

IMPROVEMENT OF FEED EFFICIENCY IN BEEF CATTLE THROUGH
SELECTION UPON RESIDUAL FEED INTAKE (RFI)

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by
NICHOLAS OLIVER MINTON

Dr. Monty S. Kerley, Thesis Advisor

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The undersigned, appointed by the Dean of the Graduate School, have examined the thesis entitled

IMPROVEMENT OF FEED EFFICIENCY IN BEEF CATTLE THROUGH
SELECTION UPON RESIDUAL FEED INTAKE (RFI).

presented by Nicholas Oliver Minton,

a candidate for the degree of Master of Science,

and hereby certify that in their opinion it is worthy of acceptance.

Dr. Monty S. Kerley

Dr. Robert L. Weaber

Dr. Mark Ellerseick

DEDICATION

To my late grandfather William Ralph Minton

A man in whom I truly admire and respect, A man whom supported me and enjoyed watching me pursue something I was truly passionate about, A man whom I know is truly proud of what I have accomplished

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IMPROVEMENT OF FEED EFFICIENCY IN BEEF CATTLE THROUGH SELECTION UPON RESIDUAL FEED INTAKE (RFI)

Nicholas Minton

Dr. Monty Kerley, Thesis Advisor

ABSTRACT

Feed cost remains the largest contributor to annual input cost within beef production. Identifying methods to reduce feed cost within the production system is crucial to the profitability of beef production. Selecting animals which metabolically, are more efficient at converting feed into gain or other sources of production is one method of reducing feed cost within beef production. The objective of this study was to investigate the improvement in feed efficiency of beef cattle through selection upon residual feed intake (RFI). Experiment one phenotyped 38 Simmental by Angus crossbred heifers for RFI over a postweaning trial as virgin heifers and then rephenotyped the same 38 heifers as mature lactating cows. Individual RFI values were used to group heifers and cows into RFI phenotype and RFI category groups. Heifers and cows with negative RFI values (RFI-) were feed efficient, while heifers and cows with positive RFI values (RFI+) were inefficient. Residual feed intake category groups (low, average, high) were determined by a 0.50 SD above and below the average RFI of the contemporary group. Residual feed intakes were not correlated ($r_p = 0.17$; $P > 0.10$) between postweaning and mature trials. Moderate correlations occurred between cow RFI with heifer category and phenotype groups ($r_p = 0.31$ and 0.35 , respectively) as well

as between cow RFI phenotype with heifer RFI and heifer category group ($r_p = 0.33$ and 0.41 , respectively). Heifer RFI phenotype was correlated ($r_p = 0.54$; $P < 0.01$) with mature cow RFI phenotype indicating heifers phenotyped as feed efficient remained feed efficient as mature cows, while heifers phenotyped as inefficient as heifers remained inefficient as mature lactating cows. Either heifer or cow RFI, RFI phenotype or RFI category group were correlated with F1 progeny feed efficiency or performance traits. Experiment two included two trials, trial one investigated the effect on progeny feed efficiency when sires and dams of known RFI phenotypes were divergently mated. Trial one further investigated the agreement in steer RFI when RFI is measured over three separate time intervals over a 120 d trial. Trial two investigated the agreement in F2 steer progeny RFI with dam RFI measured postweaning and as a mature lactating cow. Trial two further investigated the relationship between lean content and loin muscle size and development between steers produced from either feed efficient or inefficient dams. Trial one included three treatments (**TRT**): TRT 1 = RFI- sires mated to RFI- dams, TRT 2 = one RFI- sire mated to RFI+ dams and TRT 3 = one RFI+ sire mated to RFI+ dams. Residual feed intake, FCR and DMI were different among heifer progeny produced from the three treatments. Treatments one and two produced the more feed efficient heifer progeny than TRT 3 with lower RFI's (-0.31 ± 0.25 vs. -0.43 ± 0.41 vs. 0.75 ± 0.31 ; $P < 0.05$, respectively), lower FCR's (5.54 ± 0.21 vs. 5.21 ± 0.37 vs. 6.59 ± 0.26 ; $P < 0.01$, respectively) and lower DMI's (8.20 ± 0.26 vs. 8.23 ± 0.42 vs. 9.46 ± 0.33 ; $P < 0.01$, respectively) with no difference in ADG ($P = 0.52$). Differences in feed efficiency and performance did not occur among steer progeny produced from the three treatment groups between the 0 to 70 d trial and 70 to 50 d trial, however; RFI was

different among steer progeny over the 0 to 120 d trial. Steers produced from TRT 1 and 2 did had lower RFI's than steers produced from TRT 3 (-0.34 ± 0.22 vs. 0.02 ± 0.30 vs. 0.80 ± 0.37 ; $P < 0.10$, respectively). Feed conversion ratio, ADG and DMI were not different ($P > 0.10$) among steer progeny among the three treatment groups over the 0 to 120 d trial. Residual feed intakes measure over the 0 to 70 d trial and 0 to 120 d trial were moderately correlated ($r_p = 0.49$; $P = 0.03$) while RFI showed stronger correlations between the 70 to 120 d trial and the 0 to 120 d trial ($r_p = 0.92$; $P < 0.01$). Residual feed intake was not correlated between the 0 to 70 d trial and 70 to 120 d trial ($P > 0.10$).

Dam RFI phenotype measured postweaning as a heifer was correlated with steer progeny RFI ($r_p = 0.68$; $P < 0.01$), FCR ($r_p = 0.46$, $P < 0.10$), RFI phenotype ($r_p = 0.60$; $P < 0.05$) and RFI category ($r_p = 0.62$; $P < 0.05$) where dam RFI, RFI phenotype and RFI category measured as a mature cow showed no statistical correlations with steer progeny feed efficiency or feed efficiency groups. Initial and final scans of USLMA were not different between steers produced from either RFI- or RFI+ heifers, however, RFI- heifers tended to produce steers with greater developments in USLMA than steers from RFI+ heifers (19.61 ± 4.36 vs. 9.88 ± 2.28 ; $P < 0.10$). Final USLMA and gain in USLMA were larger for steers from low RFI heifers than steers from either average or high RFI heifers (91.34 ± 7.24 vs. 73.10 ± 2.41 vs. 70.00 ± 3.62 ; $P < 0.10$ and 29.82 ± 7.09 vs. 11.20 ± 2.36 vs. 9.24 ± 3.54 ; $P < 0.10$, respectively). No statistical differences in the amount of BF or development of BF occurred between steers produced from RFI- or RFI+ dams as well as among low, average or high RFI dams. In summary, phenotyping animals as feed efficient or inefficient postweaning is an accurate assessment of feed efficiency further into maturity. Divergently mating RFI- sires to RFI- dams or the inclusion of an RFI-

sire mated to RFI+ dams will improve progeny feed efficiency through later generation of production in comparison to RFI+ sires and dams. Postweaning measurement of dam RFI is a more accurate prediction of progeny feed efficiency measured postweaning than measurement of RFI in the mature cow. Higher feed efficiency dams tend to produce progeny with larger scans and developments of the longissimus muscle area, yet the conclusion of steers from higher feed efficient dams are leaner in body composition could not be made.

CHAPTER 1

REVIEW OF LITERATURE

INTRODUCTION

In recent years increased input costs have forced livestock producers to search for new methods to minimizing production costs while maintaining profitable levels of production. It is well established that feed cost is the largest contributor towards livestock producer's annual input cost (Arthur and Herd, 2008; Arthur et al., 2005; Herd and Bishop, 2000; USDA, 2009). United States Department of Agriculture Economic Research Service (USDA ERS;2009) reported between the years of 2005 to 2008 annual feed costs increased by 67% mainly due to the utilization of feed stuffs (i.e. corn and soybeans) for alternative fuel resources (i.e. ethanol). An estimated 90% (USDA, 2010c) of the total feed cost in livestock production is accounted for by corn. Corn, being a high energy dense feed ingredient commonly utilized during the growing and finishing phases of beef production is main factor in the profitability of feedlot cattle (Langemeier et al., 1992). Roughly 58 to 67% of the variation in the cost of gain can be accounted for by corn prices (Albright et al., 1993). Increased corn prices brought upon mainly by alternative fuel production and foreign demand has placed large economical strains on cattle producers. Yet without the increase in corn prices, feed costs would still remain the largest input cost in cattle production.

Although cow-calf producers utilize small percentages of corn in their feed stuffs compared to feedlots, USDA (2010b) reported in 2008 and 2009 feed costs comprised 69

and 70% of the annual operating costs of maintaining a bred U.S. beef cow. Using Standardized Performance Analysis (SPA) guidelines based from the Iowa State University Beef Cow Business Records, Lawrence and Strohben (1999) broke down annual cow feed costs into 45% pasture, 27% harvested forage, 16% purchased feeds, and 11% non-forage raised feeds (grains). With varying feedstuffs affecting feed costs, it is simple to decrease or remove the most expensive feedstuff and supplement in cheaper feed sources. However, implementing cheaper feedstuffs may only work to decrease feed cost rather than meeting maintenance requirements of the animal. Maintenance requirements of the animal are influenced by body weight, breed or genotype, sex, age, time of year, temperature, maturity level, and nutritional plane (NRC, 2000). Since metabolizable energy (**ME**) varies among different diets and intake levels, maintenance requirements and level of growth will be affected by differing diet compositions (Ferrell, 1988). Therefore, supplementation of cheaper feed sources at various times to reduce input costs may be challenging without compromising the nutritional value of the feed ration.

Dry matter intake (**DMI**) of the animal is affected by many different variables. Many factors which affect maintenance requirements (i.e. breed, sex, environment, production level) also affect DMI. Variables include: gastro intestinal capacity or “gut fill”, diet composition, and eating patterns (NRC, 1987). Koch et al. (1963) noted 38% of the variation in gain was subject of genetic differences in feed efficiency, while 25% of the variation in gain was influenced by differences in feed consumption. Independent selection of feed intake (**FI**) to increase feed efficiency in cattle; however, may only lead to negative effects on growth and production in all maturities of cattle. Selection for

reduced feed intake may only reduce appetite (Ollivier et al., 1990) without providing enough energy for maintenance and growth.

Variation in feed consumption is present in all species of animals. Increased feed consumption was observed in lines of mice selected for high growth rate in comparison to a control population (Salmon et al., 1990; Timon et al., 1970). Studies by Nielsen et al. (1997a) reported increased feed consumption was observed in mice divergently selected for high losses of heat in comparison to a control population and mice divergently selected for low heat loss (Kgwatalala and Nielsen, 2004). Laying hens differing in maintenance requirements exhibited differences in residual feed consumption (Luiting, 1991) while Mrode and Kennedy (1993) found pigs with higher growth rates to have increased feed intakes. Veerkamp et al. (1995b) found differences in residual feed intake (**RFI**) between two separate selection lines of dairy cows where one line had been divergently selected for high levels of protein and fat yield. These studies support the conclusions of differences in feed consumption for various levels of production and maintenance body weight occur across multiple species of animals. They further indicate improvements in feed efficiency are obtainable through divergent selection of a phenotypic measurement of RFI.

Various physiological mechanisms impact the variation within RFI. Factors include: feed intake, digestibility of the feed stuff, anabolic and catabolic accretion of protein and lipid tissue, physical activity, behavioral patterns in feed intake, and heat production (Herd et al., 2004b; Richardson and Herd, 2004). By accounting for these variations feed efficiency can be sustained through selection against RFI. Therefore this

review will pertain to the potential improvement in feed efficiency through divergent selection upon RFI.

Measures of feed efficiency

Common traits used to measure feed efficiency in cattle include partial efficiency of growth (**PEG**) (Archer et al., 1999; Nkrumah et al., 2004), residual body weight gain (**RG**) (Crowley et al., 2010), gross efficiency (i.e. FCR and F:G), and residual feed intake (**RFI**) (Archer et al., 1999; Veerkamp and Emmans., 1995a). Although each of these measurements account for feed intake, maintenance requirements, and production, the method in which they do so varies.

Partial efficiency of growth (PEG) equates to the ratio of average daily gain over the difference between actual feed intake and expected feed intake for maintenance (Archer et al., 1999; Carstens and Tedeschi, 2006). To accurately derive expected intakes for maintenance requirements, values must be obtained from standardized tables (Archer et al., 1999) which are determined from a population estimate of beef cattle maintenance energy requirements (Carstens and Tedeschi, 2006). Accurately recording maintenance requirements in a productive (i.e. growth or lactation) animal is challenging due to the fact that standardized maintenance requirements must be established at a constant body weight or level of production (Archer et al., 1999; Veerkamp and Emmans., 1995a). Hence, PEG or other traits which include maintenance efficiency do not phenotypically or genetically account for individual variation or accurately describe the metabolic efficiency in a growing animal (Archer et al., 1999; Carstens and Tedeschi, 2006; Veerkamp and Emmans., 1995a).

Gross efficiency also referred to as gain to feed (**G:F**) is more commonly referred to as feed conversion ratio (**FCR**) or feed to gain (**F:G**) which measures efficiency from a ratio of inputs (i.e. feed intake) to outputs (i.e. growth) (Arthur et al., 2001b). Feed conversion ratio has been the primary index of measuring growth and feed efficiency in cattle in previous years. Although FCR is a reliable indicator of efficiency for certain areas of production (Carstens and Tedeschi, 2006), selection upon these genetic accuracies can be misleading. Arthur et al. (2001d) reported highly negative phenotypic (-0.74) and genetic (-0.62 ± 0.06) correlations between FCR and average daily gain (**ADG**). Similar Pearson's correlations (-0.72 and -0.63) were derived between FCR and ADG by Lancaster et al. (2009b) and Nkrumah et al. (2004). These correlations indicated selection upon decreased FCR will lead to both a reduction in feed intake but also an increased growth rate which may lead to increased mature size of the animal. Salmon et al. (1990) reported selection upon growth dependent traits are accurate representations of mature size, indicating that selection upon decreased FCR may increase mature size of the cow herd which may lead to an increased feed cost in the mature cow herd (Archer et al., 1999) thus not decreasing the input cost of the mature cow herd.

Residual Feed Intake. In recent years RFI has gained more popularity within the research and production communities with the assistance of technological advancements in feed intake data collection. Residual feed intake, also known as Net Feed Intake (**NFI**), was first discussed by Koch et al. (1963) where he concluded feed efficiency could be determined by adjusting either feed intake for differences in growth, or growth for differences in feed intake both in reference to a measure of body weight (**BW**). Actual

feed intake consists of the average individual intakes recorded over a minimum required 70 d feed intake and growth measurement trial (Archer et al., 1997). By linear regression of intake upon metabolic body weight (average of the beginning, mid, and final body weights raised to the 0.75 power (**MMWT**)) and average daily gain (**ADG**), regression coefficients are derived in which expected feed intake is calculated (Arthur et al., 2001d; Basarab et al., 2003).

Residual feed intake represents the difference between an animal's actual intake and its expected intake independent of maintenance BW and growth (Arthur et al., 2001d; Basarab et al., 2003). The residual portion determined from the difference between actual and expected feed intake identifies efficient cattle from inefficient cattle (Archer et al., 1999; Koch et al., 1963). Negative or lower residual portions (RFI-) identify efficient animals while positive or higher residuals (RFI+) identify inefficient animals. Variation in RFI explains the differences among animals in how they utilize energy for maintenance and production (Kennedy et al., 1993; Veerkamp et al., 1995b).

Test duration of RFI

Measurement of RFI in centralized test facilities is costly (Herd et al., 2003a) to measure and hinders the growth of individual cattle being tested for RFI (Arthur et al., 2004a). Determining appropriate test durations should be kept at a minimum without compromising the accuracy of the measurement of feed intake and growth rate.

Historical test periods for accurate measurements of growth rate (ADG) in beef cattle were 112 days (Brown et al., 1991; Kemp, 1990). More recent reviews by Archer et al. (1997; 2000) and Wang et al. (2006) suggest test durations can be reduced from 112 d without compromising the accuracy of the records. Over a 119 d test duration it was

concluded individual FI could be obtained within 35 d while RFI, ADG, and FCR required a minimum 70 d test duration with BW measured every 14 d (Archer et al., 1997). With BW taken every 14 d Archer et al. (1997) concluded heritability and genetic correlations of FI, RFI, and ADG were the highest when tested over 70 d. Wang et al. (2006) conducted a 91 d trial which resulted in similar test durations for FI while test durations for FCR (42 d) and RFI (63 d) were slightly smaller than Archers possibly due to Wang's results were based off of BW taken weekly and feed intake was captured by the GrowSafe[®] feed intake system (GrowSafe Systems Ltd., Airdrie, Alberta, Canada). Although both Archer and Wang's trials consisted of either two week or weekly BW measurements respectively, Stock et al. (1983) reported BW taken on two day intervals at the beginning and end of trials resulted in sufficient measurements of ADG and G:F for steers.

More current methods of obtaining accurate measures of RFI involve a minimum 70 d feed intake and growth study where feed intake is measured by the GrowSafe[®] feed intake system with body weight measured every 14 d (Lancaster et al., 2009b) or two day consecutive BW at the beginning and end as well as single BW taken every 28 d (Basarab et al., 2007; Golden et al., 2008) to 21 d (Kolath et al., 2006). Meyer et al. (2008) and Basarab et al. (2003) both measured RFI over a minimum 70 d trial but used two day consecutive weights at the beginning and end of trial with a single mid-body weight around day 35. Additional studies utilize the Calan Gate Broadbent feeding system (American Calan, Northwood, New Hampshire) and measure BW every 14 d (Crowley et al., 2010; Lancaster et al., 2009a) while Kelly et al. (2010a; 2010b) captured feed intake utilizing the Insentec monitoring systems (Insentec, Marknesse, the

Netherlands) and captured body weights on 14 d intervals with two day consecutive BW measurements at the beginning and end of trial.

Phenotypic and genetic correlations of RFI

Unlike other measures of feed efficiency, when RFI is computed by linear regression it is phenotypically independent of its component traits, (Arthur et al., 2001b; 2001d; Herd and Bishop, 2000) thus making it a more desirable trait for selection of feed efficiency. Studies utilizing feeding standards formula to compute expected feed intake to derive RFI do not result in RFI values phenotypically independent of component traits. Fan et al. (1995) determined NFG and ADG were phenotypically correlated (-0.74) in Angus cattle while NFG and ADG were genetically correlated (-0.57 and -0.62) for both Hereford and Angus cattle respectively when RFI was calculated from the 1984 NRC. Arthur et al. (2001b) found RFI to be phenotypically correlated (-0.38 and -0.35) with ADG and BW when RFI was computed by the feeding standards formula. In the same study moderate genetic correlations (0.32 ± 0.10) were found between yearling BW and RFI when RFI was derived from regression while RFI and ADG were genetically correlated (-0.54 ± 0.09) when RFI was derived from feeding standards formulas.

Kennedy et al. (1993) stated RFI derived from regression is not genetically independent from its component traits. Jensen et al. (1992) reported genetic regressions of 0.32 ± 0.29 and -0.24 ± 0.25 between RFI and ADG. Herd and Bishop (2000) obtained genetic regressions of 0.34 ± 0.34 and 0.15 ± 0.28 between RFI and 200 and 400 d live weights respectively. To obtain full genetic independence between RFI and its component traits, RFI should be derived from genetic regression where genetic variances and co-variances are incorporated into the model to obtain full genetic improvement in

feed efficiency through selection against RFI (Arthur et al., 2001b). Selection against phenotypic RFI values can be made as phenotypic RFI and genetic RFI are highly correlated traits (Hoque et al., 2006). Archer et al. (1998) found there to be very little difference between estimates of RFI for mice when calculated phenotypically and genetically between post-weaning and mature time periods. Correlations between phenotypic and genetic measurements of RFI for postweaning measurements was 0.98 while during mature measurements the correlation was 0.96 (Archer et al., 1998). In several studies RFI has been found to be both phenotypically and genetically correlated with FCR. Herd et al. (2003a) obtained phenotypic and genetic correlations of 0.61 ± 0.03 and 0.70 ± 0.22 between RFI and FCR. Similar results were reported as 0.53 and 0.66 ± 0.05 , 0.60 and 0.78 ± 0.06 , and 0.41 and $0.48 \pm .10$ for phenotypic and genotypic correlations, respectively (Arthur et al., 2001d; Crowley et al., 2010; Hoque et al., 2009).

Although RFI and FCR are highly to moderately correlated, Arthur et al. (2001d) found low phenotypic (-0.06 and 0.02) and genetic (-0.04 ± 0.08 and -0.06 ± 0.06) correlations between RFI and ADG and MBWT. However, FCR remains highly and negatively correlated with ADG (Arthur et al., 2001d; Hoque et al., 2009) and positively to negatively correlated with MBWT (Crowley et al., 2010). Nkrumah et al. (2004) determined through Pearson's partial correlation that RFI and PEG were highly correlated (-0.89) yet PEG fails to accurately account for individual variation in maintenance cost. Kelly et al. (2010b) found no correlations with RFI between the Kleiber ratio (**KR**) and relative growth rate (**RGR**) with RFI because neither KR or RGR require feed intake in their models. Independence of RFI from its component traits allows RFI to segment total FI into functions in which it is used by the animal (Veerkamp and Emmans., 1995a) as

well as compare animals in various stages of production (Meyer, 2007). Selection against RFI to reduce feed intake should not alter growth rate or body weight of the animal, suggesting it is an affective measurement of feed efficiency in cattle (Herd and Bishop, 2000).

Range in RFI

By definition within a contemporary group the mean RFI value derived from linear regression should result in a value of 0.0. Variation above and below the mean of the group is dependent of individual contemporary groups. Twenty-four Angus x Hereford cross steers obtained a range in RFI of -0.37 to 0.38 kg/d (Castro Bulle et al., 2007), 121 contemporary groups of Japanese Black cattle had a range of -1.98 kg/d for the most efficient bull to 2.05 kg/d for the least efficient bull (Hoque et al., 2009). Residual feed intake differed between high, medium, and low RFI phenotyped steers (1.0 vs. -0.01 vs. -0.96 kg/d) (0.91 vs. -0.14 vs. -0.95 kg/d) in two separate trials by Nkrumah et al. (2007; 2004), respectively. Crews et al. (2003) reported ranges in RFI values varied on the same steers when RFI was computed during a growth and finishing phase. During the growing phase RFI ranged from -4.10 to 4.65 kg/d and from -4.77 to 3.30 kg/d during the finishing phase for the most and least efficient steers respectively. Within a contemporary group as illustrated by these studies the most efficient animal should consume close to or an equivalent amount less feed than what the least efficient calf over consumes.

Durunna et al. (2010) conducted a study in which RFI was conducted on steers during both the growing and finishing phases. Results concluded no statistical differences in the proportion of steers that maintained their efficiency groups to steers

which changed contemporary groups. Out of 490 steers phenotyped for RFI over a three year trial 17, 5, and 0 steers moved from low to high RFI efficiency groups while 12, 3, and 6 steers moved from high to low RFI efficiency groups. Durunna et al. (2010) further concluded different energy density diets alter the percentages of calves which move efficiency groups from the growing to finishing phase. Steers transitioned rations from the growing to finishing phase changed their RFI value by 31, 58, and 79% by 1.0, 0.5, and 0.25 standard deviations from the mean. In comparison, steers which remained on a constant ration over the duration of the trial changed RFI values by 30, 51, and 77% (finisher diet) and 23, 51, and 77% (grower diet) by 1.0, 0.5, and 0.25 standard deviations respectively. Thirty-seven *Bos indicus* cow's phenotyped post weaning and then again as mature cows (3 to 7 years of age) showed a 0.51 correlation between post weaning and mature RFI. Out of the 37 *Bos indicus* cows 62.2% maintained their same RFI phenotype while 37.8% of cows moved from efficient to inefficient or inefficient to efficient (Morgan et al., 2010).

Comparing RFI values on individual animals over different biological time periods as well as on different planes of nutrition may cause re-ranking within cattle. Basarab et al. (2007) noted variation in RFI occurred in four separate contemporaries from the same cow herd varied considerably from trial to trial between both phenotypic and adjusted RFI values. Residual feed intake derived on two separate cohorts of heifers varying in biological maturities during testing resulted in poor correlations with sire EBV for RFI (Bormann et al., 2010). In order to consider the same trait measured over different time periods to be genetically correlated genetic correlation of ≥ 0.90 is required (Crews et al., 2003). Although RFI values may not be genetically correlated,

biologic similarities can be made from moderate to high genetic correlations between RFI values computed over different time periods for the same animal (Crews et al., 2003). Comparison of RFI values of calves from different contemporaries where no previous selection for RFI has been conducted, computing RFI individually for each cohort through regression of DMI against ADG and MBWT results with an inclusion of season as a fixed affect in a further genetic analysis will result in the most accurate derivation of RFI (Mujibi et al., 2010).

RFI, intake, and performance

It is well cited in several studies throughout Australia, Canada, and now the United States that negative RFI cattle have decreased FI with equivalent levels of performance to positive RFI cattle. Although RFI is phenotypically independent from ADG and MBWT, RFI remains highly correlated with FI indicating selection against RFI for reduced feed intake will result in improved feed efficiencies. Arthur et al. (2001d) derived phenotypic and genetic correlations of 0.72 and 0.69 ± 0.06 between FI and RFI on Angus cattle. Lancaster et al. (2009a) reported similar correlations on 468 head of Brangus heifers where RFI_p (phenotypic RFI) and FI had a phenotypic and genetic correlation of 0.70 and 0.85 ± 0.08 while RFI_c (RFI adjusted for carcass traits) and FI had a phenotypic and genetic correlation of 0.67 and 0.86 ± 0.09 . Again with FI and RFI being highly correlated, the potential to select cattle with reduced feed intake without compromising growth can be accomplished through selection of lower RFI cattle.

Basarab et al. (2003) reported intake differences of 8.93, 8.55, and 8.00 kg/d between high, medium, and low RFI steers. When RFI was adjusted for increases in backfat and marbling low RFI steers consumed on average 6.4% less feed than medium

RFI steers and 10.4% less feed than high (Basarab et al., 2003). After dividing heifers equally in high and low RFI groups Kelly et al. (2010b) reported a 2.87 kg/d difference between the most efficient (RFI-) and least efficient (RFI+) heifers. Additional studies by Kelly et al. (2010a) reported an 8.5 and 15.9% reduction in feed consumption for low RFI heifers in comparison to medium and high RFI heifers respectively. Angus steers selected from high efficiency (RFI-) and low efficiency (RFI+) lines of cattle from NSW Agriculture Research Centre in Trangie, Australia, were placed on pasture where feed intakes were derived by method of the alkane technique. Results proved only numerical differences in feed intake between high and low efficiency lines of steers occurred where high efficiency line steers consumed (3.04 ± 0.11 kg/d vs. 3.23 ± 0.14 kg/d) less forage than low efficiency line steers, respectively (Herd et al., 2002). Meyer et al. (2008) indicated similar numerical differences in forage intake from mature Hereford cows of known RFI's on two separate grazing studies. On average RFI- cows consumed 21 and 11% less DMI of forage in experiments one and two than did RFI+ cows (Meyer et al., 2008). Studies by Golden et al. (2008), Kolath et al. (2006), Basarab et al. (2003) and Nkrumah et al. (2004) reported larger differences in intake between RFI- and RFI+ cattle.

Golden et al. (2008) found significant differences ($P < 0.001$) in feed intake between RFI- and RFI+ steers when fed a traditional feed lot ration as well as when fed a no-roughage based ration. Negative RFI steers consumed less feed on both rations with no significant differences ($P < 0.13$) in body weight or body weight gain in both trials. Positive RFI steers consumed 1.54 kg/d more feed than RFI- steers in Kolaths et al. (2006) trial. Nkrumah et al. (2004) found feed intakes to be different ($P < 0.001$) between high, medium, and low (11.05 ± 0.23 vs. 10.01 ± 0.20 vs. 9.59 ± 0.20 kg/d) RFI

steers. When RFI was calculated and adjusted for composition of gain a difference of 3.77 kg/d was found between the lowest and highest RFI steers in which follows the same trend as when RFI was adjusted for gain in back fat and marbling score, RFI- steers consumed 6.4% less feed than RFI+ steers (Basarab et al., 2003).

Residual feed intake appears to have no direct negative or positive effects on the reproductive performance of the mature cow as indicated over five years of divergent selection for RFI (Arthur et al., 2005). Cows' phenotyped post weaning for RFI and again at four years of age determined cow RFI was not correlated with body weight at four years of age (Arthur et al., 2004b). Residual feed intake computed on mature cows (3.5 to 10.7 years of age) indicated dams of low RFI heifer and steer progeny were also phenotyped as low RFI cows consuming 1.31 kg/d less feed ($P < 0.05$) than high RFI dams which also produced high RFI progeny (Basarab et al., 2007). The same study determined only small numerical differences occurred between high, medium, and low RFI dams for pregnancy, calving and weaning rate while dams of low RFI progeny tended to calve 5 to 6 days further in to the calving season.

RFI and carcass parameters

To account for additional variation in RFI unaccounted for by FI, ADG and BW, researchers have reviewed the relationship between RFI and carcass parameters.

Determination of RFI's effect on carcass parameters is also crucial to the profitability at harvest. Phenotypic (0.06, 0.11, 0.14) and Genetic (0.09 ± 0.09 , 0.06 ± 0.06 , 0.17 ± 0.05) correlations of RFI with carcass measurements of loin muscle area (**LMA**), back fat (**BF**), and rump fat were weak among young Angus bulls respectively (Arthur et al., 2001d). Studies by Hoque et al. (2006; 2009) reveal strong to moderate negative genetic

correlations between steer progeny carcass traits of hot carcass weight (**HCWT**), ribeye area (**REA**), rib thickness (**RT**), marbling score (**MARB**) and meat quality grade (**QG**) with phenotypic and genetic sire RFI's. Hoque's results inquire utilization of low RFI sires may result in progeny with undesirable hot carcass weights that have a greater ability to develop intra-muscular fat and large ribeyes. Richardson et al. (2001) found numerical variation in REA between high and low RFI steers, where low RFI steers had larger ribeyes.

Correlations between subcutaneous fat and RFI varied from weak to moderate between Hoques et al. (2006; 2009) trials, indicating small subcutaneous fat deposition would have small effects on RFI or vice versa. Jensen et al. (1992) found adjusting RFI for carcass composition accounted for little variation in total feed consumption. Herd and Bishop (2000) determined an additional 1.5% of the variation in FI is accounted for by incorporating lean content into the statistical model of feed efficiency. Differences in fat deposition between high and low RFI cattle when fat contents (i.e. intra/inter muscular fat) were combined with one another (Richardson et al., 2001). In the same study RFI-steers were found to deposit more protein growth in the LMA over the duration of the test. Unlike Richardson's results, Kelly (2010b) obtained poor agreement between RFI and carcass ultrasound measurements of BF and intra-muscular fat (**IMF**) indicating no differences in carcass composition and RFI occurred. Basarab et al. (2003) found gain in empty body fat to be positively correlated with RFI with no difference in gain in empty body protein between RFI+ and RFI- steers suggesting that lower RFI valued cattle are leaner in body composition than higher valued RFI cattle. Literature remains controversial over the relationship between RFI and fat content within cattle, however,

both high and low RFI steers appear to meet market specifications resulting in no additional profit gain or loss after divergent selection for NFE (Richardson et al., 1998; 2001).

Genetic improvement through RFI

Genetic improvement through selection on feed efficiency is sustainable with RFI being a moderate heritable trait. Arthur et al. (2001b) conducted a study utilizing data on Charolais bull calves ($n = 624$) from sires ($n = 60$) whom had previously been phenotyped for RFI utilizing the feeding standards formula. Heritability derived from feeding standards formula for RFI were 0.43 ± 0.04 for 15 months of age and 0.43 ± 0.06 for 19 months of age. Heritability's calculated from linear regression for RFI were 0.39 ± 0.04 for 15 months of age and 0.43 ± 0.06 for 19 months of age (Arthur et al., 2001b). Arthur et al. (2001d) obtained similar results on Angus cattle with a heritability of 0.39 ± 0.03 for RFI. Kennedy et al. (1993) reported large variations in heritability between phenotypic (0.03 to 0.84) and genetic (0.020 to 0.782) regressions of RFI. Given this broad range in heritability obtained by Kennedy, a larger proportion of literature shows similar heritability's to Arthur's estimates.

Korver et al. (1991) reported a heritability of 0.22 in dairy heifers, Veerkamp et al. (1995b) found a range of 0.30 to 0.38 in dairy cows, while Hoque et al. (2009) found a heritability of 0.49 ± 0.09 in Japanese black cattle. Crews et al. (2003) reported heritability of net feed efficiency during the growing phase of steers to be 0.30 ± 0.06 along with a heritability of 0.26 ± 0.07 during the finishing phase. Lancaster et al. (2009a) and others determined heritability's between phenotypic RFI (0.47 ± 0.13) and RFI adjusted for carcass traits (0.42 ± 0.13) were similar and therefore adjusting RFI for

carcass traits would not increase or decrease the heritability of DMI or feed efficiency of cattle . Archer et al. (1997) determined a 70 day test duration for intake and growth collection maximized heritability and minimized variation with a heritability of 0.42 ± 0.13 . With RFI being a moderately heritable trait consistent improvement in progeny RFI from generation to generation can be expected.

Angus and Hereford steer progeny fed on pasture from sires of a know estimated breeding value (**EBV**) for NFI indicated, every 1 kg/d decrease in the sires EBV for NFI resulted in a 19% improvement in growth rate, a 26% decrease in NFI, and a 41% improvement in FCR (Herd et al., 2004a). Single generation of selection for low and high RFI sires and dams resulted in low RFI parents producing progeny whom grew equivalent to in addition to being significantly ($P < 0.05$) lower in RFI and feed consumption (< 5%) with greater percentages of lean tissue than progeny from high RFI parents (Richardson et al., 2001). Trends in improved feed efficiency were noted in pasture fed low RFI line steers in comparison to high RFI line steers after one year of divergent selection against RFI (Herd et al., 2002). Divergent matings of the top 50% of high NFE dams to the top 5% of high NFE sires produced progeny whom consumed less feed intake and produced similar gains to progeny from lowest 50% of NFE dams and the bottom 5% of low NFE sires (Richardson et al., 1998). By combining the RFI- sires and dams whom are above or equal to the average of their contemporaries for production, improvements in progeny feed efficiency will be accomplished without negatively affecting growth rate of the animal.

Further progression of RFI as a selection tool within the cattle industry will require a genetic data base from which indexes or expected progeny difference (**EPD**)

can be derived. Australians have incorporated BREEDPLAN (Archer et al., 1999) as a central data base from which they have produced an EBV for RFI on individual sires for cattle producers to use. To the authors knowledge there are no known commercial wide indexes or EPD's available for RFI in beef cattle within the United States.

Potential profits of RFI

To the author's knowledge there has been limited work on the potential economic impact of incorporating RFI into cattle production. Exton et al. (2000) determined over a 25 year period of utilizing sires superior for NFE (high feed efficiency) that steers fed out and cows maintained within the cow herd from these sires earned annual savings in feed cost of \$35 and \$6.95 per animal respectively. These values further equate to \$52 million in feed cost savings on five million cows and \$10 million in feed cost savings on 500,000 steers. Profits from both grass and grain fed progeny were increased by 9 to 33% when a maximum of the top 10 to 20% of sires were selected for feed efficiency (Archer et al., 2004). Crews (2006) obtained an annual savings of \$26.25/hd (\$0.18/hd/d) in feed cost for lower valued RFI cattle during a 150 d finishing period when ration costs were \$0.05/d. Carstens and Tedeschi (2006) inquired slightly larger estimates in feed cost savings over a 120 d feed period where lower valued RFI cattle saved an additional \$38.00/hd compared to high RFI cattle. Exton et al. (2000) cautioned industry adoption may still remain slow at first as a result of limited cash flow with initial purchase of higher valued superior feed efficient bulls. It should be noted that additional profits are not from the single trait selection of RFI, but rather the implementation of RFI in addition to other selection criteria within the production system (Arthur and Herd, 2008). Determining a specific input cost savings is difficult to

accomplish due to the fact feed cost is determined from market prices with fluctuate periodically throughout a day's time, however it can be implied by the research cited that at each time lower RFI cattle inquired a lower feed cost at all times in comparison to medium and high RFI cattle.

Summary

Reducing input cost in time where input costs are steadily on the rise is crucial to the economic stability of the cattlemen's bottom line. Utilizing traits within the production system which promote feed efficiency without hindering the nutritional composition of the diet or negatively impacting performance or mature size of the animal are effective methods of maintaining production and profitability. The credibility of RFI has been well established throughout this review, providing an understanding that selection against RFI establishes a trait for improved feed efficiency which can be selected upon and hold true through future generations and maturities. By selecting against RFI for cattle who consume less feed and perform better than or equivalent to the average animal are the selections that need to be made to ensure profitability and production. The objective of the following studies is to review these hypotheses in the mature cow as well as through two generations of divergent selection against RFI.

CHAPTER 2

AGREEMENT BETWEEN POSTWEANING HEIFER AND MATURE COW RFI PHENOTYPES

ABSTRACT

Phenotyping cattle post-weaning for residual feed intake (**RFI**) has been established as an accurate method of identifying cattle which differ in the amount of feed required for maintenance and growth functions, limited research has been published on agreement between post-weaning and mature RFI phenotype. We hypothesized that RFI phenotypes determined post-weaning would be correlated with RFI phenotypes measured as mature cows, thus proving RFI is consistent as the animal matures. Two separate feed intake trials were conducted using a herd of Simmental x Angus (**Simm-Angus**) crossbred cattle. The initial feed intake trial phenotyped 89, 15 month old virgin Simm-Angus heifers for RFI while the second trial consisted of re-phenotyping the 20 lowest and the 20 highest RFI heifers as lactating, mature three and half year old cows. Feed intake was measured using the GrowSafe[®] feed intake system (GrowSafe Systems Ltd., Airdrie, AB, Canada) for both trials over a minimum 70 d time period. At the conclusion of each trial RFI was calculated by subtracting actual intake from expected intake, where expected feed intake was determined by the regression of intake upon ADG and average body weight^{0.75} (Basarab et al., 2003). Initial body weight (**IBW**), final body weight (**FBW**) and calf weaning weight (**CWW**) were included in the model for mature cow RFI

to account for additional variation in feed intake. Independent variables RFI phenotype and RFI category were defined by heifers and cows being categorized by RFI phenotype (RFI- or RFI+) as well as by high, average, or low RFI determined as 0.50 SD from the mean of the group. Efficient animals were noted as RFI-, while inefficient animals were noted as RFI+. No correlations ($P > 0.10$) were observed for ADG or body weight between postweaning RFI (**RFI_{hfr}**) and mature RFI (**RFI_{cow}**) or between RFI_{hfr} and RFI_{cow} category group (high, average, or low RFI). Residual feed intake phenotypes between RFI_{hfr} and RFI_{cow} were moderately correlated ($r = 0.53$; $P < 0.001$). Although RFI values were not phenotypically correlated between the two trial periods, moderate correlations between RFI phenotypes suggest no significant changes from efficient to inefficient or inefficient to efficient occur as an animal matures. Further research is necessary to confirm this conclusion as well as to study the reranking in RFI among animals within a contemporary group throughout different stages of maturity.

INTRODUCTION

Adequate provisions of feed to the cow herd represent a large portion of the annual input costs into a livestock operation. Feed cost roughly accounts for 60 to 75% of the annual non-fixed input cost to maintain a beef cow (Lemenager et al., 2008). Over the last decade a renewed interest in developing ways to decrease feed costs within beef production has arose with the continuing trend of increased prices for feedstuffs. Within the last five years implementing ways to reduce input costs have become more crucial to the profitability of beef production. From 2005 to 2009 the total gross value per bred beef cow decreased by 32% (USDA, 2010a) as feed prices continued to increase (USDA,

2010d). With lower returns on production and elevated production costs cattle producers are faced with challenging economic times. Therefore, implementing methods to reduce input costs has great potential to sustain profitability in beef production.

Several reviews have discussed potential improvements in feed efficiency through genetic selection for RFI (Arthur et al., 2001b; Herd and Bishop, 2000; Richardson and Herd, 2004). By definition, RFI is phenotypically independent of average daily gain (**ADG**) and metabolic body weight (MMWT; Crews et al. 2006) making it a more preferable trait to select upon over the more common trait, feed conversion ratio (**FCR**), also referred to as feed to gain (**F:G**). Since RFI is phenotypically independent of its component traits, selection upon RFI will not influence or skew production or body weight of the mature animal. Incorporating RFI as a selection trait in the production system can improve feed efficiency through future generations of progeny as RFI is a moderately heritable trait (Hoque et al., 2009; Lancaster et al., 2009a).

To date, a large percentage of the data on RFI has been calculated from feed intakes, production outputs and body weight measurements recorded during the postweaning phase prior to the plateau of the growth curve. Few studies have measured RFI further into maturity. Meyer et al. (2008) measured forage utilization by lactating Hereford cows which had previously been phenotyped postweaning for RFI. Their results found low RFI cows to have 11% decreased dry matter intake along with comparable body weight gains and body condition scores of RFI+ cows. Although RFI- cows continued to maintain themselves with less feed there was no indication on how well mature cow RFI agreed with postweaning heifer RFI. We hypothesized mature cow RFI and heifer RFI would be correlated. The objective of this study was to phenotype

heifers for RFI shortly after weaning and then rephenotype the same group of heifers as mature cows to determine agreement in RFI measured at different stages of maturity.

MATERIALS AND METHODS

Experimental Design

Eighty-nine Simmental by Angus crossbred heifers were purchased by the University of Missouri to develop a commercial based herd to study physiological and production effects of divergent selection for metabolic efficiency in beef cattle. These heifers were utilized on two separate feed intake and growth studies over a three year period beginning in the summer of 2007. Trial one was conducted from June 16 to August 28, 2007 at the University of Missouri Beef Research and Teaching Farm (BRTF; Columbia, MO). The 89 heifers (average initial body weight = 373.58 ± 4.20 kg; average initial age = 15.08 ± 0.07 months) were placed on a 70 d feed intake and growth trial to determine heifer RFI. After a 14 d receiving period heifers were allowed *ad libitum* access to a 100% concentrated based diet (Table 2.1) for the duration of the 70 d trial. Heifers were randomly allocated to 18 pens (4 to 5/pen 5.0 x 9.1 m) each equipped with a single GrowSafe[®] bunk (model 4000E). Intakes were collected daily using the GrowSafe[®] feed intake system. Once heifers were phenotyped for RFI they were transported to the University of Missouri's Southwest Research Facility (SWC; Mount Vernon, MO) where they were divided into three groups. The top 20 RFI- and the top 20 RFI+ cows were utilized on a forage grazing study where they were grouped by RFI phenotype and blocked by pasture. The remaining 49 cows were comingled with SWC's foundation commercial herd.

In January, 2010 trial two was conducted following the 2009 fall calving season. The 40 (top 20 RFI- and top 20 RFI+) cows used on the forage grazing trial were rephenotyped for RFI as mature lactating cows (average initial body weight = 618.86 ± 8.80 kg; average initial age = 3.84 ± 0.01 years). Cows with calves (average initial calf body weight = 176.11 ± 4.14 kg; average initial age = 4.14 ± 0.09 months) at side were randomly assigned to eight pens (4 to 5/pen 7.3 x 26 m) each containing one GrowSafe[®] feed bunk. Cows were acclimated to the test facility over a 14 d period from which they were transitioned to their study ration and were allowed *ad libitum* access to feed and water over a 71 d test duration. Diet composition is listed in Table 2.2. Prior to the concession of the study one calf and one cow died to causes unrelated to the trial resulting in the removal of two cows and two calves from the data set, leaving a total 38 cows and 38 calves to analyze. Residual feed intake and FCR were recalculated for heifer RFI using only the 38 cows in trial two to maintain the same contemporary group across both test durations.

Comparisons of progeny performance between heifer and cow RFI category groups were made to determine if RFI measured postweaning or RFI measured later in maturity was a better representation of progeny performance measured postweaning. Only 29 of the 40 rephenotyped cows were used for progeny comparisons as a result of only 29 cows produced calves from RFI phenotyped sires during the 2008 calving season. To maintain similarity between RFI measured postweaning and RFI measured later in maturity only the heifer RFI's of the 29 cows were used. Comparisons between heifer RFI and progeny performance and feed efficiency were measured using the original

heifers' RFI's. This was done as RFI's calculated from the contemporary group of 89 heifers were the RFI's in which matings were based from.

Animal Performance Measurements

For both trials body weights were recorded with two day consecutive body weight (**BW**) measurements at the beginning and end of trial along with a single BW recorded at the mid-point of each trial. Body weights were recorded early in the morning prior to delivery of feed to the GrowSafe[®] bunk; however, either feed or water was removed from pens prior to or on weigh days. Feed intakes were recorded daily by the GrowSafe[®] feed intake system with RFI calculated at the end of the trial for each individual heifer.

Average daily gain (**ADG**) was the difference between the final body weight and initial body weight divided by the total number days on trial. Residual feed intake was determined as the difference between actual intake and expected intake (Archer et al., 1997; Arthur and Herd, 2008; Herd and Bishop, 2000) where expected feed intake for postweaning RFI was calculated using the model:

$$Y_i = \beta_0 + \beta_1 \text{ADG}_i + \beta_2 \text{MMWT}_i,$$

where Y_i = average actual daily feed intake (**ADFI**) for animal i , β_0 = regression intercept, β_1 = partial regression coefficient of ADFI on ADG, β_2 = partial regression coefficient of ADFI on MMWT (average body weight^{0.75}). The model used to compute expected feed intake for trial two was:

$$Y_i = \beta_0 + \beta_1 \text{ADG}_i + \beta_2 \text{MMWT}_i + \beta_3 \text{IBW}_i + \beta_4 \text{FBW}_i + \beta_5 \text{CWW}_i,$$

where Y_i = average actual daily feed intake (**ADFI**) for animal i , β_0 = regression intercept, β_1 = partial regression coefficient of ADFI on ADG, β_2 = partial regression coefficient of ADFI on MMWT (average body weight^{0.75}), β_3 = partial regression

coefficient of ADFI on cow initial body weight (**IBW**), β_4 = partial regression coefficient on cow final body weight (**FBW**) and β_5 = partial regression coefficient of ADFI on calf weaning weight (**CWW**). Regressions were performed using PROC GLM in SAS (SAS version 9.2, SAS Inst. Inc., Cary, NC). Three heifer and three cow categories were made: 0.50 SD less than (low RFI = efficient) and greater than (high RFI = inefficient) the average RFI. Two heifer and cow RFI phenotype groups were assigned based on if animals were RFI- or RFI+. Trait abbreviations have been assigned subscripts of “hfr” and “cow” to distinguish between feed intake trials conducted when cattle were heifers and when cattle were mature, respectively.

Statistical Analysis

Individual animals were the experimental unit, where RFI category group and RFI phenotype group were the independent variables and RFI, DMI, FCR, ADG, IBW, and FBW for heifers, cows, and progeny were the dependant variables. Means of all dependent variables for each independent variable were analyzed using the GLM Procedure of SAS (SAS version 9.2, SAS Inst. Inc., Cary, NC). Correlations were analyzed through the Proc CORR command in SAS. Variables were considered different than zero at $P \leq 0.10$.

RESULTS

Correlations

Feed efficiency and performance traits. Dry matter intake (DMI) was moderately correlated with heifer RFI ($r_p = 0.64$; $P < 0.01$) while DMI showed a slightly stronger correlation with cow RFI ($r_p = 0.85$; $P < 0.01$). Weak correlations were obtained

between FCR and DMI for both heifers (Table 2.3) and cows (Table 2.4). Residual feed intake and FCR were correlated for heifers ($r_p = 0.55$) but not for cows ($r_p = 0.20$).

Strong, negative correlations between ADG and FCR were observed for both heifers and cows. Feed conversion ratio of heifers and cows tended to be moderately correlated with heifer and cow MMWT ($r_p = 0.26, P = 0.11$ vs. $r_p = -0.26 P = 0.12$; respectively).

Heifer and cow feed efficiency and performance. Pearson partial correlations between RFI_{hfr} and RFI_{cow} were weak and nonsignificant ($0.17; P > 0.10$). Residual feed intake measured as a heifer showed no relationship with DMI_{cow} or IBW_{cow} (Table 2.9). Low, average and high RFI category groups assigned as heifers and cows were not correlated ($r_p = 0.19; P > 0.10$). Residual feed intake measured as a mature cow was moderately correlated with heifer phenotype ($r_p = 0.35; P < 0.05$). Phenotype as heifers and as cows showed the most agreement among feed efficiency traits with a correlation of $0.54 (P < 0.001)$. Further correlated responses occurred amongst cow phenotype and RFI_{hfr} , RFI_{cow} and DMI_{hfr} , cow phenotype and DMI_{hfr} , IBW_{hfr} and DMI_{cow} and between DMI_{cow} and DMI_{hfr} (Table 2.9).

Feed efficiency, growth performance and feed intake as heifers and cows

Residual feed intakes ($R^2 = 0.51$) from the original 89 heifers ranged from -2.29 to 3.56 kg/d for a difference of 5.85 kg/d between the most and least feed efficient heifers. The range in RFI_{hfr} of the 38 heifers rephenotyped as cows ($R^2 = 0.60$) was -1.99 to 3.05 kg/d for a difference of 5.04 kg/d between the most and least efficient heifers. Cow RFI's ($R^2 = 0.29$) ranged from -6.91 kg/d to 8.21 kg/d for a difference of 15.12 kg/d between the most and least efficient cows. Performance data for heifer and cow category groups are summarized in Tables 2.5 and 2.7 while performance data for heifer and cow

RFI phenotype groups are summarized in Tables 2.6 and 2.8. Average RFI values for RFI- and RFI+ heifers and cows were -0.93 ± 0.18 vs. 0.75 ± 0.16 (Table 2.6) and -2.25 ± 0.41 vs. 2.38 ± 0.43 (Table 2.8), respectively. Initial and final body weights were not different ($P > 0.10$) at the onset or conclusion of each trial for both heifers and cows. Low RFI heifers and cows for both RFI category and phenotype groups consumed less feed with improved feed conversions in comparison to average or high RFI cattle. Average daily gain did not differ ($P > 0.10$) among high, average, and low RFI category groups or between RFI phenotype.

Comparison of RFI, category group, and phenotype as heifers and cows

Least square means for heifer and cow category groups and phenotype groups regressed upon one another are described in Tables 2.10 to 2.13. Mean statements for RFI_{cow} indicated low RFI heifers tended to have lower RFI's than high RFI's as mature cows (-1.10 ± 0.91 ; $P = 0.06$) and a numerically lower RFI than average RFI heifers as cows (Table 2.10). Average RFI heifers also maintained a numerically lower RFI than high RFI heifers as cows. Dry matter intake was lowest for low RFI heifers as mature cows with very little variation in DMI between average and high RFI heifers as cows. Average daily gain and FCR were virtually the same between low and average RFI heifers as cows while high RFI heifers had the smallest ADG and highest FCR as a mature cow. Average RFI heifers tended ($P < 0.10$) to be larger in body weight than high RFI cows at the onset and conclusion of the trial as mature cows.

Residual feed intakes of heifers averaged over low, average, and high RFI cows resulted in average RFI cows having the lowest numerical RFI's as heifers (Table 2.11). Low RFI cows maintained lower RFI's than high RFI cows as heifers in addition to

having the lowest DMI as heifers over both average and high RFI cows. High RFI cows were heavier than low RFI cows as heifers at the beginning and end of trial ($P < 0.05$). Numerical differences in FCR and ADG separated low, average, and high RFI heifers as mature cows.

Cow RFI and DMI were the only traits that differed between heifer RFI phenotypes (Table 2.12). As heifers, RFI- cows had lower DMI, RFI, and FCR than RFI+ cows (Table 2.13). As heifers and as cows on average there appeared to be slightly over a kilogram spread in DMI between both phenotypes; however as heifers, the difference in DMI appeared to be of greater difference than as cows ($P = 0.02$ vs. $P = 0.12$, respectively). Negative RFI cows also tended to have lower initial and final body weights than RFI+ cows as heifers. There was noticeable movement within RFI ranking among individual animals between post-weaning RFI and cow RFI measurement. Twenty-four percent of cows switched RFI phenotypes (RFI- or RFI+) between post-weaning and mature tests. Fifty-eight percent of cows moved among low, average, or high RFI category groups. Of the 58% of cows which altered their category group 18% moved within the extremes of a full standard deviation from their original category as a heifer. Cows either went from the top one-third of efficient heifers to the bottom one-third of inefficient cows, or from the bottom one-third of inefficient heifers to the top one-third of efficient cows. Eighty-two percent of cows changing category groups moved within a half standard deviation of their original phenotype, with a majority moving from efficient to average (39%). Equal amounts (22%) of cows moved from average heifers to efficient cows as inefficient heifers moved to average cows. With 58% movement in RFI category group between post-weaning and mature tests, 61% of those

heifers remained either average or better for feed efficiency as a mature cow.

Categorically ranked average RFI cows were the more feed efficient heifers post-weaning (RFI = -0.18).

Heifer and cow RFI prediction of progeny efficiency

Correlations were weak and nonsignificant between progeny traits and traits of dams as heifers and cows with the exception of a moderate correlation between progeny ADG and cow category group ($r_p = 0.38$; $P < 0.04$). Least square means statements for progeny performance for heifer and cow category, excluding progeny ADG, differed numerically. Progeny RFI's for low, average, and high RFI heifers (Table 2.14) and cows (Table 2.15) were -0.23 ± 0.38 , -0.14 ± 0.32 , -0.03 ± 0.34 and -0.15 ± 0.34 , -0.10 ± 0.34 , and -0.15 ± 0.36 , respectively. Similar to RFI only numerical differences in progeny ADG, FCR, MMWT and IBW occurred among the three heifer category groups. Progeny ADG for high RFI cows was larger ($P < 0.05$) than both the low and average RFI cow category groups. Dry matter intake, FCR, MMWT, and IBW were similar across low, average, and high RFI cows.

When dam groups were narrowed from low, average and high RFI categories to RFI phenotype larger amounts of variation between progeny traits were observed and differences were only numerical. Progeny produced from RFI- heifers consistently had lower RFI (-0.39 ± 0.26 vs. 0.15 ± 0.27 ; $P = 0.17$), FCR (5.65 ± 0.26 vs. 6.12 ± 0.27 ; $P = 0.21$) and feed intake (10.03 ± 0.31 vs. 10.75 ± 0.32 ; $P = 0.12$) than progeny from RFI+ dams, respectively. Average daily gain (1.80 vs. 1.81 ; SEM = 0.08; $P < 0.92$) and MMWT (79.29 ± 2.18 vs. 78.67 ± 2.52 ; $P < 0.84$) were both similar among progeny between RFI- and RFI+ dams phenotypes. Residual feed intake of progeny for dam

phenotype exhibited less variation than heifer phenotype as both progeny phenotypes were negative (-0.15 ± 0.28 vs. -0.11 ± 0.27 , respectively; $P = 0.91$). Surprisingly RFI- cows produced progeny with worse FCR's than RFI+ dams (5.96 ± 0.27 vs. 5.80 ± 0.26 , respectively; $P = 0.68$). Feed intake and ADG of progeny were numerically lower for RFI- dams than RFI+ (10.24 ± 0.33 vs. 10.51 ± 0.32 , respectively; $P = 0.56$).

DISCUSSION

By definition, RFI is phenotypically independent of its component traits ADG and MMWT (Archer et al., 1999). This was the case in both trials, indicating selection upon RFI can be made without influencing the growth or mature size of the animal. Studies by Golden et al. (2008) and Kolath et al. (2006) report similar results with no statistical differences between RFI groups for ADG and BW. Being independent of its component traits is the benefit to selection upon RFI rather than the more common ratio based trait FCR (Archer et al., 1999; Salmon et al., 1990). While selection upon FCR and RFI may lead to a difference in mature size of the mature cow herd, they remain correlated (Crowley et al., 2010; Hoque et al., 2009). Differences in correlations between RFI and FCR through later maturities are unsurprising in the present study, as growth rate has diminished and additional variables such as body condition, milk production, age, and stage of gestation may need to be accounted for in both traits within the mature animal to achieve accurate and correlated responses. Although, reviews by Herd and Bishop (2000) and Nkrumah et al. (2004) found strong phenotypic correlations ($r_p = 0.61$ and 0.62) between RFI and FCR on cattle younger than a year of age at the onset of trial. The accuracy of FCR may diminish as the animal grows due to an increase in feed

consumption with a decrease in skeletal and lean tissue growth; however, correlations earlier in maturity between RFI and FCR indicate selection for lower RFI cattle will also select for cattle with improved FCR's.

In agreement with the literature (Carstens and Tedeschi, 2006; Lancaster et al., 2009b) selection for FCR for improvement in feed efficiency may lead to an increased mature size of the animal. With strong correlations between RFI and DMI (Table 2.3 and Table 2.4) a reduction in feed intake can be obtained without negatively influencing production or mature size of the animal, and, thereby, reducing the input costs of production.

Heifer and cow RFI

With the original 89 heifers being partitioned into two groups within the mature cow herd as well as rephenotyped over two separate trials the focus of this chapter's discussion will pertain to the contemporary group of 38 cows phenotyped for RFI across both trials. Variation in the number of phenotyped heifers is the main factor influencing the difference in RFI_{hfr} range between the original and rephenotyped contemporary of heifers. Variation in the range of RFI values may vary among studies since feed intake is influenced by multiple variables including gender, maturity, time of year, nutrient balance, and diet composition (NRC, 1987). Additional variation in RFI among studies may also occur if RFI values are reported as DMI or actual feed intake. Research by Castro Bulle et al. (2007) and Crews et al. (2003) reported ranges in RFI from actual intake to be -0.06 to 0.06 kg/d and -4.10 to 4.65 kg/d, respectively. Hoque et al. (2009) reported a range in RFI derived from DMI to be -1.98 to 2.05 kg/d.

The average cow RFI in the current study was -0.06 kg and by definition the mean RFI should be 0.00; however, Arthur et al. (2004b) reported an average cow RFI of 0.04 on four year old cows. Cow RFI adjusted for conceptus weight, gain in backfat, body condition score and tail fat accounted for an additional 10% (39.3%) of the variation in feed intake in reference to the current study (Basarab et al., 2007). This range in RFI_{cow} is larger than that of the heifers, yet smaller than Meyer's (2007) report when cattle were fed a 100% roughage-based ration during feed intake trials using the GrowSafe[®] feed intake system. As stated by Meyer (2007), the GrowSafe[®] system is more suitable for denser diets such as pelleted or grain-based rations. When using the GrowSafe[®] system for forage-based rations the potential for increased error in feed intake is possible with a greater percentage of feed going towards unconsumed feed/waste than a pelleted or concentrate-based ration. Although wasted feed may not have significantly affected the validation of RFI, it may have contributed to a greater range in RFI values. There is, however, some variation to be expected between heifer and cow RFI values. Heifers have a greater demand to meet growth requirements in comparison to cows, and were therefore fed a higher energy dense ration at a smaller percent of body weight. With cows at a larger physical frame size and body weight than heifers, it is to be expected that cows have a greater DMI on a percent body weight basis, especially during lactation, which places a greater energetic demand on the cow.

Relationship between heifer and cow RFI, category group and phenotype

Correlations derived between trials one and two for heifer and cow RFI were indicative of re-ranking RFI values for individual animals within a contemporary group between different test periods and maturities. These correlations are contradictory to

those by Morgan et al. (2010), Archer et al. (2002) and Arthur et al. (1999) who reported phenotypic correlations of 0.40, 0.51, and 0.36, respectively, between postweaning measurement as a heifer and measurement of RFI as a mature cow. Lack of significance and weak correlations between RFI_{hfr} and RFI_{cow} within the present study may be on account of limited adjustments to RFI for variation in feed intake of the mature cow. Adjusting RFI for additional metabolic energy consuming traits of the mature animal such as actual milk production, body condition score, or fetal growth as reported by Basarb et al. (2007), may be needed to acquire a stronger phenotypic correlation between RFI_{hfr} and RFI_{cow} . Further differences between the present study and other trials with correlations between RFI computed at different maturities may reside in the variation in rations and the biological stage of production for cows. Bormann et al. (2010) concluded that RFI measured over two separate trials with two feed rations on animals differing in metabolic stage of production are not the same trait.

The present study compared phenotyped heifers and cows on two separate rations. Heifers were fed a higher energy-dense, no roughage-based ration balanced to meet nutrient requirements for their current body weight and level of growth to enable them to maximize their genetic potential for feed efficiency and growth. Lactating cows in the first trimester of gestation were fed a lower energy-dense ration which was 89% forage compared to a no-roughage based diet fed to heifers. This approach was opposite to Archer et al. (2002), whom utilized open cows which had been dried off for approximately 10 weeks and were fed the same ration as when they were phenotyped as heifers. Morgan et al. (2010) also rephenotyped cows for RFI during the dry period, yet cows were in the early stages of their first trimester and were not fed the same diet in

which heifer RFI's were derived. Given the degree of variation in biological differences affecting energy consumption within the cows between trials, one could hypothesize a stronger phenotypic correlation between heifer and cow RFI in Archer and Morgan's results were due to cows being in less of an energy demanding state of production in comparison to the current study. Nieuwhof et al. (1992) conducted a similar study to the present trial where heifer RFI during the growth stage (post-weaning) was compared to RFI's of lactating first calf heifers. Phenotypic correlations were weak ($r_p = 0.07$), yet genetic correlations were moderate ($r_g = 0.45$). Results were similar in mice with phenotypic and genetic correlations of 0.29 and 0.60, respectively, between post-weaning and mature measurements of RFI (Archer et al., 1998). Based on these results it can be suggested that larger amounts of error are liable to occur within mature cow RFI in comparison to RFI's derived as a heifer due to the additional biological variables which affect mature cow RFI.

Correlations among heifer phenotype with cow RFI and phenotype in addition to correlations between heifer category with cow phenotype and heifer RFI with cow phenotype all suggest post-weaning measurements of RFI and determination of feed efficiency status as a heifer relate to feed efficiency status later in maturity when diets vary between production cycles. Yet selection upon the phenotypic RFI value itself may be an inaccurate method of basing selection decisions to improve feed efficiency within the cow herd. Morgan et al. (2010) reported a 37.8% change in RFI phenotype from post-weaning to mature cow tests, while the current study reported a 24% alteration in RFI phenotypes between different maturities. Selection based independently on phenotypic RFI values may be biased, as animals which reside in the average range for

RFI within a contemporary can be phenotyped as a positive RFI animal as reported in the current study (Table 2.5). With an understanding that the numerical RFI value for individual animals will vary throughout maturity, a more logical approach of basing selection decisions on RFI may be to select against categorical groups rather than individual RFI values. Granted, category groups are determined from individual RFI values, and the majority of re-ranking of RFI occurs within a half standard deviation of their original category as indicated in the current study. A majority of the re-ranking (39%) occurred when efficient heifers moved to average RFI cows. Correlations ($r_p = 0.41$; $P < 0.05$) between heifer category group and RFI_{cow} suggest selection based upon heifer category group is associated with cow feed efficiency. The conclusion can be made that selection against the lower one-third of categorical ranked inefficient animals within a contemporary group will improve efficiency of the mature cow herd.

The conclusion can also be made that feed efficiency does not change from post-weaning measurements as a heifer to a mature cow from a genetic perspective; therefore, making selection decisions from RFI associated traits measured as heifers is a genetically sound approach of selecting for more feed efficient mature cows. Caution should be taken when basing selection decisions on phenotypic RFI's. Although several studies have reported strong correlations between phenotypic and genetic RFI (Archer et al., 1998; Arthur et al., 2001c), phenotypic RFI is more susceptible to error in the measurement of RFI. Efficiency in cattle during post-weaning growth may be altered later in maturity due to physiological energy-consuming states such as gestation and lactation (Archer et al., 1998). Due to differences in energy demand as well as energy consumption during these states, variation within RFI values may occur, thus altering the

rank of efficiency within a contemporary group or herd. With variation in the rank of feed efficiency throughout production, there is minimal alteration of animals going from efficient to inefficient or inefficient to efficient between post-weaning and maturity. Post-weaning measurements of RFI are accurate predictors of animal feed efficiency later in maturity.

Heifer and cow RFI prediction of progeny efficiency

An assessment of progeny RFI for both heifer category and phenotype suggest post-weaning measurements as heifers more accurately predicted progeny feed efficiency and performance than RFI's derived as mature cows. While progeny RFI was numerically lower for RFI- cows than progeny from RFI+ cows the variation between the two was minimal, along with FCR being numerically larger for RFI- cows than RFI+ cows. Potential sources of error in the agreement between progeny RFI and cow category groups may have been influenced by the difference in ADG of progeny. While sire influenced progeny RFI, it was consistently distributed across comparisons for heifers and cows.

To the author's knowledge there is limited research comparing whether RFI derived as a heifer or RFI derived as a mature cow is a more concise predictor of progeny feed efficiency. Archer et al. (1998) found heritability of postweaning RFI to be slightly higher than the heritability of RFI calculated at maturity in mice ($h^2 = 0.27$ vs. 0.24 ; respectively), although there was no comparison to determine which RFI value did a more consistent job of defining progeny RFI. Projecting progeny feed efficiency from mature RFI may be a biased estimate in comparison to RFI measured earlier in maturity. Variation in maintenance requirements of the dam in relation to the progeny due to

different stages of production, age and physiological state (NRC, 2000) will influence feed intakes and, thus, RFI. Diet composition fed to progeny in comparison to cows varied. Cows fed a higher forage diet consisted of a larger percent of cell wall content (i.e. lignin), limiting DMI of cows (NRC, 1987) in relation to progeny. When dams were phenotyped as heifers they were fed a diet much more similar to the progeny diet. The present study found postweaning measurements more accurately described mature feed efficiency rather than mature feed efficiency describing postweaning feed efficiency. With variation in the accuracy of different time points describing feed efficiency on the same animal, it should not be surprising that postweaning measurements more accurately describe postweaning measurements of progeny. Further research is needed to validate these conclusions.

CONCLUSION

Strong genetic correlations occur between RFI determined postweaning and RFI determined later in maturity. Selection for phenotypic RFI can be made with accuracy when there is limited variation in body weight, age, and level of production among animals in a contemporary. To obtain strong phenotypic correlations between RFI's among different test durations contemporaries should remain similar between tests. Further research is needed to obtain an accurate assessment on whether postweaning or mature RFI more accurately predicts progeny RFI. However, phenotyping cattle postweaning for RFI and selecting against cattle which fall in the bottom one third of their contemporary for feed efficiency will improve feed efficiency of the cow herd and reduce feed input costs into production.

Table 2.1. Ingredients and nutrient composition of diet fed to heifers.

Item ^a	As Fed basis (%)
Corn	41.30
SHP	45.00
DDGS	10.00
Supplement	2.50
Lime	1.20
Dry Matter	86.27
Crude Protein	10.97

^a = SHP = soyhull pellets; DDGS = dried distiller's grains.

Table 2.2. Ingredients and nutrient composition of diet fed to 38 head of rephenotyped cows.

Item ^a	As Fed basis (%)	Dry Matter Basis (%)
Silage Hay ^b	39.00	
Soyhull pellets	39.00	
Supplement ^c	21.00	
Dry Matter	61.32	95.20
Crude Protein	8.57	13.98
NDF	36.71	59.85
ADF	24.84	40.49
TDN	61.18	

^b = Mixed grass baleage.

^c = Dried Distillers Grain (28% protein); Mag-Oxide; mineral; lime, and salt.

Table 2.3. Pearson correlations among measures of feed efficiency, growth, and feed intake for the 38 heifers^a.

Traits ^b	RFI	FCR	DMI	ADG
MMWT	-0.00	0.26	0.58	0.16
ADG	0.00	-0.69	0.59	
DMI	0.64	0.13		
FCR	0.55			
RFI				

^a = Correlation coefficients in bold are different from zero ($P < 0.01$).

^b = RFI = residual feed intake; FCR = feed conversion ratio, DMI = dry matter intake; ADG = average daily gain; MMWT = average body weight^{0.75}.

Table 2.4. Pearson correlations among measures of feed efficiency, growth, and feed intake for the 38 cows^a.

Traits ^b	RFI	FCR	DMI	ADG
MMWT	0.01	-0.26	0.49	0.48
ADG	0.03	-0.87	0.37	
DMI	0.85	-0.04		
FCR	0.20			
RFI				

^a = Correlation coefficients in bold are different from zero ($P < 0.01$).

^b = RFI = residual feed intake; FCR = feed conversion ratio, DMI = dry matter intake; ADG = average daily gain; MMWT = average body weight^{0.75}.

Table 2.5. Means for feed efficiency and performance traits for low, medium and high RFI heifers (Ls-means).

Traits ^a	RFI Category			P-value
	Low RFI	Average RFI	High RFI	
RFI	-1.36 ± 0.15 ^d	0.01 ± 0.11 ^c	1.48 ± 0.16 ^b	< 0.0001
DMI	6.73 ± 0.35 ^d	8.79 ± 0.26 ^{b,c}	9.49 ± 0.37 ^b	< 0.0001
ADG	1.34 ± 0.12	1.58 ± 0.09	1.46 ± 0.13	0.28
FCR	5.99 ± 0.45	6.64 ± 0.33	8.11 ± 0.48	0.01
IBW	363.93 ± 13.31	376.95 ± 9.65	363.74 ± 14.03	0.63
FBW	457.91 ± 14.17	487.75 ± 10.28	465.81 ± 14.94	0.20

^a = RFI= residual feed intake; DMI = dry matter intake; ADG = average daily gain; FCR = feed conversion ratio; IBW = initial body weight; FBW = final body weight.

^{b,c,d} = Means with different letters differ across rows ($P < 0.05$).

Table 2.6. Means for feed efficiency and performance traits for RFI- and RFI+ heifers (Ls-means).

Traits ^a	RFI Phenotype		P-value
	RFI-	RFI+	
RFI	-0.93 ± 0.18	0.75 ± 0.16	< 0.0001
DMI	7.54 ± 0.32	9.11 ± 0.29	0.001
ADG	1.49 ± 0.09	1.49 ± 0.09	0.98
FCR	6.06 ± 0.35	7.43 ± 0.32	0.01
IBW	367.10 ± 10.17	373.06 ± 9.15	0.67
FBW	471.24 ± 11.19	477.50 ± 10.07	0.68

^a = RFI= residual feed intake; DMI = dry matter intake; ADG = average daily gain; FCR = feed conversion ratio; IBW = initial body weight; FBW = final body weight.

Table 2.7. Means for feed efficiency and performance traits for low, medium and high RFI cows (Ls-means).

Traits ^a	RFI Category			P-value
	Low RFI	Average RFI	High RFI	
RFI	-3.04 ± 0.41 ^d	0.12 ± 0.38 ^c	3.56 ± 0.47 ^b	< 0.0001
DMI	15.22 ± 0.41 ^d	17.24 ± 0.38 ^c	19.62 ± 0.47 ^b	< 0.0001
ADG	0.94 ± 0.08	1.00 ± 0.08	0.91 ± 0.10	0.75
FCR	28.38 ± 2.72 ^g	28.77 ± 2.53 ^{f,g}	36.09 ± 3.10 ^e	0.13
IBW	618.09 ± 15.82	610.98 ± 14.73	631.14 ± 18.04	0.69
FBW	685.05 ± 18.82	682.12 ± 17.52	695.57 ± 21.45	0.88

^a = RFI = residual feed intake; DMI = dry matter intake; ADG = average daily gain; IBW = initial body weight; FBW = final body weight.

^{b,c,d} = Means with different letters differ across rows ($P < 0.05$).

^{e,f,g} = Means with different letters differ across rows ($P \leq 0.10$).

Table 2.8. Means for feed efficiency and performance traits for RFI- and RFI+ cows (Ls-means).

Traits ^a	RFI Phenotype		<i>P</i> -value
	RFI-	RFI+	
RFI	-2.25 ± 0.41	2.38 ± 0.43	< 0.0001
DMI	15.84 ± 0.39	18.66 ± 0.41	< 0.0001
ADG	0.96 ± 0.07	0.95 ± 0.07	0.95
FCR	28.71 ± 2.25	32.62 ± 2.37	0.24
IBW	623.35 ± 12.66	613.57 ± 13.35	0.60
FBW	691.53 ± 14.96	681.25 ± 15.77	0.64

^a = RFI = residual feed intake; DMI = dry matter intake; ADG = average daily gain; IBW = initial body weight; FBW = final body weight.

Table 2.9. Pearson correlations measured between postweaning RFI and mature RFI for residual feed intake (RFI), RFI category, RFI phenotype (-/+), initial body weight, and feed intake between.

Variable ^a	RFI _{heifer}	Category _{heifer}	Phenotype _{heifer}	IBW _{heifer}	DMI _{heifer}
RFI _{cow}	0.17	0.31*	0.35**	0.34**	0.37**
Category _{cow}	0.07	0.18	0.25	0.35**	0.23
Phenotype _{cow}	0.33**	0.41**	0.54***	0.28*	0.36**
IBW _{cow}	-0.14	-0.12	-0.09	0.50***	0.21
DMI _{cow}	0.09	0.19	0.26	0.55***	0.42**

^a = RFI = residual feed intake computed postweaning and at maturity; Category = low, average or high RFI values determined from 0.50 SD from the mean of the group for; Phenotype (RFI- and RFI+); IBW = Initial BW; DMI = dry matter intake.

***Correlations are different from zero at ($P < 0.001$).

**Correlations are different from zero at ($P < 0.05$).

*Correlations are different from zero at ($P < 0.10$).

Table 2.10. Feed efficiency and performance traits for cows averaged across heifer RFI category group (Ls-means).

Traits ^a	Heifer Category			<i>P</i> -value
	Low RFI	Average RFI	High RFI	
RFI	-1.10 ± 0.91 ^c	-0.22 ± 0.66 ^{c,b}	1.46 ± 0.96 ^b	0.16
DMI	16.43 ± 0.71	17.35 ± 0.52	17.63 ± 0.75	0.46
ADG	0.99 ± 0.10	0.99 ± 0.07	0.86 ± 0.10	0.53
FCR	29.81 ± 3.22	29.28 ± 2.34	34.10 ± 3.40	0.49
IBW	614.66 ± 17.49 ^{b,c}	632.54 ± 12.69 ^b	594.07 ± 18.44 ^c	0.23
FBW	685.23 ± 20.85 ^{b,c}	702.51 ± 14.93 ^b	654.80 ± 21.70 ^c	0.21

^a = RFI = residual feed intake; DMI = dry matter intake; ADG = average daily gain; IBW = initial body weight; FBW = final body weight; CWW = calf weaning weight.

^{b,c} = Means with different letters differ across rows ($P \leq 0.10$).

Table 2.11. Feed efficiency and performance traits for heifers averaged across cow RFI category group (Ls-means).

Traits ^a	Cow Category			<i>P</i> -value
	Low RFI	Average RFI	High RFI	
RFI	0.02 ± 0.31	-0.18 ± 0.29	0.25 ± 0.36	0.64
DMI	8.10 ± 0.42	8.29 ± 0.39	9.00 ± 0.48	0.35
ADG	1.48 ± 0.11	1.50 ± 0.10	1.49 ± 0.12	0.99
FCR	6.43 ± 0.44	6.69 ± 0.41	7.52 ± 0.50	0.26
IBW	353.93 ± 11.07 ^c	370.73 ± 10.30 ^{b,c}	391.30 ± 12.62 ^b	0.10
FBW	457.43 ± 12.31 ^c	475.92 ± 11.46 ^{b,c}	495.32 ± 14.03 ^b	0.14

^a = RFI = residual feed intake; DMI = dry matter intake; ADG = average daily gain; IBW = initial body weight; FBW = final body weight.

^{b,c} = Means with different letters differ across rows (*P* < 0.05).

Table 2.12. Feed efficiency and performance traits for cows averaged across heifer RFI phenotyped (Ls-means).

Traits ^a	Heifer Phenotype		<i>P</i> -value
	RFI-	RFI+	
RFI	-1.19 ± 0.68	0.86 ± 0.61	0.03
DMI	16.55 ± 0.53	17.68 ± 0.48	0.12
ADG	0.97 ± 0.07	0.94 ± 0.07	0.76
FCR	29.79 ± 2.48	31.19 ± 2.23	0.68
IBW	624.26 ± 13.73	614.23 ± 12.36	0.59
FBW	693.38 ± 16.21	681.22 ± 14.59	0.58

^a = RFI = residual feed intake; DMI = dry matter intake; ADG = average daily gain; IBW = initial body weight; FBW = final body weight.

Table 2.13. Feed efficiency and performance traits for heifers averaged across cow RFI phenotyped (Ls-means).

Traits ^a	Cow Phenotype		<i>P</i> -value
	RFI-	RFI+	
RFI	-0.34 ± 0.24	0.38 ± 0.25	0.04
DMI	7.89 ± 0.32	8.98 ± 0.34	0.02
ADG	1.48 ± 0.09	1.50 ± 0.09	0.91
FCR	6.31 ± 0.34	7.38 ± 0.36	0.04
IBW	359.34 ± 9.01	382.68 ± 9.50	0.08
FBW	463.19 ± 9.96	487.49 ± 10.50	0.10

^a = RFI = residual feed intake; DMI = dry matter intake; ADG = average daily gain; FCR = feed conversion ratio; IBW = initial body weight; FBW = final body weight.

Table 2.14. Least square means for progeny performance for low, average, and high heifer category groups.

Trait ^a	Heifer Category			P-value
	Low RFI	Average RFI	High RFI	
RFI _{prog}	-0.23 ± 0.38	-0.14 ± 0.32	-0.03 ± 0.34	0.93
DMI _{prog}	8.74 ± 0.37	8.80 ± 0.32	9.02 ± 0.33	0.83
ADG _{prog}	1.80 ± 0.11	1.80 ± 0.10	1.81 ± 0.10	1.00
FCR _{prog}	5.72 ± 0.36	5.81 ± 0.31	6.08 ± 0.33	0.74
IBW _{prog}	263.24 ± 13.53	273.64 ± 11.54	270.68 ± 12.10	0.84
MMWT _{prog}	79.35 ± 3.04	78.71 ± 2.59	79.01 ± 2.72	0.99

^a = RFI_{prog} = residual feed intake of progeny; DMI_{prog} = dry matter intake of progeny; ADG_{prog} = average daily gain of progeny; FCR_{prog} = feed conversion ratio of progeny; IBW_{prog} = initial body weight of progeny; MMWT_{prog} = average body weight^{0.75} of progeny.

Table 2.15. Least square means for progeny performance for low, average, and high cow category groups.

Trait ^a	Cow Category			P-value
	Low RFI	Average RFI	High RFI	
RFI _{prog}	-0.15 ± 0.34	-0.10 ± 0.34	-0.15 ± 0.36	0.99
DMI _{prog}	8.66 ± 0.33	8.80 ± 0.33	9.14 ± 0.35	0.67
ADG _{prog}	1.71 ± 0.09 ^{c,d}	1.69 ± 0.09 ^d	2.01 ± 0.09 ^b	0.04
FCR _{prog}	6.01 ± 0.31	6.14 ± 0.31	5.43 ± 0.33	0.28
IBW _{prog}	261.32 ± 11.86	280.73 ± 11.86	266.92 ± 12.51	0.50
MMWT _{prog}	79.81 ± 2.70	77.68 ± 2.70	79.54 ± 2.85	0.83

^a = RFI_{prog} = residual feed intake of progeny; DMI_{prog} = dry matter intake of progeny; ADG_{prog} = average daily gain of progeny; FCR_{prog} = feed conversion ratio of progeny; IBW_{prog} = initial body weight of progeny; MMWT_{prog} = average body weight^{0.75} of progeny.

^{b,c,d} = Means with different letters differ across rows ($P < 0.05$).

CHAPTER 3

EFFECTS OF DIVERGENTLY MATING SIRES AND DAMS OF KNOWN RFI PHENOTYPES

ABSTRACT

Two separate feed intake experiments were conducted over a two year period using progeny from divergently mated sires and dams of known RFI phenotypes. The objective of the initial experiment (Yr. 1) was to determine the effect on progeny feed efficiency when sires and dams of known residual feed intakes (**RFI**) are mated and the effect on RFI when test duration was extended past 70 days. The second experiment (Yr. 2) determined if RFI obtained postweaning as heifers ($_{pw}$) or during maturity as cows ($_m$) in dams was a more accurate predictor of progeny feed efficiency. We hypothesized that parent RFI would reflect upon progeny feed efficiency and that extended test duration was necessary to accommodate for pre-test effects that could alter progeny RFI. We further hypothesized postweaning measurements of feed efficiency in dams were more accurate predictors of progeny feed efficiency than feed efficiency measured during maturity. Experiment one consisted of F1 heifer (n = 32) and steer (n = 21) progeny produced from three separate treatment groups defined as RFI- x RFI- (n = 27; TRT1), RFI- x RFI+ (n = 16; TRT 2) and RFI+ x RFI+ (n = 10; TRT 3). Fourteen F2 steers were used for the comparison of progeny feed efficiency to RFI_{pw} of dams while 13 steers were used for the comparison between progeny feed efficiency and RFI_m of dams. Feed intake (**FI**) was measured using the Growsafe[®] feed intake system (GrowSafe Systems Ltd.,

Airdrie, AB Canada) over a 70 d period for heifers (Yr. 1) and steers (Yr. 2) with an extended 120 d FI trial for steers in Yr. 1. Ultrasound images of the longissimus muscle area (**USLMA**) and backfat depth (**USBF**) were captured during the last weigh period for steers in Yr. 1 and at each consecutive weigh period for steers in Yr. 2. Independent variables of sire treatment group, dam category group and dam phenotype group were determined by their individual RFI values as being efficient (**EFF**) or inefficient (**INEFF**). Residual feed intake, dry matter intake (**DMI**), and feed conversion ratio (**FCR**) were similar between TRT 1 and TRT 2. Residual feed intake ($P < 0.02$), DMI ($P < 0.01$) and FCR ($P < 0.003$) were different between TRT 3 and both TRT 1 and 2. Average daily gain of heifers was similar among treatment groups ($P > 0.10$). Dry matter intake and FCR differed numerically among the three treatment groups for steer progeny over the 70 and 120 d FI trials. Residual feed intake was lower for TRT 1 steer progeny in comparison to TRT 3 over the 70 d (-0.44 vs. 0.71; $P < 0.09$) and 120 d (-0.34 vs. 0.80; $P < 0.02$) FI trials. Analysis of carcass traits from steers in Yr. 1 concluded USLMA differed between TRT 1 and both TRT 2 and 3 (76.16 vs. 68.35 vs. 67.47, respectively $P < 0.01$). Moderate correlations in steer progeny RFI values occurred between test durations 0 to 70 d and 0 to 120 d (0.49; $P < 0.03$), while test durations 0 to 120 d and 70 to 120 d were highly correlated (0.92; $P < 0.01$). Individual steer RFI was not correlated between test duration 0 to 70 d and 70 to 120 d (0.31; $P > 0.10$). Experiment two showed strong correlations between dam RFI phenotype_{pw} with steer RFI (0.69; $P < 0.05$), FCR (0.46; $P < 0.10$), phenotype (0.60; $P < 0.05$) and category (0.62; $P < 0.05$). Residual feed intake, RFI phenotype groups and RFI category groups for dams measured during maturity were not correlated with steer progeny traits. In conclusion, selecting against

the lower one third of INEFF dams within the population improved progeny feed efficiency. Furthermore, extending the test duration past 70 d is not required as long as animals are acclimated to the test facility and on a consistent level of feed prior to intake and body weight collection. Finally, postweaning measurement of dam RFI as a heifer is a more accurate prediction of progeny feed efficiency than RFI measured as a mature cow.

INTRODUCTION

Increased values of corn prices and pasture land rental in recent years have increased the cost of production for cattle producers. Feed cost has been commonly affiliated with being one of the largest input costs in beef cattle production. Although, many aspects of production influence the annual economical return to cattle producers, feed cost influences the economical return the most. An estimated 40 to 70% of annual production costs within cattle operations are comprised of feed and supplementation costs (Funston, 2009). Determining ways to reduce feed cost without hindering the nutritional value of the diet or decreasing performance by the animal is a challenging task, therefore, identifying animals which consume less feed and perform as well or better than an animal which consumes larger portions of feed has merit within a production system.

In previous years feed to gain (**F:G**), also reported as feed conversion ratio (**FCR**), has been the more common trait to select for feed efficiency. Feed conversion ratio is structured around selecting cattle which consume less feed for heavier gains in body weight; however, selection upon FCR and F:G have led to increased mature sizes of the cow herd (Archer et al., 1999). Residual feed intake (**RFI**), the difference between an

animal's actual intake and expected intake based on a certain level of growth performance and average body weight^{0.75} (**MMWT**), has become more popular in recent years for identifying feed efficient cattle from feed inefficient cattle. It's been determined RFI is phenotypically and genetically independent of its component traits ADG or MMWT (Arthur et al., 2001d) , and therefore selection based upon RFI will not influence the performance or mature size of the animal. Animals with negative RFI values (**RFI-**) are more feed efficient than animals with positive RFI values (**RFI+**). Being a moderately heritable trait (0.52 ± 0.14 ; Rolfe et al., 2008) selection upon RFI will influence progeny feed efficiency. Studies (Carstens and Tedeschi, 2006; Crews et al., 2006) have reported RFI- cattle consume \$38.00 to \$26.25 less feed per head in feed, respectively while direct selection upon RFI- and RFI+ lines of cattle equated to RFI- consuming \$27.00 less per head in feed (Arthur et al., 2001a).

Studies have shown divergently selecting for RFI- and RFI+ lines of cattle, RFI- lines of cattle consistently producing more feed efficient progeny with similar levels of performance and body size in to progeny from RFI+ lines of cattle (Richardson et al., 2001). While RFI remains an accurate measure of metabolic efficiency within the animal, Basarab et al. (2007) found individual animals reranked in terms of RFI over separate feed intake trials. Among the literature there appears to be controversial reports on the relationship between RFI and carcass traits of the longissimus muscle area and backfat depth. Trejo et al. (2010) found significant differences in the longissimus muscle area among low, medium, and high RFI sires while Richardson et al. (2001) observed numerical difference in the longissimus muscle area between RFI- and RFI+ steers. In mice divergently selected for heat loss, high heat loss mice had lower intakes and were

leaner in body composition than low heat loss mice (Kgwatalala and Nielsen, 2004). Hoque et al. (2006) reported selection of lower RFI animals would result in progeny in excess of subcutaneous fat cover, while Basarab et al. (2003) observed RFI- animals to be leaner in their body composition than RFI+ animals. To the author's knowledge there is limited research on the agreement between progeny RFI measured postweaning with dam RFI measured postweaning and later in maturity.

Our hypotheses were 1) divergent matings of RFI- sires to RFI- dams will improve progeny feed efficiency in comparison to divergent matings of RFI+ sires to RFI+ dams; 2) one RFI- sire mated to RFI+ dams would produce progeny which are more feed efficient with similar levels of performance to progeny produced from RFI+ sires and dams; 3) steers produced from RFI- sires and dams will be leaner in body composition with greater development in the longissimus muscle area than steers from RFI+ sires and dams; and 4) postweaning measurements of RFI in dams will be in closer relation to postweaning measurements of progeny RFI than RFI measurements made when the dam was mature.

MATERIALS AND METHODS

Experiment 1

Experimental Design

In the fall of 2007, 53 Simmental by Angus crossbred heifers (n = 27 RFI-; n = 26 RFI+) were divergently mated to four Simmental by Angus crossbred bulls (n = 3 RFI-; n = 1 RFI+) at the University of Missouri's Southwest Research Facility (SWC; Mount Vernon, MO). Sires and dams were phenotyped postweaning for RFI over a minimum 70 d feed intake trial during the summer of 2007 at the University of Missouri Beef

Research and Teaching Farm (BRTF; Columba, MO). Divergent matings listed in Table 3.4, produced 32 F1 heifer progeny and 21 F1 bull progeny. After weaning, progeny from divergently mated RFI phenotyped sires and dams were comingled with progeny from non-divergently mated dams from the SWC cow herd. Ninety-nine F1 bulls and heifers were transported to BRTF during the summer of 2009 for feed intake collection. Data analysis for experiment one (Yr. 1) consisted of 32 F1 heifers (IBW = 258.73 ± 5.04 kg; age = 10.35 ± 0.10 months) and 21 F1steers (IBW = 307.47 ± 10.18 kg; age = 10.25 ± 0.34 months) produced from 53 divergent matings of RFI phenotyped sires and dams.

Animal Management

Upon arrival to BRTF heifers and bulls were weighed and randomly allocated to 10 pens (five pens of 12 heifers/pen; 7.6 x 16.5 m and five pens of 9 to 10 bulls/pen; 7.6 x 16.5 m) each equipped with two GrowSafe[®] feed bunks. Heifers and bulls were both tagged with radio frequency identification tags (RFID; Allflex, Dallas Fort Worth, Texas) in the upper portion of the left ear within 10 cm from the base of the head. Heifers were allowed *ad libitum* access to a receiving diet (Table 3.1) and water over a 14 d receiving period to the test facility. Sixty (IBW = 258.01 ± 4.58 kg; age = 10.16 ± 0.09 months) heifers were weighed onto trial on August 3, 2009 where they were transitioned directly from the receiving to study ration (Table 3.2) and were allowed *ad libitum* access to feed and water over the entirety of the 70 d test. Steers were placed on a 35 d receiving period where *ad libitum* access to a receiving diet (Table 3.1) and water was provided while steers became acclimated to the test facility. On day 14 of the receiving period bulls were castrated by method of elastration by a licensed veterinarian using a Callicrate bander with Callicrate castration loops (NO-Bull Enterprises, St. Francis, KS). Thirty-

nine ($IBW = 309.72 \pm 7.6$ kg; age = 11.89 ± 0.07 months) steers were weighed onto trial on September 24, 2009, and were transitioned directly from the receiving to study ration (Table 3.3) and were allowed *ad libitum* access to feed and water over the entirety of the 120 d test. Growth implants were not used on either heifers or steers. Steers were marketed at two separate endpoints determined by visual appraisal of subcutaneous fat cover.

Animal Performance Measurements

Two day consecutive body weights (**BW**) were taken at the onset and conclusion of each trial with a single mid-body weight taken on d 35 for both heifers and steers. Body weights were recorded early in the morning prior to delivery of feed to the GrowSafe[®] bunk; however, neither feed or water were removed from pens prior to or on scheduled weigh days. Ultrasonic (**US**) images of steers were captured on d 120 using a 500V Aloka (Corometrics Medical Systems, Inc., Wallingford, CT) ultrasound machine with a 3.5-MHz transducer fitted to a custom beef animal standoff (a gel fitted to contour the shape of the beef animal at the 12th and 13th rib). Ultrasonic images of the longissimus muscle area (**USLMA**) and backfat depth (**USBF**) were measured on the left side between the 12th and 13th rib. Longissimus muscle area and USBF were traced on the US machine with the measurement recorded in centimeters (cm). Prior to slaughter one steer died unrelated to treatment effects. Twenty steers in total were divided into two separate harvest groups based off of visual appearance of fat cover and body weight. Group 1 (n = 7) and Group 2 (n = 13) were transported to a commercial packing plant for humane slaughter and carcass data collection. Carcass data was collected and summarized by GeneNet (Hays, KS). Days on feed (**DOF**), hot carcass weight (**HCWT**),

yield grade (**YG**), quality grade (**QG**), total feed consumed (**TFC**), cost of feed (**CF**), and yardage (**YD**) were measured or calculated for each of the 21 steers. Average daily gain (**ADG**) was the total amount of weight gained from beginning to end of the trial over the total amount of days of trial. Feed cost was figured at \$180.00 per tonnage of feed while yardage was figured at \$0.35 per day.

Feed Efficiency Measurements

At the conclusion of each feed intake trial daily feed intakes were compiled from the GrowSafe[®] feed intake system and averaged for each individual animal for the duration of each feed intake trial. Residual feed intake was measured as the difference between the animals actual and expected feed intake (Herd and Bishop, 2000).

Regression analysis of actual feed intake upon ADG and average body weight^{0.75} (**MMWT**) was used to model daily feed intake using the general linear model procedure (Proc GLM) of SAS (SAS version 9.2, SAS Inst. Inc., Cary, NC). Residual feed intake was calculated for both heifer (n = 32) and steer (n = 21) progeny produced from divergently mated sires and dams. The model fitted was,

$$Y_i = \beta_0 + \beta_1 \text{ADG}_i + \beta_2 \text{MMWT}_i,$$

where Y_i = average actual daily feed intake (**ADFI**) for animal i , β_0 = regression intercept, β_1 = partial regression coefficient of ADFI on ADG for animal i , β_2 = partial regression coefficient of ADFI on MMWT for animal i . Residual feed intake of steers was calculated over three individual time periods of 0 to 70, 0 to 120, and 70 to 120 days. Feed conversion ratio (**FCR**) was the ratio of average daily feed intake divided by average daily gain. Residual feed intake category groups (low, average, or high) were determined by one half SD above and below the mean RFI of for the contemporary.

Animals with RFI's below one half SD were categorized as low RFI animals and animals with RFI's above one half SD were categorized as high RFI animals. Animals with RFI's between low and high RFI animals were categorized as average. Residual feed intake phenotype groups were animals with either a negative RFI or a positive RFI.

Statistical Analysis

Steer and heifer progeny from experiment one were analyzed separately. Dependent variables analyzed for heifers included 70d RFI, FCR, ADG, and DMI. Dependent variables for steers included DOF, 70 d RFI, 120 d RFI, last 50 d RFI, USBF, HCWT, USLMA, QG, YG, TFC, CF, and YD. Dependent variables for both heifers and steers were analyzed using the Proc GLM procedure of SAS. Individual steers and heifers served as the experimental unit. Independent variables included treatment group, dam RFI category group, dam RFI phenotype group where treatment means were determined using the least squares mean statement of SAS. Correlations between 0 to 70 d and 0 to 120 d, 0 to 70 d and 70 to 120 d, and 0 to 120 d and 70 to 120 d were obtained through Pearson's correlations in SAS. Variables were considered different than zero with P -values ≤ 0.10 .

Experiment 2

Experimental Design

In December of 2008, 46 Simmental by Angus crossbred first calf heifers previously phenotyped postweaning for RFI ($n = 23$ RFI-; $n = 23$ RFI+) were mated to seven RFI phenotyped Simmental by Angus crossbred bulls ($n = 4$ RFI- and 3 RFI+) at SWC. Only five of the seven RFI phenotyped herd sires are represented in the current trial. Of the five herd sires, four were used for artificial insemination (**A.I.**) and one sire

was used for natural service (**N.S.**) (RFI= 0.54). Residual feed intakes for sires used for A.I. were the expected progeny differences (**EPD**) for RFI of each sire (sire A = -0.58; sire B = -0.53; sire C = 0.34; sire D = 0.66). Residual feed intake of the N.S. sire had been measured post-weaning for RFI (RFI = 0.54). Of the 46 matings, 14 produced bulls which comprised the dataset for experiment two (Yr. 2). Fourteen bulls were produced from four different combinations of divergent matings between RFI phenotyped sires and dams (n = 2 RFI- x RFI-; n = 2 RFI- x RFI+; n = 9 RFI+ x RFI+; n = 1 RFI+ by RFI-). Prior to weaning, bull calves were castrated by a licensed veterinarian using both surgical and non-surgical methods of castration. Steers greater than 272 kg of BW were castrated non-surgically using a Callicrate bander with Callicrate castration loops (NO-Bull Enterprises, St. Francis, KS), while steers less than 272 kg of BW underwent surgical castration. At weaning, the 14 steers produced from RFI phenotyped sires and dams were comingled with an additional 18 steers produced from non-divergently mated dams from the SWC cow herd. On July 22, 2010, 32 steers in total were transported to BRTF for individual feed intake measurement. Data analysis for experiment two (Yr. 2) consisted of 14 F2 steer progeny (IBW = 369.35 \pm 11.05 kg; age = 10.69 \pm 0.59 months) produced from 14 divergent matings from RFI phenotyped sires and dams.

Animal Management

Upon arrival steers (IBW = 333.77 \pm 8.54 kg; age = 10.14 \pm 0.12 months) were weighed, de-wormed (Noromectin; 1 ml/ 50 kg of BW) and randomly assigned to four pens (8/pen; 7.6 x 16.5m) each equipped with two GrowSafe[®] feed bunks. Steers were tagged with radio frequency identification tags (RFID; Allflex, Dallas Fort Worth, Texas) in the inner top portion of left ear within 10 cm from the base of the head. Growth

implants were not used. Steers were allowed *ad libitum* access to a receiving diet (Table 3.1) and water over a 14 d receiving period. On August 5, 2010 steers were weighed onto trial and directly transitioned from the receiving diet to study diet (Table 3.10) where they were allowed *ad libitum* access to feed and water over the entirety of the 70 d test duration.

Animal Performance Measurements

Two day consecutive body weights (**BW**) were taken at the onset, mid-point and conclusion of the trial. Body weights were recorded early in the morning prior to delivery of feed to the GrowSafe[®] bunk; however, neither feed or water were removed from pens prior to or on scheduled weigh days. Average daily gain (**ADG**) was the total amount of body weight gained from the initial body weight to the final body weight over the total amount of days on trial. Ultrasonic (**US**) images of the longissimus muscle area (**USLMA**) and backfat depth (**USBF**) (cm) were captured on the second day of each two day weigh period using a 500V Aloka (Corometrics Medical Systems, Inc., Wallingford, CT) ultrasound machine with a 3.5-MHz transducer fitted to a custom beef animal standoff (a gel fitted to contour the shape of the beef animal at the 12th and 13th rib). Ultrasound measurements were recorded between the 12th and 13th ribs for both USLMA and USBF. Each image was traced on the US machine with the measurement recorded in centimeters (cm). Ultrasound technician remained constant throughout the entirety of the trial.

Feed Efficiency Measurements

At the conclusion of the 70 d feed intake trial daily feed intakes were compiled from the GrowSafe[®] feed intake system and averaged for each individual animal for the

duration of the feed intake trial. Residual feed intake was measured as the difference between the animals actual and expected feed intake (Herd and Bishop, 2000).

Regression analysis of actual feed intake upon ADG and average body weight^{0.75} (**MMWT**) was used to model daily feed intake using the general linear model procedure (Proc GLM) of SAS (SAS version 9.2, SAS Inst. Inc., Cary, NC). Residual feed intake was measured amongst progeny (n =14) from RFI divergently mated sires and dams where nine of the 14 steers received creep feed prior to weaning. The model fitted was,

$$Y_i = \beta_0 + \beta_1 \text{ADG}_i + \beta_2 \text{MMWT}_i,$$

where Y_i = average actual daily feed intake (ADFI) for animal i , β_0 = regression intercept, β_1 = partial regression coefficient of ADFI on ADG for animal i , β_2 = partial regression coefficient of ADFI on MMWT for animal i . Feed conversion ratio (**FCR**) was the ratio of average daily feed intake by average daily gain. Residual feed intake category groups (low, average, or high) were determined by one half SD above and below the mean RFI of for the contemporary. Animals with RFI's below one half SD were categorized as low RFI animals and animals with RFI's above one half SD were categorized as high RFI animals. Animals with RFI's between low and high RFI animals were categorized as average. Residual feed intake phenotype groups were animals with either a negative RFI or a positive RFI.

Statistical Analysis

Individual steers served as the experimental unit in experiment two. Dependent variables analyzed for steers included 70 d RFI, FCR, ADG, DMI, USLMA, and USBF. Dependent variables were analyzed using the Proc GLM procedure of SAS. Independent variables included heifer and cow RFI, heifer and cow RFI category group and heifer and

cow RFI phenotype group. Treatment means were determined using the least squares mean statement of SAS (SAS version 9.2, SAS Inst. Inc., Cary, NC). Variables were considered different than zero with P -values ≤ 0.10 .

RESULTS

Experiment 1

Feed efficiency and performance measurements of animals

The regression of actual feed intake upon ADG and MMWT accounted for 33 and 22 percent of the variation in feed intake over a 70 d period for heifers and steers, respectively. Over the last 50 d of trial (70 to 120 d trial) an additional 14% of the variation in feed intake for steers ($R^2 = 0.36$) was accounted for in reference to the initial 70 d trial. The largest amount of variation accounted for in feed intake among steers was 56% over the 120 d ($R^2 = 0.56$) trial.

Least square means of RFI values for low, average, and high RFI heifers were -0.19 ± 0.15 , 0.08 ± 0.15 , and 1.21 ± 0.16 ($P < 0.0001$), respectively over a 70 d test duration ($R^2 = 0.33$; $P < 0.003$). Feed conversion ratio was different between low and high (5.28 ± 0.25 vs. 6.60 ± 0.26 ; $P < 0.001$) and average and high (5.60 ± 0.25 vs. 6.60 ± 0.26 ; $P < 0.01$) RFI heifers with no difference in ADG ($P > 0.10$) among the three heifer RFI categories. Range in RFI between the most and least efficient steers varied among test durations 0 to 70 d (-2.04 vs. 1.87 ; $R^2 = 0.22$), 0 to 120 d (-1.67 vs. 1.48 ; $R^2 = 0.56$) and 70 to 120 d (-1.83 vs. 2.02 ; $R^2 = 0.36$). Residual feed intakes were different among low, average and high RFI steers among test durations 0 to 70 d (-1.28 ± 0.15 , 0.20 ± 0.16 , 1.31 ± 0.17 , respectively; $P < 0.0001$), 0 to 120 d (-0.81 ± 0.13 , -0.00 ± 0.13 ,

1.00 ± 0.15, respectively; $P < 0.0001$) and 70 to 120 d (-1.37 ± 0.16; 0.04 ± 0.15; 1.48 ± 0.18, respectively; $P < 0.001$). Dry matter intakes were different among low, average and high RFI steers over the 0 to 70 d test duration (8.37 ± 0.18 vs. 9.79 ± 0.19 vs. 10.69 ± 0.21, respectively; $P < 0.0001$) and 70 to 120 d test duration (8.89 ± 0.32 vs. 10.60 ± 0.30 vs. 11.22 ± 0.35, respectively; $P < 0.0003$). Dry matter intake only differed between low and high RFI steers over the 0 to 120 d trial (9.14 ± 0.32 vs. 10.56 ± 0.37, respectively; $P < 0.01$). No differences in FCR were observed between the 0 to 120 d and 70 to 120 d intake trials among low, average or high RFI steers; however, low RFI steers had improved FCR's compared to high RFI steers over the 0 to 70d test duration (5.53 ± 0.24 vs. 6.64 ± 0.28, respectively; $P < 0.01$). Average daily gain and MMWT were not different ($P > 0.10$) among low, average and high RFI steers over the 0 to 70 d, 0 to 120 d and 70 to 120 d feed intake trials.

Correlations of feed efficiency

Ranges within RFI listed in the previous section for low, average, and high RFI steers varied as did ranking of feed efficiency among individual steers between test duration 0 to 70 d, 0 to 120 d and 70 to 120 d (Table 3.5). The largest amount of re-ranking occurred between test durations 0 to 70 d and 0 to 120 d where 67% of steers moved one half SD above or below its original RFI (low, average, or high) category group measured during the 0 to 70 d test. Of the 67% that reranked, 57% remained average or efficient while 43% remained average or inefficient. Ten percent of steers moved from either a low to high RFI ($n = 1$) category or a high to low RFI ($n = 1$) in reference to their original RFI category group determined over the initial 70 d trial. Residual feed intake category groups remained similar between 0 to 120 d and 70 to 120

d trials with only 24% of steers moving 0.50 SD above or below their RFI category group obtained over the 120 d test duration. Although RFI category groups were not similar between 0 to 70 d and 0 to 120 d trials, RFI measured between both trials was moderately correlated ($r = 0.49$; $P < 0.03$) with a stronger correlation occurring between RFI values of 0 to 120 and 70 to 120 d trials ($r = 0.91$; $P < 0.0001$).

Treatment effect

Feed efficiency and performance data among treatment groups for heifers and steers are summarized in Tables 3.6 and 3.7. Combinations of sires and dams mated by known RFI phenotype include: RFI- sires mated to RFI- dams (TRT 1), a RFI- sire mated to RFI+ dams (TRT 2) and a RFI+ sire mated to RFI+ dams (TRT 3). Heifer progeny from TRT 1 were more feed efficient than heifer progeny from either TRT 2 or TRT 3. Residual feed intake, FCR and DMI all differed between TRT 1 and TRT 3 ($P < 0.01$; $P < 0.004$; $P < 0.01$, respectively) and between TRT 2 and TRT 3 ($P < 0.03$; $P < 0.002$; $P < 0.03$, respectively) for heifer progeny. Numerical differences in RFI, FCR, and DMI occurred between TRT 1 and 2; potentially due to similar sire RFI phenotype. Average daily gain remained similar among all three treatments ($P = 0.52$).

Variation in feed efficiency and performance traits among treatment groups for steer progeny followed similar trends as their heifer mates, where TRT 1 produced low RFI steers over three consecutive test durations. Contradictive to heifers, feed efficiency and performance traits between TRT 2 and 3 only differed numerically. Residual feed intakes were different between steer progeny from TRT 1 and 3 over the 70 to 120d (-0.41 ± 0.35 vs. 0.99 ± 0.57 , respectively; $P < 0.05$) and 0 to 120 d (-0.34 ± 0.22 vs. 0.80 ± 0.37 , respectively; $P < 0.02$) trials. Over the 0 to 70 d trial RFI tended to be lower for

TRT 1 steers in comparison to TRT 3 (-0.44 ± 0.34 vs. 0.71 ± 0.56 ; $P < 0.09$) while ADG and FCR remained similar. Dry matter intake also tended to be lower for TRT 1 steers in comparison to TRT 3 steers over the 70 to 120 d (9.75 ± 0.37 vs. 11.09 ± 0.61 ; $P = 0.08$) and 0 to 120 d (9.46 ± 0.30 vs. 10.58 ± 0.50 ; $P = 0.07$) trials. Numerical differences in carcass traits and production costs separated the three treatment groups (Table 3.8).

Steers from TRT 1 scanned larger USLMA's ($P < 0.01$) than either TRT 2 or 3, while US images indicated steers produced from TRT 3 tended ($P < 0.09$) to have larger amounts of USBF than TRT 2. Numerically, TRT 2 steers had the largest HCWT (340.53 ± 15.89 kg) among the three treatment groups, while TRT 1 and TRT 3 had similar HCWT (325.27 ± 12.31 vs. 325.11 ± 19.46 kg, respectively). Treatment 3 produced steers with numerically larger USDA YG in comparison to TRT 1 and 2. USDA QG of choice was consistent among steers across all treatments of divergently mated sires and dams.

Production traits DOF, TFC, FC and CV differed numerically among treatment groups for the entirety of the production phase. Treatment group 1 recorded the lowest feed cost while TRT 2 obtained the largest profit margin over both TRT 1 and 3 ($\$684.04$ vs. $\$634.78$ vs. $\$596.73$; standard errors were excluded, respectively). A savings of almost $\$22.00$ /hd in feed was obtained by mating RFI- sires to RFI- dams (TRT 1) in comparison to mating RFI+ sires to RFI+ dams (TRT 3).

Dam effect

Dams were assigned to high, average, and low RFI category groups for both postweaning measurements as heifers and mature measurements as cows. Category groups were assigned by one half SD above and below the average RFI of the contemporary group. Dams categorized as high RFI were feed inefficient while dams in

the low RFI category were feed efficient, average RFI dams were less feed efficient than low RFI dams, yet more feed efficient than high RFI dams. Residual feed intake, DMI, FCR, ADG and MMWT differed numerically between dam RFI categories for heifer progeny. Surprisingly average RFI dams produced lower feed efficiency heifers than high RFI dams (0.30 ± 0.29 vs. -0.04 ± 0.37 , respectively). Although heifer RFI was higher for average RFI cows than high RFI cows, feed conversion ratio was numerically lower for heifers from average RFI cows in comparison heifers from high RFI cows (5.81 ± 0.27 vs. 5.90 ± 0.33). Steer progeny from high RFI (11.11 ± 0.43) cows had statistically larger DMI than progeny from low (9.86 ± 0.43 ; $P < 0.06$) and average (9.64 ± 0.43 ; $P < 0.03$) RFI cows over the 70 to 120d trial with numerically larger DMI over the 0 to 70 d and 0 to 120 d trials. As expected steer progeny from low RFI cows had numerically lower RFI's than average and high RFI cows over the 0 to 70 d test (-0.50 vs. 0.18 vs. 0.19 ; SEM = 0.44; $P = 0.47$, respectively). Average RFI dams produced numerically lower RFI steers over the 0 to 120 d (-0.33 vs. -0.20 ; SEM = 0.30; $P = 0.76$) and 70-120 d (-0.51 vs. -0.22 ; SEM = 0.44; $P = 0.65$), respectively. Residual feed intakes of steer progeny were different between average and high RFI cows over the 0 to 120 d (-0.33 vs. 0.46 , respectively; SEM = 0.30; $P < 0.08$) and 70 to 120 d (-0.51 vs. 0.67 , respectively; SEM = 0.44; $P < 0.07$) feed intake trials. Feed conversion ratio and MMWT differed numerically among dam category groups across all test durations for steers with the exception of MMWT over the 0 to 70 d test where steer MMWT was different between low and average RFI cows (93.33 vs. 82.39 ; SEM = 3.05; $P < 0.02$) and low and high RFI cows (93.33 vs. 84.67 ; SEM = 3.05, respectively; $P < 0.06$). Low RFI cows produced steers with lower FCR's with the exception of the 70 to 120 d trial

where high RFI cows had the lowest FCR; however, this may have been influenced by the numerically larger ADG. Average daily gain was different between steers from average and high RFI cows (0.87 vs. 1.28, respectively; SE = 0.12; $P < 0.03$).

When dams were categorized by RFI- and RFI+ (Table 3.9), RFI- dams produced heifers with numerically lower RFI's (-0.31 vs. 0.30; SEM = 0.27; $P < 0.11$) and FCR's (5.54 vs. 6.09; SEM = 0.24; $P < 0.12$) with similar levels of growth performance (1.73 vs. 1.76; SEM = 0.07; $P = 0.70$) and metabolic body weights (74.43 vs. 76.98; SEM = 1.43, $P = 0.21$) compared with heifers from RFI+ dams. Dry matter intake of heifers was different between RFI- and RFI+ dams (8.20 vs. 9.00 kg/d, respectively; SEM = 0.28; $P < 0.05$). Residual feed intake for steers was lower for RFI- cows than RFI+ cows over the 0 to 70 d (-0.44 ± 0.33 vs. 0.40 ± 0.35 , respectively; $P < 0.10$), 0 to 120 d (-0.34 ± 0.23 vs. 0.33 ± 0.24 , respectively; $P < 0.06$) and 70 to 120 d (-0.41 ± 0.35 vs. 0.42 ± 0.37 , respectively; $P < 0.12$) trials. Similar to RFI, DMI of steers from RFI- dams tended to be lower than steers from RFI+ dams between the 0 to 120 d (9.46 ± 0.30 vs. 10.19 ± 0.32 , respectively; $P < 0.11$) and 70 to 120 d (9.75 ± 0.36 vs. 10.71 ± 0.38 , respectively; $P < 0.08$) trials. Feed conversion ratios were numerically lower for steers from RFI- dams over the 0 to 70 d and 0 to 120 d trials while steers from RFI+ dams had numerically lower FCR's over the 70 to 120 d trial. With the exception of larger MMWT (90.37 ± 2.54 vs. 82.86 ± 2.66 ; $P < 0.06$) for steers from RFI- dams than steers from RFI+ dams over the 0 to 70 d trial, ADG and MMWT were similar between dam RFI phenotypes over the 0 to 120 d and 70 to 120 d trials.

Experiment 2

Animal performance

Correlations between steer RFI with ADG ($r_p = 0.01$; $P = 0.97$) and MMWT ($r_p = 0.00$; $P = 0.99$) were small and non-significant indicating RFI was independent of its component traits. Residual feed intake ($R^2 = 0.79$; $P < 0.001$) among 14 head of steers was the only trait which differed among low, average and high RFI categorized steers (Table 3.11). Range in RFI between the most and least efficient steers (-0.71 vs. 0.73) resulted in a 1.44 kg/d difference in RFI over the 70 d feed intake trial. Dry matter intakes were different between low and average (9.43 ± 0.40 vs. 10.51 ± 0.45 ; $P < 0.11$) and low and high (9.43 ± 0.40 vs. 10.50 ± 0.40) RFI categories. Numerical differences in FCR indicated low RFI steers had improved feed conversions with similar levels of growth and body weights to average and high RFI steers. Ultrasound scans reported USLMA and USBF were not different ($P = 0.23$ and $P = 0.92$) among steer category groups at the onset of trial. Day 70 ultrasound scans reported numerical differences in USLMA (74.78 ± 4.11 vs. 74.33 ± 4.60 vs. 70.81 ; $P = 0.77$) and USBF (1.50 ± 0.09 vs. 1.63 ± 0.10 vs. 1.48 ± 0.09 ; $P = 0.55$) separated low, average and high RFI steers with low RFI steers having larger numerical gains in USLMA with equivalent amounts of gain in USBF to high RFI steers. Average RFI steers had lower RFI's (0.11 ± 0.05 vs. 0.54 ± 0.04 ; $P < 0.0001$) and improved FCR's with numerically larger ADG and MMWT in comparison to high RFI steers. Average RFI steers also had the least amount of USLMA development and largest amount of USBF.

Residual feed intake was the only trait which differed between RFI- and RFI+ steers (Table 3.12). Numerical differences in FCR and DMI indicated RFI- steers had improved feed efficiencies with lower feed intakes. Average daily gain and MMWT were comparable between steer phenotypes. At the beginning of trial, RFI- and RFI+

steers scanned similar loin eyes (61.56 ± 2.49 vs. 61.04 ± 2.16 ; $P = 0.88$) with comparable amounts of fat cover (0.70 ± 0.05 vs. 0.60 ± 0.04 ; $P = 0.13$). Day 70 ultrasound scans indicated RFI- steers had numerically larger USLMA (74.46 ± 3.65 vs. 72.31 ± 3.16 ; $P = 0.66$) with a numerically larger amount of USLMA development over the first 70 days. Amount of back fat between RFI- and RFI+ steers on day 70 were equivalent to one another (1.53 ± 0.08 vs. 1.53 ± 0.07 ; $P = 0.94$); however, RFI- steers had numerically lower amounts of USBF development than RFI+ steers over the 70 d trial.

Progeny relationship to dam RFI

Dam feed efficiency as a heifer. With the exception to gain in USLMA, RFI and RFI category (low, average and high) of dams recorded from postweaning measurement of RFI as virgin heifers showed no correlated response with steer feed efficiency, performance traits, phenotype or category group (Table 3.13). Heifer category group was moderately correlated with USLMA growth over the 70 d trial ($r_p = -0.46$; $P = 0.10$). Pearson correlations for dam phenotype as heifers (RFI-/RFI+) showed strong correlations with steer RFI ($r_p = 0.68$; $P < 0.01$), phenotype ($r_p = 0.60$; $P < 0.05$) and category group ($r_p = 0.62$; $P < 0.05$). Feed conversion ratio and USLMA growth both showed moderate correlations ($r_p = 0.46$; $P < 0.10$ and $r_p = -0.50$; $P < 0.10$) with heifer phenotype, respectively. Dry matter intake, ADG, and gain in USBF showed no correlated response with heifer phenotype.

Feed efficiency and growth performance of steers summarized by their individual dam RFI category groups as heifers (low, average and high) indicated steer RFI was numerically different across heifer category group. Low RFI heifers produced steers with

the lowest numerical RFI, while average RFI heifers produced steers with lower RFI's than steers from high RFI heifers (Table 3.14). Feed conversion ratio tended to be lower while ADG was significantly larger for steers from low RFI heifers than steers from either average or high. Although steers from low RFI heifers were the most feed efficient they did not have the lowest DMI. Dry matter intake from steers of average RFI heifers had the lowest numerical DMI, although steers from low RFI heifers did have a numerically lower DMI than steers from high RFI heifers. Initial scans of USLMA and USBF resulted in no difference in size of USLMA or amount of USBF ($P = 0.85$ and $P = 0.94$, respectively) among progeny of low, average and high RFI heifers. Day 70 ultrasound scans of USLMA tended to be different among steer progeny of low, average and high (91.34 ± 7.24 vs. 73.10 ± 2.41 vs. 70.00 ± 3.62 ; $P < 0.10$) RFI heifers with low RFI heifers producing steers with greater ($P < 0.05$) development in USLMA than progeny from either average or high RFI heifers. Numerical differences in USBF (1.70 ± 0.20 vs. 1.48 ± 0.07 vs. 1.60 ± 0.10 ; $P = 0.43$) and gain in USBF for low, average and high heifers indicated low RFI heifers produced steers with the most amount of USBF at day 70 with the largest amount of gain in USBF over the 70 d trial than either average or high RFI heifers. Steers from average RFI heifers did scan with the least amount of USBF with the lowest amount of USBF gain over 70 days.

Similar to heifer category group, initial scans of USLMA and USBF of steer progeny from RFI- and RFI+ heifers were not different (58.83 ± 3.44 vs. 61.93 ± 1.80 ; $P = 0.44$ and 0.63 ± 0.07 vs. 0.65 ± 0.04 ; $P = 0.89$, respectively). Unlike category group, steer RFI was different ($P < 0.01$) between RFI- and RFI+ heifers (Table 3.15). Feed conversion ratio tended to be lower for RFI- heifers in comparison to RFI+ heifers ($P =$

0.10). Average daily gain was numerically larger and DMI was numerically lower for steers from RFI- heifers. Negative RFI heifers produced steers with numerically larger USLMA (78.44 ± 4.92 vs. 71.81 ; 2.57 ; $P = 0.26$) with numerically leaner body compositions (1.47 ± 0.12 vs. 1.55 ± 0.06 ; $P = 0.56$) than RFI+ steers. Gain in USBF was not different ($P = 0.68$) between heifer phenotype while gain in USLMA was, RFI- heifers produced steers with larger development in USLMA over a 70 d period (19.61 ± 4.36 vs. 9.88 ± 2.28 ; $P = 0.07$).

Dam feed efficiency as a mature cow. Pearson correlations indicated no correlated response among RFI, RFI phenotype (RFI-/RFI+) and RFI category (low, average and high) group of dams as mature cows with feed efficiency and growth performance traits of steers (Table 3.16). Average RFI cows produced steers with numerically lower RFI's with decreases in FCR than steers from either low or high RFI dams (Table 3.17). Dry matter intakes from steers of low RFI cows were larger than steers from average RFI cows ($P < 0.05$). Low RFI cows produced steers with lower RFI's than high RFI cows, DMI tended ($P = 0.12$) to be lower for steers from high RFI cows. Feed conversion ratio and ADG of steers remained numerically different between low and high RFI cows. Steers from low RFI cows initially scanned larger USLMA than steers from average and high RFI cows (72.20 ± 2.74 vs. 59.25 ± 1.58 vs. 58.83 ; $P < 0.01$, respectively). Initial scans of USBF were comparable across low, average and high RFI cows (0.75 ± 0.08 vs. 0.60 ± 0.05 vs. 0.62 ± 0.05 ; $P = 0.31$, respectively). Steers from average RFI cows scanned larger USLMA with leaner body compositions among cow categories on day 70. Steers from average RFI cows also had the most development in USLMA and the least amount of USBF accretion than steers from low and average

RFI cows over the 70 d trial. Numerical differences in RFI, FCR, ADG and DMI indicate RFI- cows produced more feed efficient steers in comparison to RFI+ dams (Table 3.18). Steers from RFI- cows scanned larger USLMA (74.59 ± 4.05 vs. 73.37 ± 3.20 ; $P = 0.82$) with comparable amounts of USBF between (1.58 ± 0.09 vs. 1.51 ± 0.07 ; $P = 0.58$) steers from RFI+ steers. However, RFI+ cows did produce steers with numerically larger developments in USLMA (13.69 ± 2.97 vs. 11.29 ± 3.75) with lower amounts of USBF (0.89 ± 0.08 vs. 0.94 ± 0.10) accretion than RFI- dams.

Divergent matings

Although contemporary groups were small and unequal among mating groups, results were similar to our hypothesis. RFI- by RFI- matings produced RFI- steers while six of the nine RFI+ by RFI+ matings produced RFI+ steers (Figure 3.3). The additional 50% of RFI- sires produced RFI+ steers; however, these sires were mated to RFI+ dams. Of the 4 RFI- steers sired from RFI+ sires three were sired by the same sire; however, one of those matings included a RFI- dam. There were no observations of RFI- dams producing RFI+ steers, where three RFI+ dams produced RFI- progeny.

DISCUSSION

Feed efficiency and performance of animals

Studies have well cited RFI- cattle consume less feed and are equivalent to their RFI+ counterparts in performance (Arthur et al., 1996; Basarab et al., 2003; Castro Bulle et al., 2007). Experiments one and two are in further agreement to these studies where both experiments showed RFI- cattle consumed lower amounts of feed with improved feed conversion and similar growth performance and body size of RFI+ cattle. The most

efficient (RFI-) Angus heifers and bulls consumed 14% less feed than expected compared to the least efficient Angus heifers and bulls consuming 11 and 16% more feed than expected, respectively (Arthur et al., 1996). Kelly et al. (2010a) found low RFI heifers to consume 8.5 to 15.9% less feed with equivalent levels of growth performance and body weights compared to average or high RFI categorized heifers. Low RFI (high feed efficiency) steers on average had a 0.98 kg/d decrease in RFI compared to high RFI steers with similar levels of growth performance (1.11 ± 0.02 vs. 1.07 ± 0.02 kg/d; Herd et al., 2009).

The large amount of variation in feed intake unaccounted for by ADG and MMWT in heifers over the 0 to 70 d trial and steers over the 0 to 70 d and 70 to 120 d feed intake trial is uncertain. Environmental effects prior to trial may have been potential causes in which the 14 d receiving period was not long enough for animals to acclimate. Herd et al. (1997) found gender did not influence feed efficiency or production traits and therefore heifer and bull progeny were combined in the analysis providing a larger contemporary group, along with a 21 d acclimation period prior to test; however, the R-square of the regression of intake on ADG and MMWT was not reported. Although Herd's study included four additional animals in their contemporary, similar results were obtained, where RFI- (high efficiency) animals consumed less feed with no difference in body size or growth performance. Combining steer and heifer progeny in the current trial could not be done as heifers and steers were phenotyped for RFI at two separate time points and were fed different feed rations.

Archer et al. (1997) reported a minimum 70 d trial is required for an accurate measurement of RFI, when BW is recorded every 14 d. Archer and Bergh (2000) found

variation in RFI to normalize on d 70 for Angus cattle while Simmental cattle required 84 days for variation in RFI to normalize, yet all breeds of cattle were fasted for 12 hours prior to BW measurements which may have influenced the accuracy of their results. Residual feed intakes measured over the 70 to 120 d trial were measured under the reported minimum number of days to acquire accurate RFI measurements; however, R^2 values indicated more variation in feed intake in comparison to the 0 to 70 d trial. Differences in the amount of feed intake between the 0 to 70 d and 70 to 120 d trials may have been influenced by the stage of maturity among steers between the two test durations. The 0 to 120 d feed intake trial compiled more measurements of feed intake, growth, and body weight potentially accounting for additional variation in feed intake. Based from these results, the number of animals within a contemporary group as well as the stage of maturity of the animal may influence the accuracy of RFI measured within the contemporary group.

Carcass parameters and composition

There remains a certain amount of uncertainty within the literature in reference to the relationship between RFI of the animal with carcass traits and body composition. Although within the current study USLMA and USBF were not different among low, average and high RFI steers as well as between RFI- and RFI+ steers, low RFI heifers did produce steers with larger USLMA with more development in USLMA over a 70 d period. Variation in USBF and development of USBF was not observed in the current study among category groups and phenotype groups for steers or dams as heifers and cows. Basarab et al. (2003) and Richardson et al. (1998) observed no differences in LMA among high, average, or low RFI steers or between progeny from high or low feed

efficiency production lines. Although Basarab et al. (2003) observed fat accretion to be different between RFI- and RFI+ steers, where RFI- steers deposited a lower amount of fat in reference to RFI+ steers. Additional studies have reported high efficiency line steers had lower amounts of BF ($P < 0.05$) between the 12th and 13th rib-interface and over the rump ($P = 0.10$) with similar percentages of intramuscular fat between selection lines (McDonagh et al., 2001). It was further observed that high efficiency crossbred steers had larger loin eye area's than low efficiency line steers, yet there was no difference in loin eye area between high and low feed efficiency lines of pure bred Angus steers (McDonagh et al., 2001). A combination of steer progeny tested over three individual 70 d feed intake trials concluded highly efficient steers were leaner with smaller loin eye area's than low feed efficiency counterparts yet it was further concluded ultrasound measurements recorded in the feedlot were phenotypically uncorrelated with RFI and did not account for any variation in RFI (Herd et al., 2003b). Carcass data on low, medium and high RFI steers concluded ribeye area (cm²) was different (92.88 vs. 87.88 vs. 89.46, respectively; $P = 0.05$) and backfat (cm) was not different (1.32 vs. 1.28 vs. 1.26, respectively; $P = 0.83$) among steer category groups (Trejo et al., 2010).

Additional research is necessary to further understand the relationship in feed efficiency with loin eye are and carcass composition. Although there appears to be an association between RFI and fat accretion, differences in maturity, breed and pre-trial nutrition may influence body composition of individual animals within a contemporary. With no reported correlations between RFI and LMA, differences in USLMA size and growth among the RFI category and phenotype groups may have been a result of genetic variation in loin eye area among sires rather than variation in energetic efficiency.

Length of trial in experiment two may have been a potential reason for no large observations of differences in USBF between low, average, and high as well as RFI- and RFI+ steers. Final US measurements in experiment one were taken on d 120 in comparison to experiment two which captured a greater portion of the growth period in comparison to the finishing period and therefore may not have been an ample amount of time to accurately compare amount or development of backfat among different RFI categories or phenotypes of steers. Studies have reported gain in ultrasound backfat to be positively correlated with RFI, with no correlation between marbling and RFI (Basarab et al., 2003). Differences in USLMA size or development of USLMA may have been a result of selection or non-selection for increased loin eye area since loin eye area is a moderately heritable trait ($h^2 = 0.46$; Arnold et al., 1991). While there appears to be an association between RFI and fat accretion in the body, research is still needed on this topic as maturity level, sex, production phase, and accuracy of measurement provide a wide range of potential error in the agreement in RFI between carcass traits and fat accretion. The assumption highly feed efficient animals will always be lower in fat content in comparison with lowly feed efficient animals should be proceeded with caution. With variation in fat content within breeds it may be presumed breeds which have the genetic ability to marble better or reach a carcass composition end point quicker are less feed efficient than other breeds do to a their higher fat content. Thus far there have been no observations of reductions in profits at market for highly feed efficient cattle being too lean or low efficiency cattle being too fat (Richardson et al., 1998).

Agreement in RFI

Re-ranking of RFI values over various trial periods indicate selection based upon individual RFI values may be misleading depending on whether the individual animal is within the growth or finishing phase of production. In reference to the current study where 67% of steers reranked in RFI by 0.50 SD, Kelly et al. (2010b) observed 54% of heifers rerank by less than 0.50 SD, yet 24 % of heifers reranked by more than a 1 SD. The current study observed only 10% of steers rerank by more than 1 SD. Differences should be expected between the present study and Kelly's, as Kelly had a five month transition period in between the growing and finishing phase where heifers were later in maturity. The current study measured intake over a consecutive 120 d trial. Differences in the strength of correlations between 0 to 70 d and 0 to 120 d and 0 to 120 d and 70 to 120 d may have been influenced by differences in tissue accretion (Arthur et al., 2001c). Residual feed intake measured within the 0 to 70 d trial consisted mainly of the growth phase where large amounts of lean tissue were being deposited in comparison to lipid. Although RFI measured over the 0 to 120 d trial included the entirety of the growth curve, it also included a percentage of the finishing phase more so than the 0 to 70 d trial. Stronger correlations with better agreements in RFI category groups between the 0 to 120 d and 70 to 120 d trials indicate RFI between the 0 to 70 d test and 0 to 120 d and 70 to 120 d tests are genetically different traits. According to Crews et al. (2003) and Arthur et al. (2001c), for measurements taken on the same trait over two separate time periods to be considered alike the genetic correlation between those traits must be ≥ 0.90 . Arthur et al. (2001c) found RFI between the weaning and yearling growth phases to be correlated ($r_p = 0.43$; $r_g = 0.75 \pm 0.12$), however the genetic correlation was < 0.90 implying RFI measured during weaning phase should be treated as a different trait than RFI measured

during the yearling growth phase. Correlations between RFI's between 0 to 70 d and 0 to 120 d imply they are genetically different traits; however, they remain associated with one another because they are moderately correlated. Therefore, cattle identified as feed efficient early in growth will continue to be more feed efficient through later stages of maturity in comparison to cattle phenotyped as RFI+.

Divergent matings effect on progeny feed efficiency

The significant amount of variation in feed efficiency between heifer and steer progeny from RFI- by RFI- (TRT 1) matings to heifer and steer progeny from RFI+ by RFI+ (TRT 3) matings indicate improvement in progeny feed efficiency is sustainable through genetic selection which is in general agreement with conclusions by Arthur et al. (1996), Veerkamp and Emmans (1995a) and Archer et al. (1998). Between 1993 to 1999 the average improvement or decrease in progeny feed efficiency between high and low feed efficiency lines of cattle were -0.32 and 0.39 kg/d, respectively (Arthur et al., 2001a). A single year of genetic selection resulted in a 68 kg decrease in feed intake by the high feed efficiency line in comparison to the low feed efficiency lines over a 120 d trial with no statistical separation in growth performance (Herd et al., 1997). Angus steers produced from high and low feed efficiency lines differed in feed intake (9.22 ± 0.18 vs. 9.78 ± 0.16 , respectively; $P < 0.05$) and net feed intake (NFI; -0.20 ± 0.11 vs. 0.17 ± 0.10 , respectively; $P < 0.05$) with no differences in performance (Richardson et al., 1998). It was suggested by Herd et al. (2004a), incorporation of high efficiency sires with low estimated breeding values for net feed intake (NFI) would decrease progeny NFI by 26%, increase growth rate by 19% and increase FCR by 41% which would be economically beneficial to producers throughout Australia. Residual feed intake

improved by 0.22 kg/d for high efficiency line steers after one year of divergent selection (Herd et al., 2003b). After five years of divergent selection upon high efficiency (RFI-/NFI-) and low efficiency (RFI+/NFI) lines of cattle no differences in growth performance were observed between the two feed efficiency lines (Arthur et al., 2001a).

Experiment two of the current study was the second generation of divergent selection for RFI. Given the small number of animals within the contemporary of experiment two along with an unequal number of divergently mated RFI sires and dams across mating groups the accuracy amongst these results were anticipated to be low. Although numbers were small, matings based upon heifer RFI produced progeny which aligned themselves close to or within their anticipated realm of feed efficiency. Steers phenotyped opposite of their anticipated RFI phenotype were potentially due to limited numbers within the contemporary. Matings were not made off of RFI measured as mature cows; therefore, additional variation in progeny RFI in relation to sire and dam RFI can be expected. Four of the sires used in experiment two obtained RFI values based from individual progeny RFI. Additional trials utilizing sires which have had RFI's assigned to them based on progeny RFI should be conducted to validate if this method is an accurate representative of the sire actual RFI phenotype. Larger differences with statistical validation in feed efficiency between RFI phenotypes is anticipated through future generations of divergent matings of RFI phenotype cattle. Nielsen et al. (1997a) noted feed intake followed the same pattern as heat loss in divergently selected mice for high and low heat loss. At the 6th and 10th generation of divergent selection upon heat loss, high heat loss mice gained an additional 35 and 85% response in increased heat production than low heat loss mice gained in response to selection (Nielsen et al., 1997b).

After 15 generations of divergent selection for high and low heat loss, high heat loss mice consumed 20.6% more feed than low heat loss mice (Nielsen et al., 1997a). Granted heritability was not calculated for the current experiment Arthur et al.(2001b; 2001d), Hoque et al. (2009) and Lancaster et al. (2009a) all reported moderate heritability for RFI thus providing additional support for divergent selection of RFI. Upon incorporation of divergent selection for RFI within a production system, improvements in progeny and herd feed efficiency can be obtained.

To the authors knowledge this is the first experiment in which sire, dam, and progeny have all been phenotyped for RFI using the GrowSafe[®] feed intake system. The GrowSafe[®] feed intake system has been validated as an accurate method of measuring individual feed intakes in cattle (DeVries et al., 2003; Schwartzkopf-Genswein et al., 2002) and has been used in other studies to measure individual feed intake for the calculation of RFI (Basarab et al., 2003; Golden et al., 2008; Kolath et al., 2006; Meyer et al., 2008). While several studies, including this one, have studied the variation in feed efficiency between high and low feed efficiency lines of cattle, to the authors knowledge this is the first experiment in which an RFI- bull was divergently mated to RFI+ females. As reported in experiment one, RFI- by RFI+ (TRT 2) matings produced progeny which were more feed efficient than the RFI+ by RFI+. Using an RFI- sire on RFI+ cows improved progeny feed efficiency in 50% of the heifers where 67% of the heifers improved their RFI category by 1 SD and 33% of heifers improved their RFI category by 0.50 SD in reference to the their dams original RFI category. Improvement in progeny feed efficiency did vary among the three separate trial periods for steers. Over the 0 to 70d trial 50% of the steers (n = 3) were categorized as high RFI from which roughly 67%

were progeny of dams which were also categorized as high RFI dams, therefore a RFI- bull did not improve progeny feed efficiency on these steers. Of the 50% of average or low RFI (high feed efficiency) progeny, 67% improved by a 0.50 SD while 33% of progeny improved by 1 SD from the original dam RFI category. Three steers did not improve in RFI category over the 0 to 120d trial in reference to their dam's original RFI category; however, 50% of steers did improve in RFI category where 67% improved by 1 SD and 33% improved by a 0.50 SD in comparison to the dam RFI category. For the 70 to 120 d trial 50% of steers showed the same RFI category group as their dams while 67% of the other half of steers improved their RFI category group by a 0.50 SD and 33% of steers improved by 1 SD. Additional research where RFI- sires are mated to RFI+ cows is necessary as these results are based from a small contemporary. Although negative RFI sires improved feed efficiency in progeny from high RFI categorized cows, maintaining the lower one third of feed efficient cows within the herd is unnecessary as they will remain a larger input cost to the operation.

Dam influence on progeny feed efficiency

Several trials have reported RFI to be a moderately heritable trait (Arthur et al., 2001d; Hoque et al., 2007; Lancaster et al., 2009a). As shown in experiment one, dam RFI category and phenotype accurately project progeny feed efficiency with the exception to heifer progeny. Sire RFI may have been a potential source of error in regards to heifers exhibiting improved feed efficiencies from high RFI dams than average RFI dams. While average and high RFI dams were mated to RFI- sires, average RFI dams were mated to a larger percentage of RFI- sires. However, the lowest RFI sire was mated to individual dams within the high RFI category which resulted in some of the

lower RFI heifers which may have skewed the results. When dams were phenotyped by RFI- or RFI+, heifer and steer progeny confirmed RFI- dams produced the most feed efficient progeny with similar ADG and body weight to progeny from RFI+ dams.

A combination of significant correlations with more uniform figures between progeny traits to heifer RFI phenotype based on the heritability of RFI, suggest RFI measured post-weaning as virgin heifers are more accurate predictions of progeny feed efficiency than RFI measured as mature cows. Basarab et al. (2007) reported comparable RFI's between progeny and mature cows, where RFI's of dams were -0.05 vs. 0.44 vs. 1.88 between low, medium, and high RFI progeny. Although progeny and cow RFI agreed with one another, a small but significant phenotypic correlation ($r_p = 0.30$; $P = 0.03$) occurred between progeny RFI and cow RFI which indicated cow RFI was a different trait than post-weaning measurement of progeny RFI (Basarab et al., 2007). Minton et al. (2010) reported progeny RFI's were in better agreement with heifer RFI category compared to cow RFI category.

Better agreement between heifer RFI and postweaning measurements of progeny may be a result of similar nutritional planes and levels of nutrition. In the current study, inclusion rates and ingredients varied between feed rations fed to steer progeny and dams as heifers; however, both trials were no-roughage based rations with similar energy densities and levels of protein. The amount of variation between progeny rations to heifer rations were much less than the amount of variation between progeny feed rations and rations fed to dams as mature cows which consisted of 39% forage. Bormann et al. (2010) suggested RFI measured on faster growing animals on a higher energy dense ration is a different trait than RFI measured on slower growing animals on a lower energy

dense ration. From a production standpoint measuring RFI on mature cows is a much less feasible task than measuring RFI on weaned heifers. With moderate correlations between steer RFI, FCR, phenotype and category with post-weaning RFI as a heifer suggests selection upon heifer RFI is an accurate prediction of progeny feed efficiency and therefore is not required to obtain RFI on mature cows.

CONCLUSION

Divergent matings of RFI phenotyped sires and dams produced progeny of similar RFI phenotype to parent RFI. More efficiently mated RFI- sires to RFI- dams consistently produced more feed efficient progeny of similar size with comparable amounts of growth to progeny produced from divergent matings of RFI+ sires and dams. Utilizing RFI- sires to service RFI+ dams appeared to improve progeny feed efficiency above that of the dam, and therefore provides additional support when retaining positive RFI valued dams which reside in the average category group. Incorporation of RFI as a genetic selection tool is an accurate traits to select upon to improve overall production efficiency and reduce input costs within the production system.

Within the literature there appears to be an association between RFI and fat deposition; indicating more feed efficient animals have less amounts of fat than inefficient animals; however these results cannot be supported from the current study as only numerical differences occurred in USBF measurements between efficient and inefficient steers and steers from efficient and inefficient mating's. Difference in USBF may not have occurred in experiment two due to as a result of the trial ending prior to the finishing phase. It can be speculated from the current trial divergently mated RFI- sires

to RFI- dams produce RFI- progeny which have the capability of depositing more lean tissue growth within the LMA than steer progeny from divergent matings of RFI+ sires and dams.

Moderate to strong correlations between steer feed efficiency traits and steer RFI phenotype with dam RFI phenotype measured postweaning indicates selection upon postweaning measurements of RFI of dams are accurate predictions of progeny RFI measured postweaning. Weak correlations between progeny RFI and RFI phenotype with RFI phenotype of dams as mature cows suggest measurements recorded on the same trait at two different biological stages of production and maturity are different traits. Further research is warranted on larger groups of RFI phenotype animals to validate these conclusions.

Table 3.1. Ingredients and nutrient composition of receiving diet.

Ingredient	% of Diet
Corn	55.00
Receiving Supplement	35.00
Hay	10.00
Nutrient Analysis ^a	
DM	86.8
CP	20.85

^a = DM = percent dry matter of diet; CP = percent crude protein of diet.

Table 3.2. Ingredients and nutrient composition of diets fed to steers in experiment one.

Ingredients ^a	% of Diet
Phase one	
Corn	57.40
Corn bran	25.00
Supplement	17.60
Nutrient Analysis	
DM	84.01
CP	12.43
Phase two	
Corn	57.40
SHP ^b	25.00
Supplement	17.60
Nutrient Analysis	
DM	83.09
CP	11.03
Phase three	
Corn	68.00
SHP	15.00
DDGS ^c	15.00
GPP supplement	2.00
Nutrient Analysis	
DM	84.14
CP	10.87

^a = DM = dry matter; CP = crude protein.

^b = SHP = soyhull pellets.

^c = DDGS = dried distillers grains.

Table 3.3. Ingredients and nutrient composition of diet fed to heifers in experiment one.

Ingredient	% of Diet
Corn	41.30
SHP ^a	45.00
DDGS ^b	10.00
Supplement	2.50
Lime	1.20
Nutrient Analysis ^c	
DM	86.27
CP	10.97

^a = SHP = soyhull pellets.

^b = DDGS = dried distillers grains.

^c = DM = dry matter; CP = crude protein.

Table 3.4. Number of progeny born per divergent mating of RFI phenotyped sires and dams.

Progeny Gender	Treatments (TRT) ^a		
	TRT 1	TRT 2	TRT 3
Heifers	16	10	6
Steers	11	6	4

^a = TRT 1 = RFI- sire by RFI- dam; TRT 2 = RFI- sire by RFI+ dam; TRT 3 = RFI+ sire by RFI+ dam.

Table 3.5. Pearson correlations among individual steer RFI and FCR between test durations 0 to 70 days, 0 to 120 days and 70 to 120 days.

Traits ^a	Test durations		
	0 to 70 d to 0 to 120 d	0 to 70 d to 70 to 120 d	0 to 120 d to 70 to 120 d
RFI	0.49 (0.03)	0.31 (<i>NS</i>)	0.92 (0.01)
FCR	0.76 (0.01)	0.08 (<i>NS</i>)	0.61 (0.01)

^a = RFI = residual feed intake; FCR = feed conversion ratio.

NS = Not Significant.

Table 3.6. Performance and feed efficiency measurements obtained over a 70 day trial on heifer progeny from divergent matings of sires and dams of known RFI phenotypes.

Traits ^b	Treatment (TRT) ^a			<i>P</i> -value
	TRT 1	TRT 2	TRT 3	
n	16	6	10	
RFI	-0.31 ± 0.25 ^c	-0.43 ± 0.41 ^{d,e}	0.75 ± 0.31 ^c	0.03
FCR	5.54 ± 0.21 ^e	5.21 ± 0.37 ^{d,e}	6.59 ± 0.26 ^c	0.003
ADG (kg)	1.73 ± 0.07	1.86 ± 0.11	1.71 ± 0.09	0.52
DMI (kg)	8.20 ± 0.26 ^c	8.23 ± 0.42 ^{d,e}	9.46 ± 0.33 ^c	0.01

^a = TRT 1 = RFI - by RFI -; TRT 2 = RFI - by RFI +; TRT 3 = RFI + by RFI +.

^b = n= number of progeny born per treatment group; RFI = residual feed intake; FCR = feed conversion ratio; ADG = average daily gain; DMI = dry matter intake.

^{cde} = Means with different letters differ across rows (*P* < 0.05).

Table 3.7. Performance and feed efficiency measurements obtained over a 120 day trial on steer progeny from divergent matings of sires and dams of known RFI phenotypes.

Traits ^b	Treatment (TRT) ^a			<i>P</i> -value
	TRT 1	TRT 2	TRT 3	
n	11	6	4	
RFI	-0.34 ± 0.22 ^e	0.02 ± 0.30 ^{d,e}	0.80 ± 0.37 ^c	0.06
FCR	7.56 ± 0.32	7.62 ± 0.44	8.34 ± 0.54	0.46
ADG (kg)	1.51 ± 0.07	1.56 ± 0.09	1.54 ± 0.12	0.92
DMI (kg)	9.46 ± 0.30 ^h	9.94 ± 0.41 ^{g,h}	10.58 ± 0.50 ^f	0.18

^a TRT 1 = RFI- sire by RFI- dam; TRT 2 = RFI- sire by RFI+ dam; TRT 3 = RFI+ sire by RFI+ dam.

^b = n = number of progeny per treatment; RFI = residual feed intake; FCR = feed conversion ratio; ADG = average daily gain; DMI = dry matter intake.

^{cde} = Means with different letters differ across rows ($P < 0.05$).

^{fgh} = Means with different letters differ across rows ($P \leq 0.10$).

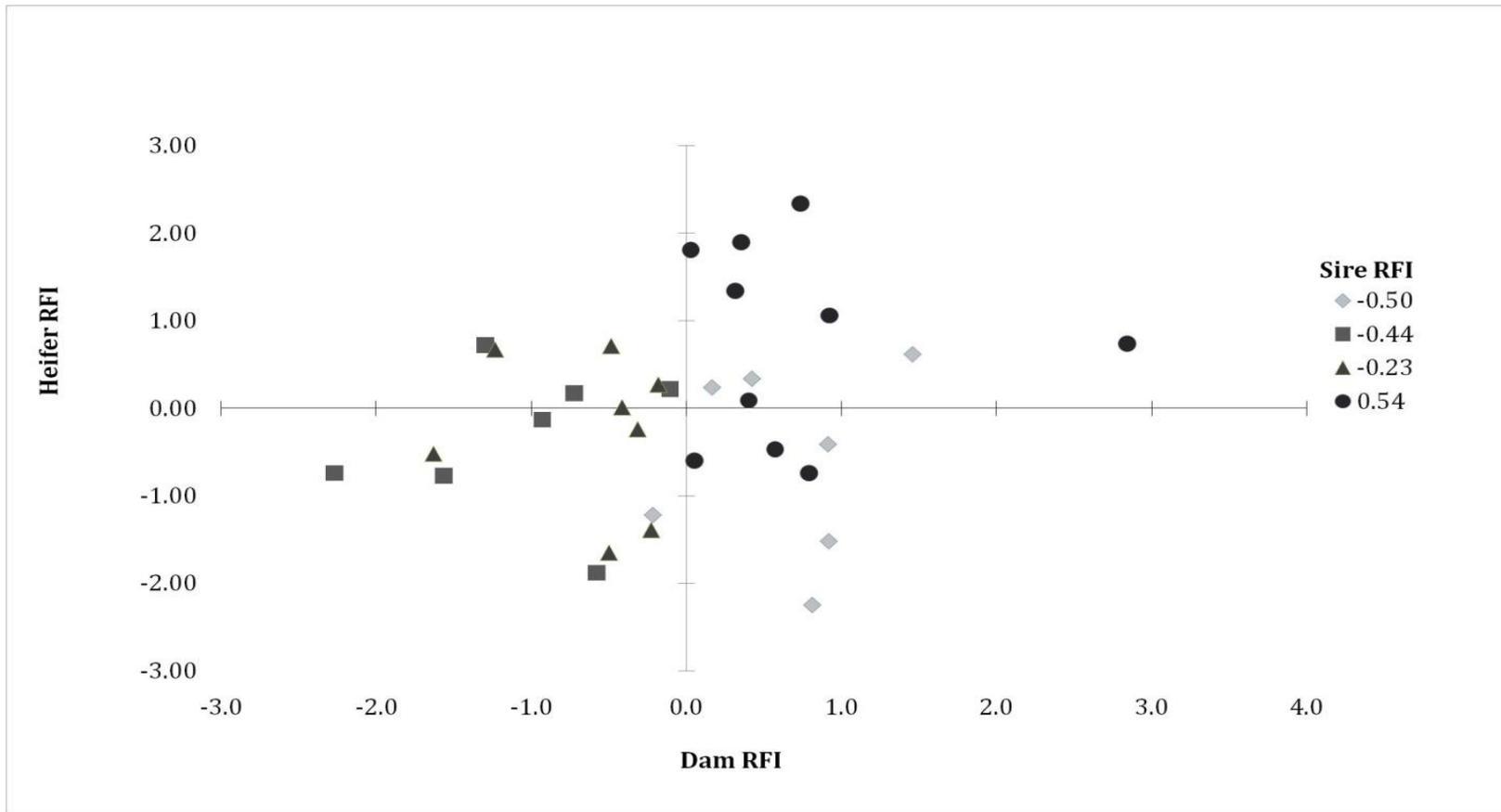


Figure 3.1. Residual feed intake of heifer progeny from divergently mated sires and dams of known RFI phenotype.

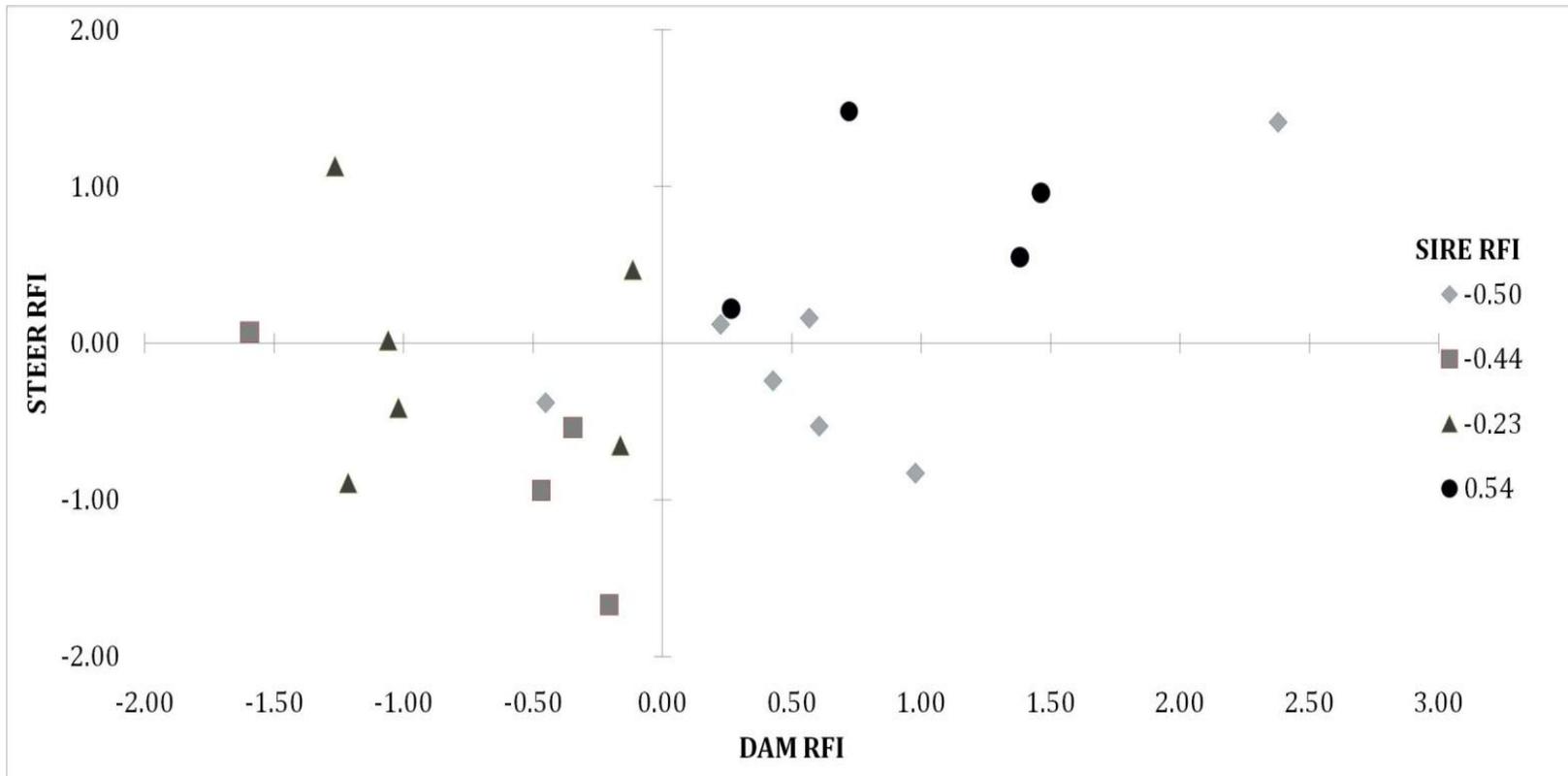


Figure 3.2. Residual feed intake of steer progeny from divergently mated sires and dams of known RFI phenotype.

Table 3.8. Carcass trait measurements and production costs for steer progeny produced from divergently mated sires and dams of known RFI phenotype.

Traits ^b	Treatment (TRT) ^a			<i>P</i> -value
	TRT 1	TRT2	TRT3	
HCWT (kg)	325.27 ± 12.31	340.53 ± 15.89	325.11 ± 19.46	0.73
REA (cm ²)	76.16 ± 1.78 ^g	67.47 ± 2.30 ^{f,g}	68.35 ± 2.82 ^f	0.01
BF (cm)	0.69 ± 0.06 ^{hi}	0.65 ± 0.08 ⁱ	0.88 ± 0.10 ^h	0.20
Quality Grade ^c	340.00 ± 15.78	383.33 ± 20.37	350.00 ± 24.95	0.26
Yield Grade	1.90 ± 0.20	1.83 ± 0.26	2.50 ± 0.31	0.23
DOF	164.60 ± 8.84	177.67 ± 11.41	159.00 ± 13.97	0.54
Feed (kg) ^d	1,883.79 ± 92.53	2,086.90 ± 119.454	1,993.78 ± 146.30	0.42
Yardage ^e	\$57.61 ± 3.09	\$62.18 ± 3.99	\$55.65 ± 4.89	0.54
Feed Cost	\$372.99 ± 18.32	\$413.21 ± 23.65	\$394.77 ± 28.97	0.42
Carcass Value	\$1,065.38 ± 55.57	\$1,159.43 ± 71.74	\$1,047.15 ± 87.87	0.52

^a = TRT 1 = RFI- by RFI- mating; TRT 2 = RFI- by RFI+ mating; TRT 3 = RFI+ by RFI+ mating.

^b = DOF = days on feed, HCWT = hot carcass weight; REA = longissimus muscle area measured between the 12th and 13th ribs; BF = back fat measured at the 12th and 13th rib.

^c = choice (400), low choice (350), select (300)

^d = \$180.00/ ton

^e = \$0.35/d

^{fg} = Means with different letters differ across rows (*P* < 0.05).

^{hi} = Means with different letters differ across rows (*P* ≤ 0.10).

Table 3.9. Least square means of steer progeny RFI for dam RFI phenotype over trials 0 to 70 days, 0 to 120 days and 70 to 120 days.

Test Duration	Dam RFI Phenotype	
	RFI-	RFI+
0 to 70 d	-0.44 ± 0.33	0.40 ± 0.35
0 to 120 d	-0.94 ± 0.42	0.99 ± 0.46
70 to 120 d	-0.41 ± 0.35	0.42 ± 0.37

Table 3.10. Ingredients and nutrient composition of diet fed to steers in year 2 of trial.

Ingredient	Percent of Diet
Whole Corn	72.35
Dried Distillers Grain Supplement	15.00
	12.65
Nutrient Analysis ^a	
DM	86.28
CP	18.12

^a = DM = percent dry matter of diet; CP = percent crude protein of diet.

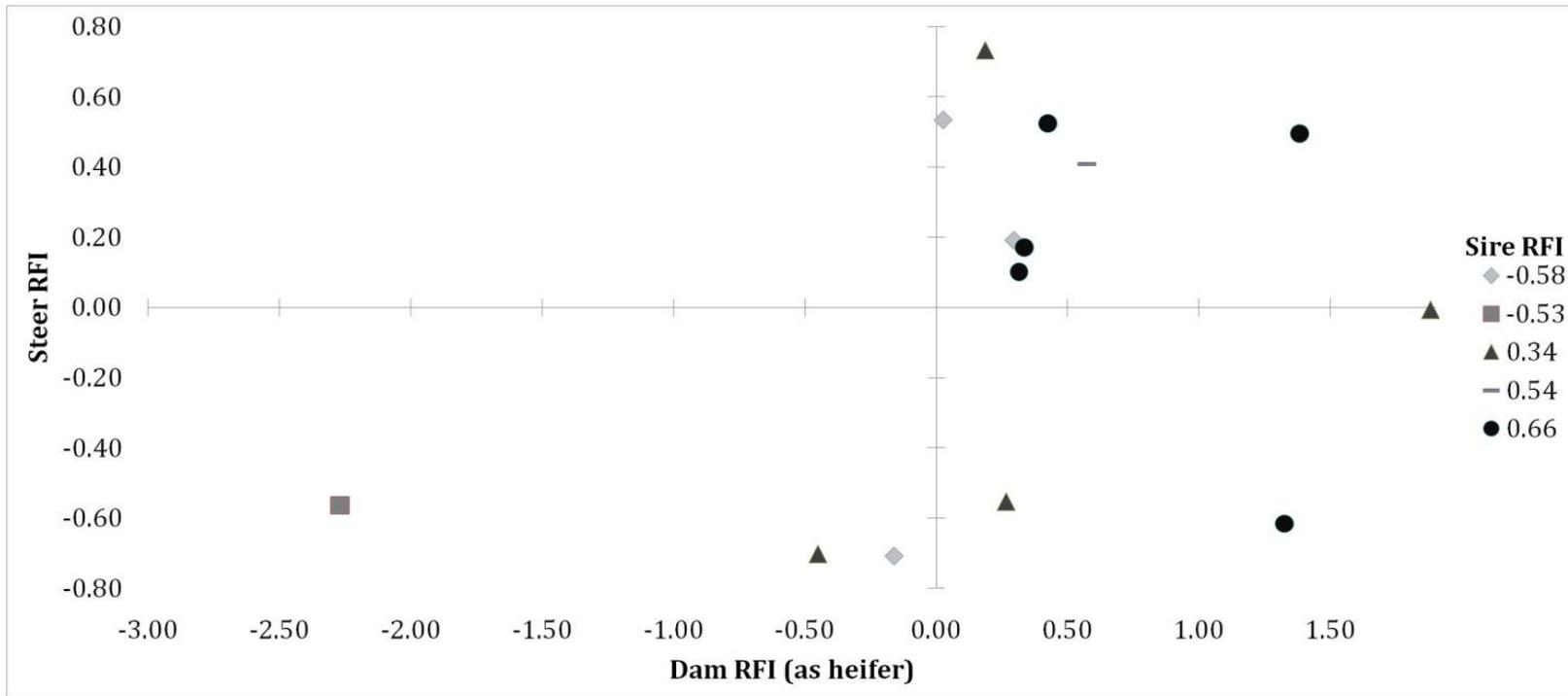


Figure 3.3. Residual feed intake of steer progeny from divergently mated sires and dams^a of known RFI phenotype. ^a = Dam RFI were measured postweaning as virgin heifers.

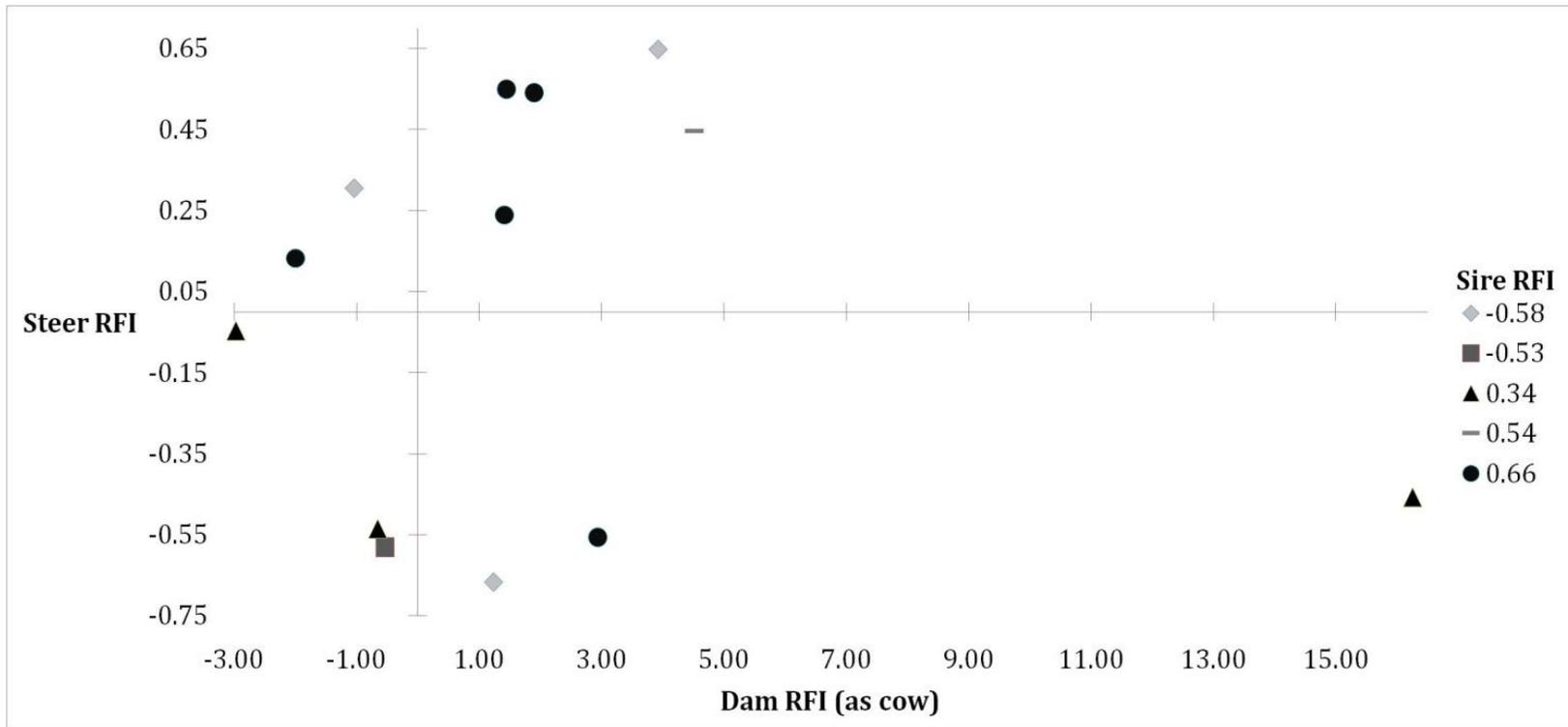


Figure 3.4. Residual feed intake of steer progeny from divergently mated sires and dams^a of known RFI phenotype. ^a = Dam RFI was measured as mature lactating cows.

Table 3.11. Feed efficiency and growth performance traits measured over a 70 day trial for low, average and high RFI steers produced from sires and dams of known RFI phenotypes in year two.

Traits ^a	Steer RFI Category			<i>P</i> -value
	Low	Average	High	
RFI	-0.63 ± 0.04 ^d	0.11 ± 0.05 ^c	0.54 ± 0.04 ^b	< 0.0001
FCR	5.56 ± 0.43	5.86 ± 0.48	6.12 ± 0.43	0.67
DMI (kg)	9.43 ± 0.40 ^f	10.51 ± 0.45 ^e	10.50 ± 0.40 ^e	0.15
ADG (kg)	2.02 ± 0.17	2.11 ± 0.19	2.03 ± 0.17	0.94
MMWT (kg)	95.94 ± 3.40	99.34 ± 3.80	96.42 ± 3.40	0.78
Gain in LMA (cm ²)	15.07 ± 3.85	8.74 ± 4.31	11.45 ± 3.85	0.56
Gain in BF (cm)	0.84 ± 0.11	1.00 ± 0.12	0.84 ± 0.11	0.54

^a = RFI = residual feed intake, FCR = feed conversion ratio; DMI = dry matter intake; ADG = average daily gain; MMWT = average body weight^{0.75}.

^{bcd} = Means with different letter differ across rows (*P* < 0.05).

^{ef} = Means with different letters differ across rows (*P* ≤ 0.10).

Table 3.12. Feed efficiency and growth performance traits measured over a 70 day trial for RFI- and RFI+ steers produced from sires and dams of known RFI phenotype in year two.

Trait ^a	Steer RFI Phenotype		<i>P</i> -value
	RFI-	RFI+	
RFI	-0.53 ± 0.10	0.39 ± 0.08	< 0.0001
FCR	5.58 ± 0.37	6.05 ± 0.32	0.36
DMI (kg)	9.82 ± 0.40	10.35 ± 0.35	0.34
ADG (kg)	2.09 ± 0.15	2.02 ± 0.13	0.74
MMWT (kg)	98.25 ± 3.00	96.21 ± 2.60	0.62
Gain in LMA (cm ²)	12.90 ± 3.53	11.27 ± 3.06	0.73
BF (cm)	0.83 ± 0.10	0.93 ± 0.08	0.49

^a = RFI = residual feed intake; FCR = feed conversion ratio; DMI = dry matter intake; ADG = average daily gain; MMWT = average mid weight^{0.75}.

Table 3.13. Pearson correlations measured among RFI, FCR, ADG, DMI, phenotype and category for year two steers with dam RFI, phenotype and category measured postweaning as a heifer.

Trait ^a	RFI _{heifer}	Phenotype _{heifer}	Category _{heifer}
RFI _{steer}	0.33	0.68***	0.22
FCR _{steer}	0.42	0.46*	0.27
ADG _{steer}	-0.27	-0.22	-0.14
DMI _{steer}	0.38	0.42	0.32
Phenotype _{steer}	0.18	0.60**	0.07
Category _{steer}	0.35	0.62**	0.30

^a = RFI = residual feed intake measured on steer progeny and dams as heifers; FCR = feed conversion ratio; ADG = average daily gain; DMI = dry matter intake; Phenotype = RFI- or RFI+ values of steers and dams as heifers; Category = low, average or high RFI values based off of a 0.50 SD from the mean of the group for steers and dams as heifers.

*** Correlations are different from zero at $P < 0.01$.

** Correlations are different from zero at $P < 0.05$.

*Correlations are different from zero at $P < 0.10$.

Table 3.14. Feed efficiency, growth performance, development in longissimus muscle area and development in backfat for steer progeny categorized by dam RFI phenotype measured postweaning as a heifer.

Trait ^a	Heifer RFI Category			<i>P</i> -value
	Low RFI	Average RFI	High RFI	
RFI	-0.56 ± 0.54	0.03 ± 0.18	0.08 ± 0.27	0.57
FCR	4.25 ± 0.86 ^f	6.00 ± 0.29 ^e	5.90 ± 0.43 ^{e,f}	0.20
ADG (kg)	2.83 ± 0.26 ^b	1.92 ± 0.09 ^d	2.15 ± 0.13 ^{c,d}	0.02
DMI (kg)	10.36 ± 0.96	9.81 ± 0.32	10.77 ± 0.48	0.28
Gain in LMA (cm ²)	29.82 ± 7.09 ^b	11.20 ± 2.36 ^{c,d}	9.24 ± 3.54 ^d	0.07
Gain in BF (cm)	1.10 ± 0.24	0.83 ± 0.08	0.95 ± 0.12	0.48

^a = RFI = residual feed intake; FCR = feed conversion ratio; ADG = average daily gain; DMI = dry matter intake.

^{bcd} = Means with different letters differ across rows (*P* < 0.05).

^{ef} = Means with different letters differ across rows (*P* ≤ 0.10).

Table 3.15. Feed efficiency, growth performance, development in longissimus muscle area and development in backfat for steer progeny categorized by dam RFI phenotype measured postweaning as a heifer.

Trait ^a	Heifer RFI Phenotype		<i>P</i> -value
	RFI-	RFI+	
RFI	-0.66 ± 0.23	0.18 ± 0.12	0.01
FCR	5.06 ± 0.49	6.06 ± 0.25	0.10
ADG (kg)	2.19 ± 0.20	2.01 ± 0.11	0.46
DMI (kg)	9.35 ± 0.54	10.33 ± 0.28	0.13
Gain in LMA (cm ²)	19.61 ± 4.36	9.88 ± 2.28	0.07
Gain in BF (cm)	0.83 ± 0.14	0.90 ± 0.07	0.67

^a = RFI = residual feed intake; FCR = feed conversion ratio; ADG = average daily gain; DMI = dry matter intake.

Table 3.16. Pearson correlations measured among RFI, FCR, ADG, DMI, phenotype and category for year two steers with dam RFI, phenotype and category measured as a mature cow.

Trait ^a	RFI _{cow}	Phenotype _{cow}	Category _{cow}
RFI _{steer}	-0.10	0.24	0.12
FCR _{steer}	0.04	0.26	0.09
ADG _{steer}	-0.22	-0.22	-0.23
DMI _{steer}	-0.29	0.08	-0.30
Phenotype _{steer}	-0.14	0.22	0.08
Category _{steer}	-0.16	0.18	0.13

^a = RFI = residual feed intake measured on steer progeny and dams as mature cows; FCR = feed conversion ratio; ADG = average daily gain; DMI = dry matter intake; Phenotype = RFI- or RFI+ values of steers and dams as mature cows; Category = low, average or high RFI values determined from 0.50 SD from the mean of the group for steers and dams as mature cows.

** Correlations are different from zero at $P < 0.05$.

*Correlations are different from zero at $P \leq 0.10$.

Table 3.17. Feed efficiency, growth performance, development in longissimus muscle area and development in backfat for steer progeny categorized by dam RFI phenotype measured as a mature cow.

Trait ^a	Cow RFI Category			<i>P</i> -value
	Low RFI	Average RFI	High RFI	
RFI	0.04 ± 0.38	-0.12 ± 0.22	0.12 ± 0.24	0.24
FCR	6.47 ± 0.60 ^d	5.25 ± 0.34 ^f	6.21 ± 0.38 ^{d,e}	0.13
ADG (kg)	2.09 ± 0.26	2.17 ± 0.15	1.93 ± 0.17	0.48
DMI (kg)	11.41 ± 0.65 ^b	9.73 ± 0.37 ^c	10.10 ± 0.41 ^{b,c}	0.13
Gain in LMA (cm ²)	2.63 ± 4.43 ^{c,d,e}	18.04 ± 2.56 ^{b,d}	10.48 ± 2.80 ^{b,c,e}	0.03
Gain in BF (cm)	0.90 ± 0.17	0.87 ± 0.10	0.96 ± 0.11	0.82

^a = RFI = residual feed intake; FCR = feed conversion ratio; ADG = average daily gain; DMI = dry matter intake.

^{bc} = Means with different letters differ across rows (*P* < 0.05).

^{def} = Means with different letters differ across rows (*P* ≤ 0.10).

Table 3.18. Feed efficiency, growth performance, development in longissimus muscle area and development in backfat for steer progeny categorized by dam RFI phenotype measured postweaning as a mature cow.

Trait ^a	Cow RFI Phenotype		<i>P</i> -value
	RFI-	RFI+	
RFI	-0.15 ± 0.23	0.09 ± 0.18	0.43
FCR	5.51 ± 0.42	5.99 ± 0.34	0.39
ADG (kg)	2.16 ± 0.16	2.01 ± 0.13	0.48
DMI (kg)	10.03 ± 0.48	10.19 ± 0.38	0.80
Gain in LMA (cm ²)	11.29 ± 3.75	13.69 ± 2.97	0.63
Gain in BF (cm)	0.94 ± 0.10	0.89 ± 0.08	0.70

^a = RFI = residual feed intake; FCR = feed conversion ratio; ADG = average daily gain; DMI = dry matter intake.

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