VARITION IN ENERGY EXPENDITURES BETWEEN GROWING STEERS WITH DIVERGENT RESIDUAL FEED INTAKES

A Thesis

by

MONTE BLAINE WHITE III

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

December 2004

Major Subject: Animal Science

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Approved as to style and content by:

Gordon E. Carstens (Chair of Committee)	Thomas H. Welsh Jr. (Member)
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ABSTRACT

Variation in Energy Expenditures Between Growing Steers with Divergent Residual Feed Intake. (December 2004)

Monte Blaine White III, B.S., Texas A&M University

Chair of Advisory Committee: Dr. Gordon E. Carstens

Objectives of this study were to determine if variation in energy expenditures contributed to differences in feed efficiency between low and high RFI steers. Nine steers with the lowest and highest residual feed intakes (RFI) were selected from 169 Braunvieh-sired crossbred steers that were individually fed a pelleted roughage-based diet for 77 d. Following the RFI measurement period, heat production (HP) measurements were obtained using indirect calorimetry while steers were fed the same roughage diet (RD) and on a high-concentrate diet (CD). Linear regression analyses of log HP or retained energy on ME intake were used to determine energy partitioning. Motion and lying activity were measured concurrently with HP on the RD and CD. During the RFI measurement period, low RFI steers had lower ($P < 0.01$) RFI (-1.7 vs. 1.6 ± 0.17 kg/d), DMI (7.7 vs. 10.2 ± 0.42 kg/d) and feed:gain ratio (F:G; 7.2 vs. 10.6 ± 0.60), but similar final BW and ADG compared to high RFI steers. However, there were smaller differences in DMI (8.4 vs. 9.7 ± 0.38 kg/d; $P < 0.05$; 7.56 vs. 8.16 ± 0.31; $P = 0.19$) and F:G (10.0 vs. 10.9 ± 0.40; $P = 0.36$; 6.5 vs. 7.5 ± 0.30; $P < 0.05$) between low and high RFI steers, on the RD and CD, respectively. ME for maintenance (ME_m; $kg^{.75}$ d^{-1}) and the partial efficiencies of ME used for maintenance and gain were similar for

low and high RFI steers. Likewise, no differences were found in fasting HP or fed HP. Motion activity was lower ($P < 0.05$) for low RFI steers compared to high RFI steers during fasting HP. Covariate analysis of HP at the same activity level yielded similar results. At slaughter, weights of lung and trachea ($P < 0.05$), spleen ($P < 0.05$) and adrenal gland ($P = 0.07$) were higher for low RFI cattle. The lack of differences in energy partitioning between divergent RFI steers may have been the result of alterations in feeding behavior or stress imposed by adapting steers to calorimetry chambers.

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CHAPTER I

INTRODUCTION

Feed input comprises more than 60 percent of the costs of producing beef, yet emphasis on improving profitability has been primarily approached through selection for output traits. Traditionally, attempts to improve genetic potential for feed efficiency in beef cattle have been accomplished by selection for feed conversion ratio (FCR), a gross measurement of feed intake to live weight gain. Feed conversion ratio does not fully depict variation in feed consumption due to the disproportionate selection pressure it places on its component traits of growth and feed intake (FI), and FCR does not attempt to account for feed requirements needed for maintenance and growth (Arthur et al. 2001a). Since FCR is inversely related to growth traits, selection for FCR in growing cattle will likely lead to larger mature cows (Herd and Bishop, 2000), increase feed costs for the breeding herd and not necessarily improve feed partitioning or profitability in an integrated beef operation.

A significant improvement in profitability could be achieved through a reduction of production costs via implementation of selection strategies to improve feed efficiency, independent of growth rate and BW. Genetic variation in maintenance energy requirements of cattle is moderately to highly heritable and, therefore, an opportunity to select for more efficient cattle may exist (Carstens et al., 1989). Residual feed intake (RFI), as first defined by Koch et al. (1963), is expressed as the difference between actual feed intake and the feed an animal is expected to consume based on its body size

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This thesis follows the style and format of Journal of Animal Science.

and growth rate. Thus, RFI is a measure of the variation in feed intake beyond that which is needed for maintenance and growth requirements (Archer et al., 1999). Residual feed intake is moderately heritable and phenotypically independent of growth rate and BW in growing cattle; however, RFI has been shown to be genetically independent of ADG, but in some cases weakly correlated with BW (Herd and Bishop, 2000; Arthur et al., 2001a, 2001c). Cattle identified as having low RFI have lower feed intakes and FCR when compared to cattle identified as having high RFI (Herd et al., 2002; Basarab et al., 2003). Similarly, cattle divergently selected for postweaning RFI have demonstrated direct selection responses equating to substantial differences in feed intake between selection lines (Arthur et al., 2001b; Richardson et al., 1998) with no changes in body weight or growth rates observed. Although negative consequences of selection for RFI are uncertain, cattle selected for low RFI have shown small associations with a reduction in carcass fat content (Richardson et al., 2001b).

Differences in efficiency of growth are partially explained by differences in composition of live weight gain (Hansson et al., 1967). It has been documented that deposition of lean tissue is energetically more efficient than fat deposition (McDonald et al., 1998) and less energy is required to maintain fat compared to lean tissue (DiCostanzo et al., 1990). However, higher maintenance requirements are more frequently associated with greater visceral organ weights and increased feed intakes (Ferrell and Jenkins, 1984b). Similarly, increases in feed intake have been associated with decreases in efficiencies of gain, suggesting maximum efficiency may not occur at maximum intake (Ferrell and Jenkins, 1998a). Physical activity has also been associated

with higher basal metabolic rates and energy expenditures (Hoffmann and Scholze, 1990). Recently Basarab et al. (2003) found in a comparative slaughter study, greater metabolizable energy (ME) intakes by high RFI steers were offset by a disproportionate increase in energy required for maintenance and heat increment of feeding. However, chemical composition of gain did account for a small portion of the greater ME intake by high RFI steers. Recently, Richardson et al. (2001a) estimated that energy expenditure associated with activity explained approximately 10% of the variation in RFI. In poultry, divergently selected for RFI 75 and 25% of observed differences in fed HP were attributed to heat increment and physical activity (Lutting et al., 1991). Further research is warranted to determine the biological sources of variation in RFI in cattle.

CHAPTER II

REVIEW OF LITERATURE

Feed efficiency in growing cattle

The most common measure of feed efficiency is feed conversion ratio or its inverse, gross efficiency. Feed conversion ratio (FCR) is simply defined as the ratio of inputs (feed) to outputs (product). In meat production systems, outputs are defined in terms of weight gain of growing animals, therefore, FCR would be the ratio between feed intake and weight gain over a defined period of time. The period of growth over which feed conversion ratio is measured is usually defined on a time-constant basis (growth and feed intake measured between two set points in time). Alternatives to the time-constant basis are a weight-constant basis (feed required for growth from weight *a* to an end weight *b*) or a maturity-constant basis (feed and growth measured from a stage of maturity *a* to *b*, or from subcutaneous fat depth *a* to *b*). Both alternatives are used in attempt to remove maturity effects from FCR comparisons.

Differences in feed efficiency have the ability to impact the profitability of an integrated production system, which has led to the universal use of FCR by livestock producers to select for more efficient poultry, swine and cattle. It has been widely demonstrated that FCR is moderately heritable (Table on p. 9). Heritability estimates for FCR in growing cattle range from 0.17 ± 0.09 (Herd and Bishop, 2000) to 0.46 ± 0.04 (Arthur et al., 2001c). It has also been well documented that FCR is both phenotypically and genetically correlated with aspects of production among livestock species. Bishop et al. (1991) found that FCR was negatively correlated with ADG (r = -0.33) and back fat

(r = -0.33) and positively correlated with feed intake (r = 0.49) and BW (r = 0.15) suggesting progeny with lower (more desirable) feed conversion ratios were fatter, gained faster and yielded carcasses with higher quality grades and less desirable yield grades. In a similar study, Brelin and Brannang (1982) reported negative phenotypic correlations between feed efficiency (ratio of feed energy to live weight gain) and carcass muscle content (r = -0.45) and daily gain (r = -0.55), but only a weak correlation with carcass fat content (r = 0.06). Arthur et al. (2001a) reported strong genetic and phenotypic correlations between FCR and ADG (r_g = -0.62; r_p = -0.74), but weak correlations between FCR and back fat (r_g = 0.03; r_p = 0.08) and longissimus muscle area (r_g = -0.12 r_p = 0.03). These studies demonstrate that strong genetic and phenotypic correlations exist between FCR and growth rate and stage of maturity. A negative correlation between feed efficiency and fat may exist in younger growing cattle, and a positive correlation may exist in older cattle when fat deposition is considerable (Brelin and Brannang, 1982).

The strong genetic correlation between FCR and growth (Table on p. 11) suggests that selection for growth will produce correlated improvements in FCR, thus reducing the justification for measuring feed intake in order to improve feed efficiency. However, it is well-known from the literature that FCR increases as animals get older (Hansson et al., 1967), which is explained by the fact that, as animals mature, maintenance energy requirements increase as a proportion of the feed consumed and the energy content of gain increases, due to greater fat deposition.

Feed efficiency in adult cattle

Maintenance requirement can be defined as the feed energy required for zero body weight change, or zero body energy change (Ferrell and Jenkins, 1985). Research has shown that 70 to 75% of total annual energy requirements for the production of beef are needed to maintain the typical breeding herd. Variation in energy requirements for maintenance appear to be greater than variation in energy requirements for growth, gestation or lactation (Ferrell and Jenkins, 1985). It has been well documented that sex (Ferrell et al., 1979), season (Blaxter and Boyne, 1982) current nutritional level and previous nutritional level (Koong et al., 1982) play important roles in determining energy requirements for maintenance in ruminant animals.

There are a number of studies demonstrating that maintenance requirements and feed conversion ratio differs between breeds of cattle. Ferrell and Jenkins (1984) found that Angus and Herford cattle had lower maintenance requirements than Simmental and Charolais cows. Frisch and Vercoe (1984) found that 15-month-old Herford x Shorthorn bulls required approximately 20% more feed to maintain the same body weight as Brahman bulls. Comerford et al. (1991) found variations in FCR between Simmental, Limousine, Polled Hereford, and Brahman and concluded that Brahman crosses have lower feed requirements for maintenance. Maintenance energy requirements have also been reported to be lower in beef breeds than dairy breeds (Blaxer and Wainman, 1966) and lower in *Bos indicus* than *Bos taurus* breeds (Frishc and Vercos, 1977). Differences in energy required for maintenance may be associated with differences among animals in their level of production (Ferrell and Jenkins, 1985; Frisch and Vercoe, 1984; Taylor et

al., 1986) or the proportion of metabolically highly active organs (Ferrell and Jenkins, 1985). Hotovy et al. (1991) suggested that there is a genetic component to variation in fasting heat production and maintenance energy requirements in beef cattle. Koong and Ferrell (1990) stated fasting heat production can differ up to 40% for animals of same age and weight, but with different nutritional backgrounds.

There are a few studies relating genetic variation in maintenance requirements within breeds. Taylor et al. (1981) found a genetic coefficient of variation of 6.4% using Ayrshire twins, indicating genetic variation in maintenance efficiency. Carstens et al. (1989) measured heat production at fasting and maintenance in pairs of monozygous Angus x Hereford and Bazona x Hereford twins at 9 and 20 months of age and found significantly more variation in maintenance energy requirements between twin pairs compared to within twin pairs. Heritability estimates for maintenance energy requirements were 0.71 ± 0.17 and 0.49 ± 0.22 at 9 and 20 months of age, respectively.

Although selection for improved FCR may improve efficiency during the growth and finishing phase of beef production it will not necessarily improve the efficiency or profitability of the entire production system. Selection for genotypes with high growth rates and hence improved FCR will also increase mature cow size (Herd and Bishop, 2000) and increase maintenance requirements (Ferrell and Jenkins, 1985). Thus, direct or indirect selection for FCR in growing animals will increase the feed costs of the breeding herd and not necessarily improve feed efficiency and profitability in integrated beef operations.

Residual feed intake

An alternative measure of feed efficiency is residual feed intake (RFI), which was first proposed by Koch et al. (1963). Koch et al. (1963) suggested that feed intake could be adjusted for BW and weight gain (or any other production trait or energy sink identified), effectively partitioning feed intake into two components: (1) the feed intake expected for a given level of production; and (2) a residual portion. Residual feed intake is expressed as the difference between actual feed intake and the feed an animal is predicted to consume based on its body size and growth rate. Therefore, larger and faster-growing cattle would be expected to consume more feed than smaller and slower-growing cattle. Cattle that consume less than their predicted feed intake based upon their BW and growth rate would have a negative RFI or a superior feed efficiency. By definition, RFI is phenotypically independent of the production traits used to calculate predicted feed intake and is a measure of feed intake beyond that needed to support maintenance and growth requirements (Archer et al., 1999). Recent studies have also shown that RFI is moderately heritable (Table 1.)

Residual feed intake has been shown to be phenotypically independent of ADG and BW in growing cattle (Arthur et al., 2001c). However, Kennedy et al. (1993) found that when RFI is calculated by phenotypic regression of production on feed intake, the resulting measure of efficiency is not necessarily genetically independent of production. Selection responses to RFI based on genotypic regression would be expected to be independent of production, and be more likely to reflect genetic differences in inherent relationships between feed intake and production. In studies where the genetic

Table 1. Summary of studies reporting heritability estimates of residual feed intake (RFI) and feed conversion ration (FCR) in growing calves

	RFI	FCR	
Breed	Heritability	Heritability	Reference
British	0.28 ± .11	ND[a]	Koch et al., 1963
Swedish Red & White	0.27 ± .33	0.35 ± .24	Berlin & Brannang, 1982
Holstein & Brown Swiss	0.28 ± .11	ND	Jensen et al., 1992
Beef cattle	ND	0.32 ± .02	Koots et al., 1994[b]
British	0.46 ± .07	ND	Archer et al., 1998
Hereford	0.16 ± .04	0.17 ± .09	Herd & Bishop, 2000
Angus	0.39 ± .03	0.29 ± .04	Arthur et al., 2001a
Charolais	0.39 ± .04	0.46 ± .04	Arthur et al., 2001c

[a]ND = not determined.
[b]Weighted averaged for 23 studies.

correlations between phenotypic RFI and production traits are close to zero, the results for phenotypic RFI would be expected to be very similar to those of genotypic RFI (Archer et al., 1999). Literature estimates of genetic correlations between RFI and ADG and BW are presented in Table 2.

Positive genetic and phenotypic correlations have been reported between RFI and FCR (Table 2), suggesting an improvement in RFI would result in an improvement in FCR. Arthur et al. (2003) more recently has shown that steers born to parents selected for low RFI (improved feed efficiency) for two generations were similar in weight and ADG, but ate 15% less feed than steers born to parents selected for high RFI. Basarab et al. (2003) reported similar results, finding that steers with low RFI (< 0.5 SD from the mean) consumed 10.4% less dry matter than high RFI steers (> 0.5 SD from the mean). Feed conversion ratio was 9.4% lower in low RFI steers compared to high RFI steers even though growth rate and body size were similar. Genetic variation in RFI has also been reported in chickens, (Gabarrou et al., 1998) swine, (Johnson et al., 1999) and dairy cattle (Veerkamp et al., 1995).

Strong evidence now exists in growing cattle that there are both phenotypic and genetic variations in feed efficiency traits (Archer et al., 1999) which are moderately heritable. This would suggest that genetic improvement could be made through selection for RFI. Since there is a strong negative correlation between FCR and growth traits and a positive correlation between RFI and FCR , RFI could be used as an alternative selection criterion for feed efficiency in current breeding programs.

Table 2. Summary of studies reporting genetic and phenotypic correlations[a] between performance and feed efficiency traits with measures of efficiency in growing steers and bulls

	Arthur et al., 2001a		Arthur et al., 2001c		Herd and Bishop, 2000		Archer et al., 1998		Jensen et al, 1992	
Trait	r_p	r_g	r_p	r_g	r_p	r_g	r_p	r_g	r_p	r_g
Residual feed intake:										
ADG	-0.06	-0.04	0.01	-0.10	-0.01	0.09	0.02	0.02	-0.04	0.42
BW[b]	0.02	-0.06	0.03	0.32	-0.01	0.15	-0.03	-0.25	ND	ND
Feed intake	0.72	0.69	0.60	0.79	0.70	0.64	0.56	ND	.09	.43
Feed conversion ratio	0.53	0.66	0.57	0.85	0.61	0.70	ND	ND	ND	ND
Feed conversion ratio:										
ADG	-0.74	-0.62	-0.46	ND[c]	ND	ND	ND	ND	ND	ND
BW[b]	0.16	-0.01	-0.08	0.24	ND	ND	ND	ND	ND	ND
Feed intake	0.23	0.31	0.48	0.64	ND	ND	ND	ND	ND	ND

[a] r_g = genetic correlation and r_p = phenotypic correlation

[b]Correlations reported in literature of RFI and FCR with BW are approximately yearling weights with the exception metabolic mid-test body weight reported by Arthur et al. (2001a).

[c]ND = Not determined.

Recent studies have suggested that heat production (Basarab et al., 2003), activity (Richardson et al., 2004), feeding behavior (Richardson et al., 2001a), body composition (Aruthur et al., 1997), visceral organ mass (Basarab et al., 2003), protein turnover (Herd et al., 2001), digestibility (Herd et al., 2004) and metabolism (Richardson et al., 2001a) may account for portions of the variation in RFI. Studies have also attempted to quantify the degree to which these parameters contribute to variation in RFI among poultry (Luiting, 1990) and swine (de Haer et al., 1993).

Heat production in poultry

There are numerous studies in poultry which have examined the variation in heat production accompanied by the difference in energy intake among poultry selected for high and low RFI. The higher energy intake of high RFI birds should be offset by either an enhanced energy expenditure in the form of basal metabolic rate, diet-induced thermogenesis or retained energy (Gabarrou et al., 1997b) compared the lower energy intake of low RFI birds. Gabarrou et al. (1997b) examined energy expenditure by indirect calorimetry in cockerels selected for low and high RFI over seventeen generations. In this study, there was no difference in fasting heat production (FHP) between the low and high RFI birds even though ME intake was 40% greater for high RFI birds compared to low RFI birds. In a similar study, Geraert et al. (1998) found that FHP was numerically higher in high RFI cockerels (17%) compared to low RFI cockerels although this difference was not significant. Diet-induced thermogenesis (DIT), expressed as the difference between fed and fasted HP, was 84% higher in the high compared to low RFI cockerels and 31% higher when calculated as a percent of ME

intake. Differences in DIT calculated from the regression between HP and physical activity explained 75% of the difference in HP and the remaining 25% could be explained by activity-related HP (Gabarrou et al., 1997b). Gabarrou et al. (1998) also found that high RFI birds exhibited a regulatory thermogenesis, which allowed them to dissipate excess energy when fed 100% and 130% of control intake, compared to low RFI birds. Gabarrou et al. (1997b) found that propranolol (β-adrenergic blocking agents) decreased HP in high RFI cockerels with no reduction in HP among low RFI cockerels, suggesting the existence of a β-adrenergic control of DIT in high RFI birds.

Studies that have shown differences in heat production have also shown variation in the ability to retain energy more efficiently between high and low RFI birds. Geraert et al. (1998) found that low RFI cockerels retained energy more efficiently ($P < 0.05$) compared to high RFI cockerels (0.991 vs. 0.809). Gabarrou et al. (1998) demonstrated no significant differences in the amount of RE fed ad libitum; however, at the same FI high RFI hens retained less energy compared to low RFI hens.

In summary, studies between high and low RFI birds (Geraert et al., 1998; Gabarrou et al., 1998) have shown no differences in fasting HP. However, higher fed HP indicates a higher heat increment of feeding in high vs. low RFI birds. The same studies, have shown that when compared at the same FI low RFI birds retain more energy compared to high RFI birds.

Heat production in cattle

Basarab et al. (2003) recently used the comparative slaughter technique to ascertain the relationships between HP, ME intake and retained energy in steers with

divergent differences in RFI. Steers with high RFI (> 0.5 SD from the mean) had significantly higher ME intakes (10.2%), retained more energy (12%) and produced more heat (9.2%) when compared to low RFI (< 0.5 SD from the mean) steers. It was concluded that differences in RFI between high and low RFI steers was partially due to a disproportionate increase in energy required for maintenance or heat increment of feeding in high RFI steers. Other researchers (NRC 1996; Ferrell and Jenkins 1998b) have reported that the efficiency of ME use for retained energy is not constant, but decreases as ME intake increases.

Richardson et al. (2001b) used comparative slaughter and reported after one generation of selection residual heat production (RHP; which is calculated to be the net of the energy used in synthesis of protein and fat gained over the test period and includes energy used for maintenance, activity and heat increment of feeding) was not different between low and high RFI steers. However, the high RFI steers had a RHP per kg of protein deposited that was 35% higher than that of low RFI steers. This implies that low RFI steers had improved efficiency of ME use for protein deposition and (or) maintaining these tissues once they were deposited. Oddy and Herd (2001) summarized that energy retention in the body accounts for only 5 to 12% of the variation in RFI, but the remaining 88-95% of the variation could be due to causes of variation in metabolism which may possibly impact heat production.

Activity and feeding behavior

It is well documented that physical activity is strongly associated with heat production (Boshouwers and Nicaise, 1985; Hoffmann and Scholze, 1990). Lutting et

al. (1991) found that White Leghorn laying hens selected for low RFI produced less heat than hens selected for high RFI, and that activity accounted for 29 to 54% of the difference in total heat production between low and high RFI hens. Gabarrou et al. (1998) found when hens were fed by crop incubation to decrease activity of feeding, high RFI hens showed an 18% decrease in heat increment (HI) compared to a 4% decrease in HI among low RFI hens. Differences between low and high RFI hens were not detected when HP and HI were measured during the dark period, where activity levels were minimal. This suggests that activity related to feeding largely contributes to differences in HI between low and high RFI hens. Luiting et al. (1991) found that 30 to 50% of the divergence in HP between lines could be accounted for by changes in physical activity. In the same study, low RFI hens were found to have shorter more frequent eating intervals, but similar total eating time compared to high RFI hens.

Richardson et al. (2001a) measured activity using pedometers in bulls progeny after one generation of selection for low and high RFI. In this study, mean pedometer counts did not differ significantly between low and high RFI bulls, but mean pedometer count was correlated ($r = 0.32$) to RFI. Richardson et al. (2001) concluded the activity measured using pedometers explained 10% of the variation in RFI in this study. In this study, low RFI steers tended to eat fewer meals per day ($P = 0.07$) and ate more DM intake per feeding ($P = 0.09$) than low RFI steers. Differences in activity associated with frequency of feeding, changes in position, walking as a result of more frequent meals and time spent eating per day was estimated to account for 3.5% of the observed difference in ME intake between low and high RFI steers. Differences in activity

associated with time spent standing and ruminating was estimated to account for 15% of the observed difference in ME intake. Activity-related HP, and HI of feeding, contribute a major role in the explanation of the increase in heat production among livestock species selected for RFI. Activity has shown to explain 79% of the variation in RFI in chickens (Luiting, 1990) and 47% of the variation in RFI in pigs has been explained by differences in eating behavior (de Haer et al., 1993).

Body composition

The association between maintenance requirement of livestock and fatness, with fatter animals tending to have lower maintenance requirements than lean animals at similar live weight, has been documented by number of studies (Cleveland et al., 1983; Ball and Thompson, 1995). Protein synthesis is energetically more efficient than fat synthesis as indicated by estimates of the ratio of energy retained to energy expended (McDonald et al., 1998). DiCostanzo et al. (1990) estimated that 804 kJ is required to maintain 1 kg of protein vs. 86.7 kJ to maintain 1 kg of fat. Therefore, body composition and the composition of gain are determinants of feed requirements. Thompson et al. (1983) found that maintenance energy costs decreased as the proportion of subcutaneous fat increased but not internal fat. This observation has been used to explain some of the differences in maintenance efficiency between dairy and beef breeds. However, Taylor et al., (1986) found consistent differences in maintenance efficiency between beef and dairy cattle when animals were compared at similar body composition, suggesting not all differences in maintenance energy requirements are explained by body composistion.

Recent studies have demonstrated that selection for RFI is correlated to changes in body composition (Arthur et al., 1997; Herd and Bishop, 2000; Richardson et al., 1998). Basarab et al. (2003) most recently demonstrated that gain in empty body fat was significantly higher in high RFI steers compared to low RFI steers. In this study, RFI was significantly correlated with gain in empty body fat ($r = 0.44$), but not gain in empty body protein ($r = -0.06$). In contrast, steer progeny from low RFI parents gained more empty body protein than steer progeny from high RFI parents (Richardson et al., 2001b). This implies that low RFI steers had an improved efficiencies in depositing energy as protein and (or) in maintaining these tissues once they were deposited. The compilation of these studies suggest that selection for low RFI may result in indirect selection for leanness but whether it is due to slower rates of fat deposition or increase lean gain is not entirely clear. Associations with body composition may also reflect differences in maturity patterns between RFI lines or measurement periods. However, Richardson et al. (2001b) concluded that less than 5% of the variation in sire RFI was explained by the variation in body composition in steer progeny selected for RFI after one generation. Variation among RFI in cattle for differences in body composition can be adjusted for by ultrasound measurements of backfat thickness and marbling score at the beginning and end of the test period (Basarab et al., 2003).

Results from studies conducted in poultry have demonstrated that selection for low RFI increase abdominal fat content compared to selection for high RFI (El-Kazzi et al., 1995). El-Kazzi et al. (1995), after 17 generations of selection, found that abdominal fat content was significantly higher in low vs. high RFI birds at 52 weeks of age. Katle

et al. (1991) found, after one generation of selection, abdominal fat content was higher in low vs. high RFI birds at 44 weeks of age. However, after two generations of selection no differences were found in abdominal fat content between low and high RFI birds at 41 weeks of age. The study notes that the lack of differences may be attributable to the hens being young at the time of scanning in which case the hens may not have reached the level where differences would be visible. Bentsen (1983) findings support this conclusion. This study observed a positive phenotypic correlation between RFI and abdominal fat from 16 to 40 weeks of age and a negative correlation from 40 to 66 weeks of age.

In growing cattle, several studies (Arthur et. al., 2001a; Basarab et al., 2003; Richardson et al., 2001b) have found a positive phenotypic correlation between RFI and fatness. Few studies have been conducted to examine differences in body composition between mature RFI cattle. Arthur et al. (1999) found no differences in fat depth between divergent lines of RFI cows (Arthur et al., 1999).

Visceral organs

Ferrell and Jenkins (1998b) have shown that cattle with higher ME intake have heavier organ weights of stomach complex, intestines, liver, heart, lung, kidney and spleen. Ferrell and Jenkins (1985) demonstrated that energy expenditure by visceral organs constituted a major proportion of the energy required for basal metabolism. They suggested that the high rates of energy expenditure of these tissues appear to be associated with the high rates of protein synthesis in these tissues. Thus, the relative proportion of these visceral organs in the body is likely to influence the maintenance

requirements of cattle. Smith and Baldwin (1974) found the liver, heart, mammary tissue and tissues of the gastrointestinal tract to be among the more metabolically active tissues. Evidence suggest that energy expenditures of the metabolically active tissues account significantly more towards basal metabolic activity than the proportional weights of these tissues (Ferrell and Koong, 1986). Influence of plane of nutrition has also been shown to have a positive relationship with weights of visceral organs (Ferrell and Koong, 1986).

Richardson et al. (2001b) found that the component weights of external organs (hide, head, hooves and tail) and internal organs (kidney, lung, liver, heart, spleen, gall bladder, bladder, neck, diaphragm and esophagus) to be similar between high and low RFI steers. Basarab et al. (2003) reported no differences in gut fill between low and high RFI steers. However, Basarab et al. (2003) found that low RFI steers had specifically lower weights of liver, small and large intestine, stomach and intestine and kidney fat compared to steers with high RFI.

Protein turnover

Mersmann et al. (1984) suggested that differences in plasma urea concentrations observed between lean and fat selection lines of pigs occurred as a result of a more efficient use of amino acids for protein synthesis, and as a consequence reduced the requirement to deaminate amino acids, in the lean line. In cattle, there is substantiated variation in supply of amino acids due in part to variation in efficiency of microbial protein production in the rumen (Kahn, 1996; Lush et al., 1991). McDonagh et al. (1998) found higher rates of myofibril disassembly and lower levels of calpastatin in

high RFI steers compared to low RFI steers (Herd et al., 2001). Metabolizable energy lost as heat appeared to be more closely related to protein mass than fat mass, as evidenced by the association between RFI and residual heat production per unit gain in protein, but not in fat (Richardson et al., 2001b). This implies the low RFI steers had superior efficiencies in depositing energy in protein gain and (or) maintaining these tissue once they were deposited.

Digestibility

It is known from the literature that as the level of intake relative to maintenance increases the digestion of feed decreases (Oddy and Herd, 2001). Richardson et al. (1996) found small but significant differences in digestibility between cattle of high and low RFI. Richardson et al. (2001b) found that low RFI cattle were better able to digest a pelleted roughage ration and a feedlot ration when compared to high RFI cattle. The apparent decrease in digestibility for high RFI cattle could contribute up to at least 10% of the difference in ME intake (Richardson et al., 2001b). However, Katle (1991) examined chickens for causal factors of variation in RFI and concluded that results for digestibility were unclear, and suggested that investigation of the relationship between digestibility and RFI should continue. The lack of a relationship between digestibility and RFI have been confirmed in chickens by Luiting et al. (1994) and in growing pigs by de Haer et al. (1993).

Methane

Methane output ranges from 5 to 12% of gross energy intake and plays a significant role in energy balance and feed efficiency (Van Soest, 1994) in cattle. Herd

et al. (2002) estimated that cattle selected for low RFI produced 15% less enteric methane per day than those selected for high RFI. The reduction in methane among low RFI cattle is accountable by having a lower daily gross intake and a lower methane production as a percent of gross energy. Okine et al. (2001) estimated that yearly methane emissions were 21% lower for low RFI than high RFI steers, based on the assumption that methane emissions as a percent of gross energy were similar among RFI groups. As a result of reduced feed intakes, Okine et al. (2001), also reported significant reduction of manure (14.5%), nitrogen (16.9%), phosphorous (17%) and potassium (17.1%) production in low vs. high RFI steers. The current global trends for stronger environmental regulations will provide an economic incentive to beef producers able to reduce production of manure and methane.

Physiological indicators of residual feed intake

Blood urea nitrogen. Differences in plasma urea concentration have been observed in Southdown ram hoggets selected for backfat thickness (Van Maanen et al., 1989), in pigs selected for fatness (Mersmann et al., 1984), Romney sheep selected for fleece weight (McCutcheon et al., 1987; Clark et al., 1989), and in dairy cattle selected for increases of milk or milk solids (Sinnett-Smith et al., 1987). In all of these studies, higher plasma urea concentrations were found in the less productive line. Carter et al. (1989) found that the use of plasma urea concentrations were predictive of genetic merit for lean meat production in sheep. These are analogous to a study comparing high and low RFI steers which demonstrated a significantly higher concentration of blood urea nitrogen (9.98 vs. 8.60 ± 0.36 mg/dL; $P < 0.001$) among high RFI steers in blood

samples taken at the end of the study (Theis, 2002). Richardson et al. (1996) also demonstrated that a significant increase of total plasma protein in high RFI steers compared to low RFI steers (70.05 vs. 65.20 ± 0.68 g/L; $P < 0.01$).

Thyroid hormones. A number of studies have demonstrated that thyroid hormones play a major role in thermogenesis in birds (Gabarrou et al., 1994) and mammals (May, 1989). Triiodothyronine (T_3) and thyroxine (T_4) concentrations have been related to variations of diet-induced thermogenesis among birds selected for high and low RFI. Gabarrou et al. (2000) demonstrated significantly higher concentrations of T_3 when fed and T_4 when fasted among high RFI cockerels compared to low RFI cockerels. There were no differences in concentrations of T_3 when fasted and T_4 when fed. In a similar study, Gabarrou et al. (1997a) found that cockerels selected for high RFI had higher concentrations of T_3 after feeding, lower concentrations of T_3 after fasting but similar T_4 concentrations compared to cockerels selected for low RFI. Gabarrou et al. (1997b) also reported lower serum concentrations of T_3 in feed deprived high RFI cockerels, but no differences in T_3 when fed or in T_4 at any level of intake. Bordas and Minvielle (1999) looked at the gradual divergence of RFI in two lines of laying poultry between the ages of 4 and 34 weeks. The study reported that differences between lines in RFI and feed intake became significant only after the ages of 12 and 18 weeks of age, respectively. The study also reported that concentrations of T_3 were progressively divergent with age and as differences in feed intake gradually increased. The difference in T_3 concentrations were significantly lower among low RFI birds at 17

weeks of age with no difference in concentrations of T_4. Levels of T_3 decreased faster in the low RFI line compared to high RFI line.

In birds, as stated previously, high RFI birds have demonstrated enhanced heat production derived from enhanced diet-induced thermogenesis. Studies have shown physical activity to be partially accountable for this difference. However, differences between RFI lines are likely to exist in the regulation of thermogenic expenditure. Injection of propranolol (a $ß_2$-adrenergic receptor blocker) reduced DIT only in high RFI chickens (Gabarrou et al., 1994) which suggested that the adrenergic system is partly involved in the divergence between lines of RFI. Injections of iopanic acid (IOPA) reduced both plasma T_3 concentrations and heat production to the same levels in which high RFI birds were shown to exhibit higher concentrations of T_3 and heat production compared to low RFI birds (Gabarrou et al., 1997a). IOPA caused a greater increase in plasma T_4 and decrease in plasma T_3 in the high RFI birds than in low RFI birds, suggesting a higher turnover of T_3 in high RFI birds. Gabarrou et al. (1997a) suggested that the increased hepatic deiodinase activity dependent on the availability of endogenous sulfhydryl groups appeared to be related to the enhanced DIT of high RFI birds.

Studies relating thyroid hormones to the variation among lines selected for RFI in cattle are limited. Theis (2002) found low and high RFI steers (± 1 SD from the mean) had similar T_3 concentrations, but low RFI steers had significantly lower T_4 concentrations at day 0 of the trial. White et al. (2003) reported no phenotypic correlation between thyroid hormones and RFI; however, lower concentrations of T_3 and

T_4 at the end of the study were found in low RFI steers (< 0.5 SD) compared to high RFI (< 0.5 SD) steers. Brown et al. (2004) found that RFI was not correlation with T_3 and T_4 in Bonsmara bulls.

Insulin-like growth factor-1. Insulin-like growth factor (IGF-1) has been shown to be related to a number of traits including growth, body size, feed conversion ratio and carcass characteristics (Davis and Bishop, 1995). Johnston et al. (2002) recently demonstrated that IGF-1 was positively correlated genetically with both RFI and FCR in cattle. The study also suggested that selection for reduced IGF-1 will result in a correlated reduction in RFI, FCR and fatness based upon the positive correlation between IGF-1 and P8 fat in a previous study (Johnston et al., 2001). Brown et al. (2004) also found a positive correlation between IGF-1 and RFI in which low RFI (< 0.5 SD) steers and bulls had 29% and 25% lower concentrations of serum IGF-1 compared to high RFI (> 0.5 SD) steers and bulls. However, Richardson et al. (1996) found no significant differences in concentrations of IGF-1 between high and low RFI cattle. Further investigation is required in this area to consider the magnitude of the correlation with RFI and the optimal time to measure IGF-1 in order to make major selection decisions and culling management (Johnston et al., 2002).

CHAPTER III

OBJECTIVES

The objective of this study was to determine differences in maintenance energy requirements, basal metabolic rate and heat increment of feeding in steers identified as having the lowest and highest RFI when fed high roughage and high grain diets. An additional objective of this research was to examine the relationships between RFI and performance traits, ultrasound estimates of carcass composition, body composition, physical activity and methane production in steers with low and high RFI. Quantifying possible sources of variation contributing to differences in RFI will help to better understand how differences in RFI may impact selection programs, production scenarios and profitability of beef production.

CHAPTER IV

MATERIALS AND METHODS

Experimental design

One-hundred and sixty-nine Braunvieh-sired crossbred steers obtained from a Texas cattle ranch (Spade Ranches, Lubbock, TX) were used during the 77-d RFI measurement period. The steers were Branvieh-sired progeny from a four-breed rotational breeding program (Angus, Simmental, Hereford and Braunvieh) and originated from three ranch locations. Steers were stratified by initial BW and ranch origin and randomly assigned to one of two feeding locations (College Station; n = 57 and McGregor; n = 112). Within feeding location, steers were randomly allotted by BW blocks to pens (74.3 m^2 and 10.54 m^2 per animal at College Station and McGregor) equipped with individual Calan gate feeders (American Calan, Northwood, NH). Steers were individually fed a pelleted roughage-based diet formulated to meet or exceed all nutrient requirements for growing steers (Table 3). Following a 30-d adaptation period, weekly BW and feed intakes (FI) were measured for 77 d. Growth of each animal was modeled by linear regression of weekly BW against days on feed to obtain a modeled ADG. Residual feed intake was calculated as the difference between actual dry matter intake (DMI) and DMI predicted from a multiple linear regression of DMI on mid-test $BW^{.75}$ and ADG (Carstens et al., 2002).

At the conclusion of the 77-d RFI measurement period, nine steers with the lowest and highest RFI (College Station; n = 6 and McGregor; n = 12) were selected to measure additional physiological and metabolic parameters on a roughage and high-

concentrate diet (Table 3). The 12 selected RFI steers from McGregor were transported to the individual feeding facility in College Station. Following a 28-d adaptation period, weekly BW and FI were measured on the selected 18 RFI steers until slaughter. During the roughage feeding period (d 105 to 189), the selected 18 steers were fed the same pelleted roughage-based diet described in the 77-d RFI measurement period (Table 3). At the conclusion of the roughage period, the selected low and high RFI steers were adjusted to a high-concentrate diet (Table 3). Steers were started on an intermediate-concentrate diet (60% steam-flaked corn, 30% cottonseed hulls, 10% protein supplement; as-fed basis) fed ad libitum and supplemented coastal hay (10% of ad libitum as-fed FI). Over the next 14 days the steers were adjusted from the intermediate-concentrate diet to a high-concentrate (80% steam-flaked corn; as-fed basis) diet (Table 3). During the high-concentrate feeding period (d 187 to 322), steers were fed twice daily. Separate batch samples of the pelleted roughage-based and high-concentrate diets were pooled, sub-sampled and sent for analysis (Dairy One Forage Laboratory; Ithaca, NY).

Heat production and heart rate

All 18 steers were halter broken and housed to respiration chambers for a 12-h adaptation period, with free access to full feed and water, nine and five days prior to HP measurements. Steers were paired (one low; one high RFI phenotype) and randomly assigned to the respiration chambers. Steers were fed at 1.1 x maintenance for 6 d and, on d 5 and 6 of feed restriction, HP was measured. Steers were then fasted for 4 d and HP measured on d 3 and 4 of fasting. Measurements of heart rate (HR) were made for

Table 3. Ingredient and nutrient composition of the growing diet fed during the 77-d RFI measurement and roughage feeding period and the finishing diet fed during the high-concentrate feeding period

Growing diet		Finishing diet	
Item	Amount	Item	Amount
Ingredients (As-fed basis):		Ingredients (As-fed basis):	
Alfalfa meal	35	Stem-flaked Corn	80
Cottonseed hulls	30	Cottonseed Hulls	10
Soybean hulls	13.5	Protein Supplement[b]	10
Wheat midds	10	Cottonseed meal	74.5
Rice bran	5	Ground limestone	11
Molasses	5	Urea	5
Premix[a]	1.5	Salt	2.3
Nutrients (Dry matter basis):		Nutrients (Dry matter basis):	
Dry matter, %	89.9	Dry matter, %	87.6
Crude protein, %	15.7	Crude protein, %	14.9
Metabolizable energy, Mcal/kg	2.2	Metabolizable energy, Mcal/kg	3.2
Acid detergent fiber, %	40.5	Acid detergent fiber, %	7.3
Neutral detergent fiber, %	55.7	Neutral detergent fiber, %	16.3
Calcium, %	0.86	Calcium, %	1.02
Phosphorus, %	0.33	Phosphorus, %	0.58
Magnesium, %	0.33	Magnesium, %	0.24
Iron, ppm	376	Iron, ppm	475
Zinc, ppm	93	Zinc, ppm	106
Copper, ppm	32	Copper, ppm	23

[a]Premix contained 12% CP, 0.3 % P, 43 ppm Zn, 11.4 IU/kg Vitamin E, 13 ppm Cu and 0.2 ppm Se.
[b]Protein supplement contained 53% CP, 4.9% Ca, 2.4% Na, 1% P, 0.53% Mg, 211 g/ton Rumensin, 68 g/ton Tylan, 853 ppm Fe, 436 ppm Zn, 149 ppm Cu, 1.27 ppm Se, 9185 IU/kg Vit A, 65 IU/kg Vit E on a dry matter basis.

each animal simultaneously with maintenance and fasting HP measurements. Data were averaged over a one-min sampling interval and recorded on a data logger module (Mini-Mitter, Mini-Mitter Co., Sunriver, OR). For analysis, HR data were filtered and corrected for erroneous data using an excel spreadsheet.

Prior to the start of HP measurements during the high-concentrate period, steers were placed into respiration chambers for two additional 24-h adaptation periods during which the steers had free access to feed and water. Steers were then placed into respiration chambers at full feed and HP measured. Full feed was estimated as the average of ad libitum FI from the 7 d prior to starting full feed HP measurements. Steers were then fed at 1.1 x maintenance for 6 d and on d 5 and 6 HP measured. All HP measurements using indirect calorimetry, were measured as two consecutive 22.5-h periods (3 h were needed for bank time, calibration, and shutdown procedures). Heat production was calculated as HP (kcal) = 3.867 O2 (L) + 1.20 CO2 (L) – 0.518 CH4 (L) (Brouwer, 1965).

Respiration chambers

Oxygen consumption and carbon dioxide and methane production were measured using an automated indirect calorimetry system which consisted of two individual respiration chambers. The internal dimensions of the chambers are 1.65 x 2.82 x 2.47 m and are designed to be airtight in order to facilitate accurate measurements of gas exchange by the animal. The chambers were equipped with an adjustable free stall with a waterer, feed trough and two feed dispensers. The chambers were also equipped with water hoses and a stainless steel pit covered by a slatted grate to allow manure and urine

excreted by the animal to be removed. To maintain a constant climate (max humidity 60%, heat 13° C, and AC 24° C) a heating/air conditioning unit and a humidity controlling device was mounted within each unit.

The air flow rate (standard temperature and pressure; STP) through each chamber was measured by means of a mass flow meter with a range of 25-500 L/min (FLOWKIT 500H; Sable Systems, Henderson, NV). The STP flow rate was set to maintain a targeted CO_2 concentration (0.8% and 0.9% for roughage and high concentrate periods) in the chamber. Concentrations of O_2 were measured by a fuel cell oxygen (FC-1B, Sable Systems, Henderson, NV) gas analyzer which, contains an acidic electrolyte to eliminate sensitivity to CO_2. Carbon dioxide and CH_4 concentrations were continuously monitor and measured with an infrared carbon dioxide (CA-2A, $\lambda = 4.26$ µm) and methane (MA-1, $\lambda = 4.26$ µm) gas analyzer. Each gas analyzer measures barometric pressure and corrects the output to a standard barometric pressure which compensates for changes in barometric pressure and eliminates drift. Accuracy's, resolutions and ranges of each analyzer are < 0.1% and < 1% for 02 and CO_2, 0.0001%, 0.001% and 0.001% and 1-100%, 0-10% and 0-5%, respectively. Daily variations in the gas analyzers were corrected and monitored by calibration using a standard gas (20.95% O2, 1.1% CO_2, and 0.1% CH4) and a zero or nitrogen gas. Relative humidity, dew point and water vapor pressure of each respiration chamber was measured in conjuntion with the gas analyzers using a flow-through system (RH-100). Temperature in each chamber was measured during HP measurements using a TC-100 thermocouple meter with a range of –75 to +125° C and a resolution of .01° C.

Gas samples from outside air (baseline) were pumped to the analysis system using a mass flow sub-sampler unit (TR-SS1). Gas samples of air exiting from each of the two respiration chambers were pumped to the analysis system using sub-sampler pumps mounted within the Flowkit 500H mass flow meters. Air from each of the three sources (Baseline, Chamber A, and Chamber B) were sampled successively for four min each, with the baseline being sampled every fourth sample. An automated data acquisition program (Distributed MR v2.2; Sable Systems; Henderson, NV) was used to cycle analysis from each of the three sources and to record (average of the final 30 s of the 4 min sampling interval) chamber environment and gas concentrations.

Physical activity

In conjunction with maintenance and fasting HP measurements during the roughage feeding period, a motion-activity detector (Sable System Henderson, NV) was mounted within the chamber and positioned to face the broad side of the steer to detect any general movement the steer made within the chamber. The detector has a 0-5 V analog output which reflects the percentage of time the animal was active during the previous five minutes. It is scaled linearly such that activity 50% (or more) of the time = 5 volts and complete motionlessness = 0 volts. The automated data acquisition program recorded motion activity for two consecutive 22.5-h measurement periods.

In conjuntion with full feed and maintenance HP measurements during the high concentrate feeding period, a lying-activity monitor was placed within the chamber along the broad side of the steer to determine if the steers were standing or lying. The monitor placed an infrared line, within the chamber, level with the mid-line of the steer

and a reflector on the opposite side. A separate data logger (L430 Simple Logger; AEMC instruments, Dover, NH) with a sample rate of 4096 reading/hr (decreases 50% each time memory is full) and data storage of 8182 readings recorded either a non-zero voltage (complete circuit) or a 0 voltage (circuit impeded). A zero voltage corresponds to an animal standing. Data was then transferred to a desktop computer and quantified to determine lying-activity for two consecutive 22.5-h measurement periods.

Carcass and body composition

Initial ultrasound measures of 12th rib fat thickness were obtained on day 0 of the 77-d RFI measurement period using a Scanner 200 real-time ultrasound unit (Pie Medical Equipment Co., Maastrict, The Netherlands) equipped with a 18-cm, 3.5 MHz linear array transducer. Ultrasound measures of 12th rib (BF), longissimus muscle area (LMA) and percentage intramuscular (IM) fat were taken on d 70, 217 and 294 of the study. Images for rump fat thickness were obtained at the juncture of the gluteus medius and biceps femoris muscles between the hook and pin bones and parallel to the backbone. Gains in BF, LMA and IM fat for the RFI measurement, roughage and high-concentrate periods were calculated from d 0 to 70, 70 to 217 and 217 to 294, respectively.

At the conclusion of the high-concentrate feeding period, the selected low and high RFI steers were randomly (three high; three low each day) slaughtered on d 321, 322 and 323 at the Rosenthal Meat Science and Technology Center (Texas A&M University). Steers were stunned with captive bolt and exsanguinated. Weights of hot carcass, blood, head, hooves, tail, hide, spleen, liver, gall bladder, lungs and trachea,

heart, kidneys, adrenal glands, pancreas, small and large intestine (full and empty), stomach complex (full and empty) and non carcass fat (trim) removed from the internal organs were recorded. Empty body weight was calculated as the weight at slaughter minus gut contents. After a 48-h chill, carcass cooler data was collected and 9 - 11th rib sections removed, dissected and fat and lean tissue ground for subsequent analysis of fat, protein and moisture concentrations. Triplicate samples of four to six grams were placed in a convention oven at 100 °C for a 24-h to determine moisture loss. Crude fat was determined by petroleum ether extract. Nitrogen content determined by Leco analysis (Leco Corp, St. Joseph, MI). Duplicate samples were pooled and crude protein was calculated as 6.25 x N.

Data editing and calculation

During maintenance HP measurements on the roughage and high-concentrate diet, ME required for maintenance was estimated as a function of metabolic body size in order to determine feed intake at 1.1 x maintenance. The equation for FI was:

FI at 1.1 x maintenance (AF kg/d) = ((110(BWkg$^{.75}$)/ME diet)*1.1)

where ME of the diet is expressed on an as-fed basis. The estimation of ME required for maintenance was also used to estimate liters of CO_2 produced by the animal while in the respiration chamber for all HP measurements. The equation was:

CO_2 (L/min) = 110 x BW kg$^{.75}$ + 0.5 (ME intake – 110 x BW kg$^{.75}$)

where ME intake is metabolizable energy intake (kcal/d) and CO_2 is expressed in liters per min and ME in kcal/d. In order to maintain targeted CO_2 concentrations (0.8% and 0.9% for roughage and high-concentrate diets), STP flow rates were estimated as a

function of liters of CO_2 produced by the animal in the respiration chamber by the equation:

STP flow rate (l/min) = CO_2 l/min x Chamber CO_2%.

During HP measurements on the roughage diet, specific adjustments to concentrations of O2, CO_2 and CH4 were made based upon differences in sub-sampler flow rates between the three sources. Relationships between sub-sampler flow rate and gas concentrations for each of the three gas analyzers were developed and used to derive adjustment equations for each chamber and gas. The equations were:

(Adj) Baseline O2% = Base O2% + (△ flow/11407); △ flow = -186.53;

(Adj) Chamber A O2% = A O2% + (△ flow/11407); △ flow = 153.3;

(Adj) Chamber A CO_2% = A CO_2 + (△ flow/46339); △ flow = 153.3;

(Adj) Baseline CH4% = Base CH4% + (△ flow/512478);

△ flow = -186.53;

(Adj) Chamber A CH4% = A CH4% + (△ flow/-37859);

△ flow = -153.3; Only made on maintenance HP measurements

(Adj) Chamber A CH4% = A CH4% + (△ flow/512478);

△ flow = 153.3; Only made on fasting HP measurements

where △ flow represents the difference in sub-sampler flow rate measured as mL/min between the specified source and chamber B. Therefore, gas concentrations in the baseline and chamber A are adjusted to sub-sampler flow rates corresponding to

chamber B. During HP measurements on the high-concentrate diet, sub-sampler flow rates from the three sources were set, monitored for drift and no adjustments to recorded gas concentrations were warranted.

Six steers were reevaluated in the respiration chambers during the roughage HP measurements and eight steers during the high-concentrate HP measurements. Reevaluations were based upon adaptability (FI in the respiration chambers relative to ad libitum FI in the pen) to respiration chambers and data acquisition program failure. Substitution of reevaluated HP measurements were subjected to a predetermined list of selection criterion (chamber FI as a percent of ad libitum FI, methane analyzer drift, equipment failure and missing calorimetry, heart rate and activity data). Two steers during the high-concentrate full fed HP measurements were removed from the study due to extremely depressed feed intakes (evaluated as a percent of normal ad libitum) in the respiration chambers likely caused by a lack of adaptability to respiration chambers. Measured methane gas production of three steers during full fed HP measurements were withheld from the study due to methane analyzer drift.

Statistical analyses

At the end of the 77-d RFI measurement period, 11 steers were omitted due to illness based on examination of weekly BW and feed intake patterns. As a result, data from 169 steers were included in the final analysis (College Station; n = 57 and McGregor; n = 112). To minimize measurement errors of animal growth due to fluctuations in gut fill, growth rates of individual steers were modeled by linear regression of weekly BW against time using the regression procedure of SAS Inst. Inc.

(Cary, NH). These regression coefficients were used to derive initial (d 0) and final (d 77) BW, mid-test metabolic BW ($BW^{0.75}$) and ADG for each steer for the 77-d RFI measurement period. To calculate residual feed intake, ADG and mid-test $BW^{0.75}$ were used to model expected daily dry matter feed intake using the GLM procedure of SAS. A separate model was fitted for steers within each feeding location, with ranch origin of steers included as a class variable. The model fitted was:

Model 1: $Y_{ij} = ß_0 + ß_1$mid-test $BW^{.75}_i + ß_2ADG_, + e_{ij}$,

where Y_{ij} = expected DMI for the i^{th} animal from the j^{th} origin, $ß_0$ = regression intercept, $ß_1$ = partial regression of expected DMI on mid-test $BW^{.75}$, $ß_2$ = partial regression of expected DMI on ADG and e_i = residual error in expected DMI for the i^{th} animal from the j^{th} origin. Residual feed intake was then calculated as the difference between expected and actual feed intake (RFI = expected FI – actual FI). Thus, steers with low or negative RFI values are more efficient than steers with high or positive RFI values.

For the 169 steers, partial correlation coefficients were determined using the MANOVA function of Proc GLM with feeding location and ranch origin included in the model as class variables to examine the relationships between RFI and performance and carcass composition. To further characterize RFI, steers were ranked by RFI within each feeding location and separated into low, medium and high groups that were < 0.5 SD, ± 0.5 SD and > 0.5 SD, respectively, from the mean RFI of 0.0 ± .82 kg/d (mean ± SD). All data were analyzed using Proc GLM (SAS, 1996) with a model that included RFI group, feeding location and ranch of origin as class variables.

During the roughage and high-concentrate feeding periods growth rates of individual animals were modeled by linear regression of weekly BW against time to minimize measurement errors caused by periods of feed restriction, fasting and stresses imposed by adaptation to respiration chambers. The regression coefficients were used to derive ADG and final BW during the roughage (d 189) and high-concentrate (d 322) feeding periods. Residual feed intake for the 18 steers during the roughage and high-concentrate feeding periods were calculated as described previously; however, were not reported due to inherent manipulations and disruptions in FI for HP measurements. All data from the 77-d RFI measurement, roughage and high-concentrate feeding periods for the selected 18 steers were analyzed by Proc GLM (SAS, 1996) with RFI group used as a class variable.

Linear regressions of log heat production or retained energy (RE) on ME intake [kcal/$(kg^{.75}$ $d)^{-1}$] for individual steers and RFI groups were tested to evaluate effects of efficiency characterized by postweaning RFI on the slope and intercept. Group analysis of the linear regression of log HP or RE on ME intake was accomplished using Proc GLM (SAS, 1996) with RFI group as a class variable. Linear regressions of log HP or RE on ME intake for individual animals were used to further evaluate effects of post weaning RFI on energy partitioning. Physical activity evaluated as motion or lying in the respiration chambers was tested for its effects on the relationship between log HP or RE on ME intake between RFI groups. Slopes between RFI groups were similar, therefore, physical activity expressed as motion or lying was used as a covariate for HP measurements on roughage and high-concentrate diets. Covariate analysis enabled HP

and energy partitioning to be evaluated at the same activity level. Individual analysis of log HP and RE on ME intake adjusted and unadjusted from covariate analysis was analyzed using Proc GLM (SAS, 1996) with RFI group as a class variable.

CHAPTER V

RESULTS AND DISCUSSION

Growth and performance traits

During the 77-d RFI measurement period, the overall ADG, DMI and RFI were 1.01 (SD = 0.21), 8.96 (SD = 1.35) and 0.0 (SD = 0.82). Dry matter intakes were strongly correlated with growth rates ($r = 0.66$; $P < 0.0001$) and BW measured on d 77 ($r = 0.72$; $P < 0.0001$) but, were less than unity suggesting that opportunities exist to alter relationships between feed intake and growth traits in cattle. As expected, RFI was not correlated with ADG or BW measured on d 0 or 77 (Table 4) as the model used to determine RFI adjusts for these traits. Results reported in this study, are in agreement with recent studies that found RFI to be phenotypically independent of growth and body size (Archer et al., 1998; Arthur et al., 2001a, 2001c; and Herd and Bishop, 2000). The same literature found that RFI was genetically independent of ADG; however, moderate genetic correlations were found between RFI and BW.

RFI was not phenotypically correlated with growth rate (Table 4). However, there was a large negative correlation between FCR and growth rate ($r = -0.74$; $P < 0.0001$). Arthur et al. (2001a, 2001c) also found large negative correlations between FCR and growth rate ($r = -0.74$ and -0.54). During the 77-d RFI measurement period, RFI was positively correlated with DMI ($r = 0.62$; $P < 0.0001$) and FCR ($r = 0.49$; $P < 0.0001$) which are similar to phenotypic correlations reported by Herd and Bishop (2000), Arthur (2001a, 2001c) and Archer et al. (1998).

The average RFI for steers identified as having low (< 0.5 SD below the mean), medium (± 0.5 SD from the mean) and high (> 0.5 SD above the mean) RFI were – 0.89, -0.05 and 0.79 ± 0.06 kg/d, respectively (Table 5). Low RFI (more efficient) steers consumed 17% less dry matter per day and had 19% lower FCR compared to high RFI (less efficient) steers. Body weight on d 0 and 77 and growth rates were similar for low, medium and high RFI steers (Table 5). Similar results were found in a study involving 176 steers fed a high barley diet in which Basarab et al. (2003) found low RFI steers consumed 10.4% less and had a 9.4% lower FCR with no differences in BW or ADG.

Ultrasound measures of rump fat and backfat thickness on d 70 of the 77-d RFI feeding period were positively correlated with RFI (Table 4). However, ultrasound measures of longissmus muscle area (LMA) and intramuscular fat (IM) obtained on d 70 were not correlated with RFI. Low RFI steers had lower ($P < 0.05$) backfat and rump thickness than high RFI steers (Table 5). Arthur et al. (2001a) reported positive phenotypic and genetic correlations of 0.14 and 0.17, respectively, between backfat thickness and RFI.

During the 77-d RFI measurement period, the selected nine steers with the lowest and highest RFI had average RFI of –1.69 and 1.64 kg/d (Table 6), respectively. The low RFI (selected nine lowest RFI steers) steers consumed 24.5% less dry matter and had 32.4% lower FCR during the 77-d RFI measurement period compared to the high RFI steers (selected nine highest RFI steers). During the roughage feeding period the low RFI steers consumed 12.6% less dry matter and had 8.4% lower FCR compared to high RFI steers. During the high-concentrate feeding period low RFI steers consumed

Table 4. Partial correlations of residual feed intake (RFI) and feed conversion ratio (FCR) with other performance traits and ultrasound estimates of carcass composition in growing steers during the 77-d RFI measurement period

Trait[a]	RFI	FCR
Body weight:		
Initial (d 0), kg	0.002 (0.98)	0.26 (0.0009)
Final (d 77), kg	0.002 (0.98)	-0.15 (0.05)
ADG, kg/d	0.00 (1.00)	-0.74 (0.0001)
DMI, kg/d	0.62 (0.0001)	-0.04 (0.61)
Feed conversion ratio, feed DM/gain	0.49 (0.0001)	--
Initial backfat, mm[b]	0.11 (0.16)	0.18 (0.02)
Final backfat, mm[c]	0.22 (0.004)	-0.05 (0.54)
Final rump fat, mm	0.18 (0.02)	0.05 (0.54)
Final LMA, cm^2	0.03 (0.68)	0.05 (0.55)
Final IM fat, %	0.10 (0.22)	0.03 (0.72)

[a]LMA = longissimus muscle area; IM = intramuscular fat.

[b]Initial ultrasound measurements of carcass composition were obtained on d 0 of the 77-d RFI measurement period.

[c]Final ultrasound measurements of carcass composition were obtained on d 70 of the 77-d RFI measurement period.

Table 5. Characterization of performance traits and ultrasound measures of carcass composition in steers with low, medium and high residual feed intake (RFI)[a] during the 77-d RFI measurement period

Trait[b]	Low RFI	Medium RFI	High RFI	SE	P-value
Number of steers	54	63	51	--	--
RFI, kg/d	-0.89	-0.05	0.79	0.06	0.0001
Body weight:					
Initial (d 0), kg	246.5	244.9	245.0	4.4	0.94
Final (d 77), kg	325.1	324.5	323.7	5.4	0.98
ADG, kg/d	1.02	1.03	1.02	0.03	0.92
DMI, kg /d	7.94	8.77	9.59	0.17	0.0001
FCR, feed DM/gain	7.90	8.65	9.71	0.25	0.0001
Initial backfat, mm[c]	3.10	3.16	3.18	0.11	0.77
Final backfat, mm[d]	3.95	4.08	4.22	0.11	0.13
Final rump fat, mm	3.89	4.21	4.24	0.13	0.04
Final LMA, cm^2	52.9	52.9	53.3	0.95	0.92
Final IM fat, %	2.82	2.84	2.89	0.08	0.70

[a]Low, medium and high RFI steers were < 0.5 SD, ± 0.5 SD, and > 0.5 SD from the mean RFI of 0.0 ± 0.82 kg/d (mean ± SD) respectively.

[b]FCR = feed conversion ratio; LMA = longissimus muscle area; IM = intramuscular fat.

[c]Initial ultrasound measurements of carcass composition were obtained on d 0 of the 77-d RFI measurement period.

[d]Final ultrasound measurements of carcass composition were obtained on d 70 of the 77-d RFI measurement period.

7.4% less dry matter and had 13.5 % lower FCR compared to high RFI steers. Growth rates and BW on d 0, 77, 189 and 322 were similar during the 77-d RFI measurement, roughage and high-concentrate feeding periods (Table 6). Differences in DMI and RFI between low and high RFI steers were reduced during the roughage and high-concentrate feeding periods, although consistent with 77-d RFI measurement period. Similar findings were reported in a study involving 410 steers fed for an 84-d growing and 112-d finishing period in which Crews et al. (2003) found the phenotypic variance estimate for RFI during the growing period was more than twice that of RFI during the finishing period. Indicating that observed variance in RFI on the growing diet was higher than on the finishing diet. However, the lack of differences in DMI, FCR and RFI during the roughage and high-concentrate feeding periods could have been due to alterations in feeding behavior (time spent at the bunk, meals per day, and meal size) or activity imposed by adapting steers to respiration chambers or periods of feed restriction for HP measurements.

Ultrasound measures of initial backfat, final backfat and rump fat thickness obtained during the 77-d RFI measurement period were less ($P < 0.05$) among low RFI steers compared to high RFI steers (Table 7). Low RFI steers had lower ($P = 0.01$) final backfat thickness obtained during the high-concentrate feeding period than high RFI steers (Table 7). Gain in backfat thickness from d 70 to 294 was greater (4.23 vs. 5.87 mm; $P = 0.08$) for high RFI steers compared low RFI steers. Higher gains in backfat thickness among high RFI steers were mostly attributed to a higher ($P = 0.03$) gain in

Table 6. Performance traits of the selected low and high residual feed intake (RFI) steers during the 77-d RFI measurement, roughage feeding and high-concentrate feeding periods

Trait[a]	Low RFI	High RFI	SE	P-value
Number of steers	9	9	--	--
77-d RFI measurement period				
RFI, kg/d	-1.69	1.64	0.17	0.0001
Body weight				
Initial (d 0), kg	253.0	247.8	7.9	0.65
Final (d 77), kg	336.7	325.4	10.2	0.44
ADG, kg/d	1.09	1.01	0.07	0.46
DMI, kg/d	7.70	10.20	0.42	0.01
Feed conversion ratio, feed DM/gain	7.16	10.59	0.60	0.01
Roughage feeding period				
Final (d 189) BW, kg	424.9	424.7	12.0	0.99
ADG, kg/d	0.87	0.91	0.05	0.57
DMI, kg/d	8.46	9.68	0.36	0.03
Feed conversion ratio, feed DM/gain	9.95	10.86	0.69	0.36
High-concentrate feeding period				
Final (d 322) BW, kg	596.4	587.3	14.2	0.66
ADG, kg/d	1.17	1.11	0.07	0.53
DMI, kg/d	7.56	8.16	0.31	0.19
Feed conversion ratio, feed DM/gain	6.49	7.50	0.30	0.03

[a]Performance data for the 77-d RFI measurement, roughage feeding and high-concentrate feeding periods were calculated from d 0 to 77, 105 to 189 and 189 to 322 of the study.

backfat on the high-concentrate diet. No differences in ultrasound measures of LMA or IM were found between high and low RFI steers during either of the three trail periods (Table 7). Richardson et al. (1998) reported similar findings in steer progeny from RFI bulls selected as the top and bottom 5% after a 120 d feeding trial. In the study, low RFI cross-bred steer progeny fed a 75% rolled barley finishing diet were found to have lower ($P < 0.05$) initial rib (3.8 vs. 4.7 ± 0.30 mm) and rump (4.28 vs. 5.88 ± 0.38) fat and lower ($P < 0.05$) final rib (7.1 vs. 8.4 ± 0.47 mm) and rump (8.3 vs. 10.3 ± 0.62) fat. Basarab et al. (2003) reported a positive phenotypic correlation of ($r = 0.22$) between gain in ultrasound backfat thickness and RFI. Phenotypic and genetic correlations between RFI and ultrasound measures of fat depth ($12/13^{th}$ rib fat $r_p = 0.14$, $r_g = 0.17 \pm 0.05$; rump P8 fat $r_p = 0.11$, $r_g = 0.06 \pm 0.06$; Arthur et al., 2001c) and carcass fat ($r_p = 0.14$, $P = 0.09$; Basarab et al., 2003) reported in literature are similar to trends represented in this data set. However, differences in ultrasound body composition may have been affected by alterations in feeding behavior due to stresses imposed by halter breaking or periods of feed restriction for heat production measurements.

Body composition

Protein concentrations of 9 - 11^{th} rib samples were higher ($P = 0.03$) in low RFI steers with no differences in lipid content to high RFI steers. No differences were found in BW at slaughter or hot carcass weight between RFI steers (Table 8). The low and high RFI steers had similar weights of hide, blood, head, hooves, tail, stomach, small intestine, large intestine, heart, lung and trachea, liver, pancreas, adrenal gland, pituitary, anterior pituitary and dissected compared to high RFI steers. No differences in empty

Table 7. Ultrasound measures of carcass composition of the selected low and high residual feed intake (RFI) steers during the 77-d RFI measurement, roughage feeding and high-concentrate feeding periods

Parameter[a]	Low RFI	High RFI	SE	P-value
Number of steers	9	9	--	--
77-d RFI measurement period				
Initial backfat, mm[b]	2.89	3.67	0.22	0.02
Final backfat, mm[c]	3.87	4.49	0.20	0.04
Final LMA, cm^2	53.48	53.19	1.37	0.88
Final IM fat, %	2.78	2.94	0.14	0.43
Gain in backfat, mm[d]	0.98	0.82	0.31	0.73
Roughage feeding period				
Final backfat, mm	5.64	6.41	0.40	0.20
Final LMA, cm^2	70.13	69.71	1.97	0.88
Final IM fat, %	2.95	3.18	0.12	0.19
Gain in backfat, mm	1.78	1.92	0.52	0.85
Gain in LMA, cm^2	16.65	16.52	2.03	0.97
Gain in IM fat, %	0.16	0.24	0.20	0.77
High concentrate feeding period				
Final backfat, mm	8.10	10.36	0.53	0.01
Final LMA, cm^2	79.00	73.86	2.11	0.11
Final IM fat, %	2.80	2.91	0.08	0.33
Gain in backfat, mm	2.46	3.95	0.46	0.03
Gain in LMA, cm^2	8.87	4.15	2.62	0.22
Gain in IM fat, %	-0.15	-0.27	0.15	0.57

[a]LMA = longissimus muscle area; IM = intramuscular fat.

[b]Initial ultrasound measurements of carcass composition were obtained on d 0 of the study.

[c]Final ultrasound measurements of carcass composition measured for the 77-d RFI measurement, roughage feeding and high-concentrate feeding periods were obtained on d 70, 217 and 294 of the study.

[d]Gain in ultrasound measures of carcass composition measured for the 77-d RFI measurement, roughage feeding and high-concentrate feeding periods were calculated from d 0 to 70, 70 to 217 and 217 to 294 of the study.

body weight (EBW) or gut fill were found between low and high RFI steers (Table 9). Expressed as a percent of EBW, low RFI steers had heavier weights of spleen (P = 0.02), adrenal gland (P = 0.07) and lungs and trachea (P = 0.03) (Table 9) compared to high RFI steers. Weights of internal organs (heart, lungs, trachea, kidney, liver and spleen) expressed as a percentage of EBW was similar among low and high RFI steers but approached significance at P = 0.11 (Table 9). Richardson et al. (2001) also reported that low and high RFI steers had similar external (hide, head, hooves and tail) and internal (kidney, lung, liver, heart, spleen, gall bladder, neck, diaphragm and esophagus) organ weights. Similarly Basarab et al. (2003) reported that low (< 0.5 SD below the mean) and high (> 0.5 SD above the mean) RFI steers (RFI adjusted for measures of backfat and marbling gain) were similar in EBW, gut fill, hide, head, feet and tail, kidney, lung and trachea, heart spleen, gall bladder and bladder. However, Basarab et al. (2003) found that low RFI steers had lower (P < 0.01) weights of liver, small and large intestine, stomach and intestine and noncarcass fat compared to high RFI steers. Ferrell and Jenkins (1998) have shown that cattle with higher ME intakes have heavier organ weights of stomach complex, intestines, liver, heart, lung, kidney and spleen.

Energy partitioning on a high-roughage diet

During the roughage feeding period, there were no differences in fasting HP, metabolizable energy for maintenance (ME_m) or respiratory quotient (RQ) between low and high RFI steers (Table 10). This is in agreement with RFI studies in adult poultry using indirect calorimetry that found no differences in fasting HP between selection lines divergently selected for RFI over multiple generations (Gabarrou et al. 1997b, 1998;

Table 8. Least square means for weights of organs and tissues at slaughter and slaughter body weight in the selected low and high residual feed intake (RFI) steers.

Parameter	Low RFI	High RFI	SE	P-value
Slaughter BW, kg	572.7	570.6	14.8	0.92
Hot carcass weight, kg	349.1	352.9	9.7	0.79
9th, 10th and 11th rib protein, %	17.31	15.28	0.61	0.03
9th, 10th and 11th rib fat, %	33.02	34.51	1.31	0.43
External tissues, kg[a]	68.21	65.95	1.68	0.36
Hide, kg	38.46	37.53	1.30	0.62
Blood, kg	13.22	11.66	0.76	0.16
Head, kg	15.82	15.19	0.48	0.36
Hoove, kg	12.42	11.66	0.38	0.18
Tail, kg	1.51	1.57	0.06	0.48
Internal organs, kg[b]	14.55	13.87	0.49	0.34
Heart, kg	2.00	1.88	0.52	0.13
Lungs and trachea, kg	3.74	3.38	0.52	0.13
Kidney, kg	1.13	1.03	0.12	0.57
Liver, kg	6.58	6.68	0.30	0.82
Spleen, kg	1.10	0.91	0.05	0.01
Pancreas, mg[c]	45.11	46.73	8.87	0.90
Adrenal gland, mg[d]	18.48	17.17	0.85	0.28
Pituitary, mg	2.37	2.24	0.08	0.29
Anterior pituitary, mg	1.84	1.74	0.08	0.40
Dissected noncarcass fat, kg	45.55	48.07	2.65	0.51
Stomach complex, kg	14.01	13.53	0.70	0.64
Small intestine, kg	4.21	4.43	0.28	0.59
Large intestine, kg	2.40	2.35	0.16	0.83

[a]External organs include: hide, head, hooves and tail.
[b]Internal organs include: heart, lungs, trachea, kidney, liver and spleen.
[c]Pancreas weight for the 9 low RFI n = 6 and 9 high RFI n = 8.
[d]Adrenal gland weight for the 9 low RFI n= 8 and high RFI n = 9.

Table 9. Least square means for weights of various organs and tissues at slaughter expressed as a proportion[a] of empty body weight (EBW) in the selected low and high residual feed intake (RFI) steers

Parameter	Low RFI	High RFI	SE	P-value
Empty body weight (EBW), kg	532.5	532.7	15.4	0.99
Gut fill, kg[b]	40.25	37.83	3.13	0.59
External tissues	128.65	124.05	3.14	0.32
Hide	72.36	70.70	2.38	0.63
Blood	24.85	22.08	1.42	0.19
Head	29.83	28.51	0.73	0.22
Hoove	23.62	21.88	0.96	0.22
Tail	2.84	2.96	0.12	0.51
Internal organs	27.30	26.10	0.50	0.11
Heart	3.78	3.53	0.12	0.15
Lungs and trachea	7.00	6.34	0.19	0.03
Kidney	2.10	1.93	0.19	0.53
Liver	12.32	12.56	0.41	0.69
Spleen	2.09	1.70	0.11	0.02
Pancreas, (mg kg^{-1} EBW)[c]	0.085	0.090	0.019	0.87
Adrenal gland, (mg kg^{-1} EBW)[d]	0.035	0.032	0.001	0.07
Anterior pituitary, (mg kg^{-1} EBW)	0.004	0.003	0.000	0.29
Total dissected fat	84.92	90.15	3.46	0.30
Pituitary, (mg kg^{-1} EBW)	0.005	0.004	0.000	0.27
Stomach complex	26.49	25.41	1.30	0.57
Small intestine	7.93	8.29	0.50	0.62
Large intestine	4.57	4.38	0.33	0.69

[a]Organs and tissues at slaughter are represented as (g kg^{-1} EBW).

[b]Gut fill is calculated as the difference between slaughter BW and EBW; external organs include: hide, head, hooves and tail; internal organs include: heart, lungs, trachea, kidney, liver and spleen; total dissected fat includes all the dissected non carcass fat.

[c]Pancreas weight for the 9 low RFI n = 8 and 9 high RFI n = 9.

[d]Adrenal gland weight for the 9 low RFI n= 6 and high RFI n = 8.

Geraert et al., 1998). In the current study, there were no differences in HP when high and low RFI steers were fed at 1.1 x maintenance (Table 10). Residual feed intake studies in poultry have also repeatedly shown no differences in HP when FI was restricted to the same amount (Gabarrou et al., 1998). There were no mean differences in RE while high and low RFI steers were fed at 1.1 X maintenance (Table 10). No differences in the partial efficiency for ME use for maintenance, $k_{m,}$ were found between high and low RFI steers (Table 10). Values of k_m were similar to those reported for growing cattle on an adequate or high plane of nutrition (Birkelo et al., 1989). Retained energy while fed at 1.1 X maintenance was less than predicted for all steers.

Methane produced (kcal/d) during measurements of maintenance HP on the roughage diet were similar between high and low RFI steers (Table 10). No differences in methane production expressed as a percent of gross energy (GE) intake were found between high and low RFI steers (Table 10). Methane production expressed as a percent of GE intake is similar to the accepted ranges of 5 to 12 % in literature (Van Soest 1994).

Regression equations of RE on ME intake ($RE = ß_0 + ß_1$ x ME intake) for the two RFI groups found neither the slope, $ß_1$ (partial efficiency of ME use for maintenance, k_m), nor intercept, $ß_0$ (RE extrapolated to zero) were different for high and low RFI steers (Table 11). Maintenance, estimated as ME intake at which RE equals zero, was similar for high and low RFI steers. The partial efficiency of ME use for maintenance (k_m) obtained from the regression analysis was 0.67 which is similar to values of k_m using equations of Blaxter & Boyne (1979) for a roughage diet.

Table 10. Least square means of energy partitioning for the selected low and high residual feed intake (RFI) steers during the roughage feeding period

Parameter[a]	Low RFI	High RFI	SE	P-value
Maintenance heat production period[b]				
BW, kg	366.13	354.16	2.47	0.47
ME intake, kcal (kg $^{.75}$ .d) $^{-1}$	111.93	117.48	3.02	0.21
Heat production, kcal (kg $^{.75}$ .d) $^{-1}$	137.46	138.47	2.89	0.81
Retained energy, kcal (kg $^{.75}$ .d) $^{-1}$	-25.53	-20.99	3.20	0.33
Respiratory quotient	0.97	0.96	0.01	0.40
CH_4, % of GE intake	4.49	3.56	0.50	0.21
CH_4, kcal/d	1090.99	863.54	126.94	0.22
Fasting heat production period				
BW, kg	349.77	342.64	2.45	0.66
Heat production, kcal (kg $^{.75}$ .d) $^{-1}$	98.51	102.07	3.08	0.43
Respiratory quotient	0.74	0.73	0.01	0.12
ME_m, kcal (kg $^{.75}$ d) $^{-1}$ [c]	151.02	148.37	4.07	0.65
Partial efficiency of ME use for maintenance, k_m [c]	0.65	0.69	0.02	0.14

[a] ME = metabolizable energy; CH_4 = methane produced during calorimetry experiments; ME_m = calculated maintenance energy requirement.

[b] During maintenance heat production period steers were fed at 1.1 x maintenance.

[c] k_m = FHP/ ME_m; maintenance is estimated as the ME intake [(kg $^{.75}$ .d) $^{-1}$] at which energy retention is zero from the regression equation of RE on ME intake (RE = $ß_0 + ß_1$ x ME intake).

Motion activity expressed on a scale from 0 to 5 was significantly higher (P = 0.05) among high RFI steers compared to low RFI steers during the fasting HP measurements (Table 12). This is in agreement to RFI studies in poultry (Gabarrou et al., 1997) and cattle (Richardson et al., 2001a) which have shown animals identified as having low RFI have lower measures of physical activity and can partially account for differences in ME intake between lines of RFI. Motion activity was positively correlated ($r = 0.67$; $P < 0.0001$) with HP. There were no differences in the slopes of the regression of motion activity on HP indicating there were no differences in the incremental cost of physical activity measured by motion between high and low RFI steers. As a result, motion activity was used as a covariate in order to evaluate HP at the same activity level. Regression adjustments for activity are similar to activity adjusted fasting HP reported by Baker et al., (1991) for beef cattle of similar age (104.7 ± 1.0). There were no mean differences in adjusted fasting HP (99.9 vs. 100.7 ± 2.6), adjusted ME required for maintenance (150.7 vs. 149.1 ± 3.9) or k_m (0.66 vs. 0.68 ± 0.01) between high and low RFI steers. Regression analysis of RE on ME intake indicated similar results.

Energy partitioning on a high-concentrate diet

During the high-concentrate feeding period there were no differences in mean ME_m, retained energy or respiratory quotient during full fed or maintenance HP measurements between high and low RFI steers (Table 13). High and low RFI steers expressed no differences in ME intake (Table 13) or daily DMI (7.01 vs. 7.47 ± 0.42) during full feed HP measurements. Although ad-libitum daily DMI were not different

Table 11. Relationship between retained energy and ME intake for the selected low and high residual feed intake (RFI) steers during the roughage feeding period

Model [a]	$ß_1$ (± SE)	$ß_0$ (± SE)	R^2	n	Maintenance[b]	k_m
Roughage						
Low RFI steers	0.651 ± 0.026	-98.44 ± 2.21	0.97	9	151.2	0.65
High RFI steers	0.690 ± 0.041	-102.08 ± 3.39	0.95	9	147.9	0.69

[a] Model: retained energy $= ß_0 + ß_1$ x ME intake. All variables are expressed as kcal/$(kg^{.75} .d)^{-1}$.

[b] From the model maintenance is estimated as the ME intake [kcal/$(kg^{.75} .d)^{-1}$] at which energy retention is zero and the slope is the partial efficiency of ME use for maintenance, k_m.

Table 12. Least square means for motion and lying activity during measurement of heat production during the roughage and high-concentrate feeding periods in the selected low and high residual feed intake (RFI) steers

Parameter	Low RFI	High RFI	SE	P-value
Motion[a] activity during Roughage period				
Maintenance heat production, scale (0-5)	1.38	1.36	0.07	0.86
Fasting heat production, scale (0-5)	0.83	1.05	0.08	0.05
Lying[b] during High-concentrate period				
Full-feed heat production, h	19.50	13.71	2.69	0.11
Maintenance heat production, h	18.48	14.70	2.41	0.28

[a]Motion activity is scaled linearly such that activity 50% (or more) of the time = 5 volts and complete motionlessness = 0 volts.

[b]Lying activity on d 1and 2 of full fed heat production (n = 9 low RFI and n = 5 high RFI).

between RFI groups in the respiration chamber, differences were reflective of differences in DMI during the high-concentrate feeding period (7.56 vs. 8.16 ± 0.31 kg/DM) and the previous seven days before entering the respiratory chambers (8.26 vs. 8.57 ± 0.28 kg/DM) for low and high RFI steers. Individual regression of RE on ME intake found no differences in mean partial efficiencies of gain (k_r) between low and high RFI steers (Table 13). Partial efficiency of maintenance (k_m), estimates from the regression of log HP on ME intake, were similar among high and low RFI steers (Table 13). This is in contrast to Basarab et al. (2003) who found by comparative slaughter, that high RFI steers had significantly higher ME intakes, retained more energy and produced more heat. Contrasts in results between the current study and Basarab et al. (2003) may have resulted from differences in methodology. Comparative slaughter techniques used in Basarab et al. (2003) may have allowed a larger range in ME intakes in cattle displaying differences in feed efficiency; therefore, allowing differences in energy partitioning to be observed. However, HP measurements using comparative slaughter techniques are not a direct measurement. The lack of differences in ad libitum HP and energy partitioning efficiency measures in the current study may have been due to the lack of differences in FI between high and low RFI steers caused by alterations in feeding behavior (time spent at the bunk, meals per day, and meal size) imposed by adaptations to respiratory chambers.

Methane produced (kcal/d) during measurements of HP on the high-concentrate diet were similar between high and low RFI steers (Table 13). No differences in methane production expressed as a percent of gross energy (GE) intake were found

Table 13. Least square means of energy partitioning for the selected low and high residual feed intake (RFI) steers during the high-concentrate feeding period

Parameter[a]	Low RFI	High RFI	SE	P-value
Number of steers	7	9	--	--
Full-feed heat production period				
BW, kg	527.55	525.15	14.91	0.91
ME intake, kcal (kg $^{.75}$ .d) $^{-1}$	232.65	248.89	12.84	0.36
Heat production, kcal (kg $^{.75}$ .d) $^{-1}$	164.06	162.22	4.33	0.75
Retained energy, (kg $^{.75}$ .d) $^{-1}$	68.59	86.67	11.08	0.24
Respiratory quotient	1.08	1.10	0.01	0.44
CH_4, % of GE intake	2.12	2.00	0.37	0.84
CH_4, kcal/d	640.97	658.09	131.79	0.93
Maintenance heat production period[b]				
BW, kg	504.46	500.77	14.81	0.87
ME intake, kcal (kg $^{.75}$ .d) $^{-1}$	124.16	124.56	0.52	0.58
Heat production, kcal (kg $^{.75}$ .d) $^{-1}$	125.79	122.57	2.26	0.30
Retained energy, kcal (kg $^{.75}$ .d) $^{-1}$	-1.63	1.99	2.34	0.27
Respiratory quotient	0.98	0.97	0.01	0.60
CH_4, % of GE intake	3.42	3.90	0.01	0.60
CH_4, kcal/d	621.49	704.19	108.66	0.60
ME_m, kcal (kg $^{.75}$ .d) $^{-1}$ [c]	125.41	121.47	3.99	0.47
Partial efficiency of ME use for gain, k_r[c]	0.62	0.68	0.04	0.29
Partial efficiency of ME use for maintenance, k_m[d]	0.72	0.76	0.02	0.27

[a]ME = metabolizable energy; CH_4 = methane produced during calorimetry experiments; ME_m = calculated maintenance energy requirement.

[b]During maintenance heat production period steers were fed at 1.1 x maintenance.

[c]Maintenance is estimated as the ME intake [(kg $^{.75}$ .d) $^{-}$1] at which energy retained is zero from the regression of RE on ME intake (RE = $ß_0 + ß_1$ x ME intake) and the slope is the partial efficiency of ME use for gain or k_r.

[c]k_m = fasting HP / ME_m; where maintenance is estimated as the point on the regression at which heat production is equal to ME intake from the regression of log heat production on ME intake (log HP = $ß_0 + ß_1$ x ME intake) and fasting HP is the antilog of the intercept.

between high and low RFI steers. This is similar to previous studies using calculations to derive predictive values of methane emissions (Okine et al., 2001 and Basarab et al., 2003). However, those studies demonstrated high RFI steers to produce significantly more methane per day compared to low RFI steers.

Neither the slope, ß$_1$ (partial efficiency of ME use for gain, k_r), nor intercept, ß$_0$ (RE extrapolated to zero) from the regression analysis of RE on ME intake were different for high and low RFI steers (Table 14). Maintenance, estimated from the regression of RE on ME intake, was similar for high and low RFI steers (Table 14). Likewise, neither the slope nor the intercept of the regression of log HP on ME intake were different for high and low RFI steers (Table 14). There were no differences in k_m or maintenance estimated from the regression (Table 14). The regression analysis of log HP on ME intake indicated that k_m for all 18 steers was 0.77 which are similar to values of k_m using equations of Blaxter & Boyne (1979) for a high-concentrate diet.

There were no differences in lying activity during HP measurements on the high-concentrate diet. Although not different, high RFI steers spent 30% less time lying during the full feed HP measurements. Lying activity measured during full feed HP measurements was negatively correlated ($r = -0.40$; $P = 0.04$) with full feed HP. The slope of the regression of time spent lying on HP or incremental cost of standing was 5.4 kJ $(kg^{.75}\ d)^{-1}$ and is similar to the range accepted for cattle and sheep of 6 to 12 kJ $(kg^{.75}\ d)^{-1}$ (Blaxter, 1989). There were no differences in the slopes of the regression of time spent lying, therefore, there were no differences in the incremental cost of standing between high and low RFI steers. As previously described, physical activity expressed

as time spent lying was used as covariate in order to evaluate HP at the same activity level. Although not different, full feed HP adjusted for lying activity was 2.6% higher for high RFI steers on the high-concentrate diet. No differences in RE were found between low and high RFI steers. This agrees more with the findings of Gabarrou et al. (1997b; 1998). These data suggest that HP and measures of energy partitioning may have been influenced by alternations in activity imposed by stress caused by adaptation to respiration chambers.

No differences were found in ME_m between high and low RFI steers on either the roughage or high-concentrate diets. Regression analysis indicated similar results. Lack of differences in HP between RFI steers could have been caused by decreasing divergence in RFI and FI between high and low RFI steers throughout the roughage and high-concentrate feeding periods. Studies using indirect calorimetry to assess differences in metabolism in poultry have been conducted using lines of high and low RFI birds selected for numerous generations allowing considerable differences in RFI and ME intake between lines. In this study, influences of handling and halter breaking may have altered natural behavior traits in feeding behavior (time spent at the bunk, meals per day, meal size) and activity which may have contributed to differences in residual feed intake. Therefore, steers may have not expressed differences in RFI to the same extent in the 77-d RFI measurement period. More research is warranted to directly measure energy partitioning in cattle expressing vast differences in RFI. Either, studies with cattle divergently selected for residual feed intake or studies directly measuring energy expenditure in a production environment may allow sustainable differences in

RFI and ME intake in order to determine differences in energy balance among high and low RFI steers.

Table 14. Regression equations describing energy partitioning for low and high residual feed intake (RFI) steers during the high-concentrate feeding period

Model [a]	ß$_1$ (± SE)	ß$_0$ (± SE)	R^2	n	FHP[b]	Maintenance[c]	k_r / k_m [d]
Model I							
Low RFI steers	0.671 ± 0.042	-86.31 ± 7.93	0.95	7	86.3	128.6	0.67
High RFI steers	0.698 ± 0.030	-85.91 ± 5.79	0.97	9	85.9	123.1	0.70
Model II							
Low RFI steers	0.0001 ± 0.0001	1.983 ± 0.023	0.83	7	96.3	128.2	0.75
High RFI steers	0.0009 ± 0.0001	1.977 ± 0.018	0.86	9	94.8	123.0	0.77

[a]Model I: retained energy = ß$_0$ + ß$_1$ x ME intake. Model II: log heat production = ß$_0$ + ß$_1$ x ME intake. All variables are expressed as kcal/(kg$^{.75}$ .d)$^{-1}$.

[b]Fasting HP (FHP) is expressed as the absolute value of the intercept for Model I and the antilog of the intercept for Model II.

[c]Maintenance is estimated as the ME intake at which energy retained is zero for Model I and the point at which heat production is equal to ME intake for Model II.

[d]The slope of Model I represents the partial efficiency of ME use for gain (k_r). The partial efficiency of ME use for maintenance (k_m) is estimated as k_m = fasting heat production / maintenance; where fasting heat production and maintenance are derived from Model II.

CHAPTER VI

SUMMARY

The data reported herein document that residual feed intake is highly correlated to feed conversion ratio and thus residual feed intake may be used as an alternative measure of feed efficiency independent of body weight and growth rate. There were observed differences of 28% in DMI and 39% in FCR between high and low RFI steers with no differences in BW or growth rate. Low RFI steers gained 28% less backfat from d 70 to d 294 compared to high RFI steers. Higher gains in backfat may have contributed to a reduction in feed efficiency in high RFI steers compared to low RFI steers. However, substantial differences in postweaning RFI and composition of gain did not equate to differences in energy partitioning, maintenance energy requirements or heat increment of feeding between RFI steers. Less physical activity among low RFI steers, found in this study, may provide a source of variation in feed efficiency among high and low RFI steers. Data reported herein suggest that selection for RFI may improve feed efficiency and therefore profitability of beef production. However, reductions in backfat among low RFI cattle suggest more research is warranted to determine the impact of selection pressure on RFI cattle in terms of carcass quality, time spent in the feedyard and reproductive efficiency.

Even though, there were no differences in energy partitioning, influences of handling and halter breaking may have altered natural behavioral traits in feeding behavior (time spent at the bunk, meals per day, meal size) and activity which may have contributed to the divergence in high and low RFI steers during the RFI measurement

period. Given the magnitude of the difference in feed efficiency more research is warranted on physiological factors involved in accounting for the observed differences in RFI. Studies with, either, cattle divergently selected for residual feed intake or studies directly measuring energy expenditure in a production environment may provide sustainable differences in RFI and ME intake in order to determine differences in energy balance among high and low RFI steers.

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APPENDIX A

Table A1. Performance data from d 0 to 77 of the study

ID	RFI Group	Model ADG, kg/d	BW d 0, kg	BW d 77,kg	DMI, kg/d	FCR	$BW^{.75}$, kg	RFI, kg/d
112	1	1.14	248	336	7.46	6.53	70.58	-1.96
142	1	1.37	239	345	9.03	6.60	70.65	-1.36
164	1	1.00	258	335	7.59	7.58	71.49	-1.93
172	1	0.83	265	329	7.72	9.29	71.56	-1.26
210	1	1.25	243	339	7.60	6.09	70.44	-2.39
239	1	1.08	262	345	8.18	7.60	72.75	-1.43
246	1	1.11	277	362	8.61	7.78	75.58	-1.37
272	1	0.98	243	319	6.54	6.65	68.62	-1.66
295	1	1.03	241	320	6.51	6.34	68.58	-1.83
132	3	1.52	279	396	12.82	8.45	78.77	1.32
133	3	1.12	289	376	11.83	10.56	77.85	1.91
148	3	0.74	235	292	10.02	13.48	65.35	2.52
165	3	1.10	276	361	11.21	10.20	75.38	1.28
204	3	1.01	215	292	10.82	10.76	63.50	2.75
263	3	0.52	267	307	7.98	15.20	69.69	1.33
294	3	1.03	210	289	8.96	8.74	62.85	1.08
307	3	1.07	215	297	9.01	8.41	64.02	1.31
311	3	0.96	245	319	9.13	9.50	68.76	1.28

Table A2. Performance data from d 105 to 189 of the study

ID	RFI Group	BW d 189, kg	Model ADG, kg/d	FCR	DMI, kg/d
112	1	417	0.80	9.92	7.95
142	1	439	0.80	14.00	11.17
164	1	417	0.85	10.29	8.77
172	1	413	0.85	9.74	8.25
210	1	462	1.18	6.63	7.83
239	1	442	1.00	9.10	9.06
246	1	454	0.89	8.33	7.41
272	1	406	0.87	9.84	8.53
295	1	373	0.61	11.71	7.20
132	3	498	0.91	12.07	11.00
133	3	461	0.79	12.89	10.18
148	3	384	0.83	12.46	10.39
165	3	469	1.00	8.62	8.58
204	3	391	0.94	10.08	9.48
263	3	381	0.72	12.86	9.20
294	3	390	0.90	10.82	9.79
307	3	421	1.16	6.81	7.92
311	3	427	0.94	11.16	10.55

Table A3. Performance data from d 189 to 322 of the study

ID	RFI Group	BW d 322, kg	Model ADG, kg/d	FCR	DMI
112	1	536	0.84	6.88	5.76
142	1	622	1.29	6.18	7.96
164	1	583	1.26	5.84	7.34
172	1	585	0.94	7.22	6.77
210	1	663	1.44	6.56	9.43
239	1	634	1.31	6.51	8.52
246	1	626	1.13	6.80	7.69
272	1	539	0.99	6.49	6.44
295	1	581	1.38	5.90	8.15
132	3	634	0.76	10.33	7.86
133	3	632	1.21	7.20	8.71
148	3	533	1.00	7.91	7.94
165	3	642	1.36	6.72	9.12
204	3	575	1.24	6.62	8.22
263	3	546	1.14	6.69	7.64
294	3	541	0.90	7.88	7.11
307	3	598	1.34	6.68	8.96
311	3	584	1.06	7.45	7.90

Table A4. Carcass composition data from d 0 to 70 of the study

ID	RFI Group	Initial 12th rib fat, mm	Final 12th rib fat, mm	Final rump fat, mm	Final IM fat, mm	Final REA, cm^2	Initial BCS, 1-5	Final BCS, 1-5
112	1	4	3.3	4.1	2.37	54.2	4	5
142	1	2	4.1	3.3	2.84	51.0	3	4
164	1	3	2.8	4.6	2.81	48.4	3	5
172	1	2	4.1	3.0	2.78	52.3	4	5
210	1	2	3.6	3.8	2.56	52.3	3	5
239	1	3	4.1	3.8	2.84	52.3	4	5
246	1	3	4.8	5.3	2.71	59.4	3	6
272	1	3	4.1	4.6	2.40	54.8	4	4
295	1	4	4.1	3.0	3.75	56.8	3	5
132	3	4	4.8	3.0	2.48	60.0	5	5
133	3	4	4.6	5.3	3.56	58.1	4	4
148	3	4	5.1	3.8	2.52	52.3	3	4
165	3	3	4.8	4.6	3.37	56.8	4	5
204	3	3	5.3	5.1	2.51	47.1	3	5
263	3	4	4.1	4.6	2.65	50.3	4	5
294	3	4	4.3	3.8	3.04	56.8	4	4
307	3	3	3.6	3.8	3.25	47.1	3	4
311	3	4	3.8	3.0	3.07	50.3	4	4

Table A5. Carcass composition data on d 217 of the study

ID	RFI Group	Final 12th rib fat, mm	Final rump fat, mm	Final IM fat, mm	Final REA, cm^2	Final BSC, 1-5
112	1	5.08	3.30	2.93	72.39	5
142	1	5.59	6.86	2.83	63.48	5
164	1	6.35	6.86	2.85	66.32	6
172	1	5.59	5.33	3.70	69.94	5
210	1	7.11	8.38	2.52	74.84	7
239	1	5.08	6.86	2.47	84.13	6
246	1	5.59	6.10	2.76	69.55	5
272	1	4.83	5.33	3.46	68.32	5
295	1	5.59	4.57	3.00	62.19	5
132	3	6.35	7.62	2.82	67.35	6
133	3	8.89	9.91	2.90	79.81	6
148	3	5.59	5.33	3.71	67.23	5
165	3	5.59	7.62	3.12	74.00	6
204	3	5.33	7.62	3.46	64.06	6
263	3	5.59	6.86	2.84	67.74	5
294	3	4.32	6.86	3.40	72.90	6
307	3	8.64	7.62	2.98	64.13	6
311	3	7.37	6.86	3.41	70.19	5

Table A6. Carcass composition data on d 294 of the study

ID	RFI Group	Final 12th rib fat, mm	Final rump fat, mm	Final IM fat, mm	Final REA, cm^2
112	1	6.10	6.10	2.93	79.35
142	1	7.87	7.62	2.94	81.61
164	1	10.67	8.89	3.10	83.87
172	1	6.60	7.62	2.38	76.84
210	1	10.41	8.89	2.89	65.87
239	1	8.38	8.38	2.57	89.29
246	1	6.86	6.86	2.92	79.74
272	1	8.13	5.59	2.82	70.71
295	1	7.87	7.62	2.66	83.68
132	3	8.64	6.86	2.66	77.35
133	3	12.95	12.45	3.20	75.81
148	3	9.65	5.59	3.17	67.23
165	3	11.94	10.41	2.95	81.87
204	3	9.40	11.18	2.84	73.03
263	3	10.67	8.89	2.71	77.42
294	3	9.40	9.65	2.52	76.65
307	3	11.94	6.10	3.06	70.71
311	3	8.64	7.62	3.08	64.71

Table A7. Body composition data for the study

ID	RFI Group	Slaughter BW, kg	Hot carcass weight, kg	Empty BW, kg	Weight of blood, kg	Weight of head, kg	Weight of hooves, kg	Weight of tail, kg
112	1	508	310	464	12.65	14.20	13.80	1.30
142	1	599	350	538	14.25	15.90	12.00	1.40
164	1	566	342	537	10.10	17.70	11.75	1.60
172	1	539	322	497	13.70	15.75	13.55	1.55
210	1	648	407	621	12.20	16.00	11.85	1.70
239	1	610	367	578	19.60	18.00	11.20	1.60
246	1	595	371	549	14.50	15.00	12.70	1.55
272	1	513	313	468	10.40	14.80	12.55	1.60
295	1	576	359	540	11.55	15.05	12.40	1.25
132	3	629	385	577	10.00	17.65	14.85	1.70
133	3	605	384	573	9.95	15.80	11.70	1.75
148	3	520	319	478	10.90	13.15	10.65	1.60
165	3	621	385	576	12.20	15.50	11.40	1.90
204	3	555	347	531	13.40	13.65	10.60	1.55
263	3	532	336	493	14.10	15.40	11.00	1.35
294	3	524	325	485	11.80	13.15	10.85	1.70
307	3	595	358	563	10.50	16.55	12.85	1.45
311	3	554	338	519	12.05	15.85	11.00	1.15

Table A7. Continued

ID	RFI Group	Weight of hide, kg	Weight of spleen, kg	Weight of liver, kg	Weight of gall bladder, kg	Weight of lungs and trachea, kg	Weight of heart, kg	Weights of kidney, kg
112	1	36.50	1.14	5.54	0.35	3.30	1.90	1.00
142	1	40.20	1.10	7.48	0.60	3.45	2.20	1.20
164	1	37.50	0.95	6.86	0.55	3.75	1.85	0.85
172	1	44.05	1.34	4.92	0.35	3.50	1.95	0.85
210	1	40.65	1.05	7.33	0.45	4.80	2.05	1.10
239	1	43.90	1.10	7.52	0.65	4.45	2.05	2.40
246	1	39.80	1.08	6.36	0.70	3.40	1.80	0.85
272	1	27.55	1.14	5.35	0.20	3.25	2.05	0.85
295	1	36.00	1.01	7.86	0.50	3.75	2.15	1.05
132	3	40.00	1.17	6.42	0.30	3.75	2.15	1.20
133	3	39.10	1.00	7.58	0.55	3.55	2.05	1.00
148	3	34.45	0.79	6.88	0.25	3.10	2.00	0.95
165	3	38.55	0.76	7.70	0.50	3.30	2.00	1.20
204	3	34.70	0.69	6.62	0.35	3.40	1.85	0.85
263	3	35.35	1.06	5.86	0.25	3.75	1.70	0.90
294	3	38.95	0.78	6.29	0.25	2.60	1.55	0.95
307	3	36.50	0.94	6.72	0.40	3.85	1.80	1.20
311	3	40.20	0.94	6.03	0.40	3.10	1.80	1.00

Table A7. Continued

ID	RFI Group	Weight of adrenal gland, mg	Weight of pancreas, mg	Weight of stomach, kg	Weight of small intestine, kg	Weight of large intestine, kg	Dissected noncarcass fat, kg	Weight of Pituitary, mg
112	1	19.0	57.5	14.25	3.30	2.20	31.41	2.6
142	1	18.7	ND	19.95	5.20	2.75	45.56	2.5
164	1	18.7	34.6	14.15	3.80	2.50	54.80	2.3
172	1	17.3	65.2	11.60	3.20	1.95	41.56	2.5
210	1	21.3	63.3	14.35	4.65	2.20	55.06	2.7
239	1	ND[a]	ND	10.50	3.65	1.95	55.45	2.0
246	1	16.8	12.9	14.91	4.50	2.36	48.25	2.2
272	1	14.6	ND	12.50	4.77	3.55	33.53	2.3
295	1	21.4	37.2	13.90	4.80	2.10	44.35	2.2
132	3	19.8	21.6	15.05	4.75	2.70	47.55	2.5
133	3	17.0	46.9	13.40	5.75	2.80	47.65	2.3
148	3	15.2	90.8	13.20	3.85	1.95	39.26	2.1
165	3	20.4	ND	15.55	5.05	2.90	57.87	2.5
204	3	16.2	25.4	12.90	3.50	2.10	59.46	1.9
263	3	13.6	50.7	12.85	3.45	1.95	41.16	2.1
294	3	14.7	ND	11.86	5.23	1.68	44.06	1.9
307	3	20.3	40.9	14.95	5.15	2.45	49.20	2.5
311	3	17.3	50.8	12.05	3.10	2.60	46.41	2.4

[a] ND = denote not discernible values of weights due to collection errors.

Table A7. Continued

ID	RFI Group	Weight of Anterior Pituitary, mg	Percent protein of the 12th rib, %	Percent moisture of the 12th rib, %	Percent fat of the 12th rib, %
112	1	1.8	21.34	78.24	20.24
142	1	2.1	16.64	76.02	22.51
164	1	1.7	16.50	66.54	32.17
172	1	1.9	15.32	74.87	23.68
210	1	2.2	14.43	66.99	31.71
239	1	1.5	16.26	69.59	29.06
246	1	1.5	17.09	73.39	25.19
272	1	2.0	20.99	77.72	20.78
295	1	1.9	17.27	63.09	35.69
132	3	2.1	17.54	71.12	27.50
133	3	1.8	14.29	65.25	33.48
148	3	1.5	14.33	69.17	29.49
165	3	2.0	16.19	64.03	34.73
204	3	1.5	15.18	63.05	35.73
263	3	1.6	15.52	68.14	30.54
294	3	1.5	15.38	61.46	37.35
307	3	2.0	13.86	66.00	32.72
311	3	1.7	15.28	63.92	34.84

Table A8. Hip height measured on d 0, 70, 217 and 294 and physical activity data for the study

ID	RFI Group	Hip height d 0, cm	Hip height d 70, cm	Hip height d 217, cm	Hip height d 294, cm	Motion activity during maintenance HP, 1-5	Motion activity during fasting HP, 1-5	Time spend lying during full feed HP, hr	Time spent lying during maintenance HP, hr
112	1	117	125	135	136	1.37	0.92	21.96	26.49
142	1	110	125	133	135	1.28	0.84	20.33	19.60
164	1	118	126	134	137	1.39	0.84	23.00	24.93
172	1	118	126	133	137	1.40	0.69	19.08	24.31
210	1	113	120	131	133	1.48	1.15	15.53	20.19
239	1	115	118	126	130	1.46	0.93	14.33	8.98
246	1	118	124	131	133	1.84	0.88	25.03	19.34
272	1	119	124	133	138	1.02	0.64	20.50	9.64
295	1	113	124	133	135	1.15	0.52	15.74	12.83
132	3	117	126	133	138	1.36	0.79	22.36	13.61
133	3	125	124	133	137	0.79	1.02	ND[a]	11.83
148	3	115	122	130	130	1.11	1.04	20.01	21.84
165	3	117	126	135	139	1.42	0.70	0.00	0.01
204	3	110	118	128	131	1.92	1.65	ND	20.95
263	3	117	124	128	133	1.09	0.62	ND	15.98
294	3	111	121	132	133	1.70	1.80	16.60	15.29
307	3	117	120	131	131	1.30	1.30	ND	7.27
311	3	114	123	132	135	1.35	0.76	9.58	25.50

[a] ND = denotes not discernible values due to equipment failure at time of recording.

Table A9. Energy partitioning data on the roughage diet

ID	RFI Group	Respiratory quotient during maintenance HP	$BW^{.75}$, kg during HP	HP fed at maintenance, kcal ($kg^{.75}.d^{-1}$)	Retained energy fed at maintenance, kcal ($kg^{.75}.d^{-1}$)	ME intake fed at maintenance, kcal ($kg^{.75}.d^{-1}$)	Partial efficiency of ME use for maintenance estimated from linear regression	Linearly estimated maintenance requirement, kcal ($kg^{.75}.d^{-1}$)
112	1	0.93	85.53	125.47	-43.61	81.86	0.66	148.36
142	1	0.98	86.14	148.52	-28.21	120.31	0.65	163.64
164	1	0.97	79.82	130.78	-29.36	101.42	0.69	143.72
172	1	0.97	84.52	134.86	-17.04	117.82	0.61	145.71
210	1	0.89	81.16	144.88	-32.01	112.87	0.68	160.09
239	1	0.97	81.16	143.65	-25.78	117.87	0.67	156.20
246	1	1.04	91.94	129.18	-9.67	119.51	0.67	133.90
272	1	1.05	86.07	139.05	-24.66	114.39	0.58	156.69
295	1	0.96	76.96	140.73	-19.43	121.30	0.66	150.88
132	3	0.92	89.44	145.14	-29.09	116.04	0.59	165.10
133	3	1.02	93.29	124.46	-8.09	116.37	0.72	127.56
148	3	0.96	80.69	139.07	-21.05	118.03	0.73	146.90
165	3	0.98	85.76	141.15	-22.67	118.49	0.60	156.03
204	3	0.96	73.89	139.27	-21.96	117.30	0.69	149.32
263	3	0.96	76.15	124.00	-6.37	117.63	0.68	127.00
294	3	0.98	77.12	134.50	-15.71	118.79	0.76	139.47
307	3	0.90	73.41	148.84	-32.63	116.21	0.77	158.58
311	3	0.93	84.98	149.80	-31.35	118.45	0.67	165.38

Table A9. Continued

ID	RFI Group	Partial efficiency of ME used for maintenance estimated from semi-log regression	Estimated maintenance requirement from seim-log regression	Respiratory quotient during fasting HP	$BW^{.75}$, kg during fasting HP	HP at fasting, ($kg^{.75}.d^{-1}$)	Retained energy at fasting, kcal ($kg^{.75}.d^{-1}$)	Methane produced during maintenance HP, kcal/d
112	1	0.61	159.91	0.77	81.79	97.29	-97.29	289
142	1	0.62	170.68	0.73	84.29	106.53	-106.53	1390
164	1	0.67	148.16	0.73	77.20	99.76	-99.76	1166
172	1	0.58	152.29	0.73	82.34	89.01	-89.01	1089
210	1	0.65	165.97	0.72	79.27	108.53	-108.53	1341
239	1	0.65	161.12	0.73	78.15	105.06	-105.06	989
246	1	0.66	135.64	0.76	88.98	89.98	-89.98	1123
272	1	0.53	171.54	0.77	81.00	91.33	-91.33	1509
295	1	0.64	155.23	0.73	74.87	99.13	-99.13	922
132	3	0.54	180.77	0.72	88.83	97.91	-97.91	1208
133	3	0.72	128.36	0.75	89.51	92.25	-92.25	ND[a]
148	3	0.72	148.92	0.76	77.91	107.08	-107.08	422
165	3	0.57	166.01	0.73	83.35	94.20	-94.20	1356
204	3	0.67	152.86	0.73	73.00	102.42	-102.42	785
263	3	0.67	128.05	0.73	74.78	86.25	-86.25	973
294	3	0.75	140.49	0.72	75.59	105.96	-105.96	1106
307	3	0.76	160.50	0.71	69.22	122.11	-122.11	962
311	3	0.64	171.83	0.71	84.60	110.49	-110.49	910

[a] ND = denotes not discernible values due to equipment failure.

Table A10. Energy partitioning data on the high-concentrate diet

ID	RFI Group	Respiratory quotient during full fed HP	$BW^{.75}$, kg during full fed HP	HP fed at full feed, kcal ($kg^{.75}.d^{-1}$)	Retained energy fed at full feed, kcal ($kg^{.75}.d^{-1}$)	ME intake fed at full feed, kcal ($kg^{.75}.d^{-1}$)	Partial efficiency of ME use for growth estimated from linear regression	Linearly estimated fasting HP, kcal ($kg^{.75}.d^{-1}$)
112	1	1.04	106.43	147.89	9.89	157.79	0.39	-51.57
142	1	1.03	109.44	142.60	87.29	229.89	0.84	-105.35
164	1	1.11	103.98	163.38	40.16	203.54	0.54	-70.07
172	1	1.09	115.47	149.63	2.55	152.18	0.23	-32.41
210	1	1.10	115.29	183.70	76.24	259.94	0.62	-85.78
239	1	1.09	113.68	163.63	102.16	265.80	0.73	-92.23
246	1	1.10	118.01	164.50	42.09	206.59	0.56	-73.45
272	1	1.04	105.79	154.20	28.18	182.38	0.35	-35.21
295	1	1.11	104.05	176.42	103.99	280.42	0.68	-85.32
132	3	1.07	117.87	160.23	40.67	200.89	0.69	-98.18
133	3	1.07	117.84	171.41	80.06	251.47	0.59	-67.43
148	3	1.04	102.09	154.70	52.35	207.05	0.68	-87.53
165	3	1.13	114.87	177.50	116.12	293.63	0.68	-82.79
204	3	1.13	105.07	168.20	103.35	271.55	0.70	-85.88
263	3	1.07	101.58	144.94	100.81	245.75	0.75	-83.89
294	3	1.12	108.80	158.10	76.71	234.82	0.63	-70.36
307	3	1.11	105.35	160.03	123.08	283.11	0.77	-95.02
311	3	1.12	113.33	164.84	86.91	251.74	0.63	-71.76

Table A10. Continued

ID	RFI Group	Linearly estimated maintenance requirement, kcal ($kg^{.75}.d^{-1}$)	Estimated fasting HP from semi-log regression, kcal ($kg^{.75}.d^{-1)}$	Partial efficiency of ME used for maintenance estimated from semi-log regression	Estimated maintenance requirement from seim-log regression	Respiratory quotient during maintenance HP	$BW^{.75}$, kg during HP	HP fed at maintenance, kcal ($kg^{.75}.d^{-1}$)
112	1	132.39	73.10	0.56	131.53	1.00	107.29	126.09
142	1	125.72	107.94	0.86	125.69	0.98	105.93	125.32
164	1	129.38	85.63	0.66	128.93	0.99	100.19	127.03
172	1	141.09	63.57	0.46	138.73	0.99	109.01	124.96
210	1	137.62	98.51	0.72	136.72	0.97	110.22	133.29
239	1	126.11	99.62	0.79	126.05	1.00	110.15	125.76
246	1	131.34	87.92	0.67	130.68	0.95	115.85	127.72
272	1	101.30	63.50	0.60	106.71	0.98	102.02	115.83
295	1	126.38	95.95	0.76	126.21	0.99	100.41	125.60
132	3	142.05	105.32	0.74	141.55	0.97	114.31	136.16
133	3	114.97	83.11	0.72	116.09	0.99	114.31	119.03
148	3	129.56	95.97	0.74	129.31	0.92	98.87	127.53
165	3	122.21	94.01	0.77	122.58	1.00	108.58	123.78
204	3	123.24	95.12	0.77	123.19	0.98	102.75	122.99
263	3	111.62	90.41	0.81	112.14	1.01	97.54	114.94
294	3	112.34	83.10	0.73	113.35	0.97	105.43	116.78
307	3	123.34	101.02	0.82	123.47	0.97	100.63	124.14
311	3	113.85	84.78	0.74	114.81	0.93	110.36	117.77

Table A10. Continued

ID	RFI Group	Retained energy fed at maintenance, kcal ($kg^{.75}.d^{-1}$)	ME intake fed at maintenance, kcal ($kg^{.75}.d^{-1}$)	Methane produced during full fed HP, kcal/d	Methane produced during maintenance HP, kcal/d
112	1	-4.02	122.07	167.56	450.26
142	1	-2.04	123.28	251.18	407.31
164	1	-2.78	124.26	670.75	622.20
172	1	-4.81	120.15	820.17	1109.05
210	1	-7.16	126.13	826.72	729.19
239	1	-0.96	124.80	ND[a]	906.55
246	1	-4.59	123.13	1449.23	405.85
272	1	7.74	123.58	549.16	426.00
295	1	-1.62	123.98	393.02	537.04
132	3	-13.19	122.97	ND	1013.81
133	3	5.76	124.79	624.51	1205.25
148	3	-4.23	123.29	625.09	638.20
165	3	3.30	127.08	997.27	776.87
204	3	-0.56	122.43	NA	920.14
263	3	10.04	124.97	482.92	746.28
294	3	7.45	124.24	664.02	863.41
307	3	2.67	126.81	113.34	158.32
311	3	6.68	124.46	1099.50	15.45

[a] ND = denotes not discernible values due to equipment failure.

APPENDIX B

Protocol for calibration of instrumentation

Analyzers of O_2, CO_2 and CH_4, are calibrated using nitrogen gas, a standard gas (19.5% O_2, 1.1% CO_2 and 0.1% CH_4) and outside air (atmospheric air is 20.95% O_2). Before calibration, check dry-rite columns to ensure dry air is being pumped through gas analyzers. During calibration, gases used for calibration are set to flow through the analyzers at a specified flow rate (approximated 200 ml/min). Specific adjustments were made for variable flow rates going into the analyzers and are described previously in the materials and methods section. The O_2 analyzer is spanned (calibrated to a known concentration) using outside air and adjusted to zero using nitrogen gas. The CO_2 and CH_4 analyzers are spanned with standard gas and adjusted to zero using nitrogen gas. Note that adequate time (10-15 min) must be allowed for analyzers to equilibrate each time a calibration gas is set to flow through the analyzers. Any adjustments to span or zero analyzers while equilibrating will result in a false calibration. At the end of a measurement period standard gas is set to flow through the analyzers to check for instrumentation failure and drift (a noticeable increase or decrease in gas concentration read by the analyzer for a known concentration). Record standard gas concentrations read by the analyzers at the beginning and end of a measurement period in order to track analyzer performance. Presented in Table B1, listed by run number, are standard gas concentrations recorded before and after each measurement period. Animal ID, cross-listed with run number and run type are given in Table B2. Specifications for selection criterion and data editing for analyzer malfunction are described in the material and methods section.

Table B1. Data for standard gas concentrations read by O_2, CO_2 and CH_4 analyzers before and after HP measurements

Measurement number	Initial O_2 concentration, %	Final O_2 concentration %	Initial CO_2 concentration, %	Final CO_2 concentration, %	Initial CH_4 concentration, %	Final CH_4 concentration, %
105	19.5047	19.3486	1.0990	1.0570	0.1000	0.0920
107	19.6700	19.7700	1.1260	1.1200	0.0990	0.1050
108	19.7500	19.4052	1.1010	1.0600	0.1000	0.1010
109	19.3520	19.3465	1.1010	1.0900	0.1000	0.0990
111	19.3600	19.3438	1.1000	1.1040	0.1000	0.1020
113	19.4267	19.3956	1.1000	1.0920	0.1010	0.0940
114	19.3600	19.4054	1.1020	1.1000	0.1000	0.0920
115	19.3552	19.2656	1.1000	1.1010	0.1000	0.1000
116	19.3784	19.5813	1.1000	1.1200	0.1000	0.0940
118	19.3600	19.4085	1.1010	1.0930	0.1000	0.0890
119	19.3650	19.3348	1.0990	1.0880	0.1000	0.0920
121	19.3827	19.4086	1.1000	1.0300	0.1000	0.0920
124	19.4256	19.4035	1.1000	1.0850	0.0990	0.0960
126	19.3367	19.3414	1.1000	1.1000	0.1000	0.0880
127	19.4465	19.4722	1.1000	1.1000	0.1010	0.0990
128	19.3650	19.3580	1.1010	1.1020	0.1010	0.0990
129	19.3970	19.2710	1.1000	1.0960	0.1000	0.0870
131	19.3544	19.3611	1.1000	1.1000	0.1000	0.0990
132	19.3840	19.3612	1.1000	1.1040	0.0990	0.0980
133	19.3987	19.4206	1.1000	1.0980	0.0990	0.0980
134	19.3585	19.3741	1.1000	1.0960	0.1000	0.0990
135	19.3356	19.3886	1.1000	1.0990	0.1000	0.0860
136	19.3790	19.3662	1.1000	1.0960	0.0990	0.0980
143	19.7308	19.3762	1.0980	1.0800	0.1000	0.0810
144	19.3962	19.3703	1.0980	1.0960	0.0990	0.0990
145	19.4109	19.4137	1.0980	1.1020	0.1000	0.0990
146	19.5081	19.5705	1.0980	1.1040	0.0990	0.0980
149	19.3371	19.3735	1.0990	1.0980	0.1000	0.1030
150	19.3645	19.4032	1.0980	1.0940	0.1010	0.1010

Table B1. Continued

Measurement number	Initial O_2 concentration, %	Final O_2 concentration %	Initial CO_2 concentration, %	Final CO_2 concentration, %	Initial CH_4 concentration, %	Final CH_4 concentration, %
152	19.3400	19.3894	1.0990	1.0840	0.0990	0.0860
153	19.4144	19.4280	1.0980	1.0990	0.1000	0.1020
155	19.3214	19.4320	1.0990	1.0920	0.1000	0.0990
157	19.3272	19.3948	1.0980	1.0940	0.1000	0.1000
158	19.3452	19.3810	1.0990	1.1070	0.1000	0.0950
159	19.3287	19.3646	1.0980	1.1100	0.1000	0.1000
160	19.3480	ND[a]	1.0980	ND	0.0990	ND
162	19.3520	19.3428	1.0980	1.1010	0.1000	0.0990
163	19.3537	19.3756	1.1000	1.1060	0.1000	0.0990
165	19.3136	19.3948	1.0980	1.0960	0.1000	0.0980
166	19.3676	19.4000	1.0980	1.0940	0.1000	0.0990
167	19.3800	19.3560	1.0990	1.1080	0.1000	0.1020
168	19.3377	19.4168	1.0990	1.0890	0.1010	0.1010
169	19.3782	19.4200	1.0980	1.0990	0.1010	0.0980
170	19.3542	19.3833	1.0980	1.0960	0.1000	0.1010
171	19.3430	19.3910	1.0980	1.0940	0.1010	0.1020
173	19.3874	ND	ND	ND	ND	ND
174	19.3813	19.3836	1.0980	1.0980	0.0990	0.0990
175	19.3831	19.3680	1.0990	1.0940	0.1000	0.0960
176	19.3455	19.3385	1.0980	1.1000	0.1000	0.0880
177	19.3348	19.3744	1.0980	1.0870	0.0990	0.0840
178	19.3604	19.3469	1.0990	1.1020	0.1000	0.0860

[a] ND = denotes not discernible values not recorded.

Table B2. Animal ID, measurement number, type and diet

Animal ID	Measurement Type	Diet	Measurement number
112	Maintenance HP	Roughage	129
112	Fasting HP	Roughage	132
112	Full fed HP	High-concentrate	160
112	Full fed HP	High-concentrate	162
112	Maintenance HP	High-concentrate	165
112	Maintenance HP	High-concentrate	173
112	Full fed HP	High-concentrate	177
112	Maintenance HP	High-concentrate	178
132	Maintenance HP	Roughage	105
132	Fasting HP	Roughage	107
132	Maintenance HP	Roughage	131
132	Fasting HP	Roughage	133
132	Full fed HP	High-concentrate	143
132	Maintenance HP	High-concentrate	146
133	Maintenance HP	Roughage	127
133	Fasting HP	Roughage	128
133	Full fed HP	High-concentrate	162
133	Maintenance HP	High-concentrate	166
142	Maintenance HP	Roughage	116
142	Fasting HP	Roughage	118
142	Full fed HP	High-concentrate	153
142	Maintenance HP	High-concentrate	158
148	Maintenance HP	Roughage	129
148	Fasting HP	Roughage	132
148	Maintenance HP	High-concentrate	165
148	Full fed HP	High-concentrate	169
148	Full fed HP	High-concentrate	169
148	Maintenance HP	High-concentrate	173
164	Maintenance HP	Roughage	111
164	Fasting HP	Roughage	113
164	Full fed HP	High-concentrate	145
164	Maintenance HP	High-concentrate	150
164	Full fed HP	High-concentrate	168
164	Maintenance HP	High-concentrate	171
165	Maintenance HP	Roughage	111
165	Fasting HP	Roughage	113
165	Maintenance HP	Roughage	134
165	Fasting HP	Roughage	135
165	Full fed HP	High-concentrate	145
165	Maintenance HP	High-concentrate	150

Table B2. Continued

Animal ID	Measurement Type	Diet	Measurement number
172	Maintenance HP	Roughage	124
172	Fasting HP	Roughage	126
172	Full fed HP	High-concentrate	163
172	Maintenance HP	High-concentrate	167
172	Full fed HP	High-concentrate	170
172	Maintenance HP	High-concentrate	176
172	Full fed HP	High-concentrate	177
172	Maintenance HP	High-concentrate	178
204	Maintenance HP	Roughage	114
204	Fasting HP	Roughage	115
204	Full fed HP	High-concentrate	152
204	Maintenance HP	High-concentrate	152
210	Maintenance HP	Roughage	108
210	Fasting HP	Roughage	109
210	Full fed HP	High-concentrate	144
210	Maintenance HP	High-concentrate	149
239	Maintenance HP	Roughage	114
239	Fasting HP	Roughage	115
239	Full fed HP	High-concentrate	152
239	Maintenance HP	High-concentrate	157
246	Maintenance HP	Roughage	127
246	Fasting HP	Roughage	128
246	Maintenance HP	Roughage	136
246	Maintenance HP	High-concentrate	166
246	Full fed HP	High-concentrate	170
246	Maintenance HP	High-concentrate	174
246	Full fed HP	High-concentrate	175
263	Maintenance HP	Roughage	116
263	Fasting HP	Roughage	118
263	Maintenance HP	Roughage	134
263	Fasting HP	Roughage	135
263	Full fed HP	High-concentrate	153
263	Maintenance HP	High-concentrate	158
272	Maintenance HP	Roughage	105
272	Fasting HP	Roughage	107
272	Maintenance HP	Roughage	108
272	Fasting HP	Roughage	133
272	Full fed HP	High-concentrate	143
272	Maintenance HP	High-concentrate	146
272	Full fed HP	High-concentrate	168
272	Maintenance HP	High-concentrate	171

Table B2. Continued

Animal ID	Measurement Type	Diet	Measurement number
294	Maintenance HP	Roughage	119
294	Fasting HP	Roughage	121
294	Full fed HP	High-concentrate	155
294	Full fed HP	High-concentrate	155
294	Maintenance HP	High-concentrate	159
294	Maintenance HP	High-concentrate	174
295	Maintenance HP	Roughage	119
295	Fasting HP	Roughage	121
295	Full fed HP	High-concentrate	155
295	Maintenance HP	High-concentrate	159
307	Maintenance HP	Roughage	108
307	Fasting HP	Roughage	109
307	Full fed HP	High-concentrate	144
307	Maintenance HP	High-concentrate	149
311	Maintenance HP	Roughage	124
311	Fasting HP	Roughage	126
311	Full fed HP	High-concentrate	163
311	Maintenance HP	High-concentrate	167
311	Full fed HP	High-concentrate	175
311	Maintenance HP	High-concentrate	176

Protocol for heat production calculations

In order make necessary calculations for heat production, data acquisition files for each measurement must be imported into a macro (excel spreadsheet with preset equations). Volumes of O_2 (V_{O2}) consumed and CO_2 (V_{CO2}) and CH_4 (V_{CH4}) produced are calculated as the difference in concentrations of O_2, CO_2 and CH_4 entering and exiting the chamber multiplied by the flow rate (VE) at STPD (standard temperature and pressure of dry air). STP flow rate is measured as air pulled through the chamber and is therefore, flow rate exiting the chamber. The equations (McLean and Tobin, 1987) for (VE) are as follows :

Equation 1: VE (l/min) = STP flow rate x Dry air (%) ;

where,

Equation 2: Dry air (%) = ((1- P_w)/ P_{tot})) x ((P_{tot} / 273) x (273/273 x temp));

where temp refers to the temperature within the respiration chamber and P_w is the saturating vapor pressure (kpa) and P_{tot} is the barametric pressure (kpa). The equations for P_w and P_{tot} are as follows:

Equation 3: P_w (kpa) = $e^{(16.78 \text{ x temp} - 116.9/ \text{ temp} + 237.3)}$;

and

Equation 4: P_{tot} (kpa) = 101.3 [(293 – 0.0065 El) / 293]$^{5.26}$

where El is the elevaltion above sea level. STPD flow can then be used to calculate volumes of gases consumed and produced.

Gas concentrations of outside air (inlet air) and air exiting the chamber (outlet air) are used to determine the change in concentration which is multiplied by the volume

of STPD air moving through the chamber to get the volume of gas consumed or produced by the animal. In general, volume of air and oxygen exiting and entering a chamber is of similar magnitude but not equal. In other words the total volume of oxygen consumed by the animal is not necessarily equal to the total volume of carbon dioxide and methane produced by the animal. Therefore, when concentrations of all respiratory gases are analyzed the relationship between volume of air entering and exiting can be obtained by equating the quantity of nitrogen in inlet and outlet airstreams, i.e. the Haldane transformation. Correction terms for carbon dioxide and methane are negligible and thus the Haldane transformation is only incorporated into equations for volume of O_2 consumed (V_{O2}). The equations (J.A. Mclean and G. Tobin, 1987) are as follows

Equation 5: V_{O2} (l/min) = VE (l/min)[ΔF_{O2} + (FI_{O2} / FI_{N2}) x (ΔF_{O2} + ΔF_{CO2} + ΔF_{CH4})]

Equation 6: V_{CO2} (l/min) = VE (l/min)[ΔF_{CO2} /100]

Equation 7: V_{CH4} (l/min) = VE (l/min)[ΔF_{CH4} /100]

where

Equation 8: $\Delta F = FI - FE$

and F is the concentration of the specified gas, FI is the concentration of the specified gas in the inlet airstream and FE is the concentration of the specified gas in the outlet airstream. In this system, the gas concentration of the inlet airstream in quantified with measurements of outside air. The concentration of nitrogen in the air is determined as gas that is not O_2, CO_2 or CH_4. In other words

Equation 9: $F_{N2} = 100 - (F_{O2} + F_{CO2} + F_{CH4})$

Once the volumes of gases consumed and produced are calculated, respiratory quotient and heat production (HP) can be calculated. The equations are as follows

Equation 10: Respiratory quotient = V_{O2} / V_{CO2}

Equation 11: HP (kJ/ min) = 16.179 (V_{O2}) + 5.022 (V_{CO2}) -2.168 (V_{CH4})

(Brouwer, 1965)

Heat production is then converted from kJ to kcal. In the macro the same set of calculations are performed for each measurement taken at four minute intervals for a predetermined 45-hr measurement period. Average HP is then calculated for two 22.5-hr periods and a 45-hr period and is expressed in kcal ($kg^{.75} .d^{-1}$).

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