMF of -0.25. This correlation was similar to the age adjusted correlation reported in this study (-0.24) but was much smaller in magnitude than the weight adjusted correlation reported (-0.07). These genetic correlations indicate that as bull's *longissimus* muscle area increases they tend to deposit less intramuscular fat in their *longissimus* muscle.

Genetic correlations between ultrasound measured traits (USFAT, USREA and USIMF) and SC varied in sign and magnitude for age and weight adjusted analyses. Genetic correlations adjusted to a common age between SC and USFAT, USREA and USIMF were 0.03, -0.24 and 0.27, respectively. Genetic correlations adjusted to a common weight between SC and USFAT and USREA were -0.13 and -0.20, respectively. A genetic correlation adjusted to a common weight was not calculated between SC and USIMF. There were no genetic correlations between SC and ultrasound measured traits reported in the literature.

Residual Feed Intake (RFI) Results

Comparison Between RFI Groups. No significant differences were detected between low RFI and high RFI group bulls for size and growth traits (ADG, initial weight (IW), frame score (FS), adjusted 365 day weight (YW), SC, USIMF and TG) when final weight or age was used as a covariate (Table 12 and Table 13). Significant differences ($P < 0.05$) were seen in low RFI and high RFI group bulls for USFAT, USREA, FCR, feed intake (FI), and RFI when final weight or age was used as a covariate (Table 12 and Table 13). The low RFI group bulls were leaner, had a larger *longissimus* muscle area, better FCR while consuming less feed over the duration of the test than the high RFI group bulls. These results were inconsistent with most studies done involving comparison of low RFI groups and high RFI groups in beef cattle (Herd et al., 2003; Baker et al., 2006).

Breed Effect on Post-Weaning Gain and Ultrasound Measurements. Differences among breeds can be seen in Table 14 and Table 15. As expected, there were breed differences ($P < 0.05$) among the following traits: ADG, IW, FS, YW, USFAT, USREA, USIMF, SC, FCR, and TG. Continental breeds are larger framed cattle than British breeds and consequently tend to weigh more. Also, Continental breeds of cattle are generally leaner and have a larger *longissimus* muscle area than British breeds of cattle. The results published in this study for both weight and age adjusted traits was consistent with the findings reported in previous studies with beef cattle (Marshall, 1994; Bidner et al., 2002).

Year Effect on Post-Weaning Gain and Ultrasound Measurements. Least squares means can be seen in Table 16 and Table 17 for the main effect of year of RFI on post-weaning gain and ultrasound measured traits. As expected there were differences ($p < 0.05$) among years for traits analyzed (ADG, IW, FS, YW, USFAT, USREA, USIMF, SC, FCR, and TG).

Implications

Results of this study indicate all traits analyzed were low to moderately heritable. Almost all heritability estimates were lower than published reports, except TG. TG was within published estimates for field data. Most heritability estimates reported throughout the literature were from designed studies not field data estimates like what was reported in this study.

Genetic correlations of RFI adjusted to a weight or age basis with TG, ADG, USFAT and SC were low or uncorrelated. However genetic correlations of RFI adjusted to a weight or age basis with FCR, USIMF and USREA were correlated. Selection for improved RFI would cause an increase in *longissimus* muscle area, a decrease in marbling and an improvement in FCR.

There was no difference between low RFI and high RFI groups when adjusted to a weight or age basis for most post-weaning growth and ultrasound measured traits. However, differences were detected between low RFI and high RFI group bulls for USFAT, USREA, FCR, RFI and FI. Low RFI bulls had less subcutaneous fat thickness, larger longissimus muscle areas, better FCR and RFI values while consuming less feed throughout the duration of the test. Results indicate selection of lower RFI animals should not cause a change in size or weight of the animal. Ultrasound traits should remain similar in size and measure also.

Finally, these individual performance records collected on bulls centrally tested can be added to NCE models to predict EPD's. Producers can then use their respective breed's EPD's to select a total package bull for their breeding program.

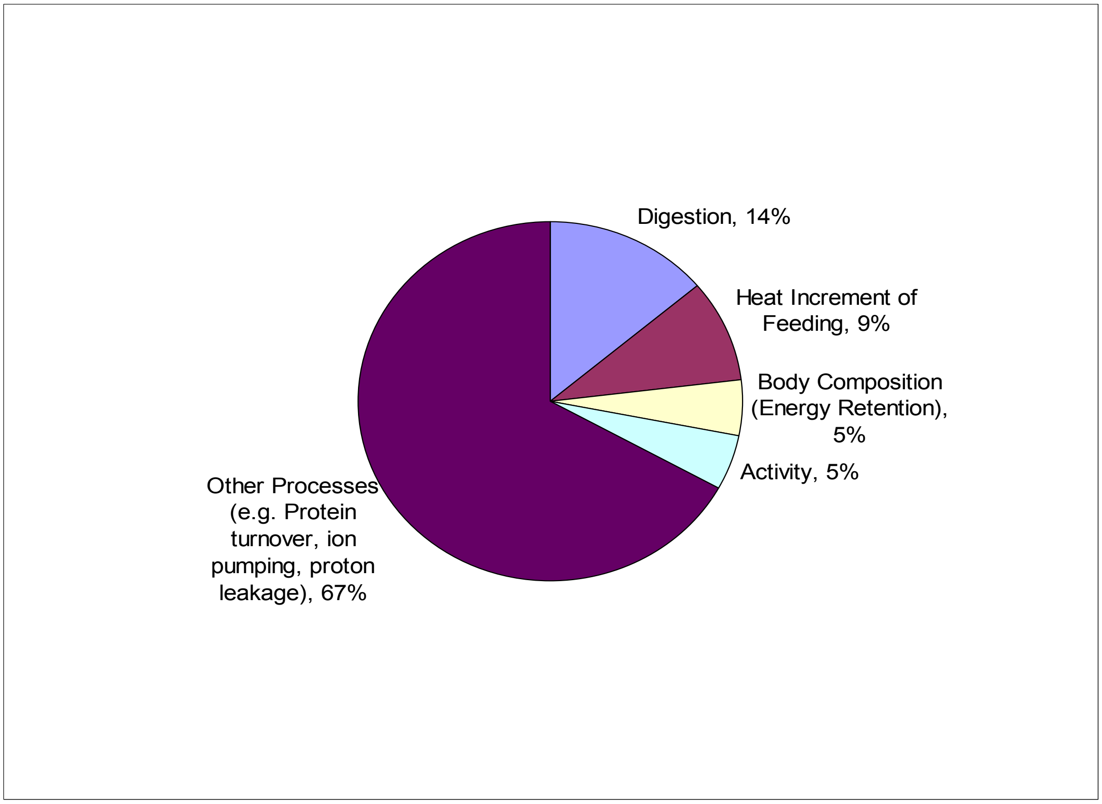

Figure 1. Estimates of the percentage contribution of different mechanisms to variation in residual feed intake in beef cattle (Herd et al., 2004).

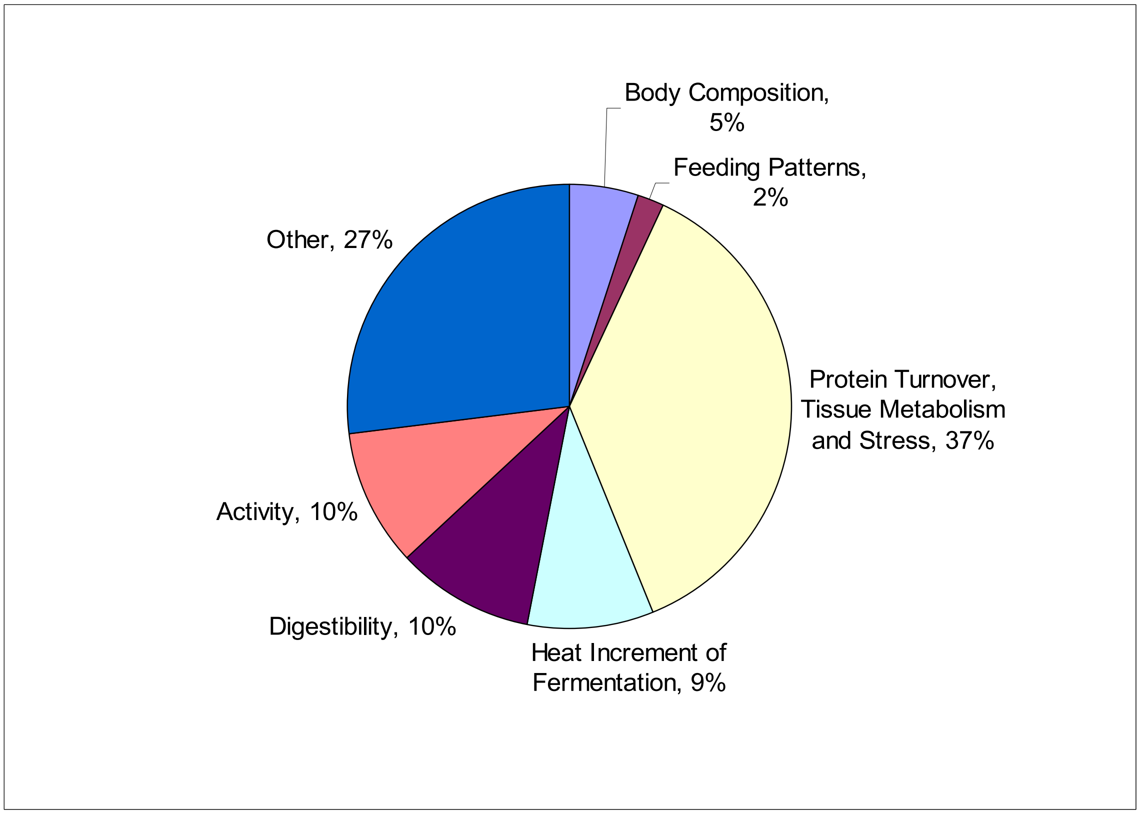

Figure 2. Contributions of biological mechanisms to variation in residual feed intake as determined from experiments on divergently selected cattle (Richardson and Herd, 2004).

Table 1. Nutrient analysis of diet fed to bulls by year[a]

Year	TDN, %	CP, %	CF[b], %
1978 – 1984	71.50	12.30	16.10
1985 – 1986	70.52	12.00	16.10
1987 – 1988	68.97	12.10	19.27
1989 – 1990	69.80	12.12	18.38
1991 – 1992	69.46	12.49	19.18
1993 – 1994	70.00	12.72	18.41
1995	70.07	12.77	17.67
1996 – 2004	71.03	Not < 12.50	Not > 20.00

[a] Percent dry matter basis

[b] Crude fiber, %

Table 2. Estimates of additive (co)variance components of centrally tested bulls adjusted to a common age[a].

Trait	TG	FCR	RFI	ADG	USFAT	USREA	USIMF	SC
TG[b]	1841							
FCR[c]	-18.82	0.34						
RFI[d]	-1.61	0.19	0.44					
ADG[e]	-	-0.13	-0.02	0.15				
USFAT[f]	0.69	-0.002	-0.007	0.007	0.01			
USREA[g]	3.28	-0.21	-0.39	0.02	0.01	0.59		
USIMF[h]	0.86	0.06	0.25	0.009	0.01	-0.09	0.24	
SC[i]	15.19	-0.04	0.15	0.15	0.005	-0.36	0.25	3.65

[a] Variance on diagonal and covariance on off-diagonal
[b] Total gain over duration of test (final weight – initial weight)
[c] Feed conversion ratio defined as kilograms of feed required to put on one kilogram of gain
[d] Residual feed intake as outlined by Appendix A
[e] Average daily gain, kg/d
[f] Ultrasound fat thickness taken at 12th and 13th rib
[g] Ultrasound longissimus muscle area, cm^2
[h] Ultrasound percent intramuscular fat
[i] Scrotal circumference, cm

Table 3. Estimates of environmental (co)variance components of centrally tested bulls adjusted to a common age[a]

Trait[b]	TG	FCR	RFI	ADG	USFAT	USREA	USIMF	SC
TG	9029							
FCR	-88	2.28						
RFI	0.93	1.84	3.77					
ADG	-	-0.64	0.01	0.77				
USFAT	1.52	0.04	0.06	0.01	0.04			
USREA	51.25	-0.16	-0.51	0.49	0.05	5.69		
USIMF	-8.60	0.18	0.10	-0.10	0.08	-0.24	1.50	
SC	93.27	0.09	0.04	0.81	0.04	1.30	-1.02	19.33

[a] Variance on the diagonal and covariance on the off diagonal
[b] See Table 2 for trait abbreviations

Table 4. Estimates of additive (co)variance components of centrally tested bulls adjusted to a common weight[a].

Trait[b]	TG	FCR	RFI	ADG	USFAT	USREA	USIMF	SC
TG	1237							
FCR	-17.41	0.36						
RFI	2.20	0.17	0.40					
ADG	-	-0.17	0.02	0.11				
USFAT	-0.03	0.0002	-0.001	0.001	0.01			
USREA	1.30	-0.20	-0.37	0.02	0.004	0.71		
USIMF	1.77	0.06	0.22	0.03	0.12	-0.03	0.23	
SC	0.60	0.17	0.21	0.02	-0.02	-0.32	-	3.65

[a] Variance on the diagonal and covariance on off-diagonal

[b] See Table 2 for trait abbreviations

Table 5. Estimates of environmental (co)variance components of centrally tested bulls adjusted to a common weight[a]

Trait[b]	TG	FCR	RFI	ADG	USFAT	USREA	USIMF	SC
TG	6627							
FCR	-94.82	2.55						
RFI	2.86	1.94	3.84					
ADG	-	-0.83	0.02	0.59				
USFAT	-0.89	0.04	0.06	-0.01	0.03			
USREA	-8.45	-0.03	-0.37	-0.12	-0.0085	4.52		
USIMF	-9.67	0.22	0.12	-0.11	0.08	-0.28	1.51	
SC	21.40	-0.09	-0.31	0.18	-0.02	0.02	-	17.48

[a] Variance on the diagonal and covariance on off-diagonal

[b] See Table 2 for trait abbreviations

Table 6. Simple means ± standard deviations for performance and ultrasound traits of bulls used in analyses adjusted by age

Trait	N	Mean
Age, days	2,008	405 ± 31
WWT[a], kg	1,905	299 ± 37
YWT[b], kg	1,995	540 ± 53
ADG[c], $kg \cdot d^{-1}$	1,998	1.73 ± 0.27
FCR[d]	1,998	7.54 ± 1.12
USFAT[e], mm	1,830	7.98 ± 3.46
USIMF[f], %	475	3.17 ± 0.86
SC[g], cm	1,574	36.32 ± 2.91
USREA[h], cm2	1,012	95.48 ± 10.52
TG[i],kg	1,998	205 ± 35
RFI[j]	1,998	0.00 ± 1.05

[a] Weaning weight adjusted to 205 days and adjusted for age of dam using national breed association adjustments
[b] Yearling weight adjusted to 365 days as outlined by BIF (2002)
[c] Average daily gain on test
[d] Feed efficiency defined as kilograms of feed required to put on one kilogram of gain
[e] Ultrasound Fat Thickness measured at the 12th and 13th rib
[f] Ultrasound percent Intramuscular Fat measured in the ribeye muscle
[g] Scrotal circumference measured at conclusion of test
[h] Ultrasound *longissimus* muscle area measured at the 12th and 13th rib
[i] Total gain over duration of test (final test weight – on test weight)
[j] Residual feed intake as outlined by Appendix A

Table 7. Simple means ± standard deviations for performance and ultrasound traits of bulls used in analyses adjusted by final weight

Trait	N	Mean
FW[a], kg	2,005	586 ± 60
WWT[b], kg	1,912	299 ± 37
YWT[c], kg	2,002	540 ± 53
ADG[d], $kg \cdot d^{-1}$	2,005	1.73 ± 0.28
FCR[e]	2,005	7.56 ± 0.62
USFAT[f], mm	1,836	7.96 ± 3.46
USIMF[g], %	475	3.17 ± 0.86
SC[h], cm	1,576	36.32 ± 2.91
USREA[i], cm^2	1,012	95.48 ± 10.19
TG[j], kg	2,005	205 ± 35
RFI[k]	2,005	0.00 ± 1.05

[a] Final weight (average of two consecutive weigh days at conclusion of test)

[b] Weaning weight adjusted to 205 days and adjusted for age of dam using national breed association adjustments

[c] Yearling weight adjusted to 365 days as outlined by BIF (2002)

[d] Average daily gain on test

[e] Feed efficiency defined as kilograms of feed required to put on one kilogram of gain

[f] Ultrasound Fat Thickness measured at the 12th and 13th rib

[g] Ultrasound percent Intramuscular Fat measured in the ribeye muscle

[h] Scrotal circumference measured at conclusion of test

[i] Ultrasound *longissimus* muscle area measured at the 12th and 13th rib

[j] Total gain over duration of test (final test weight – on test weight)

[k] Residual feed intake as outlined in the Appendix

Table 8. Simple means ± SEM for performance and ultrasound traits of bulls by breed used in analyses adjusted by age

	Breed															
	Angus		Brangus		Charolais		Gelbvieh		Limousin		Hereford		Santa Gertrudis		Simmental	
Trait	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean
Age, days	829	408 ± 1.07	33	389 ± 5.74	337	402 ± 1.68	100	384 ± 2.43	74	405 ± 3.01	183	412 ± 2.58	85	399 ± 2.98	367	405 ± 1.50
WWT[a], kg	771	296 ± 1.38	32	293 ± 5.11	322	303 ± 1.99	91	305 ± 3.22	71	290 ± 3.09	177	268 ± 2.29	84	298 ± 3.30	357	317 ± 1.64
YWT[b], kg	825	541 ± 1.90	33	522 ± 6.15	334	549 ± 2.62	98	548 ± 4.31	73	509 ± 4.10	183	488 ± 3.32	84	524 ± 4.21	365	565 ± 2.24
ADG[c] kg·d^{-1}	825	1.74 ± 0.01	33	1.58 ± 0.03	334	1.79 ± 0.02	100	1.80 ± 0.02	73	1.63 ± 0.02	183	1.50 ± 0.02	85	1.57 ± 0.02	365	1.81 ± 0.01
FCR[d]	825	7.67 ± 0.04	33	7.83 ± 0.18	334	7.25 ± 0.07	100	7.08 ± 0.09	73	6.92 ± 0.09	183	7.76 ± 0.11	85	7.67 ± 0.11	365	7.65 ± 0.07
USFAT[e], mm	771	10.16 ± 0.12	29	8.02 ± 0.58	314	5.62 ± 0.11	89	4.82 ± 0.20	67	5.48 ± 0.23	151	9.69 ± 0.22	70	7.30 ± 0.31	339	5.90 ± 0.11
USIMF[f], %	240	3.59 ± 0.06	1	2.16 ± 0.00	79	2.77 ± 0.06	37	2.68 ± 0.07	20	2.47 ± 0.10	14	2.93 ± 0.10	3	2.63 ± 0.26	81	2.77 ± 0.07
SC[g], cm	632	36.24 ± 0.11	30	36.01 ± 0.48	281	36.07 ± 0.15	95	35.23 ± 0.24	65	33.25 ± 0.26	70	35.11 ± 0.34	57	35.14 ± 0.49	344	38.02 ± 0.15
USREA[h], cm^2	457	92.41 ± 0.41	14	88.98 ± 2.47	182	99.00 ± 0.79	69	95.73 ± 1.27	39	106.17 ± 1.83	19	79.83 ± 1.90	12	90.37 ± 1.75	220	98.83 ± 0.61
TG[i], kg	825	204 ± 1.19	33	189 ± 3.90	334	212 ± 1.91	100	192 ± 3.91	73	188 ± 3.55	183	200 ± 2.50	85	208 ± 3.56	365	211 ± 1.84
RFI[j]	825	0.28 ± 0.03	33	0.12 ± 0.22	334	-0.28 ± 0.06	100	-0.17 ± 0.13	73	-1.07 ± 0.12	183	-0.39 ± 0.06	85	-0.26 ± 0.11	365	0.15 ± 0.06

[a] Weaning weight adjusted to 205 days and adjusted for age of dam using National Breed Association adjustments
[b] Yearling weight adjusted to 365 days as outlined by BIF (2002)
[c] Average daily gain of bulls for entire test period
[d] Feed conversion ratio defined as pounds of feed required to put on one pound of gain
[e] Ultrasound fat thickness measured at the 12th and 13th rib
[f] Ultrasound percent intramuscular fat measured in the *longissimus* muscle area
[g] Scrotal circumference measured at conclusion of test
[h] Ultrasound *longissimus* muscle area measured at the 12th and 13th rib
[i] Total gain over duration of test (final test weight – on test weight)
[j] Residual feed intake as outlined in Appendix A

Table 9. Simple means ± SEM for performance and ultrasound traits of bulls by breed used in analyses adjusted by final weight

	Breed															
	Angus		Brangus		Charolais		Gelbvieh		Limousin		Hereford		Santa Gertrudis		Simmental	
Trait[a]	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean
FW, kg	825	591 ± 2.14	33	547 ± 9.83	334	594 ± 2.86	100	566 ± 4.64	73	554 ± 4.95	183	542 ± 3.94	87	565 ± 5.13	370	610 ± 2.88
WWT, kg	771	296 ± 1.38	32	293 ± 5.11	322	303 ± 1.99	91	305 ± 3.23	71	290 ± 3.09	177	268 ± 2.29	86	298 ± 3.24	362	317 ± 1.64
YWT, kg	825	541 ± 1.90	33	522 ± 6.15	334	549 ± 2.62	98	548 ± 4.31	73	509 ± 0.36	183	488 ± 3.32	86	524 ± 4.25	370	564 ± 2.26
ADG $kg{\cdot}d^{-1}$	825	1.74 ± 0.01	33	1.58 ± 0.03	334	1.79 ± 0.02	100	1.80 ± 0.02	73	1.63 ± 0.02	183	1.50 ± 0.02	87	1.56 ± 0.02	370	1.80 ± 0.01
FCR	825	7.67 ± 0.04	33	7.83 ± 0.18	334	7.25 ± 0.07	100	7.08 ± 0.09	73	6.92 ± 0.09	183	7.76 ± 0.11	87	7.69 ± 0.11	370	7.67 ± 0.07
USFAT, mm	771	10.16 ± 0.12	29	8.02 ± 0.58	314	5.62 ± 0.11	89	4.82 ± 0.20	67	5.48 ± 0.23	151	9.69 ± 0.22	72	7.29 ± 0.30	343	5.86 ± 0.11
USIMF, %	240	3.59 ± 0.06	1	2.16 ± 0.00	79	2.77 ± 0.06	37	2.68 ± 0.07	20	2.47 ± 0.10	14	2.93 ± 0.10	3	2.63 ± 0.26	81	2.77 ± 0.07
SC, cm	632	36.24 ± 0.11	30	36.01 ± 0.48	281	36.07 ± 0.15	95	35.23 ± 0.24	65	33.24 ± 0.26	70	35.11 ± 0.34	58	35.06 ± 0.49	345	38.03 ± 0.15
USREA, cm^2	457	92.41 ± 0.41	14	88.98 ± 2.47	182	99.00 ± 0.79	69	95.73 ± 1.27	39	106.17 ± 1.83	19	79.83 ± 1.90	12	90.37 ± 1.75	220	98.83 ± 0.61
TG, kg	825	204 ± 1.19	33	189 ± 3.90	334	212 ± 1.91	100	192 ± 3.91	73	188 ± 3.55	183	200 ± 2.50	87	208 ± 3.49	370	211 ± 1.83
RFI	825	0.28 ± 0.03	33	0.12 ± 0.22	334	-0.28 ± 0.06	100	-0.17 ± 0.13	73	-1.07 ± 0.12	183	-0.39 ± 0.06	87	-0.26 ± 0.11	370	0.17 ± 0.06

[a] See Table 8 for trait abbreviations

Table 10. Estimates of heritability and genetic and phenotypic correlations of post-weaning traits of centrally tested bulls adjusted to a common age[a]

Trait[b]	TG	FCR	RFI	ADG	USFAT	USREA	USIMF	SC
TG	0.17	-0.63	0.00	-	0.11	0.21	-0.06	0.22
FCR	-0.76	0.13	0.61	-0.50	0.11	-0.09	0.11	0.01
RFI	-0.06	0.49	0.10	0.00	0.12	-0.17	0.13	0.02
ADG	-	-0.60	-0.08	0.17	0.08	0.21	-0.07	0.21
USFAT	0.20	-0.05	-0.13	0.23	0.16	0.11	0.35	0.04
USREA	0.10	-0.47	-0.77	0.07	0.18	0.09	-0.10	0.08
USIMF	0.04	0.22	0.77	0.05	0.34	-0.24	0.14	-0.12
SC	0.19	-0.04	0.12	0.20	0.03	-0.24	0.27	0.16

[a] Heritability estimates on the diagonal, genetic correlations below the diagonal and phenotypic correlations above the diagonal

[b] See Table 2 for trait abbreviations

Table 11. Estimates of heritability and genetic and phenotypic correlations of post-weaning traits of centrally tested bulls adjusted to a common weight[a]

Trait[b]	TG	FCR	RFI	ADG	USFAT	USREA	USIMF	SC
TG	0.16	-0.74	0.03	-	-0.06	-0.04	-0.07	0.05
FCR	-0.82	0.12	0.60	-0.70	0.10	-0.06	0.12	0.01
RFI	0.10	0.46	0.09	0.02	0.35	-0.16	0.13	0.04
ADG	-	-0.82	0.08	0.16	-0.06	-0.05	-0.08	0.05
USFAT	-0.01	0.01	-0.02	0.03	0.15	-0.01	0.36	-0.04
USREA	0.04	-0.39	-0.70	0.08	0.07	0.13	-0.10	-0.03
USIMF	0.04	0.19	0.73	0.17	0.45	-0.07	0.13	-
SC	0.01	0.15	0.17	0.04	-0.13	-0.20	-	0.17

[a] Heritability estimates on the diagonal, genetic correlations below the diagonal and phenotypic correlations above the diagonal

[b] See Table 2 for trait abbreviations

Table 12. Least squares mean ± SEM between residual feed intake (RFI) groups for post-weaning gain and ultrasound traits of central test bulls adjusted for weight.

	Group[a]		
Trait[b]	Low-RFI	High-RFI	P > F
ADG	1.70 ± 0.01	1.69 ± 0.01	0.50
IW	381 ± 0.98	382 ± 1.21	0.52
FS	6.83 ± 0.03	6.79 ± 0.04	0.40
YW	537 ± 1.37	535 ± 1.66	0.34
USFAT	7.33 ± 0.13	8.45 ± 0.17	0.0001*
USREA	96.62 ± 0.65	93.28 ± 0.78	0.001*
USIMF	2.80 ± 0.11	3.00 ± 0.10	0.16
SC	35.67 ± 0.12	36.01 ± 0.15	0.08
FCR	7.11 ± 0.04	8.10 ± 0.05	0.0001*
TG	203 ± 0.98	202 ± 1.21	0.52
FI	1435 ± 4.31	1621 ± 5.30	0.0001*
RFI	-0.90 ± 0.03	0.79 ± 0.04	0.0001*

[a] Low-RFI group = RFI < 0, High-RFI group = RFI ≥ 0

[b] Average daily gain (ADG, kg/d), initial weight (IW, kg), frame score (FS), yearling weight adjusted to 365 days as outlined by BIF (2002) (YW, kg), ultrasound fat thickness (USFAT, mm), ultrasound *longissimus* muscle area (USREA, sq cm), ultrasound percent intramuscular fat (USIMF), scrotal circumference (SC, cm), feed conversion ratio (FCR), total gain on test (TG, kg), total feed intake on test (FI, kg), residual feed intake (RFI, kg)

*Means are significantly different ($P < 0.05$)

Table 13. Least squares mean ± SEM between residual feed intake (RFI) groups for post-weaning gain and ultrasound traits of central test bulls adjusted for age.

	Group[a]		
Trait[b]	Low-RFI	High-RFI	P > F
ADG	1.67 ± 0.01	1.65 ± 0.01	0.28
IW	374 ± 1.59	371 ± 1.94	0.23
FS	6.7 ± 0.03	6.7 ± 0.04	0.30
YW	527 ± 1.85	524 ± 2.23	0.34
USFAT	7.11 ± 0.13	8.22 ± 0.17	0.0001*
USREA	95.41 ± 0.69	91.76 ± 0.83	0.0007*
USIMF	2.82 ± 0.11	2.99 ± 0.10	0.23
SC	35.44 ± 0.12	35.72 ± 0.16	0.17
FCR	7.08 ± 0.04	8.12 ± 0.05	0.0001*
TG	199 ± 1.14	197 ± 1.40	0.28
FI	1414 ± 5.76	1587 ± 7.04	0.0001*
RFI	-0.87 ± 0.03	0.78 ± 0.04	0.0001*

[a] Low-RFI group = RFI < 0, High-RFI group = RFI ≥ 0

[b] Average daily gain (ADG, kg/d), initial weight (IW, kg), frame score (FS), yearling weight adjusted to 365 days as outlined by BIF (2002) (YW, kg), ultrasound fat thickness (USFAT, mm), ultrasound *longissimus* muscle area (USREA, sq cm), ultrasound percent intramuscular fat (USIMF), scrotal circumference (SC, cm), feed conversion ratio (FCR), total gain on test (TG, kg), total feed intake on test (FI, kg), residual feed intake (RFI, kg)

*Means are significantly different ($P < 0.05$)

Table 14. Least squares mean ± SEM for breed effect of residual feed intake (RFI) on post-weaning gain and ultrasound traits of central test bulls adjusted for weight

	Trait[a]											
Breed	ADG	IW	FS	YW	USFAT	USREA	USIMF	SC	FCR	TG	FI	RFI
Angus	1.71 ± 0.01^{ab}	380 ± 0.78^{b}	6.1 ± 0.03^{d}	536 ± 1.06^{bc}	10.39 ± 0.10^{ab}	92.24 ± 0.36^{c}	3.62 ± 0.05^{a}	36.29 ± 0.10^{b}	7.66 ± 0.03^{ab}	204 ± 0.78^{b}	1553 ± 3.41^{a}	0.14 ± 0.02^{a}
Brangus	1.62 ± 0.03^{c}	392 ± 3.49^{a}	6.9 ± 0.11^{bc}	535 ± 4.86^{bc}	9.75 ± 0.42^{b}	89.72 ± 2.06^{cd}	-	36.55 ± 0.41^{b}	7.85 ± 0.15^{a}	192 ± 3.49^{c}	1501 ± 15.32^{cd}	0.00 ± 0.11^{bc}
Charolais	1.75 ± 0.01^{a}	376 ± 1.15^{c}	7.1 ± 0.04^{b}	539 ± 1.58^{ab}	5.85 ± 0.14^{d}	97.91 ± 0.57^{b}	2.88 ± 0.08^{bc}	35.94 ± 0.14^{b}	7.37 ± 0.05^{c}	209 ± 1.15^{a}	1527 ± 5.04^{bc}	-0.09 ± 0.04^{bc}
Gelbvieh	1.75 ± 0.02^{a}	375 ± 2.23^{c}	6.9 ± 0.07^{c}	543 ± 3.08^{a}	5.39 ± 0.25^{d}	98.73 ± 0.91^{b}	2.79 ± 0.11^{bc}	36.31 ± 0.25^{b}	7.45 ± 0.09^{bc}	210 ± 2.23^{a}	1550 ± 9.80^{a}	0.05 ± 0.07^{ab}
Limousin	1.64 ± 0.03^{c}	387 ± 3.06^{a}	6.9 ± 0.10^{c}	516 ± 4.19^{d}	6.20 ± 0.40^{d}	109.56 ± 1.48^{a}	2.55 ± 0.16^{c}	33.90 ± 0.35^{d}	7.62 ± 0.13^{abc}	198 ± 3.06^{c}	1491 ± 13.46^{d}	-0.33 ± 0.10^{d}
Hereford	1.71 ± 0.02^{ab}	380 ± 1.82^{bc}	6.1 ± 0.06^{d}	533 ± 2.51^{c}	11.06 ± 0.38^{a}	84.84 ± 1.77^{d}	3.11 ± 0.19^{b}	35.16 ± 0.31^{c}	7.57 ± 0.08^{abc}	205 ± 1.82^{ab}	1536 ± 8.02^{ab}	-0.14 ± 0.06^{cd}
Santa Gertrudis	1.67 ± 0.02^{bc}	385 ± 2.22^{ab}	7.4 ± 0.07^{a}	543 ± 3.07^{a}	8.68 ± 0.32^{c}	89.23 ± 2.18^{cd}	2.49 ± 0.41^{c}	34.86 ± 0.31^{c}	7.68 ± 0.09^{ab}	199 ± 2.22^{bc}	1520 ± 9.78^{bcd}	-0.13 ± 0.07^{bcd}
Simmental	1.71 ± 0.01^{ab}	380 ± 1.15^{b}	7.1 ± 0.04^{b}	543 ± 1.58^{a}	5.80 ± 0.13^{d}	97.36 ± 0.51^{b}	2.88 ± 0.08^{bc}	37.68 ± 0.13^{a}	7.63 ± 0.05^{ab}	204 ± 1.15^{b}	1545 ± 5.06^{a}	0.03 ± 0.04^{b}

[a] See Table 2 for trait abbreviations

Columns with different superscripts differ at $P < 0.05$

Table 15. Least squares mean ± SEM for breed effect of residual feed intake (RFI) on post-weaning gain and ultrasound traits of central test bulls adjusted for age

	Trait^{a}											
Breed	ADG	IW	FS	YW	USFAT	USREA	USIMF	SC	FCR	TG	FI	RFI
Angus	1.72 ± 0.01^{b}	382 ± 1.27^{b}	6.1 ± 0.03^{c}	542 ± 1.45^{b}	10.51 ± 0.10^{a}	92.78 ± 0.39^{c}	3.61 ± 0.05^{a}	36.43 ± 0.10^{b}	7.59 ± 0.04^{a}	206 ± 0.91^{b}	1560 ± 4.60^{a}	0.12 ± 0.02^{a}
Brangus	1.53 ± 0.04^{d}	372 ± 5.69^{bc}	6.6 ± 0.12^{b}	508 ± 6.63^{d}	9.17 ± 0.43^{b}	86.82 ± 2.23^{d}	-	35.90 ± 0.42^{c}	7.91 ± 0.16^{a}	182 ± 4.10^{e}	1441 ± 20.64^{e}	0.03 ± 0.11^{abc}
Charolais	1.75 ± 0.01^{a}	379 ± 1.88^{b}	7.2 ± 0.04^{a}	542 ± 2.16^{b}	5.89 ± 0.15^{c}	98.16 ± 0.62^{b}	2.87 ± 0.08^{bc}	36.00 ± 0.15^{c}	7.32 ± 0.05^{b}	210 ± 1.35^{a}	1535 ± 6.81^{b}	-0.10 ± 0.04^{cd}
Gelbvieh	1.70 ± 0.02^{bc}	367 ± 3.65^{c}	6.7 ± 0.08^{b}	527 ± 4.22^{c}	5.19 ± 0.26^{d}	97.67 ± 0.98^{b}	2.79 ± 0.11^{bc}	36.13 ± 0.26^{bc}	7.53 ± 0.10^{ab}	204 ± 2.63^{bc}	1522 ± 13.24^{bc}	0.07 ± 0.07^{ab}
Limousin	1.53 ± 0.03^{d}	345 ± 4.96^{d}	6.6 ± 0.11^{b}	489 ± 5.67^{de}	5.47 ± 0.41^{cd}	105.11 ± 1.58^{a}	2.55 ± 0.16^{c}	32.88 ± 0.36^{e}	7.56 ± 0.14^{abc}	184 ± 3.57^{e}	1383 ± 18.00^{f}	-0.31 ± 0.10^{d}
Hereford	1.65 ± 0.02^{c}	362 ± 2.96^{c}	5.9 ± 0.06^{d}	516 ± 3.41^{d}	10.74 ± 0.39^{a}	82.47 ± 1.92^{d}	3.11 ± 0.19^{b}	34.70 ± 0.33^{d}	7.59 ± 0.08^{a}	198 ± 2.14^{cd}	1488 ± 10.76^{d}	-0.12 ± 0.06^{cd}
Santa Gertrudis	1.63 ± 0.02^{c}	380 ± 3.68^{b}	7.3 ± 0.08^{a}	530 ± 4.25^{c}	8.36 ± 0.34^{b}	87.48 ± 2.36^{cd}	2.52 ± 0.41^{c}	34.67 ± 0.33^{d}	7.72 ± 0.10^{a}	195 ± 2.65^{d}	1502 ± 13.36^{cd}	-0.09 ± 0.07^{bcd}
Simmental	1.74 ± 0.01^{ab}	390 ± 1.15^{a}	7.2 ± 0.04^{a}	551 ± 2.18^{a}	5.98 ± 0.13^{c}	98.16 ± 0.55^{b}	2.87 ± 0.08^{bc}	37.93 ± 0.13^{a}	7.59 ± 0.05^{a}	208 ± 1.37^{ab}	1570 ± 6.90^{a}	0.02 ± 0.04^{bc}

[a] See Table 2 for trait abbreviations

Columns with different superscripts differ at $P < 0.05$

Table 16. Least squares mean ± SEM by year of residual feed intake (RFI) on post-weaning gain and ultrasound traits of central test bulls adjusted for weight

	Trait[a]											
Year	ADG	IW	FS	YW	USFAT	USREA	USIMF	SC	FCR	TG	FI	RFI
1978	1.57 ± 0.03^{hij}	367 ± 3.01^{ijk}	5.4 ± 0.10^{lm}	502 ± 4.12^{h}	-	-	-	-	7.04 ± 0.13^{no}	217 ± 3.01^{def}	1530 ± 13.24^{g}	-0.12 ± 0.09^{ab}
1979	1.43 ± 0.02^{l}	386 ± 2.68^{de}	5.3 ± 0.09^{m}	491 ± 3.67^{i}	-	-	-	-	9.34 ± 0.11^{a}	198 ± 2.68^{jk}	1782 ± 11.79^{ab}	-0.10 ± 0.08^{b}
1980	1.49 ± 0.02^{kl}	379 ± 2.66^{fg}	5.6 ± 0.08^{l}	508 ± 3.64^{h}	-	-	-	-	8.13 ± 0.11^{cd}	205 ± 2.66^{hi}	1623 ± 11.70^{f}	-0.06 ± 0.08^{ab}
1981	1.56 ± 0.02^{ij}	366 ± 2.60^{ijk}	6.3 ± 0.08^{j}	510 ± 3.55^{h}	-	-	-	-	7.63 ± 0.11^{hijk}	218 ± 2.60^{def}	1650 ± 11.41^{ef}	-0.02 ± 0.08^{ab}
1982	1.56 ± 0.02^{ij}	366 ± 2.60^{ijk}	6.3 ± 0.08^{j}	507 ± 3.56^{h}	-	-	-	-	8.00 ± 0.11^{cdef}	219 ± 2.60^{def}	1738 ± 11.42^{cd}	-0.02 ± 0.08^{ab}
1983	1.53 ± 0.02^{jk}	370 ± 2.69^{hij}	5.5 ± 0.09^{lm}	503 ± 3.69^{h}	-	-	-	36.98 ± 0.30^{b}	8.51 ± 0.11^{b}	214 ± 2.69^{efg}	1807 ± 11.84^{a}	-0.06 ± 0.08^{ab}
1984	1.61 ± 0.02^{ghi}	360 ± 2.69^{klmn}	6.0 ± 0.09^{k}	525 ± 3.68^{g}	-	-	-	-	7.78 ± 0.11^{efghi}	224 ± 2.69^{abcd}	1718 ± 11.81^{d}	-0.04 ± 0.08^{ab}
1985	1.57 ± 0.02^{hij}	366 ± 2.82^{ijkl}	6.2 ± 0.09^{jk}	521 ± 3.92^{g}	7.59 ± 0.31^{efgh}	-	-	37.78 ± 0.31^{b}	7.69 ± 0.12^{fghij}	219 ± 2.82^{cdef}	1666 ± 12.39^{e}	-0.16 ± 0.09^{b}
1986	1.58 ± 0.02^{hij}	364 ± 2.87^{jkl}	6.7 ± 0.09^{i}	531 ± 3.92^{fg}	7.63 ± 0.32^{efgh}	-	-	37.20 ± 0.32^{b}	7.39 ± 0.12^{jklm}	221 ± 2.87^{cde}	1620 ± 12.60^{f}	-0.14 ± 0.09^{b}
1987	1.61 ± 0.02^{ghi}	359 ± 2.36^{lmn}	7.3 ± 0.08^{cdef}	526 ± 3.23^{g}	7.14 ± 0.28^{ghij}	-	-	38.71 ± 0.28^{a}	7.86 ± 0.10^{defgh}	226 ± 2.36^{abc}	1762 ± 10.39^{bc}	-0.03 ± 0.07^{ab}
1988	1.59 ± 0.02^{ghij}	361 ± 2.44^{klm}	7.3 ± 0.08^{def}	530 ± 3.34^{g}	7.51 ± 0.28^{fgh}	-	-	36.97 ± 0.28^{b}	8.05 ± 0.10^{cde}	224 ± 2.44^{bcd}	1785 ± 10.72^{ab}	-0.02 ± 0.08^{ab}
1989	1.64 ± 0.02^{g}	354 ± 2.32^{h}	7.5 ± 0.07^{bc}	548 ± 3.17^{de}	6.65 ± 0.28^{ij}	-	-	35.60 ± 0.28^{cdef}	7.16 ± 0.10^{mno}	231 ± 2.32^{a}	1637 ± 10.18^{ef}	-0.01 ± 0.07^{ab}
1990	1.63 ± 0.02^{gh}	355 ± 2.33^{mn}	7.5 ± 0.07^{bcd}	548 ± 3.19^{de}	7.77 ± 0.28^{efg}	-	-	36.05 ± 0.28^{cd}	7.85 ± 0.10^{defgh}	229 ± 2.33^{ab}	1790 ± 10.26^{ab}	0.01 ± 0.07^{ab}
1991	1.78 ± 0.02^{def}	386 ± 2.31^{def}	7.7 ± 0.07^{a}	548 ± 3.16^{de}	7.74 ± 0.28^{efg}	-	-	35.45 ± 0.28^{cdefg}	7.46 ± 0.10^{jkl}	199 ± 2.31^{ijk}	1468 ± 10.16^{h}	-0.07 ± 0.07^{ab}
1992	1.82 ± 0.02^{cd}	382 ± 2.29^{efg}	7.4 ± 0.07^{cde}	549 ± 3.13^{de}	6.47 ± 0.28^{j}	101.03 ± 0.93^{a}	-	35.47 ± 0.28^{cdefg}	7.69 ± 0.10^{ghij}	203 ± 2.29^{hij}	1542 ± 10.06^{g}	0.12 ± 0.07^{a}
1993	1.64 ± 0.02^{g}	402 ± 2.30^{c}	7.4 ± 0.07^{cde}	541 ± 3.14^{ef}	8.36 ± 0.28^{cde}	94.17 ± 0.95^{de}	-	35.97 ± 0.26^{cd}	8.08 ± 0.10^{cd}	183 ± 2.30^{l}	1471 ± 10.09^{h}	-0.09 ± 0.07^{b}
1994	1.74 ± 0.02^{f}	390 ± 2.27^{d}	7.3 ± 0.07^{ef}	543 ± 3.11^{de}	8.08 ± 0.27^{def}	92.06 ± 0.95^{ef}	-	35.68 ± 0.26^{cde}	7.95 ± 0.10^{cdefg}	195 ± 2.27^{k}	1534 ± 9.99^{g}	-0.06 ± 0.07^{ab}
1995	1.80 ± 0.02^{de}	383 ± 2.32^{efg}	7.6 ± 0.07^{ab}	564 ± 3.17^{ab}	7.35 ± 0.28^{ghij}	100.94 ± 0.97^{ab}	-	36.09 ± 0.26^{c}	8.14 ± 0.10^{c}	202 ± 2.32^{hij}	1626 ± 10.19^{f}	-0.14 ± 0.07^{b}
1996	1.91 ± 0.02^{ab}	371 ± 2.27^{hi}	7.1 ± 0.07^{fg}	551 ± 3.40^{cd}	7.35 ± 0.28^{fghi}	97.22 ± 0.93^{c}	-	35.46 ± 0.25^{cdefg}	7.02 ± 0.10^{no}	214 ± 2.27^{fg}	1484 ± 9.99^{h}	-0.07 ± 0.07^{ab}
1997	1.79 ± 0.02^{de}	385 ± 2.34^{def}	6.9 ± 0.07^{hi}	523 ± 3.20^{g}	8.63 ± 0.26^{bcd}	96.39 ± 0.92^{cd}	-	34.50 ± 0.26^{h}	7.19 ± 0.10^{lmn}	200 ± 2.34^{ijk}	1415 ± 10.28^{i}	-0.12 ± 0.07^{b}
1998	1.77 ± 0.02^{def}	387 ± 2.35^{de}	7.0 ± 0.07^{gh}	551 ± 3.22^{cd}	8.79 ± 0.27^{bc}	96.08 ± 0.93^{cd}	3.89 ± 0.14^{a}	34.79 ± 0.26^{gh}	7.11 ± 0.10^{mno}	198 ± 2.35^{jk}	1392 ± 10.33^{i}	-0.09 ± 0.07^{b}
1999	1.87 ± 0.03^{bc}	376 ± 2.91^{gh}	6.8 ± 0.09^{hi}	550 ± 3.99^{cde}	9.40 ± 0.33^{ab}	98.34 ± 1.11^{bc}	2.20 ± 0.11^{e}	35.23 ± 0.32^{defgh}	6.84 ± 0.12^{o}	208 ± 2.91^{gh}	1407 ± 12.81^{i}	-0.11 ± 0.09^{b}
2000	1.76 ± 0.02^{ef}	388 ± 2.39^{de}	7.2 ± 0.08^{efg}	547 ± 3.27^{de}	9.94 ± 0.27^{a}	90.73 ± 0.94^{fg}	2.96 ± 0.10^{c}	35.10 ± 0.27^{efgh}	7.52 ± 0.10^{ijk}	197 ± 2.39^{k}	1461 ± 10.50^{h}	-0.01 ± 0.08^{ab}
2001	1.93 ± 0.02^{a}	421 ± 2.46^{b}	7.4 ± 0.08^{cde}	572 ± 3.37^{a}	9.87 ± 0.28^{a}	96.52 ± 0.97^{cd}	2.90 ± 0.10^{c}	34.88 ± 0.28^{fgh}	7.01 ± 0.10^{no}	163 ± 2.46^{m}	1141 ± 10.82^{j}	0.05 ± 0.08^{ab}
2002	1.89 ± 0.02^{ab}	427 ± 2.70^{b}	7.3 ± 0.09^{efg}	569 ± 3.73^{a}	6.98 ± 0.30^{ghij}	89.48 ± 1.03^{g}	3.01 ± 0.11^{b}	34.81 ± 0.30^{fgh}	7.00 ± 0.11^{no}	157 ± 2.70^{m}	1088 ± 11.86^{k}	-0.14 ± 0.09^{b}
2003	1.76 ± 0.02^{def}	437 ± 2.56^{a}	6.8 ± 0.08^{hi}	559 ± 3.50^{bc}	7.69 ± 0.29^{efg}	90.43 ± 1.00^{fg}	2.65 ± 0.10^{d}	34.64 ± 0.29^{h}	7.36 ± 0.11^{klm}	147 ± 2.56^{n}	1077 ± 11.26^{k}	-0.07 ± 0.08^{ab}
2004	1.91 ± 0.02^{ab}	424 ± 2.35^{b}	7.2 ± 0.07^{efg}	558 ± 3.21^{bc}	6.85 ± 0.27^{hij}	90.95 ± 0.93^{fg}	2.69 ± 0.10^{d}	35.23 ± 0.26^{efgh}	6.50 ± 0.10^{p}	161 ± 2.35^{m}	1039 ± 10.31^{l}	-0.14 ± 0.07^{b}

[a] See Table 2 for trait abbreviations

Columns with different superscripts differ at $P < 0.05$

Table 17. Least squares mean ± SEM by year of residual feed intake (RFI) on post-weaning gain and ultrasound traits of central test bulls adjusted for age

	Trait[a]											
Year	ADG	IW	FS	YW	USFAT	USREA	USIMF	SC	FCR	TG	FI	RFI
1978	1.44 ± 0.03^{o}	314 ± 4.87^{l}	5.0 ± 0.11^{lm}	473 ± 5.57^{mn}	-	-	-	-	6.94 ± 0.14^{klm}	202 ± 3.51^{fgh}	1397 ± 17.70^{i}	-0.01 ± 0.09^{abc}
1979	1.28 ± 0.03^{p}	317 ± 4.41^{kl}	4.8 ± 0.10^{m}	458 ± 5.05^{o}	-	-	-	-	9.17 ± 0.12^{a}	180 ± 3.18^{l}	1613 ± 16.02^{de}	-0.10 ± 0.09^{bc}
1980	1.33 ± 0.03^{p}	326 ± 4.24^{jkl}	5.1 ± 0.09^{kl}	469 ± 4.84^{no}	-	-	-	-	8.13 ± 0.12^{bcd}	187 ± 3.05^{jkl}	1485 ± 15.38^{h}	-0.02 ± 0.08^{abc}
1981	1.47 ± 0.03^{no}	328 ± 4.35^{jk}	6.0 ± 0.09^{ij}	488 ± 4.98^{lm}	-	-	-	-	7.57 ± 0.12^{fgh}	207 ± 3.14^{def}	1555 ± 15.80^{fg}	0.01 ± 0.08^{abc}
1982	1.50 ± 0.03^{no}	333 ± 4.26^{j}	6.2 ± 0.09^{i}	496 ± 4.87^{jkl}	-	-	-	-	7.89 ± 0.12^{def}	211 ± 3.07^{cde}	1658 ± 15.45^{c}	-0.04 ± 0.08^{abc}
1983	1.48 ± 0.03^{no}	333 ± 4.44^{j}	5.3 ± 0.10^{k}	496 ± 5.08^{kl}	-	-	-	35.73 ± 0.32^{def}	8.34 ± 0.12^{b}	208 ± 3.20^{def}	1722 ± 16.13^{b}	-0.07 ± 0.09^{abc}
1984	1.53 ± 0.03^{mn}	337 ± 4.40^{ij}	5.8 ± 0.10^{j}	506 ± 5.03^{jk}	-	-	-	-	7.81 ± 0.12^{defg}	215 ± 3.17^{cd}	1654 ± 15.97^{cd}	-0.04 ± 0.09^{abc}
1985	1.52 ± 0.03^{no}	347 ± 4.66^{hi}	6.0 ± 0.10^{ij}	509 ± 5.41^{j}	7.05 ± 0.33^{efgh}	-	-	37.10 ± 0.33^{b}	7.67 ± 0.13^{efgh}	213 ± 3.36^{cd}	1617 ± 16.91^{cde}	-0.16 ± 0.09^{c}
1986	1.55 ± 0.03^{lm}	353 ± 4.69^{gh}	6.7 ± 0.10^{h}	526 ± 5.38^{hi}	7.23 ± 0.33^{defgh}	-	-	36.66 ± 0.33^{bc}	7.38 ± 0.13^{hij}	218 ± 3.38^{bc}	1595 ± 17.04^{ef}	-0.13 ± 0.09^{c}
1987	1.59 ± 0.02^{kl}	348 ± 3.88^{hi}	7.3 ± 0.08^{cdef}	525 ± 4.43^{i}	6.87 ± 0.29^{fgh}	-	-	38.30 ± 0.29^{a}	7.81 ± 0.11^{efg}	224 ± 2.79^{b}	1738 ± 14.07^{b}	-0.03 ± 0.08^{abc}
1988	1.61 ± 0.03^{jkl}	362 ± 4.00^{fg}	7.4 ± 0.09^{bcd}	539 ± 4.57^{defgh}	7.40 ± 0.29^{fgh}	-	-	36.79 ± 0.29^{bc}	7.99 ± 0.11^{cde}	227 ± 2.88^{ab}	1793 ± 14.52^{a}	-0.04 ± 0.08^{abc}
1989	1.65 ± 0.02^{ijk}	363 ± 3.80^{fg}	7.5 ± 0.08^{ab}	548 ± 4.34^{bcd}	6.66 ± 0.29^{gh}	-	-	35.72 ± 0.29^{def}	7.22 ± 0.11^{ijk}	232 ± 2.74^{a}	1656 ± 13.79^{c}	-0.01 ± 0.07^{abc}
1990	1.66 ± 0.02^{hi}	371 ± 3.81^{ef}	7.6 ± 0.08^{ab}	556 ± 4.36^{ab}	7.78 ± 0.29^{cde}	-	-	36.12 ± 0.29^{cd}	7.87 ± 0.11^{def}	234 ± 2.75^{a}	1829 ± 13.85^{a}	0.00 ± 0.07^{abc}
1991	1.77 ± 0.02^{def}	393 ± 3.80^{d}	7.7 ± 0.08^{a}	543 ± 4.34^{cdefg}	7.62 ± 0.29^{cde}	-	-	35.40 ± 0.29^{defg}	7.55 ± 0.11^{gh}	198 ± 2.74^{gh}	1481 ± 13.79^{h}	-0.06 ± 0.07^{abc}
1992	1.83 ± 0.02^{cd}	394 ± 3.76^{d}	7.4 ± 0.08^{bcd}	549 ± 4.30^{bcd}	6.49 ± 0.29^{h}	101.02 ± 1.01^{a}	-	35.62 ± 0.29^{def}	7.77 ± 0.11^{efg}	204 ± 2.71^{efg}	1569 ± 13.65^{fg}	0.13 ± 0.07^{a}
1993	1.64 ± 0.02^{ijk}	405 ± 3.76^{c}	7.4 ± 0.08^{bc}	540 ± 4.31^{defg}	8.24 ± 0.29^{bc}	93.29 ± 1.04^{ef}	-	35.77 ± 0.27^{de}	8.11 ± 0.11^{bcd}	184 ± 2.71^{kl}	1479 ± 13.66^{h}	-0.08 ± 0.07^{bc}
1994	1.75 ± 0.02^{efg}	398 ± 3.73^{cd}	7.3 ± 0.08^{cdef}	544 ± 4.26^{cdef}	7.94 ± 0.28^{bcd}	91.04 ± 1.03^{fg}	-	35.57 ± 0.27^{def}	7.99 ± 0.10^{cde}	196 ± 2.69^{hi}	1552 ± 13.53^{g}	-0.05 ± 0.07^{abc}
1995	1.70 ± 0.02^{ghi}	359 ± 3.78^{g}	7.3 ± 0.08^{cde}	535 ± 4.32^{efghi}	6.63 ± 0.28^{gh}	97.00 ± 1.02^{bc}	-	35.22 ± 0.27^{efgh}	8.23 ± 0.11^{bc}	190 ± 2.72^{ijk}	1554 ± 13.70^{fg}	-0.11 ± 0.07^{c}
1996	1.90 ± 0.02^{ab}	376 ± 3.74^{e}	7.1 ± 0.08^{fg}	546 ± 4.67^{bcde}	7.22 ± 0.29^{defgh}	96.38 ± 1.00^{bcd}	-	35.29 ± 0.26^{defgh}	7.12 ± 0.11^{jk}	212 ± 2.69^{cd}	1489 ± 13.57^{h}	-0.06 ± 0.07^{abc}
1997	1.81 ± 0.02^{cde}	377 ± 3.85^{e}	7.0 ± 0.08^{g}	532 ± 4.40^{ghi}	8.32 ± 0.28^{bc}	94.17 ± 1.03^{de}	-	33.97 ± 0.28^{j}	6.79 ± 0.11^{lm}	202 ± 2.77^{fgh}	1407 ± 13.98^{i}	-0.12 ± 0.07^{c}
1998	1.75 ± 0.02^{efg}	392 ± 3.86^{d}	7.0 ± 0.08^{g}	542 ± 4.42^{cdefg}	8.55 ± 0.28^{b}	94.65 ± 1.00^{cde}	3.89 ± 0.14^{a}	34.60 ± 0.28^{hij}	7.07 ± 0.11^{jkl}	196 ± 2.78^{hi}	1398 ± 14.02^{i}	-0.06 ± 0.07^{abc}
1999	1.93 ± 0.03^{a}	399 ± 4.76^{cd}	7.0 ± 0.10^{g}	563 ± 5.44^{a}	9.54 ± 0.34^{a}	98.90 ± 1.20^{ab}	2.21 ± 0.12^{e}	35.50 ± 0.34^{defg}	6.66 ± 0.13^{m}	215 ± 3.43^{cd}	1466 ± 17.27^{h}	-0.10 ± 0.09^{bc}
2000	1.74 ± 0.02^{fg}	390 ± 3.92^{d}	7.2 ± 0.08^{defg}	539 ± 4.48^{defgh}	9.65 ± 0.28^{a}	88.97 ± 1.01^{g}	2.96 ± 0.10^{b}	34.83 ± 0.28^{ghi}	7.46 ± 0.11^{hi}	195 ± 2.82^{hij}	1461 ± 14.23^{h}	0.01 ± 0.08^{abc}
2001	1.85 ± 0.03^{bc}	427 ± 4.13^{b}	7.0 ± 0.09^{g}	537 ± 4.72^{defghi}	9.48 ± 0.30^{a}	94.73 ± 1.06^{cde}	2.90 ± 0.10^{bc}	34.74 ± 0.30^{ghij}	7.33 ± 0.12^{hij}	153 ± 2.97^{m}	1130 ± 14.99^{j}	0.11 ± 0.08^{ab}
2002	1.87 ± 0.03^{abc}	443 ± 4.48^{a}	7.1 ± 0.10^{efg}	554 ± 5.17^{abc}	6.85 ± 0.32^{fgh}	88.86 ± 1.12^{g}	3.01 ± 0.11^{b}	34.91 ± 0.32^{fghi}	7.12 ± 0.12^{jk}	155 ± 3.23^{m}	1112 ± 16.27^{jk}	-0.12 ± 0.09^{c}
2003	1.73 ± 0.03^{fgh}	441 ± 4.22^{a}	6.7 ± 0.09^{h}	543 ± 4.83^{cdefg}	7.36 ± 0.30^{defg}	88.66 ± 1.08^{g}	2.65 ± 0.10^{d}	34.41 ± 0.30^{ij}	7.51 ± 0.12^{ghi}	143 ± 3.04^{n}	1075 ± 15.33^{k}	-0.03 ± 0.08^{abc}
2004	1.84 ± 0.02^{bc}	423 ± 3.88^{b}	7.0 ± 0.08^{g}	533 ± 4.43^{fghi}	6.43 ± 0.28^{h}	88.90 ± 0.99^{g}	2.70 ± 0.10^{d}	34.90 ± 0.28^{fghi}	6.70 ± 0.11^{m}	153 ± 2.79^{m}	1022 ± 14.07^{l}	-0.08 ± 0.08^{bc}

[a] See Table 2 for trait abbreviations

Columns with different superscripts differ at $P < 0.05$

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APPENDIX

CALCULATION OF RESIDUAL FEED INTAKE (RFI)

A. General
  a. Daily feed intake was converted to total feed intake of each animal during the entire feeding period.
  b. Convert total feed intake to total energy intake by multiplying total Dry Matter (DM) intake by metabolizable energy of the diet fed determined by indirect calorimetry.
    i. Look up energy values of feedstuffs in diet using nutrient requirements of beef cattle (National Research Council, 1996). The following is a list of feedstuffs used to calculate RFI for Auburn University BCIA bull test.
      1. Corn = 3.25 Mcal kg^{-1}
      2. Cottonseed Hulls = 1.52 Mcal kg^{-1}
      3. Oats = 2.78 Mcal kg^{-1}
      4. Soybean Meal = 3.04 Mcal kg^{-1}
      5. Molasses = 2.60 Mcal kg^{-1}
      6. Cottonseed Meal = 2.71 Mcal kg^{-1}
      7. Barley Grain #2 = 3.03 Mcal kg^{-1}
      8. Fat = 7.30 Mcal kg^{-1}
  c. Change pounds of each ingredient to a percent of ingredient in diet by dividing pounds of each ingredient into total pounds of diet.
    i. Example: Pounds of ingredient ÷ Total pounds of diet = % of ingredient in diet
  d. Multiply percent of ingredient in diet by NRC values looked up.
    i. Example: Corn = 0.30 * 3.25 = 0.975
    ii. Then take the sum of all feedstuffs calculated previously (in d.i).
  e. Take the sum (from d.ii) and multiply it by total feed intake (kg). This number is the total energy intake.
  f. Convert total energy intake (from e) to Mj by multiplying it by 4.184
  g. Total energy intake is then divided by 10 to give total DM intake standardized to an energy density of 10 MJ ME kg^{-1} DM.
  h. Total standardized feed intake (SFI) is then divided by the number of days on test to give average standardized daily feed intake (SFI, kg d^{-1}).
  i. Calculate mid-weight (MWT): MWT = Final Weight – (0.50 * Days on Test * Average Daily Gain)
  j. Calculate metabolic mid-weight (MMWT): MMWT = (MWT)$^{0.73}$
  k. Convert MMWT to Kg: MMWT ÷ 2.20462

l. Convert daily feed intake to Kg: total feed intake(kg)/days on test

m. Convert ADG from pounds per day to kg per day: ADG (lbs/d)/2.20462

n. Next calculate expected feed intake (EFI, kg d^{-1})

    i. Calculate expected feed intake (EFI) using a regression equation in a statistical analysis software program (SAS, SAS Inst. Inc., Cary, NC).

        1. Model fitted is basically of the form:

            a. $Y_i = a + b_1 ADG_i + b_2 MMWT + e_i$

               Where

               Yi = SFI for animal i

               a = regression intercept

               b_1 = partial regression coefficient of SFI on ADG

               b_2 = partial regression coefficient on MMWT

               e_i = residual error in SFI of animal i

    ii. Regress feed intake against some descriptor of maintenance (e.g. bodyweight to the power of 0.73) and production (e.g. growth rate). The predicted value from this regression is the expected feed intake.

        1. Measures of average daily gain (ADG, kg d^{-1}) and metabolic mid-weight (MMWT, $kg^{0.73}$) are used to model daily EFI.

o. Calculate RFI by the following equation: RFI = Average standardized feed intake per day (from h) – expected feed intake (from n.ii.1)