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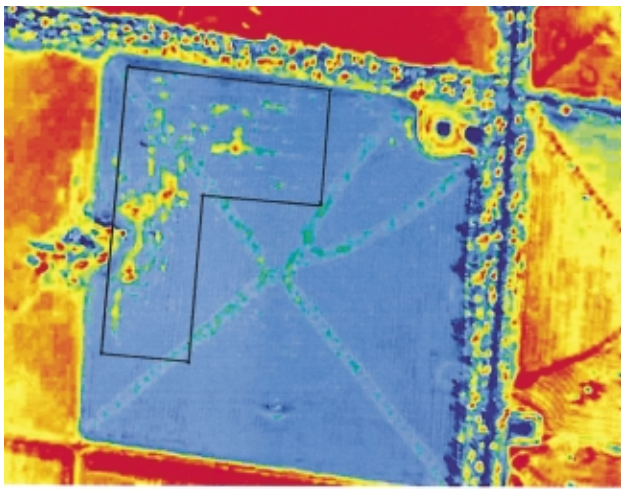

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Body composition and implications for heat production of Angus steer progeny of parents selected for and against residual feed intake

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Abstract. Yearling Angus steer progeny of parents selected for low residual feed intake (RFI; high efficiency) or high RFI (low efficiency) were evaluated for feed intake, growth and differences in body composition. RFI is the difference between actual feed intake and expected feed intake based on an animal's size and growth over a test period. Individual intakes of a high grain content ration and growth rates were recorded for 140 days and then the steers were slaughtered for measurement of body composition. All internal organs and non-carcass fat depots were removed, weighed and ground for chemical analysis. Carcasses were kept overnight in the chiller and the left half of every carcass physically dissected into retail cuts, and then into total fat, lean and bone. Carcass fat and lean were then combined and ground for chemical analysis. Steers from low RFI parents ate less ($P<0.05$) than the steers from high RFI parents, for similar rates of growth. Improvement in RFI was accompanied by small changes in body composition towards greater lean and less fat in the progeny of low RFI parents. Correlations of sire estimated breeding values for RFI with end of test whole body chemical protein, chemical fat and a principal component that condensed information on fat and lean body composition at the end of the test, were statistically significant. These confirmed there was a genetic association between body composition and RFI, with fatness being associated with higher RFI (i.e. lower efficiency). However, the correlations were small and suggested that less than 5% of the variation in sire RFI was explained by variation in body composition of their steer progeny. There was no evidence that a difference in the chemical composition of gain over the test explained the greater intake of metabolisable energy (ME) by the high RFI steers. The results suggest that the difference in ME intake following a single generation of divergent selection for RFI was due to metabolic processes rather than to changes in body composition.

Additional keywords: cattle, feed efficiency.

Introduction

Selection of beef cattle on genetic merit for average daily gain has successfully been used to improve the growth rate of beef cattle over many years. However whether this has been accompanied by improvement in the feed efficiency of maintaining herds of cows that are larger in size is questionable. Within the beef cattle population there is considerable variation in feed efficiency that is independent of size and growth rate (Arthur *et al.* 1997). This can be measured as residual feed intake (RFI), being the difference between an animal's actual feed intake and its expected feed intake based on its size and growth over a specified test period. Selection to improve RFI should reduce the cost of feeding cattle without compromising growth performance (Arthur *et al.* 1997).

Post-weaning tests for RFI on British breed cattle fed a medium quality ration have demonstrated that genetic variation in RFI exists, and that the trait is moderately heritable (Archer *et al.* 1998). Preliminary results suggest a single generation of selection for negative (i.e. more efficient) post-weaning RFI improved the efficiency of young bulls and heifers in post-weaning tests for RFI (Herd *et al.* 1997) and of steers when fed in a feedlot (Richardson *et al.* 1998). The genetic associations between post-weaning RFI and body composition, carcass traits and meat quality in Australian cattle are not known. However, Herd and Bishop (2000) have demonstrated both a phenotypic and genetic correlation between post-weaning RFI and estimated lean content of the carcass of British Hereford cattle, such that improvement in RFI is associated with increased lean content. In Australian cattle, a single generation of selection to improve RFI has been accompanied by a reduction in subcutaneous fat thickness in feedlot steers (Richardson *et al.* 1998), supporting the underlying genetic correlation

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between post-weaning RFI and subcutaneous rib fat depth in the preliminary report by Herd *et al.* (1998).

This paper reports the differences in feed intake, growth, body composition and implications for heat production of Angus steer progeny of parents divergently selected for and against post-weaning RFI. A preliminary report on the feedlot phase of this experiment was given by Richardson *et al.* (1998) and on the full experiment by Richardson *et al.* (1999*a*).

Materials and methods

Animals

The animals used were yearling Angus steers resulting from a single generation of divergent selection for post-weaning RFI. Cattle breeding and post-weaning tests for RFI were conducted at the NSW Agriculture Research Centre, Trangie, New South Wales, Australia. Post-weaning RFI tests were conducted on Trangie-bred Angus bulls and heifers, and Angus, Shorthorn, Hereford and Poll Hereford heifers purchased from industry herds, using the method described by Arthur *et al.* (1997).

At the end of each test, the heifers and bulls were ranked for RFI. The top 50% of heifers were then mated to the top 5% of bulls, and the bottom 50% of heifers mated to the bottom 5% of bulls to produce progeny bred for either high RFI or low RFI. The entire drop of steer progeny born in March and April 1996 from the industry-herd Angus heifers was available to this study. Following weaning in October 1996, the steers (17 low RFI steers from 4 sires; 21 high RFI steers from 4 sires) were transported from Trangie to the CRC research feedlot 'Tullimba'.

Feed intake and growth evaluation

The steers were grown on improved pastures until entry to the research feedlot in November 1996. They were then divided by age into 2 groups containing roughly equal numbers of low RFI and high RFI cattle: group 1, the older steers, consisting of 9 low RFI steers and 10 high RFI steers; group 2, the younger steers, 8 low RFI and 11 high RFI steers. Over a 2-week period the steers were accustomed to rations of increasing grain content. They were then fed a ration containing oat grain (70%, by fresh weight), hay (15%), protein meal (5%), mineral additives (2%) and a proprietary mixture of molasses, monensin, urea, vitamins, minerals and water (8%). The ration had a dry matter (DM) content of 89%, an *in vitro* metabolisable energy (ME) content of 10.75 MJ/kg DM (calculated as $12.54 - 0.124 \times$ acid-detergent fibre% $+ 0.393 \times$ N%), 14.3% crude protein (as N $\times$ 6.25) and a final urea content of 1%.

Three weeks after entry to the feedlot, each group of steers was split into 2 smaller groups (comprising low RFI and high RFI animals) and moved into 4 pens, each containing an automated self-feeder. Steers were individually identified by a transponder worn as an eartag. They were allowed 2 weeks to adapt to feeding from the automated feeders. Individual daily *ad libitum* feed intake and weekly liveweight were then recorded until February 1997 for the group 1 steers (over a total of 70 days) and March 1997 for the group 2 steers (over 106 days). Following evaluation in the feedlot, the steers were transported to the Beef Research Unit at the University of New England, Armidale, NSW. Here their *ad libitum* intake of feedlot ration and weight gain continued to be recorded: over 72 days for group 1 steers and 32 days for group 2 steers. At the start of the feedlot test period and end of the animal-house period, subcutaneous rib (12th/13th) and rump (Australian P8 site) fat depths were measured using an Aloka 500 ultrasound scanner. The cross-section area of the eye-muscle (*M. longissimus dorsi*; EMA) was measured subsequently by computer analysis of stored images.

Slaughter and dissection

One low RFI steer was removed from the experiment whilst in the feedlot and 3 high RFI steers that had not been evaluated in the animal house were excluded from this slaughter. The remaining 34 steers were killed in 2 groups of 17 (8 low RFI, 9 high RFI) in April and June 1997. The steers had been fed the feedlot ration for about 180 days and had attained an average age of 14 months and liveweight of 426 kg.

Each group was transported 500 km by road to the Food Science Australia abattoir at Cannon Hill, Brisbane, for slaughter. After an overnight curfew without food but with water available, the steers were killed using a captive-bolt pistol, and then bled. Electrical stimulation was not applied. External body parts (head, hide, hooves and tail) were collected from the slaughter floor, weighed and then discarded. Internal organs and trimmings from the carcass were dissected free of visible fat, and the weights of the 'fat-free' organs and various fat depots recorded. The internal organs were combined, as was separately the internal fat, and both portions separately minced, thoroughly mixed, subsampled and stored frozen for subsequent chemical analysis. The carcasses were chilled at 1°C and the next morning the left half of each carcass was dissected into boneless retail cuts (3 mm fat trim left on cuts). The weights of the chilled carcass and of retail beef, carcass fat and carcass bone were recorded. The carcass fat and retail beef were combined, then minced and subsampled for subsequent chemical analysis.

Laboratory analysis

After thawing and further mixing, subsamples of minced carcass, gut and internal fat were taken and freeze-dried for determination of DM content, following which the dried samples were ground before determination of nitrogen, fat and ash content.

Prior to chemical analysis samples were oven dried either at 105°C for the carcass and gut samples or at 70°C for the internal fat samples. Nitrogen content was measured on 1 g of dried sample of carcass mince and gut, and a 0.5 g sample of internal fat, using a Leco Nitrogen Analyser (model FP-200). Protein was calculated as N multiplied by 6.25. Fat was measured on a 3 g dried sample as the weight loss from the thimble following two, 65 min extractions with chloroform in a Soxtec 1043 Extraction Unit. Ash content was determined on a 2 g dried sample of minced carcass and gut, and on a 3 g sample of internal fat by combustion at 550°C for 6 h. Nitrogen and fat determinations were done in duplicate, and ash content in triplicate for all samples. Results for protein, fat and ash content are presented as a percent of DM.

Derived values

The chemical composition of external organs (head, hide, tail and hooves) blood and bones was not determined. Results for grain-fed steers (900 lb) published by Haecker (1920) were used to estimate the amount of fat and protein in the hide, blood and bones of our steers (assuming selection for RFI has no effect on the chemical composition of these organs). Results from Early *et al.* (1990*a*, 1990*b*) were used to estimate the amount of protein in the tail, head, lower leg and hooves (assuming no difference between low RFI and high RFI steers in the percentage of protein for each organ). No data was available to make estimations for the amount of fat in each of these external organs. These calculated values for external organs were added to the chemical composition measured for the remainder of the animal to give total chemical protein and fat for each animal at the end of the test period.

Energy retained (ER) due to the increase in body mass over the test period was calculated as the increase in energy stored in body tissues between the start and end of the test. Energy stored in body tissues was determined assuming 23.6 MJ of energy per kilogram of protein and 39.3 MJ of energy per kilogram of fat (Pullar and Webster 1977). To calculate the chemical composition of liveweight gain and ER over the test period it was necessary to estimate the chemical composition at the start of the test. The number of steers available for this study was not

sufficient to include start-of-test slaughters. The start of test weights of chemical protein and fat were estimated using multiple regression equations derived from the end of test slaughter data. These equations are:

$$\text{Protein (kg)} = 0.117 \times \text{LW} + 84.1 \times \text{EMA} - 74.3 \times \text{rib fat/LW} + 11.3 \times \text{rump fat/LW} \quad (R^2 = 0.49,\ n = 33,\ P<0.001)$$

$$\text{Fat (kg)} = 0.233 \times \text{LW} - 95.8 \times \text{EMA/LW} + 331 \times \text{rib fat/LW} + 36.2 \times \text{rump fat} \quad (R^2 = 0.50,\ n = 33,\ P<0.001)$$

where protein and liveweight (LW) are expressed in kg, EMA in mm^2/kg and rib and rump fat in mm/kg.

Heat production (HP) was calculated as the difference between the intake of ME over the test and ER in body mass gain over the test. As calculated, HP includes energy expended in the processes of protein and fat synthesis, energy used for the maintenance of body tissues over the test, energy used for activity and energy lost through the heat increment of feeding. Estimates from Geay (1984) for the efficiency of protein and fat synthesis of 0.2 and 0.75 respectively were used to calculate the ME theoretically expended in protein and fat gained over the test period. This value was subtracted from HP to estimate residual heat production (RHP), which includes energy used for maintenance, activity and lost through heat increment of feeding.

Statistical analysis

One high RFI steer had an atypically low feed intake while in the beef research unit and did not gain any weight over this period. Results for this animal were not used. The individual animal data for feed intake and liveweight used in this analysis were recorded over 142 days for the group 1 steers and 138 days for the group 2 steers. These are longer periods than the 70- and 56-day periods used in the preliminary report on feedlot performance by Richardson *et al.* (1998). Weekly liveweight for each steer was regressed on time using a simple linear regression to calculate start of test weight, mid test weight and average daily gain. This reduces the variation associated with gut fill if single start of test weights were to be used. The test period started following adaptation of the cattle to the feedlot diet and environment, the end of the test period was determined as the final feed intake and liveweight collected the day before transport to the abattoir for slaughter. The average daily feed intake by the steers was regressed against their average daily gains and $\text{midweight}^{0.73}$, and RFIs were calculated as the residuals from this regression (these being the difference between predicted and observed feed intake). Feed conversion ratio was determined as the ratio of total feed DM eaten to total liveweight gain for the test period.

Results for 33 steer progeny (16 low RFI, 17 high RFI) from 4 high RFI and 4 low RFI sires were obtained in this experiment. Differences between progeny of low RFI or high RFI parents were analysed using the general linear model (GLM) procedure of SAS (1989). Group (1 or 2) and the interaction of group with parental efficiency class (low RFI or high RFI) were included as fixed effects in the preliminary analysis. The interaction of efficiency class and group was not significant ($P>0.05$) for any of the measures of performance or body composition in this experiment, indicating that the differences between progeny of the parental efficiency classes were similar within both groups of animals tested. Therefore group was dropped from the final analysis. It was possible that comparisons using efficiency class might be unduly influenced by individual sires. The traditional method to guard against this is to fit sire within efficiency class as a random effect in the GLM and to test efficiency class differences against the sire within efficiency class mean squares. The low number of animals in this experiment meant this approach lacked the power to detect all but large differences between efficiency classes. An alternate approach was used to detect whether there was evidence for a genetic association of parental RFI with variation in traits measured on their progeny. Trial estimated breeding values (EBVs) for sire post-weaning RFI were obtained (Anon. 1999). The correlation procedure of SAS (1989) was used to examine correlations between the sire EBVs for RFI and values for traits measured on their steer progeny. Statistically significant correlations were presumed evidence for a genetic association.

To describe and evaluate biologically meaningful differences in body composition this paper presents results for many traits. The principal component analysis of SAS (1989) was used to condense the information on body composition contained within these many traits into just 1 or 2 new traits. These new traits were then analysed for evidence of genetic association with variation in parental RFI. The traits used in the principal component analysis were selected as describing elements of fatness and lean at the end of the experiment: thickness of subcutaneous rib and rump fat; total chemical fat; weight of internal fat; carcass subcutaneous fat and intermuscular fat; retail beef; total chemical protein; and the weight of internal organs, digestive tract and external organs.

Results

Growth, feed intake and efficiency

At the start of the experiment there was no difference ($P>0.05$) in age or liveweight of the progeny of the low RFI and high RFI parents (Table 1). Average daily gain over the test period and final liveweight did not differ between the 2 classes of steers. Progeny of the low RFI parents demonstrated a lower RFI ($P<0.05$) than progeny of high RFI parents: therefore steers will be referred to as low and high RFI steers from this point onwards. High RFI steers consumed 5% more per day ($P<0.05$) than the low RFI steers. The low RFI steers had less P8 rump fat ($P<0.05$) and rib fat ($P<0.1$) than the high RFI steers at the start of the test period. By the end of the test there was no significant difference in subcutaneous fat depth or EMA between the low RFI and high RFI steers. Both groups deposited a similar amount of subcutaneous rib fat (7.4 ± 0.8 and 7.8 ± 0.7 mm; n.s.) and rump fat (9.0 ± 0.6 and 8.3 ± 0.7 mm; n.s.) over the test, while the low RFI steers gained more EMA (16.7 ± 1.3 and 12.8 ± 1.3 cm^2; $P<0.05$) over the test. While the latter results suggest that the composition of gain over the test was similar by low and high RFI steers, correlations between sire EBV for RFI and the ultrasound scans suggest selection for RFI will lead to changes in body composition and to the composition of gain over time.

Carcass and non-carcass components

The low RFI and high RFI steers did not differ significantly for cold carcass weights (Table 2) and dressing percentages (56.2 ± 0.3 and 57.1 ± 0.4%; n.s.). There were no differences between the steer groups in the weights of dissected subcutaneous, intermuscular fat and non-carcass fat, but correlations between these traits and sire EBV for RFI were all positive, indicating selection against RFI had slightly increased the amount of fat in these depots. Total dissected carcass fat (intermuscular + subcutaneous) was significantly higher in high RFI steers, and total carcass fat

plus internal fat (total dissected fat) also tended ($P<0.10$) to be higher in the high RFI steers than in the low RFI group.

There was no difference in the absolute weight of any of the external organs for the low RFI and high RFI steers. Although, low RFI steers had more external organs as a percentage of their final liveweight ($P<0.1$) than did high RFI steers (Table 2). The correlations for external organs and external organs expressed as a percentage of carcass weight with sire EBV for RFI ($r = –0.42$; $P<0.01$ and $r = –0.52$; $P<0.01$ respectively) affirmed these results. While there was no difference for the high and low RFI steers in weight of bones, low RFI steers had significantly more bones as a proportion of their final liveweight ($P<0.05$) compared to high RFI steers. Bones were also significantly correlated with sire EBV for RFI, when expressed as a percentage of final liveweight ($r = –0.46$; $P<0.01$). There was no difference in absolute weights for any of the internal organs; however, there was a trend for the low RFI steers to have more intestines (6.26 ± 0.20 *v.* 5.80 ± 0.16; $P<0.10$) than high RFI steers. The negative correlation between total weight of intestines and sire EBV for RFI supported this trend ($r = –0.33$; $P<0.10$).

Chemical composition, energy retention and energy balance

There was no difference between the low RFI and high RFI steers in weight of whole-body chemical protein and chemical fat when slaughtered at the end of the test period, or in gain of fat over the test (Table 3). However, low RFI steers gained more protein than high RFI steers, and contained a greater proportion of protein in the final liveweight, than the high RFI steers ($P<0.10$). Statistically significant correlations between measures of body composition and sire EBV for RFI presented in Table 3 provide evidence for a genetic association between RFI and body composition. Positive correlations between RFI with end-of-test chemical fat (both total whole body and as a percentage of final liveweight), and negative correlations with chemical protein (both gain and total whole body as a percentage of final liveweight), are consistent with increased fatness being associated with higher RFI (i.e. lower efficiency). There was no difference in ER in body tissues, in HP or in RHP over the test period. The low RFI steers had a lower RHP per kg of protein gained over the test ($P<0.05$) and this difference was affirmed by the correlation between RHP per kg of protein gain and sire EBV for RFI. Variations in sire EBV for RFI was not accompanied by differences in RHP per kg of fat gain.

Principal component analysis of body composition

The first 2 principal components together accounted for 62% of the standardised variance of the body composition data. The first principal component accounted for 36% of the standardised variance of the body composition data and was a measure of all components contributing to body composition, as shown by approximately equal loadings of all the fatness and lean variables. The second principal component accounted for 26% of the standardised variance and had positive loadings for measures of fatness and negative loadings for measures of lean. These loadings were: subcutaneous rib fat 0.38, subcutaneous rump fat 0.31, total chemical fat 0.32, internal fat 0.40, carcass intermuscular fat 0.39, carcass subcutaneous fat 0.19, retail beef –0.26, total chemical protein –0.32, internal organs (excluding GIT) –0.18, digestive tract –0.20 and external organs –0.26. The

Table 1. Feed intake, growth and efficiency of yearling Angus steer progeny of parents selected for low RFI (high efficiency) or high RFI (low efficiency)

Values are means ± standard error, and correlations of the trait with sire estimated breeding value for RFI

Trait	Low RFI	High RFI	Signif.	Correlation
Number of animals	16	17		
Start age (days)	279 ± 3	284 ± 3	n.s.	
Start liveweight (kg)	283 ± 7	292 ± 7	n.s.	0.20
Final liveweight (kg)	423 ± 6	428 ± 8	n.s.	0.09
Daily liveweight gain (kg/day)	1.00 ± 0.04	0.97 ± 0.04	n.s.	–0.15
Daily feed intake (kg DM)	8.03 ± 0.10	8.45 ± 0.17	*	0.34†
Residual feed intake (kg/day)	–0.15 ± 0.08	0.16 ± 0.10	*	0.35*
Feed conversion ratio	8.23 ± 0.34	8.97 ± 0.40	n.s.	0.28
Start rib fat depth (mm)	3.8 ± 0.33	4.7 ± 0.35	†	0.35*
Start rump fat depth (mm)	4.3 ± 0.30	5.7 ± 0.45	*	0.49**
Start eye-muscle area (cm^2)	43.3 ± 0.90	46.1 ± 1.40	n.s.	0.42*
Final rib fat depth (mm)	11.2 ± 0.69	12.4 ± 0.76	n.s.	0.29
Final rump fat depth (mm)	13.3 ± 0.69	14.0 ± 0.90	n.s.	0.12
Final eye-muscle area (cm^2)	59.9 ± 1.34	58.9 ± 1.06	n.s.	–0.07
Change in eye-muscle area (cm^2)	16.7 ± 1.28	12.8 ± 1.26	*	–0.44**

† $P<0.10$; * $P<0.05$; ** $P<0.01$; n.s., $P>0.10$.

third principal component explained only an additional 12% of the variance and as interpretation of the loadings was not obvious results for it are not presented. There was no difference ($P>0.05$) between the low and high RFI steers in their loading on the first principal component nor was there a significant ($P>0.05$) correlation between these loadings and sire EBV for RFI. Low RFI steers tended ($P = 0.06$) to have loadings on the second component that were negative (i.e. in the direction associated with lean) and high RFI steers loadings that were positive (i.e. in the direction associated with fatness; -0.56 ± 0.43 and 0.53 ± 0.37 respectively). The correlation between loadings on the second component and EBV for RFI were positive ($r = 0.43$; $P<0.05$). This implies a genetic association between RFI and body composition, with increased fatness associated with higher RFI (i.e. lower efficiency), and is in agreement with the correlations for protein and fat presented in Table 3.

Discussion

Yearling age Angus steer progeny of parents who had been selected for low post-weaning RFI demonstrated improved efficiency when fed over 140 days on a high grain content feedlot ration compared with steer progeny of parents selected for high post-weaning RFI. The progeny of low RFI parents demonstrated a lower RFI compared with the progeny of high RFI parents, the difference in RFI being 0.31 kg DM/day, or about 3.8% of the average daily DM intake for all the steers (8.24 kg). This is slightly less than the 5% difference calculated from the preliminary report by Herd *et al.* (1997). Both results confer with the report by Arthur *et al.* (1997) stating that post-weaning RFI has a genetic component with a moderate heritability. The steers in this study expressed differences in RFI on a ration that differed from the pelleted lucerne diet on which their parents were tested. This indicates that improvement in RFI is not restricted to the test diet and environment on which the parent generation is selected, and that improvement in performance may be expressed under different feeding systems.

Post-weaning RFI used to select the parents of the steers tested in this study was calculated to be phenotypically independent of size and growth rate. The 2 groups of steers produced following a single generation of divergent selection for post-weaning RFI showed no change in start of

Table 2. Weights of carcass and non-carcass components for yearling Angus steer progeny of parents selected for low RFI (high efficiency) or high RFI (low efficiency)

Values are the means ± standard error, and correlations of the trait with sire estimated breeding value for RFI

Organ	Low RFI	High RFI	Signif.	Correlation
	Carcass component weights			
Cold carcass weight (kg)	240 ± 3.10	245 ± 4.70	n.s.	0.23
Subcutaneous fat (kg)	16.8 ± 1.18	19.6 ± 1.17	n.s.	0.35*
Intermuscular fat (kg)	25.3 ± 1.13	28.9 ± 1.92	n.s.	0.34†
Carcass fat (intermuscular + subcutaneous; kg)	42.1 ± 1.76	48.5 ± 2.08	*	0.47**
Retail beef (kg)	151 ± 1.73	151 ± 3.03	n.s.	0.03
Retail beef yield from carcass (%)	63.0 ± 0.45	61.6 ± 0.64	†	–0.36*
Bones (kg)	45.5 ± 1.03	43.9 ± 0.85	n.s.	0.23
	Non-carcass component weights			
External organs (kg)[A]	56.32 ± 0.78	54.81 ± 0.90	n.s.	–0.27
Internal organs (kg)[B]	13.52 ± 0.41	13.34 ± 0.27	n.s.	–0.18
Gastrointestinal tract (GIT; kg)	16.4 ± 0.52	15.9 ± 0.41	n.s.	–0.20
Non-carcass fat (kg)[C]	33.18 ± 1.45	35.78 ± 1.32	n.s.	0.30†
Total dissected fat (kg)[D]	84.2 ± 2.86	92.4 ± 3.30	†	0.42*
	Body component percentages			
Internal organs/final liveweight (%)	3.2 ± 0.07	3.1 ± 0.04	n.s.	–0.27
External organs/final liveweight (%)	13.2 ± 0.15	12.8 ± 0.15	*	–0.42*
Non-carcass fat/final liveweight (%)	7.8 ± 0.35	8.4 ± 0.31	n.s.	0.28
Carcass fat/final liveweight (%)	9.9 ± 0.39	11.3 ± 0.39	*	0.50**
Bones/final liveweight (%)	10.73 ± 0.15	10.27 ± 0.12	*	–0.46**
Total dissectible fat/final liveweight (%)	19.8 ± 0.66	21.5 ± 0.61	†	0.42*
Retail beef/final liveweight	35.4 ± 0.36	35.2 ± 0.49	n.s.	–0.36*

[A]External organs include: hide, head, hooves and tail.
[B]Internal organs: kidney, lung, liver, heart, spleen, gall bladder, bladder, neck, diaphragm, oesophagus.
[C]Non-carcass fat: mesenteric, omental, kidney and channel fat, plus fat trimmed from the lungs and heart.
[D]All fat dissected from the carcass (carcass fat plus non-carcass fat).
† $P<0.10$; * $P<0.05$; ** $P<0.01$; n.s., $P>0.10$.

test liveweight and final liveweight. Steer groups did not differ significantly for average daily gain over the test period, but the high RFI steers had a reduced average daily feed intake ($P<0.05$) and would have been more profitable to feed. When slaughtered at the end of the test there was no difference between the low RFI and the high RFI steers in subcutaneous fatness and EMA. Therefore both groups of steers would have equally met market specifications for liveweight and fatness.

The trend towards increased lean content of the carcasses associated with selection to reduce RFI is in agreement with the negative genetic correlation between post-weaning RFI and estimated lean content of the carcass reported for British Hereford cattle (r_g = –0.43; Herd and Bishop 2000). The apparent lack of change in subcutaneous fat thickness in the small sample of cattle used in this study presumably reflects the much lower genetic correlation with RFI reported in the Australian cattle tested thus far (r_g = 0.22; Herd *et al.* 1998). Correlations between the sire EBV for RFI and several measures of fatness of their progeny were generally less than 0.4 but confirmed that there was a genetic association between fatness and selection for RFI. The second principal component condensed information on fat and lean body composition at the end of the experiment into a single trait that had positive loadings for measures of fatness and negative loadings for measures of lean. The positive correlation of this new trait with sire EBV for RFI provided additional evidence for a genetic association between body composition and RFI, with fatness being associated with higher RFI (i.e. lower efficiency). However, with a correlation of 0.43 it explained only 18% of the variation in principal component 2, which itself explained only 26% of the standardised variance in body composition. This meant that less than 5% (i.e. $0.18 \times 0.26 = 0.0468$) of the variation in parental RFI was explained by variation in these measures of body composition of their steer progeny.

The small changes in external organs, bones and measures of protein and fat suggest that changes in body composition do occur following selection for RFI. High RFI steers had a greater start of test EMA, a lower end of test EMA, a lesser proportion of external organs and bones in their final liveweight, and deposited more fat and less protein over the test than low RFI steers. Together these changes in composition imply there may be differences in the maturity pattern of these steers. However there is as yet no evidence that selection for RFI has been accompanied by a change in mature size, and as a corollary, changed stage of maturity (liveweight as a proportion of mature liveweight) in divergently selected progeny when compared at the same age. In this study, yearling-aged low RFI and high RFI steers did not differ in liveweight at the start and end of the test period, nor did low RFI and high RFI bulls and heifers at the end of a post-weaning test for RFI (Herd *et al.* 1997). Preliminary data from the Trangie breeding herd suggests that mature cow weight is phenotypically independent from post-weaning RFI (Arthur *et al.* 1999). Moreover, Herd and Bishop (2000) reported post-weaning RFI to be genetically independent of mature cow size using data from an experiment on British Hereford cattle. Given this evidence, the differences observed in this experiment may be a reflection of different patterns of maturity rather than mature cow size.

The whole-body content of chemical protein of these steers was estimated to be about 60 kg, of which the

Table 3. Chemical composition, energy retained in body tissues and energy balance over a 140-day test for yearling Angus steer progeny of parents selected for low RFI (high efficiency) or high RFI (low efficiency)

Values are means ± standard error, and correlations of the trait with sire estimated breeding value for RFI

Trait	Low RFI	High RFI	Signif.	Correlation
Whole body end of test chemical protein (kg DM)[A]	60.2 ± 0.75	59.2 ± 0.81	n.s.	–0.18
Whole body end of test chemical fat (kg DM)[A]	92.9 ± 2.11	99.1 ± 3.84	n.s.	0.34 †
Chemical protein as % final liveweight	14.2 ± 0.15	13.9 ± 0.17	†	–0.33 †
Chemical fat as % final liveweight	21.9 ± 0.43	23.1 ± 0.62	n.s.	0.38 *
Gain in protein (kg DM)	15.1 ± 0.59	12.8 ± 0.79	*	–0.50 **
Gain in fat (kg DM)	36.5 ± 2.29	40.2 ± 3.60	n.s.	0.23
Energy retained (ER; GJ)[B]	1.79 ± 0.09	1.88 ± 0.14	n.s.	0.15
Intake of ME during test (MEI; GJ)	12.1 ± 0.16	12.8 ± 0.27	†	0.33 †
Heat production (HP, = MEI – ER; GJ)	10.3 ± 0.21	10.9 ± 0.30	n.s.	0.22
Residual heat production (RHP; GJ)[C]	6.64 ± 0.33	7.27 ± 0.43	n.s.	0.17
RHP/gain in protein (kJ/kg DM)[D]	455 ± 34.5	615 ± 54.4	*	0.46 **

[A]Includes literature values for hide, blood, bones, hide, head, hooves and tail.
[B]Includes ER as fat or protein (calculated as kg tissue energy content).
[C]Calculated as HP less energy expended in tissue energy gain (efficiencies of gain k_f = 0.75; k_p = 0.2), includes energy used for tissue maintenance.
[D]RHP/total weight of tissue gained over test.
† $P<0.10$; * $P<0.05$; ** $P<0.01$; n.s., $P>0.10$.

3 components that were actually measured comprised about 33 kg, or about 55% (carcass: about 28 kg; non-carcass lean: about 4 kg; non-carcass fat: about 1 kg). The remaining 45% of whole-body chemical protein was not measured in this experiment, so literature values were used to calculate chemical composition, and assumed no difference in composition between low RFI and high RFI steers. The largest depot of protein measured was that in the carcass and the low RFI steers contained 36% chemical protein in their carcasses compared with 33% in the high RFI steers (although the difference was not statistically significant). Had external organs actually been measured and a similar difference in protein content been present then the estimated chemical content of the low RFI steers would have increased. A greater chemical protein content of the low RFI steers compared with the high RFI steers may be expected, given the low RFI steers had a greater proportion of protein in their bodies as a percentage of their final liveweight compared with the high RFI steers (Table 3).

The only difference in gain of chemical composition over the test period was a small increase in protein gain by the low RFI steers. The increased intake of ME by high RFI steers could not be attributed to a difference in ER in body tissues. The difference in ME intake was the extra energy lost as heat production by the high RFI steers. Residual heat production was calculated to be net of the energy used in synthesis of the amounts of protein and fat gained over the test period, and is analogous to maintenance energy expenditure used in Herd and Bishop (2000). Those authors reported a positive genetic correlation between maintenance energy expenditure and RFI in young British Hereford cattle indicating that high RFI was associated with high maintenance energy expenditure. While RHP did not differ (P>0.05) for the low RFI and high RFI steers, the high RFI steers had a RHP per kg of protein deposited that was 35% higher than that of the low RFI steers, and there was no evidence of association between RFI and RHP per kg of fat gained. This implies the low RFI steers had superior efficiencies in depositing energy in protein gain and/or in maintaining these tissues once they were deposited.

Protein turnover in living animals is an energetically expensive process. Moreover, protein in gut tissues has a turnover rate perhaps 20 times that of protein in skeletal muscle (Wassner and Li 1982; Rennie and Millward 1983). It was then perhaps surprising that the low RFI steers had more external organs as a proportion of final liveweight, and more whole body chemical protein, than the high RFI steers. In this experiment, ME 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 gain in fat. One explanation for this would be a difference between the groups of steers in protein turnover. Variation in protein metabolism has been shown to accompany genetic selection for growth and other traits in domestic animals (reviewed by Oddy 1999). Compared with the low RFI steers, higher rates of myofibre disassembly and lower levels of calpastatin (an inhibitor of the calpain enzymes thought responsible for myofibre disassembly) have being reported from skeletal muscle from the high RFI steers. This is indicative of higher rates of protein breakdown in the high RFI steers (McDonagh 1998).

A single generation of selection for improved post-weaning RFI has produced steers with a lower feed intake, similar growth rate, similar carcass weight and fat finish, and with an improvement in retail beef yield, compared with steer progeny of parents selected against RFI. Correlations for measures of body composition with sire EBV for RFI are evidence of a genetic association with body composition. But variation in body composition explained only a small part of variation in RFI and is but a small component of the physiological basis for variation of this trait in beef cattle. The remainder of this variation is likely due to differences in tissue protein turnover, the difference in feed intake, and perhaps differences in activity (Richardson *et al.* 1999*b*).

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References

Anon. (1999) 'Trial net feed intake estimated breeding values for Angus sires.' Australian Angus Group Breed Plan Genetic Evaluation Report, Angus Society of Australia. pp. 106–107.

Archer JA, Arthur PF, Herd RM, Richardson EC (1998) Genetic variation in feed efficiency and its component traits. *Proceedings of the 6th World Congress of Genetics Applied to Livestock Production* **25**, 81–84.

Arthur PF, Archer JA, Herd RM, Richardson EC, Wright JH, Dibley KCP, Burton DA (1997) Genotypic and phenotypic variation in feed intake, feed efficiency and growth rate in beef cattle. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* **12**, 234–237.

Arthur PF, Archer JA, Herd RM, Richardson EC (1999) Relationship between postweaning growth, net feed intake and cow performance. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* **13**, 484–487.

Early RJ, McBride BW, Ball RO (1990*a*). Growth and metabolism in somatotrophin-treated steers. II. Carcass and noncarcass tissue components and chemical composition. *Journal of Animal Science* **68**, 4144–4152.

Early RJ, McBride BW, Ball RO (1990*b*) Growth and metabolism in somatotrophin-treated steers. III. Protein synthesis and tissue energy expenditures. *Journal of Animal Science* **68**, 4153–4166.

Geay Y (1984) Energy and protein utilisation in growing cattle. *Journal of Animal Science* **58**, 3766–3778.

Haecker TL (1920) Investigations in beef production. I. The composition of steers at various stages of growth and fattening. *Bulletin* **193**, 1–105.

Herd RM, Archer JA, Arthur PF, Richardson EC, Wright JH, Dibley KCP, Burton DA (1997) Performance of progeny of high vs. low net feed conversion efficiency cattle. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* **12**, 742–745.

Herd RM, Archer JA, Arthur PF, Richardson EC (1998) Reducing the cost of beef production through the genetic improvement of net feed efficiency. In 'Proceedings of The British Society of Animal Science' 1998. p. 45.

Herd RM, Bishop SC (2000) Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. *Livestock Production Science* **63**, 111–119.

McDonagh MB (1998) Calpain activity affects muscle protein turnover and meat tenderisation. PhD Thesis, University of New England, Armidale, Australia.

Oddy VH (1999) Genetic variation in protein metabolism and implications for variation in efficiency of growth. *Recent Advances in Animal Nutrition in Australia* **12**, 23–29.

Pullar JD, Webster AJF (1977) The energy cost of fat and protein deposition in the rat. *British Journal of Nutrition* **37**, 355–363.

Rennie MJ, Millward DJ (1983) 3-methylhistidine excretion and the urinary 3-methylhistidine/creatinine ratio are poor indicators of skeletal muscle protein breakdown. *Clinical Science* **65**, 217–225.

Richardson EC, Herd RM, Archer JA, Woodgate RT, Arthur PF (1998) Steers bred for improved net feed efficiency eat less for the same feedlot performance. *Animal Production in Australia* **22**, 213–216.

Richardson EC, Herd RM, Oddy VH, Woodgate RT, Archer JA, Arthur PF (1999*a*). Body composition explains only part of the intake difference between high and low efficiency Angus steers. *Recent Advances in Animal Nutrition in Australia* **12**, 4A.

Richardson EC, Kilgour RJ, Archer JA, Herd RM (1999*b*). Pedometers measure differences in activity in bulls selected for high and low net feed efficiency. *Proceedings of the Australian Society for the Study Animal Behaviour* **26**, 16.

SAS Institute Inc. (1989) 'SAS/STAT Users Guide. Version 6 (4th edn).' (SAS Institute Inc.: Cary, NC, USA)

Wassner SJ, Li JB (1982) Nt-methylhistidine release: contributions of rat skeletal muscle, GI tract and skin. *American Journal of Physiology* **243**, 293–297.

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