Residual Feed Intake: Animal Performance, Carcass Quality and Body Composition

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Introduction

Feed efficiency has a major influence on the unit cost of beef cattle production. Gibb and McAllister (1999) have reported that a 5% improvement in feed efficiency has an economic impact four times greater than a 5% improvement in average daily gain. In addition, the cost of feed is second only to fixed costs in importance to the profitability of commercial beef operations (Basarab, 1999). The relative importance of the cost of feeding in beef operations is due to the fact that 70-75% of the total dietary energy cost in beef production is used for maintenance (Ferrell and Jenkins 1985; NRC 1996). However, genetic variation in maintenance energy requirement of cattle is moderately heritable (h^2 = 0.22-0.71), suggesting an opportunity to select for more efficient cattle (Carstens et al. 1989; Bishop 1992). Selection for lower maintenance requirements is difficult and measures of feed efficiency such as Kleiber ratio and feed conversion efficiency are related to measures of body size, growth rate, composition of gain and appetite (Arthur et al. 2001a). A new concept called residual feed intake (RFI) is a feed efficiency trait that has been found to be independent of body weight and weight gain (Koch et al. 1963), and is defined as the difference between an animal's actual feed intake and its expected feed requirements for maintenance and growth. The trait is moderately heritable (h^2 = 0.29-0.46), implying that improvements could be made in feed efficiency without affecting body size, and thus maintenance requirements or growth rate (Archer et al. 1998; Arthur et al. 2001a). However, differences in efficiencies of growth may also be due to differences in composition of live weight gain (Pullar and Webster 1977; Ferrell and Jenkins 1998). For example, differences in rates of water and protein accretion have an influence on rate and efficiency of body weight gain, primarily because of the lower energy content of water and protein relative to fat (Ferrell and Jenkins 1998). Conversely, higher maintenance costs are frequently associated with greater visceral organ weights and increased feed intake (Ferrell and Jenkins 1998). In addition, higher maintenance costs are more associated with body protein than with body fat (Pullar and Webster, 1977). Thus, the negative consequences of selecting for RFI are uncertain, although selection for RFI has been associated with reduced carcass

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fat content (Richardson et al. 2001). This review explores current literature on the relationships between RFI and carcass quality, body composition and growth rate.

Relationships between RFI and Animal Performance

Growth Rate and Body Size

Residual feed intake as a measure of feed efficiency and by definition, adjusts for feed intake for gain and metabolic mid-point weight (Koch et al. 1963). Thus, in theory the phenotypic correlation between RFI and measures of growth and body size are automatically zero. Several studies; Archer et al. (1998), Arthur et al. (2001c), Arthur et al. (2001a) in Australia and France, Basarab et al. (2003) Crews et al. (2003) in Canada, and Koch et al (1963), Jensen et al. (1992) in the United States have demonstrated that the phenotypic correlations between RFI and ADG and body size are close to zero. For example, among 148 steers with RFI values from -1.95 to 1.82 kg/day, we did not observe any phenotypic correlations between RFI and ADG, and RFI and metabolic mid-point weight (Figure. 1) (Basarab et al. 2003).

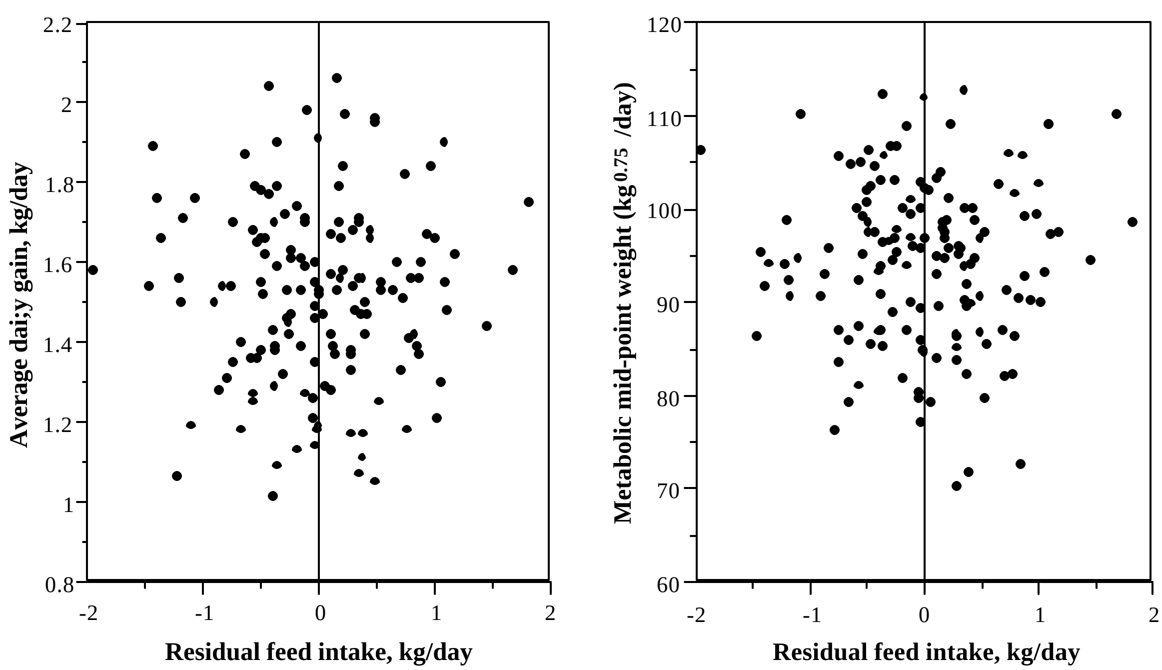

Figure 1. Relationships between residual feed intake and average daily gain and metabolic mid-point weight in 148 crossbred steers on a finishing diet.

In theory, RFI is thus, phenotypically independent of growth and body size. However, Archer et al. (1998) and Herd and Bishop (2000) reported genetic correlations between RFI and yearling weight of –0.25 and 0.15, respectively. Jensen et al. (1992) obtained genetic correlations between RFI and ADG of 0.32 and –0.24 for two different test periods, while Arthur et al. (2001a) reported genetic correlations between RFI and ADG of -0.10 for Charolais bulls (n=792) fed *ad libitum*. On the other hand Arthur et al. (2001c), reported that RFI was genetically independent of ADG (r_g = -0.04) and metabolic mid-point weight or body size (r_g = -0.06). These data are thus, equivocal on the direction or magnitude of the genetic correlations between RFI and production traits. A large study of a divergent selection started in 1993 by Australian researchers has helped in determining the impact of selection for RFI on production traits. In this study, the top 5% of efficient bulls (negative RFI) were mated to the top 50% of efficient heifers, while the bottom 5% of inefficient bulls (positive RFI) were mated to the bottom 50% of inefficient heifers (Arthur et bal. 2001b). Their results revealed that after two generations of divergent selection for RFI, no differences were observed in the yearling weight or ADG of progeny from negative or positive RFI parents (Table 1).

Table 1. Performance of progeny from low or high residual feed intake bulls and heifers after five years of selection[a]

Traits	Low residual feed intake parents	High residual feed intake parents	Yearly Correlated response
Number of animals	62	73	
Residual feed intake, kg/day	-0.54b	0.71c	0.25
365 day live weight, kg	384.3	380.7	0.72
Average daily gain, kg/day	1.44	1.40	0.01
Actual feed intake, kg/day	9.4b	10.6c	0.24
kg gain/kg feed	0.15b	0.13c	0.24

[a]Adapted from Arthur et al. (2001b)
b,c means in the same row differ, P<0.05

Feed Intake and Feed Conversion Ratio

Various researchers including Herd and Bishop (2000), Arthur et al. (2001a), and Arthur et al (2001c) have reported moderate and positive phenotypic correlations (r_p) between RFI and dry matter intake (DMI). These values have ranged from r_p = 0.64 in Hereford, r_p = 0.60 in Charolais, and r_p = 0.72 in Angus cattle. Similarly, the r_p between RFI and feed conversion ratio (FCR) ranged between 0.53 and 0.70 in these same studies. Figure 2 shows the results of a Canadian study using 148 feedlot steers from five genetic strains on a finishing diet by Basarab et al. (2003). The study showed that

RFI was correlated positively with DMI ($r_p = 0.42$, $P < 0.01$) and FCR ($r_p = 0.44$, $P < 0.01$). This study also reported that low RFI steers consumed 10.4% less dry matter ($P<0.01$) and had a 9.4% improvement in FCR ($P < 0.01$) compared to high RFI steers. Genetically, RFI is also moderately and positively related to DMI ($r_g = 0.69$ and 0.79; Arthur et al. 2001a, c) and FCR ($r_g = 0.66$ and 0.85; Arthur et al. 2001 a,c).

These results indicate that selection for low RFI will result in reduced feed intake and improved FCR, with no adverse affect on growth and body size.

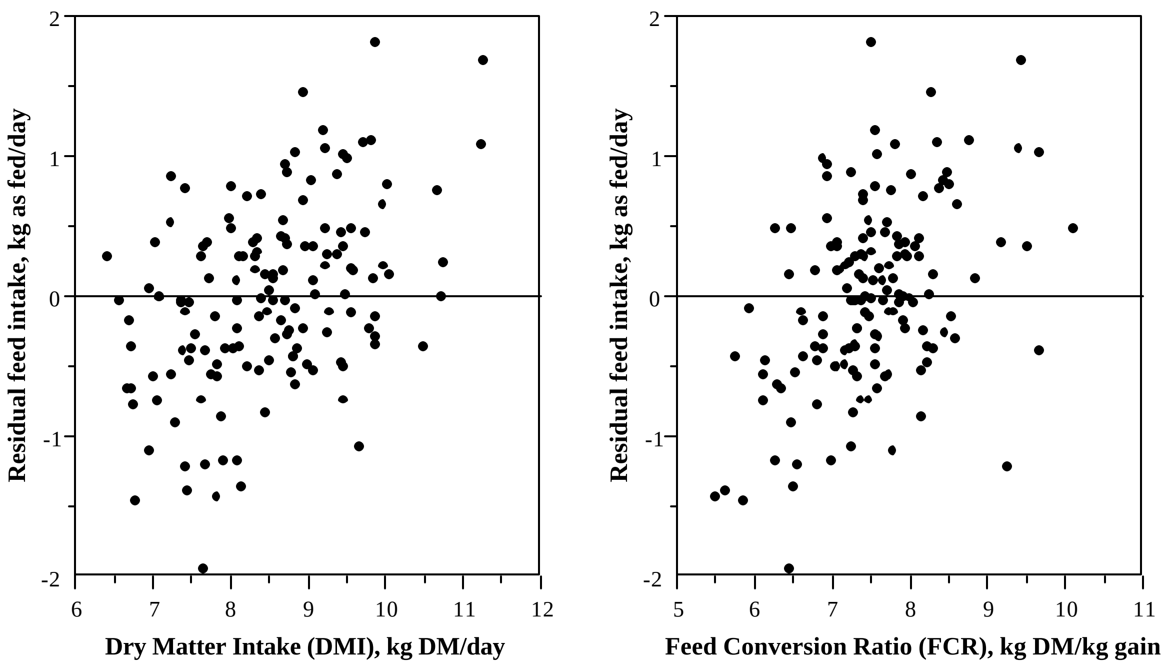

Figure 2. Relationship between residual feed intake and dry matter intake (RFI = -2.30±0.41 + 0.27±0.05DMI, $R^2 = 0.177$, $P<0.0001$), and residual feed intake and Feed Conversion Ratio (RFI = -2.63±0.45 + 0.35±0.06FCR, $R^2 = 0.193$, $P<0.0001$).

Cow Reproduction Performance

There is not a lot of data in the literature on the consequences and impact of selecting for RFI on cow reproductive performance. Herd et al. (2002) and Herd and Bishop (2000) have been the researchers to report that the genetic correlations between post-weaning RFI and cow mature size are low ($r_g = -0.22$) or near zero ($r_g = -0.09$;) indicating that selection for low post-weaning RFI will not be accompanied by an increase in cow weight. Herd et al (2002) also reported a strong, positive genetic correlation between post-weaning RFI and feed intake of the cow ($r_g = 0.64$). Post-weaning RFI of heifers is also strongly correlated ($r_g = 0.58$) with RFI during first lactation (Niewhof et al. 1992). These results suggest that selection for low post-weaning RFI will reduce feed intake by the cow, with no increase in cow weight or body size. On the other hand, these positive impacts of RFI on cow reproductive performance would not occur if we selected for low FCR, because post-weaning FCR and cow size is negatively related (r_g = -0.54) and post-weaning FCR and cow feed intake is poorly related (r_g = 0.20; Herd et al. 2002).

Several studies are presently underway in Canada and Australia on the longer-term consequences of selecting for post-weaning RFI on cow reproduction and efficiency.

Relationships between RFI and Carcass Quality and Composition

Carcass characteristics

The relationships between RFI and carcass characteristics have been the most contentious since the introduction of the concepts of RFI. Arthur et al. (2001c) reported low phenotypic correlations between RFI and ultrasound backfat thickness (r_p = 0.14), rump P8 fat depth (r_p = 0.11) and longissimus muscle area (r_p = 0.06). Basarab et al. (2003) found no relationships between RFI and ultrasound backfat thickness (r_p = 0.02; P=0.82), longissimus muscle area (r_p = -0.01; P=0.94), gain in longissimus muscle area (r_p = 0.04; P=0.65) and marbling score (r_p = 0.13; P=0.11). However, these researchers did report low, positive relationships between RFI and gain in ultrasound backfat thickness (r_p = 0.22, P < 0.01), gain in ultrasound marbling (r_p = 0.22, P < 0.01), carcass marbling (r_p = 0.15, P = 0.07) and dissectible carcass fat (r_p = 0.14, P = 0.09) and a low, negative relationship between RFI and dissectible carcass lean (r_p = -0.21, P = 0.01). These relationships indicate a small and positive association between RFI and fatness. However, Crews et al. (2003) reported low, negative genetic correlations between RFI and backfat thickness (r_g = -0.24±0.30 and r_g = -0.09±0.36) on a growing and finishing diet respectively. They also reported a moderate, negative genetic correlation between RFI and marbling score (r_g = -0.44±0.36 on a finishing diet). Jensen et al. (1992) also reported negative genetic correlations between RFI and carcass fat percentage. These results indicate that RFI was genetically associated with the increased potential for deposition of subcutaneous and intramuscular fat. However, in all cases the genetic correlations are low and the standard errors relatively high, indicating that the relationships may not be different from zero. Thus it is unclear from these studies whether RFI is related to carcass fatness.

Richardson et al. (2001) reported on the longer-term consequence of selecting for port-weaning RFI. In their study progeny from cattle selected for low RFI had 13.2% less subcutaneous and intermuscular fat than the progeny from cattle selected for high RFI (Table 2). The efficient progeny also had 12.4% less carcass fat than the inefficient progeny. This lower carcass fat content in the efficient progeny raises several concerns, such as the potential genetic antagonisms of RFI with marbling and reproductive fitness and the effect that composition of gain has on the true energetic efficiency of the animal. Thus it is possible that differences in RFI are partially due to differences in fattening and not due to inherent differences in the energy required for maintenance and growth of specific animal types. Indeed, Basarab et al (2003) concluded that attempts should be made to adjust RFI equations for changes in ultrasound backfat thickness and marbling score.

Table 2. Weight of carcass fat for yearling Angus steer progeny of parents selected for low (efficient) or high (inefficient) residual feed intake.[a]

Traits	Low residual feed intake parents	High residual feed intake parents	Sign.
Number of animals	16	17	
Cold carcass weight, kg	240	245	NS
Carcass fat (IM and SQ)[b] kg	42.1	48.5	$P < 0.05$
Carcass fat/final weight, %	9.9	11.3	$P < 0.05$
Total dissectible fat/final weight, %	19.8	21.5	$P < 0.10$

[a] Adapted from Richardson et al. (2001).
[b]IM = Intermuscular fat; SQ = Subcutaneous fat.

Body Composition and Composition of Gain

Differences in feed efficiency between animals have been attributed to differences in the composition of live weight gain (Pullar and Webster 1977; Ferrell and Jenkins 1998). For example, differences in rates of water and protein accretion have an influence on rate and efficiency of body weight gain, primarily because of the lower energy content of water and protein relative to fat (Ferrell and Jenkins 1998). In addition, higher maintenance costs are highly associated with greater visceral organ weights and increased feed intake (Ferrell and Jenkins 1998), and higher body protein than body fat (Pullar and Webster, 1977). DiCostanzo et al (1990) estimated that 9.3 times more energy is required to maintain 1 kg of protein (807.1 KJ/kg) than to maintain 1 kg of fat (86.6 KJ/kg) because of the higher turn-over rate for protein than fat. Basarab et al. (2003) found no relationship between RFI and empty body fat ($r_p = 0.12$, $P = 0.14$), but observed a negative trend between RFI and empty body protein ($r_p = -0.14$, $P = 0.09$). The phenotypic correlation between RFI and gain in empty body fat was low ($r_p = 0.26$, $P < 0.01$, Fig. 3), with no relationship between RFI and gain in empty body protein. Basarab et al. (2003) also reported that low RFI steers had 3.1% more empty body water, 6.0% less empty body fat than high RFI steers (Table 3). These results suggest that steers with low RFI had a slightly slower rate of empty body fat deposition than steers with high RFI. Thus, we suggest that adjustment for this bias in body composition

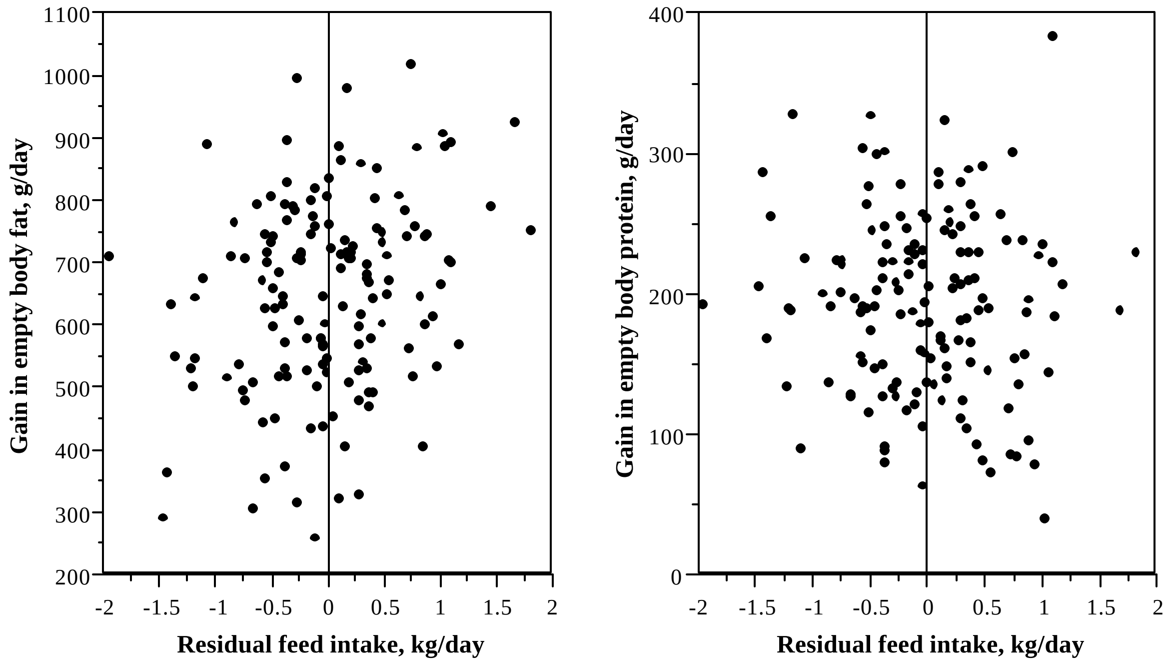

Figure 3. Relationship between residual feed intake and gain in empty body fat (r_p = 0.26, P = 0.002, n=148) and gain in empty body protein (r_p = -0.11, P = 0.164, n=148).

needs to be made by measuring animals for ultrasound backfat thickness and marbling score at the beginning and end of the test period.

Table 3. Body composition and daily accretion rates of water, protein, fat and ash in steers with high, medium and low residual feed intake.[a]

Traits	Residual feed intake group[b]			SEM	Probability
	High	Medium	Low		
Number of steers	43	61	44		
Empty body composition					
Water, g/kg	510b	513b	526a	3.0	0.015
Fat, g/kg	282a	281a	265b	3.8	0.021
Protein, g/kg	167	165	167	1.5	0.733
Ash, g/kg	41	40	42	0.6	0.152

[a] Adapted from Basarab et al. (2003)
[b]Residual feed intake groups are defined as follows: High = RFI is > 0.5 SD above the

mean; Medium = RFI is ± 0.5 SD above and below the mean; Low = RFI is < 0.5 SD below the mean.

Partitioning of Energy

Results of recent studies (Basarab et al. 2003) suggest that there are differences in the use of energy between low- and high-RFI cattle. There is a strong, positive phenotypic correlation between RFI and metabolizable energy intake (MEI; r_p = 0.80, P<0.01; Basarab et al. 2003). Thus, high RFI steers consumed 4.6% more MEI and produced 5.3% more heat than medium RFI steers and consumed 11.3% more MEI and produced 10.3% more heat than low RFI steers (Table 4). High RFI steers also partitioned more of the increase in MEI towards heat production and less toward retained energy than either medium or low RFI steers. Reasons for these difference may relate to the finding that low and medium RFI steers had lower weights of liver (P <0.01), small and large intestine (P = 0.09), and stomach and intestine (P < 0.01) than high RFI steers. Other researchers (NRC 1996; Ferrell and Jenkins 1998) have reported that the efficiency of ME use for retained energy is not constant, but decreases as MEI increases. Ferrell and Jenkins (1998) suggested that a portion of non-linearity in the relationship of retained energy on MEI was due to a depression in metabolizability of the diet at high levels of intake, higher maintenance cost or heat increment of feeding at higher levels of feed intake and heavier organ weights of stomach complex, intestines, heart, lung, kidney and spleen. This later point is significant since visceral organs can account for 50% of the energy cost of maintenance.

Table 4. Metabolizable energy intake (MEI), retained energy, heat production and weights of various organs at slaughter in steers with high, medium and low residual feed intake.[z]

Traits	Residual feed intake group			SEM	Probability
	High	Medium	Low		
Number of steers	43	61	44		
Empty body component gain, g/(kg$^{0.75}$ .day)					
MEI, KJ/(kg$^{0.75}$ .day)	1083a	1035b	973c	4.4	< .001
Retained energy, KJ/(kg$^{0.75}$ .day)	332a	322a	292b	6.1	0.002
Heat Production, KJ/(kg$^{0.75}$ .day)	751a	713b	681c	7.3	< .001
Weight of organs at slaughter, kg					
Liver	6.57a	6.18b	6.06b	0.08	0.007
Stomach and intestine	48.73a	45.98b	45.05b	0.56	0.004
Small and large intestine	30.15	28.47	27.18	0.67	0.093

[z] Adapted from Basarab et al. (2003).

Physical activity

In poultry and pigs, the level of physical activity is strongly associated with feed efficiency, accounting for 29-79% of the variation in maintenance requirements in chickens (Luiting et al. 1991) and 47% of the variation in RFI in pigs (DeHaer et al. 1993). These results have given credence to the assertions that the physiological mechanisms associated with differences in RFI in cattle undoubtedly include variation in activity. Although few studies have examined the relationships between level of physical activity and RFI in cattle, Basarab et al. (2003) reported that low, medium and high RFI steers did not differ ($P > 0.1$) in the number of visits to the feeder or in the total time spent eating each day. Phenotypic correlations between RFI and number of visits to the feeder ($r_p = 0.14$, $P = 0.08$) and total time spent eating each day ($r_p = 0.13$, $P = 0.12$) did show a small, positive trend toward high RFI steers making more visits to the feeder and spending more time eating each day. In addition, Nkrumah et al. (2003) reported a strong, positive phenotypic correlation ($r_p = 0.75$, $P < 0.01$) between RFI and total time spent eating each day in 90 hybrid beef calves (299 kg). We suggest that these results point to subtle but increasing evidence of differences in physical activity contributing to differences in RFI in cattle.

Summary and Conclusion

Feed efficiency has a major influence on the unit cost of beef cattle production. Residual feed intake has been proposed as a measure of feed efficiency that is moderately heritable and independent of growth and body size. Residual feed intake is not phenotypically related to measures of animal growth and body size, while genetically these relationships are either low or near zero. Residual feed intake is moderately and positively related to feed intake and Feed Conversion Ratio in beef cattle. Phenotypic correlations for ultrasound and carcass backfat thickness and marbling are low, implying a small positive association between RFI and fatness. However, the genotypic correlations between RFI and carcass backfat and marbling ranged from +0.17 to -0.44 and these measures have had relatively high standard errors, indicating that the genetic relationships may not differ from zero. Residual feed intake tended to be negatively related to empty body protein and positively related to gain in empty body fat suggesting that low RFI animals have a slightly slower rate of fat deposition than high RFI animals. Residual feed intake is positively related to metabolizable energy intake, heat production and retained energy, indicating that as RFI increased, more of the MEI was partitioned toward heat production and less toward live weight gain. Weight of liver, small and large intestine, and stomach and intestine were heavier in high RFI animals. There is some evidence to show that a portion of the greater MEI consumed by high RFI animals may be due to differences in the chemical composition of gain. However, a greater proportion may be due to differences in visceral weight, maintenance and heat increment of feeding and inherent differences in metabolic processes affecting metabolizable energy intake. We suggest that some effort may be required to adjust residual feed intake for differences in the chemical composition of gain so as not to adversely affect carcass characteristics in feeder cattle and fat deposition in breeding females.

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