Genetics of growth and feed efficiency

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Introduction

The CRC for Cattle and Beef Quality was established in 1993 to identify the genetic and non-genetic factors affecting beef quality and other production traits of economic importance. Providing feed for cattle is the single largest input cost in beef production enterprises. Advances in computing and electronics has allowed the development of reliable automatic feed intake recorders making it easier to measure feed intake, and this in association with increased producer demand for a means of selecting on the basis of efficiency, has led to increased research in feed efficiency. Understanding genetic variation in feed efficiency and providing the tools for genetic improvement in the efficiency of feed utilization can have a major impact on profitability.

Progress of research within the CRC, and internationally, for beef cattle feed efficiency has been regularly reviewed and published (Archer et al. 1999; Herd et al. 2003a; Arthur et al. 2004; Arthur and Herd 2005, 2006). This paper summarises the CRC's major contributions to new knowledge and applications for genetic improvement of growth and feed efficiency.

Measuring feed efficiency

Net feed intake is the measure of feed efficiency that has been recommended by scientists as the trait to be adopted by the Australian Beef Industry for the purpose of genetic improvement. Net feed intake (NFI), sometimes also called residual feed intake (RFI), is the difference between the amount of feed that an animal eats during a feed intake test and the amount expected for an average animal of its weight and growth rate. By this measure, the more efficient cattle are those that eat less than expected. It allows a fair comparison of cattle of different liveweight and permits selection of feed efficient cattle of any desired weight.

The use of NFI for selection to improve feed efficiency is preferable to use of feed conversion ratio (FCR, kilograms of feed eaten per kilogram of liveweight gain) as selection on FCR can lead to heavier cattle, which may not suit all environments (Herd et al. 2003a).

To allow scientists to measure the feed intake on large numbers of research cattle, the CRC in conjunction with local company Cosign Ltd, developed an automatic feed intake recorder, and now has 26 units installed at the CRC 'Tullimba' Research Feedlot. To assist cattle breeders measure feed intake and the efficiency of their own cattle the CRC granted a license to manufacture and sell the feed intake recorder to the Ruddweigh International Scale Company. This machine has been purchased by a number of progressive cattle breeders and government research agencies.

The minimum length of test required to obtain accurate data on liveweight gain and feed intake by an animal to compute NFI was determined to be 70 days, preceded by a 21 day introductory period to allow the animal to become accustomed to the test ration and feeding system (Archer et al. 1997). This is shorter than usually recommended for growth-rate tests overseas, but still imposes significant inconvenience and feeding costs on the test animal owner. Automatic animal weighing systems offer the potential to reduce the length of the test (Kearney et al. 2004) but the 70-day test remains the current Australian standard until reliable automatic weighing systems are installed in feed-intake test stations.

To ensure accurate collection of feed efficiency data, clear guidelines on how cattle are to be tested and an accreditation system for the conduct of tests were developed in consultation with the Performance Beef Breeders Association, representing the major Australian beef cattle breed societies. The standards manual for testing cattle is now in its second edition and there are currently 14 accredited testing facilities.

CRC cattle breeding programs

Four major cattle breeding programs and their associated pedigree and performance data have given CRC scientists an internationally-unique resource for estimation of genetic relationships. These pedigree populations are:

1. The Trangie Angus Feed Efficiency herd and divergent NFI selection lines, with

approximately 2,000 bull, heifer or steer progeny measured.

2. The CRCI straight breeding experiment involving 7 Australian cattle breeds in which almost 8,000 progeny were measured for growth; carcase and meat quality traits, and approximately 1500 for feed efficiency (as NFI).
3. The CRCI northern crossbreeding progeny test project involving Brahman cows joined to 9 sire breeds, with around 1,800 progeny measured for growth; carcase and meat quality traits, with 469 also with NFI data.
4. The CRCII northern breeding project, based on Brahman and Tropical Composite cattle with some 2,200 steers measured for growth, carcass and meat quality traits, and 1465 for feed-intake and NFI, and 2,200 heifer half-sibs measured for age at puberty and subsequent fertility.

Most animals in these populations have had DNA samples stored. The Australian Beef Industry will continue to benefit form this unique database which now forms the foundation for new CRC for Beef Genetic Technologies research in gene discovery and accelerated genetic improvement.

1. Trangie Angus feed efficiency herd

Research in Australia into NFI began at the Trangie Agricultural Research Centre, NSW, prior to commencement of the CRC, with funding provided by the former Meat Research Corporation. This major project demonstrated the presence of genetic variation in NFI measured postweaning in young bulls and heifers from the Angus breed, and also in heifers from the Shorthorn and Hereford breeds.

Postweaning NFI performance tests

Records on 1,180 young Angus bulls and heifers involved in performance tests were used to estimate genetic and phenotypic parameters for feed intake, feed efficiency, and other postweaning traits. The mean age was 268 days at the start of the performance test, which comprised 21-day adjustment and a 70-day test period. Traits studied included 200-day weight, 400-day weight, scrotal circumference, scanned rib and rump fat depths and eye-muscle area, average daily gain, metabolic mid-test liveweight, daily feed intake, FCR and NFI.

In brief, the results showed daily feed intake, average daily gain, 200-day weight, 400-day weight, rib and rump fat depth, average daily gain, eye-muscle area, FCR and NFI were all moderately heritable (Table 1). Feed conversion ratio was genetically (rg=0.66) and phenotypically (rp=0.53) correlated with NFI. Feed conversion ratio was correlated (rg=-0.62, rp= -0.74) with average daily gain, whereas NFI (which includes ADG in its calculation) was not (rg=-0.04, rp= -0.06). Genetically, both NFI and FCR were negatively correlated with direct effects of 200-day weight and 400-day weight. The correlations between the remaining traits and the feed efficiency traits were close to zero, except between feed intake and FCR (rg=0.31, rp=0.23), feed intake and NFI (rg=0.69, rp=0.72), and rib fat depth and NFI (rg=0.17, rp=0.14). These results indicated that genetic improvement in feed efficiency could be achieved through selection and, in general, correlated responses in growth and the other postweaning traits would be minimal. Full results are reported in Arthur et al. (2001b) and were used to develop BREEDPLAN NFI EBVs.

Direct response to selection

Comprehensive evaluation of the correlated responses to selection for NFI selection was a major area of research within the CRC. Starting with the 1993-born Angus cattle at the Trangie Research Centre, a postweaning feed intake and NFI test was conducted each year. Creation of the NFI selection lines commenced in 1994. The 1993-born and 1994-born cattle formed the foundation herd. After completing their NFI test, the females were allocated to their selection lines based on their individual NFI values. Those with low NFI (<0; more efficient) were allocated to the low NFI

Table 1. Trangie Angus Feed Efficiency Project: Postweaning NFI test and mature cow NFI test heritabilities (on the diagonal) and genetic correlations (above the diagonal) for feed intake (FI), test average daily gain (ADG), metabolic mid-test liveweight (MMWT), net feed intake (NFI), feed conversion ration (FCR) and end-of-test scanned P8 fat depth, and genetic correlations between postweaning traits (below diagonal) and mature cow traits (above diagonal). (Adapted from Arthur et. al. 2001b and Archer et al. 2002)

Trait	Mean	FI	ADG	MMWT	NFI	FCR	P8 fat
Postweaning test							
FI (kg/day)	9.65	***0.39***	0.54	0.65	0.69	0.31	0.14
ADG (kg/day)	1.26		***0.28***	0.53	-0.04	-0.62	-
MMWT (kg)	68.8			***0.40***	-0.06	-0.01	-
NFI (kg/day)	0.05				***0.39***	0.66	0.06
FCR (kg/kg)	7.79					***0.29***	-0.04
P8 fat (mm)	5.44						***0.38***
Mature cow test							
FI (kg/day)	15.7	***0.28***	0.57	0.45	0.71	-0.57	
ADG (kg/day)	1.19		***0.33***	0.37	0.02	-0.87	
MMWT (kg)	110			***0.71***	-0.21	-0.12	
NFI (kg/day)	-0.54				***0.23***	-0.21	
FCR (kg/kg)	14.3					***0.26***	
Genetic correlations between postweaning and mature cow test traits							
FI (kg/day)		0.94	0.67	0.69	0.69	-0.12	
ADG (kg/day)		0.73	0.72	0.91	0.20	-0.30	
MMWT (kg)		0.51	0.39	0.82	0.06	0.05	
NFI (kg/day)		0.64	0.22	-0.22	0.98	-0.06	
FCR (kg/kg)		0.15	-0.33	-0.54	0.75	0.20	

Table 2. Trangie NFI Divergent Selection lines: Means for production traits for young bulls and heifers postweaning and steers from cattle lines divergently selected for low NFI (high efficiency) or high NFI (low efficiency), and regression co-efficient with NFI EBV.

Trait	Selection Line Low NFI	 High NFI	Level of Significance	Regression with NFI EBV
Postweaning test of bulls and heifers[1]				
Feed intake (kg/day)	9.4	10.6	*	
Average daily gain (kg/day)	1.44	1.40	ns	
Yearling liveweight (kg)	384	381	ns	
Net feed intake (kg)	-0.54	0.71	*	
Steer performance on pasture[2]				
Feed intake (kg/day)	3.0	3.2	ns	0.28^{ns}
Average daily gain (kg/day)	0.50	0.42	†	-0.11*
Feed conversion ratio (kg/kg)	6.4	8.5	ns	2.9†
Steer performance in the feedlot[3]				
Feed intake (kg/day)	12.3	12.5	ns	0.04 ^{ns}
Average daily gain (kg/day)	1.53	1.49	ns	-.09*
Feed conversion ratio (kg/kg)	7.6	8.2	†	0.59†
Net feed intake (kg/day)	-0.12	0.10	*	0.42*
Preslaughter P8fat depth (mm)	13.1	14.8	*	2.4*
Body composition of steers, percentages of final liveweight[4]				
Non-carcass fat	7.8	8.4	ns	0.28
Carcass fat	9.9	11.3	*	0.50**
Retail beef	35.4	35.2	ns	-0.36*

ns P>0.1, † P<0.1,* P<0.05, ** P<0.01.

[1] After 2 generations of selection, adapted from Arthur et al. (2001a)

[2] After 1 generation of selection, adapted from Herd et al. (2002)

[3] After 1 generation of selection, adapted from Herd et al. (2003b)

[4] After 1 generation of selection, adapted from Richardson et al. (2001)

line; those with high NFI (>0; less efficient) to the high NFI line. The 3-6 lowest NFI and 3-6 highest NFI bulls tested each year were allocated to the low and high-NFI lines, respectively. Divergent selection, based solely on individual postweaning NFI, continued to 1998, with the first progeny of selected parents born in 1995 and the last in 1999.

Direct and correlated responses in postweaning feed efficiency and growth traits resulting from 5 years of divergent selection were evaluated using 62 low-NFI (high efficiency) line cattle and 73 high-NFI (low efficiency) line cattle (Arthur et al. 2001a). Direct selection response (high-line minus low-line) in NFI per year was 0.249 kg/day. Correlated responses in yearling weight and average daily gain were not significant. However, annual correlated responses in feed intake (0.24 kg/day) and feed conversion ratio (0.24) were significant (P<0.05). After approximately two generations of divergent selection, low-NFI line progeny that ate significantly less feed than progeny in the high-NFI line, but did not differ in average daily gain over the test period or in final liveweight (Table 2).

Steer performance on pasture

After a single generation of divergent selection, steer progeny from the low-NFI line grew faster than steers from the high-NFI, with no difference in feed intake, and therefore displayed superior feed conversion during growout on summer pasture in northern NSW (Table 2). Further evidence for favourable association of steer growth and feed efficiency on pasture, with genetic variation in NFI, was reported by Herd et al. (2004). A cohort of Angus and Hereford steers in the CRCI Straight Breeding Project were also evaluated for their growth and feed intake on pastures in northern NSW. Significant regression coefficients with EBV NFI provided evidence for favourable associations for average daily gain, NFI and FCR with superior EBV for NFI. Lack of a significant regression coefficient for feed intake with NFI EBV provided evidence that it was not differences in pasture intake that resulted in superior feed conversion but rather superior average daily gain when pasture conditions limited growth rate of the steers, as occurred in both experiments.

Steer performance in the feedlot

Feedlot performance and carcase attributes of steer progeny from parents selected for low (n=144 steers) or high NFI (n=165 steers) was investigated using 3 cohorts of Trangie-bred calves born in 1997, 1998 and 1999, and fed for slaughter at light, heavy and medium market weights respectively (Herd et al. 2003a). Selection for low NFI produced steer progeny that ate less per unit liveweight gain compared to steers from high NFI parents over a 70-day test period in the feedlot, with no adverse effects on growth (Table 2). Low-NFI line steers tended to have lower (superior) FCR than the high-NFI line steers (7.6 v 8.2 kg/kg) and had lower NFI (-0.12 v 0.10kg/day). Significant positive regressions of FCR and NFI with EBV for NFI provided further evidence for favourable genetic associations with postweaning NFI. Ultrasound measurement before slaughter showed that low-NFI line steers had less fat over their rib and rump and a smaller eye-muscle area than high-NFI line steers (10.2 v 11.6mm, 13.1 v 14.8mm, 66.9 v 70.6cm2; all P<0.05). The Low-NFI line steers had less fat depth at the rump on the hot carcass and there was a small difference in dressing percentage (14.9 v 16.5mm, 52.1 v 52.9%;

both P<0.05). Significant (P<0.05) regressions for the three subcutaneous fat measurements, eye-muscle area and dressing percentage with NFI EBV provided additional evidence of genetic association.

Body composition

Evidence exists that there is a genetic relationship between NFI and subcutaneous fat depth, with more efficient (lower NFI) animals being leaner than less efficient (high NFI) animals. Using total tissue dissections of bodies of steers selected for NFI, Richardson et al. (2001) reported significant selection line differences in percent carcass fat but not in percent retail beef yield (Table 2), thus confirming the trend in the genetic correlation with subcutaneous fat. The significant regression coefficient for retail beef yield percentage with NFI EBV is favourable provides market specifications for fatness are met. Detailed studies into the biological factors contributing to variation in NFI conclude that differences in body composition are a minor contributor, and that other physiological processes and behaviour explain most of the variation (Richardson and Herd, 2004).

Meat tenderness

After a single generation of divergent selection on postweaning NFI, meat samples taken from the M. longissimus dorsi of feedlot-finished steers showed no difference between selection lines in shear force and compression values after 1 and 14 days of ageing, nor in initial concentrations in muscle of m- and μ-calpain (enzymes associated with initiation of muscle fibre breakdown; McDonagh et al. 2001). However, muscle from low-NFI line steers contained a slightly higher concentration of calpastatin (an inhibitor of the action of the calpain enzymes) and lower level of myofibre fragmentation, than LD muscle from high-NFI line steers. These results provide evidence that on-going selection for low NFI (high efficiency) could negatively affect meat tenderness, and this association needs to be monitored. Small differences in myofibre fragmentation are consistent with differences in protein degradation and turnover proposed as one of the mechanisms contributing to variation in NFI (Richardson and Herd, 2004).

Maternal feed efficiency and productivity

Individual pasture intakes by 41 lactating cows that had previously being ranked as above or below average for postweaning NFI were measured by alkane capsule technology. The experiment demonstrated a phenotypic association between NFI of the young female and her later efficiency at pasture. Low-NFI cows were 7% heavier, had similar subcutaneous fat levels and reared calves of similar weight to high-NFI cows, but consumed no more feed than the high-NFI cows (Table 3). The advantage in efficiency of the low-NFI cows, when expressed as a ratio of calf weight to cow feed intake, whilst numerically large (15%) was only statistically significant at P=0.07, presumably due to small number of animals in the experiment.

Following the postweaning test, all heifers entered the cow herd. After the birth of their second calf cows were not mated, and approximately 10 weeks after the calf was weaned the cows were re-tested for feed intake and growth. Data on 751 cows tested in 7 groups was available. The 70-day test was conducted in a similar manner to the postweaning tests. Genetic parameters for the mature cow test traits are given in Table 1. All traits were moderately to highly heritable. The results indicated that there is significant genetic variation in daily feed intake by the cows and the two measures of cow efficiency: NFI and FCR. Daily feed intake was strongly related to NFI at both phenotypic and genetic levels.

The phenotypic and genetic relationships between traits measured during the postweaning and mature cow tests are presented in Table 1. At the phenotypic level, most traits (with the exception of metabolic mid-test liveweight) were only moderately correlated from postweaning heifers to mature cows. However at the genetic level all traits, with the exception of FCR, were highly correlated across the two ages. In particular, the relationships between postweaning and mature daily feed intake and NFI were strong, with the genetic correlations approaching unity.

The results show that selection for lower postweaning NFI will lead to a reduction in the intake of a pelleted ration by dry, non-pregnant cows, together with a slight increase in cow weight, thus improving the efficiency of the cow herd. These strong relationships present the opportunity to utilise selection to improve feed efficiency of growing animals and mature cows simultaneously, based on measurements taken postweaning prior to selection decisions being made.

Data on 185 Angus cows were used to study the effect of divergent selection for NFI on maternal productivity across 3 mating seasons, starting from 2000. The cows were the result of 1 to 2.5 generations of selection (mean of 1.5), and differed in NFI EBV by 0.8 kg/day. In general, cows lost subcutaneous fat (measured 2 times a year) during the period when they were nursing calves, and gained fat thereafter. No significant selection-line differences in fatness were observed except for those measured at the start of the 2000 (10.8 v. 9.3mm), 2001 (11.3 v.9.8mm) and 2002 (7.0 v. 5.7mm) mating seasons, where high residual feed intake cows had significantly (P<0.05) higher rib fat depths. No significant selection line differences in weight (measured 4 times a year) were observed. However, the cows either maintained or lost weight during the calf nursing period, and gained weight thereafter, with mean weights ranging from 450 to 658kg. There were no significant selection-line differences in pregnancy (mean 90.4%), calving (mean 88.7%) and weaning (mean of 80.8%) rates, milk yield (mean 7.7 kg/day) and weight of calf weaned per cow exposed to bull (mean 195 kg) (Table 3). The study indicates that after 1.5 generations of divergent selection for NFI there are no significant selection-line differences for maternal productivity traits. Complete results are reported in Arthur et al. (2005).

Table 3. Trangie NFI Divergent Selection lines: Means for production traits for cows from cattle lines divergently selected for low NFI (high efficiency) or high NFI (low efficiency).

Trait	Selection Line		Level of Significance
	Low NFI	High NFI	
Pasture intake[1]			
Cow feed intake (kg/day)	12.5	13.2	ns
Cow liveweight (kg)	618	577	*
Calf liveweight (kg)	111	104	ns
Calf weight/cow feed intake (kg/kg)	9.3	8.1	†
Reproductive rate[2]			
Pregnancy Rate (%)	90.5	90.2	ns
Calving Rate (%)	89.2	88.3	ns
Weaning Rate (%)	81.5	80.2	ns
Growth of calves[2]			
Birth Weight (kg)	36.9	36.2	ns
Pre-weaning Average Daily Gain (kg/day)	0.88	0.89	ns
220 Day Weight (kg)	231	231	ns
Maternal productivity[2]			
Calving Day	215	210	†
Milk Yield (kg/day)	7.5	7.8	ns
Weight of calf born per cow mated (kg)	33.6	31.8	ns
Weight of calf weaned per cow mated (kg)	191	198	ns

ns P>0.1, † P<0.1, *P<0.05.

[1] Foundation generation, phenotypically ranked low or high for NFI, adapted from Herd et al. (1998)

[2] After 1.5 generations of selection, adapted from Arthur et al. (2005)

Summary from Trangie work

- There is significant genetic variation in postweaning NFI in young bulls and heifers, and in mature cows fed medium-quality pelleted rations ad libitum.
- NFI is moderately heritable (similar to growth rate).
- NFI responds to selection.
- Differences in feed efficiency are due in only very small part to differences in body composition, but rather reflect a large number of integrated physiological and behavioural factors.
- Selection for low NFI can produce young cattle that have
  1. better growth and feed efficiency on pasture
  2. similar growth and more efficient in the feedlot
  3. equal carcass and meat quality traits.
- Selection for low NFI can produce cows that
  1. appear to be more efficient at pasture
  2. with little or no increase in mature size
  3. with similar calving rates
  4. with similar milk production
  5. with slight trend to less subcutaneous fat.

2. CRCI straight breeding project

From 1993 - 2000, seven breeds were involved in this major CRC 'progeny test'. The purpose bred cattle included purebred progeny from commercial herds linked to known genetic material. Angus, Murray Grey, Hereford, Shorthorn, Brahman, Belmont Red and Santa Gertrudis breeders provided weaners by BREEDPLAN sires.

Growth and body composition

7622 cattle were measured for several weight and body composition traits in temperate and tropically adapted breeds. Traits included: liveweight, hip height, body fat score, muscle score, flight time, ultrasound scanned fatness, and eye muscle area. Measurements were taken at 3 stages during the project: post-weaning, start of finishing, and end of finishing (i.e. pre-slaughter). Animals were finished to 3 target market-weight end-points ('Domestic' 220kg, 'Korean' 280kg, or 'Japanese' 340kg carcass weight), either on pasture or in a feedlot, and in 2 different geographic regions for the tropically adapted breeds (Queensland: sub-tropical and New South Wales: temperate). These data were used to estimate genetic parameters for the traits at each stage, and also to estimate the effect of market weight and finishing regimes on the phenotypic and genetic expression of each trait measured at the end of finishing stage. The design of the project is summarised in Figure 1.

Feedlot finishing decreased the age at slaughter, and increased fatness and muscling compared with pasture-finished animals. Heritabilities ranged from 0.13 to 0.58, with subjectively scored traits generally being lower than objectively measured traits (Table 4). Additive genetic variances generally increased with stage of measurement, and with increasing market weight. Genetic correlations of the same measure across stages or market weights were all close to unity (Table 5). Additive genetic variances of the various traits were similar for feedlot versus pasture finished groups, and the genetic correlation between each measure for feedlot and pasture finish was greater than 0.70. The effect of finishing region (i.e. temperate versus subtropical environments) for the tropically-adapted breeds had little effect on the magnitude of the additive genetic variances or genetic correlations between traits across geographic regions. Full results are presented in Johnston et al. (2003).

The results imply that changing the production system had a significant impact on the phenotypic expression of growth and body composition traits but little effect on the underlying genetic expression and subsequent ranking of sires (i.e. no major genotype by production environment interactions). Therefore, these live animal measures could be used as selection criteria in genetic evaluation programs and may also be genetically correlated with abattoir carcass and meat quality traits.

Feed intakes

Feed intake, daily weight gain, metabolic mid-test liveweight, NFI and FCR were recorded on 1481 steers and heifers feedlot finished on a grain-based diet for three market endpoints. Also measured were subcutaneous fat at the rump P8 site, 12/13th rib, eye-muscle area and intra-muscular fat (IMF%) by scanning, time spent eating and number of feeding sessions per day. Estimated heritabilities for these traits ranged from 0.13 to 0.45 (Table 6). NFI had a high genetic correlation with rump P8 fat (0.72) but lower with IMF% (0.22). Feeding behaviour was also heritable and genetically linked with NFI. Selection for lower NFI (higher efficiency) is therefore possible in feedlot finished cattle, but fatness will decrease. When appropriate, multivariate selection is therefore recommended to achieve increased feed efficiency together with the desired level of fatness, using an index including NFI, on-test weight gain and fat measurements.

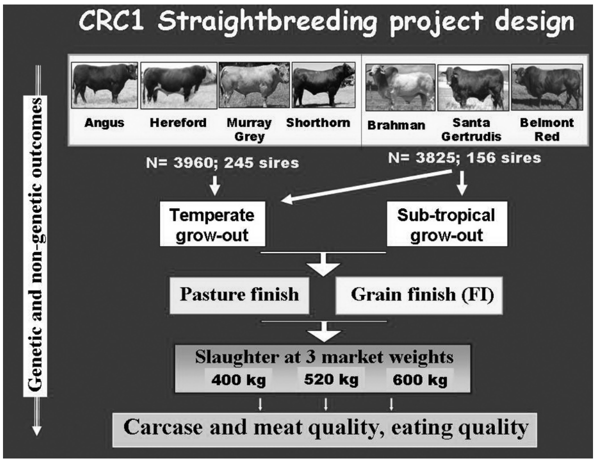

Figure 1. CRCI straight breeding project design

There were large breed differences for number of feeding sessions per day: Brahman cattle ate more frequently than Belmont Red and Santa Gertrudis breeds which ate more often than temperate breed cattle. Within breeds, there was a tendency for more efficient animals to have fewer feeding sessions per day. In contrast, breeds adapted to harsher tropical conditions ate more meals per day. Full results are presented in Robinson and Oddy (2004).

Summary from CRCI straightbreeding

- There was no major re-ranking of sires for liveweight and carcase traits across different market end-points, finishing systems (grain vs grass) or (in the case of tropically-adapted cattle) sub-tropical vs temperate environments.

1. Sires performed similarly whether their progeny were grain finished or grass finished. While the average values of the progeny were affected markedly by finishing regime, the sires tended to rank the same, that is, a sire that produced the fattest progeny under grain finishing still produced the fattest progeny under grass finishing.
2. Sires performed similarly when their steer progeny were finished to different market endpoints. Again raw values changed but the sires were ranked similarly when their steer progeny were killed at the different target carcase weights that ranged from slaughter group averages of 200kg to almost 350kg across the three market destinations of Domestic, Korean and Japanese.
3. Progeny of

Table 4. CRCI Straight Breeding Project: Number of measurements, heritability (h2) and additive genetic variances (σ2A) for liveweight, scanned eye-muscle area (EMA) and P8 fat depth in Temperate and Tropically-adapted breeds measured at post weaning, at start of finishing and end of finishing. (Adapted from Johnston et al. 2003)

Trait	Temperate breeds			Tropically adapted breeds		
	n	h^2	σ^2_A	n	h^2	σ^2_A
Liveweight (kg)						
Post-Weaning	3613	0.58	333	3851	0.57	303
Start of finishing	3771	0.48	495	3851	0.31	297
End of finishing	3771	0.45	836	3851	0.32	553
Scanned EMA (cm^2)						
Post-Weaning	3029	0.32	4.65	3270	0.23	5.17
Start of finishing	3355	0.30	7.22	2629	0.23	4.96
End of finishing	3190	0.20	7.26	3649	0.19	6.43
Scanned P8 (mm)						
Post-Weaning	3301	0.38	0.43	3427	-	-
Start of finishing	3485	0.38	1.05	2630	0.19	0.54
End of finishing	3428	0.36	3.25	3767	0.44	5.74

Table 5. CRCI Straight Breeding Project: Least squares means (LS-mean), heritabilities (h2), and genetic correlations (rg) between feedlot and pasture performance for liveweight (LWT) scanned P8 fat depth and scanned eye muscle area (EMA) measured in temperate and tropically adapted breeds at the end of finishing. (Adapted from Johnston et al. 2003)

Finishing Regime	Variable	Trait LWT	 P8 fat	 EMA
			Temperate Breeds	
Feedlot South	LS-mean	515	12.3	66.1
	h^2	0.46	0.34	0.29
Pasture South	LS-mean	499	9.7	60.5
	h^2	0.53	0.52	0.13
	r_g	0.85	0.73	1.00
			Tropically Adapted Breeds	
Feedlot North	LS-mean	484	12.9	70.8
	h^2	0.33	0.34	0.15
Pasture North	LS-mean	489	10.8	65.9
	h^2	0.45	0.6	0.17
	r_g	0.92	0.94	0.91
			Tropically Adapted Breeds	
Feedlot North	LS-mean	484	12.9	70.8
	h^2	0.33	0.34	0.15
Feedlot South	LS-mean	489	11.0	64.8
	h^2	0.33	0.60	0.17
	r_g	0.99	1.00	0.99

tropically adapted sires performed similarly whether the progeny were raised in the north or in the more temperate south.

- This suggests that there is no need for two separate breeding schemes for grain- and grass-finishing production systems.
- Feed intake and NFI were moderately heritable in the feedlot-finished cattle and had moderate genetic correlations with fatness. Selection for lower NFI to improve feed efficiency is therefore possible but fatness will also decrease on average in the population not measured. Multi-trait selection is recommended to achieve increased feed efficiency together with the desired level of fatness.

3. CRCI northern crossbreeding project

From 1993 to 2000, the CRC had a large crossbreeding experiment in central Queensland. Brahman cows, from co-operating breeders, were joined to 9 sire breeds: Angus (AA), Brahman (BB), Belmont Red (BR), Charolais (CC), Charbray (CB), Hereford (HH), Limousin (LL), Santa Gertrudis (SG) and Shorthorn (SS). The crossbred progeny were grown out on pasture and finished on pasture and grain in the north and grain in the south (see Figure 2).

Feed intakes

Individual daily feed intake and liveweights were measured on 469 beef cattle representing 9 sire breeds joined to Brahman cows. Sire-breed differences for daily feed intake and NFI are presented in Table 7. Progeny of European and British breed sires were heavier at the start of the feed test, had higher growth rates and consumed more feed compared to progeny from Brahman and Belmont Red sires. Progeny from Brahman and European sire breeds had significantly lower NFI compared to progeny of Angus, Shorthorn and Belmont Red sire breeds. Hereford and Santa Gertrudis sired progeny had significantly lower NFI compared to Angus and Shorthorn sire breeds.

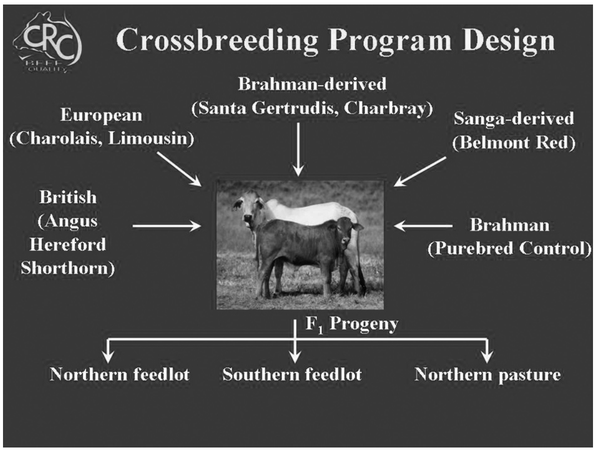

Figure 2. Design of the CRC Crossbreeding Program

Summary of CRCI crossbreeding

- Sire breed had large effects on growth and most carcase and beef quality attributes
- European sires had progeny with heaviest, leanest and highest yielding carcases
- No major re-ranking of sire breeds occurred across market (domestic, Korean, Japanese), finish (grain versus grass) or environment (north versus south) for carcase and beef quality attributes.
- Provided evidence for significant sire-breed

Table 6. CRCI Straight Breeding Project: Means, additive genetic variance (σ2A), heritability (on diagonal) and genetic correlations (above diagonal) for feed intake, NFI, daily feeding time, daily number of feeding sessions and feedlot-exit scans of P8 fat depth and intramuscular fat measured (IMF%) under feedlot test conditions. (Adapted from Robinson and Oddy, 2004)

Trait	Mean	σ^2_A	FI	NFI	Time feeding	No. Sessions	P8 fat	IMF%
FI (kg/d)	12.3	0.64	***0.27***	0.43	0.03	0.16	0.59	0.39
NFI (kg/d)	-2.63	0.14		***0.18***	0.35	0.43	0.72	0.22
Time feeding (min.)	91.4	120			***0.36***	-0.08	0	-0.25
No. sessions	12.0	9.5				***0.44***	0.02	0.16
P8 fat (mm)	12.7	5.3					***0.33***	0.48
IMF%	4.8	0.63						***0.43***

Table 7. Sire-breed least square means for start of test weight (SWT), average daily gain (ADG), daily feed intake (DFI), feed conversion ratio (FCR) and net feed intake (NFI) of feedlot finished steers and heifers of 9-sire breeds mated to Brahman cows. See text for sire-breed abbreviations. (Adapted from Moore et al. (2005)

Sire-Breed	EWT	ADG	DFI	FCR	NFI
BB	371.2	1.12	9.96	8.9	-0.61
CC	454.8	1.42	12.31	9.4	-0.57
LL	433.6	1.44	12.04	8.8	-0.50
HH	446.8	1.57	12.62	8.7	-0.30
SG	426.3	1.48	12.17	8.5	-0.27
BR	402.0	1.23	11.23	9.5	0.01
SS	452.6	1.52	12.98	8.8	0.16
AA	445.7	1.56	13.45	9.1	0.30
CB	NE	1.31	11.01	-	-
Mean SED	6.93	0.06	0.35	0.39	0.23

differences in feed intake and feed efficiency (as NFI) under feedlot conditions. Although based on a small number of sires from each breed, the results showed that progeny of Brahman and European breed sires had lower NFI (more efficient) than the progeny of the Angus, Shorthorn and Belmont Red sires, with the progeny of the Hereford and Santa Gertrudis sires being intermediate in feed efficiency (Moore et al. 2005a).

- Provided data to help produce BREEDPLAN Multibreed EBV adjustments.

4. CRCII Project 2.3

This project investigated links between carcase and feed efficiency traits and female reproductive fitness in northern Australia. Brahmans and Tropical Composites, representing 54 and 51 sires respectively, were bred using AI and natural service in cooperating herds in 1999 through 2002. Tropical Composites were approximately 50% Bos indicus or African Sanga and 50% non-adapted Bos taurus. Following weaning, steers were run in cohorts on cooperating properties and, following the growout phase, were feedlot finished for a mean of 112 days. Steers received an oestradiol-based growth promotant during grow-out and finishing. Heifers were run in cohorts on 4 research stations across Queensland. In line with industry practice, Brahman heifers were run on stations representing a full range of industry environments, while Tropical Composite heifers were run in all but the harshest environment.

Table 8. CRCII Northern Breeding Project: Genetic correlations (with SE) between feed intake (FI) and net feed intake (NFI), and growth and fatness traits, and plasma insulin-like growth factor-I concentration (IGF-I) for purebred Brahmans and Tropical Composites measured at feedlot entry and feedlot exit. (Adapted from Wolcott et. al. 2006)

Feedlot Entry						
Liveweight	0.67 (0.18)	-0.19 (0.32)	0.69 (0.12)	-0.07 (0.23)	0.68 (0.11)	-0.04 (0.18)
Average daily gain	0.25 (0.27)	-0.68 (0.30)	0.75 (0.14)	0.17 (0.24)	0.53 (0.14)	-0.01 (0.20)
P8 fat depth	-0.60 (0.19)	-0.41 (0.26)	-0.14 (0.22)	0.01 (0.24)	-0.38 (0.15)	-0.11 (0.18)
Hip height	0.23 (0.22)	-0.56 (0.26)	0.55 (0.16)	0.05 (0.24)	0.39 (0.14)	-0.17 (0.19)
IGF-I	-0.16 (0.25)	0.03 (0.30)	-0.41 (0.26)	-0.51 (0.29)	-0.33 (0.18)	-0.28 (0.20)
Feedlot Exit						
Liveweight	0.92 (0.05)	-0.01 (0.29)	0.92 (0.04)	0.18 (0.21)	0.89 (0.04)	0.11 (0.17)
Average daily gain	0.97 (0.04)	0.07 (0.27)	0.90 (0.05)	0.26 (0.22)	0.91 (0.03)	0.20 (0.17)
P8 fat depth	0.29 (0.22)	0.18 (0.28)	0.48 (0.17)	0.38 (0.20)	0.41 (0.13)	0.33 (0.16)
Hip height	0.28 (0.22)	-0.60 (0.23)	0.50 (0.20)	-0.12 (0.25)	0.35 (0.15)	-0.32 (0.17)
IGF-I	-0.16 (0.25)	0.03 (0.30)	-0.41 (0.26)	-0.51 (0.29)	-0.33 (0.17)	-0.56 (0.18)

Genetic correlations for steer feed intake and NFI with growth traits and fatness were estimated separately for the Brahman and Tropical Composite cattle. Heritability of NFI was 0.24 and 0.38 for the Brahmans and Tropical Composites respectively (Table 8). Genetic correlations between NFI and growth rate, hip height and P8 fat depth at feedlot entry (rg = -0.68, -0.41, -0.56 respectively) indicated that these traits could be exploited to indirectly improve NFI in Brahmans, but were of little use for the Tropical Composites. IGF-I, sampled at feedlot entry and feedlot exit, had a negative correlation with NFI for these cattle treated with hormonal growth promotant.

Genetic correlations for corresponding measures of steer and heifer growth and live body composition were examined for Brahman and Tropical Composite cattle to examine the extent of genotype x environment and sex interactions when production systems differ markedly for the sexes (Barwick et al. 2006). Steer measures were at feedlot entry and feedlot exit. Heifer measures were at the end of the first "wet" and second "dry" season experienced post-weaning. A number of correlations differed from unity (Table 9). For certain growth and scanned body composition measures, genetic evaluation and selection in these genotypes may need to distinguish heifer wet and dry seasons and steer growth and feedlot environments as separate traits, especially for Brahman heifers and Tropical Composite steers.

Summary for CRCII Project 2.3

- Feedlot feed efficiency (as NFI) was moderately heritable in both genotypes.
- Genetic correlations between NFI and growth rate prior to feedlot entry, P8 fat depth, and hip height measured at feed entry indicated that these traits could be exploited through selection

to indirectly improve NFI in Brahmans, but appear to be of limited use for Tropical Composites.

- Selection for improved NFI will on average result in taller leaner cattle.
- Results are consistent with Brahman being more adapted to harsh, tropical heifer environments and with Tropical Composite being better able to exploit feedlot conditions.
- For certain growth and scanned body composition measures, genetic evaluation and selection of Brahman and Tropical Composite cattle for these environments may need to distinguish heifer season and steer growth environments as separate traits, especially for Brahman heifers and Tropical Composite steers.
- The new parameter estimates, data on many traits and genetic linkage from this project will also further strengthen BREEDPLAN for tropical breeds.

Insulin-like Growth Factor-I (IGF-I) blood test

The inconvenience and cost of testing seedstock cattle for NFI lead the CRC research team to look for gene markers and physiological tests to increase the accuracy of the NFI EBV and/or to reduce cost of finding superior stock. The first of these, a blood test for the protein IGF-I, was introduced to BREEDPLAN in 2004. It followed from research using feed intake, NFI, and IGF-I records for cattle in the Trangie Angus feed efficiency herd and CRCI straight breeding project, both described above. The results showed that IGF-I concentration in plasma taken postweaning to be heritable and genetically correlated with growth and feed efficiency (Table 10). The study concluded that this provided an opportunity to use this early-in-life measure as a selection criterion for the genetic improvement of feed efficiency and carcass traits, but that further research to investigate the optimal age to measure IGF-I was needed (Johnston et al. 2002).

Table 10. Heritability (h2) of concentration of IGF-I and genetic correlations (rg) (with SE) between IGF-I and average daily gain (ADG) and mid-feed test weight (WT), feed intake (FI), net feed intake (NFI) and feed conversion ratio (FCR), for cattle from the Trangie Angus feed efficiency herd and the CRCI straight breeding project. (Adapted from Johnston et al. 2002).

	h^2	r_g				
	IGF-I	ADG	WT	FI	FCR	NFI
Trangie	0.43 (0.12)	-0.20 (0.17)	0.03 (0.14)	0.27 (0.14)	0.55 (0.16)	0.39 (0.13)
CRCI	0.34 (0.09)	-0.23 (0.32)	0.25 (0.32)	0.01 (0.30)	0.37 (0.42)	0.56 (0.35)

Table 9. CRCII Northern Breeding Project: Genetic correlations (with SE) between repeat measurements of liveweight, average daily gain, scanned P8 fat depth and scanned eye-muscle area in Brahman and Tropical Composite steers and heifers. (Adapted from Barwick et. al. 2006)

Trait	Sex / Measurement time / Genotype	
	Steer Feedlot Entry vs. Steer Feedlot Exit	
	Brahmans	Tropical Composites
Liveweight	0.79 (0.11)	0.90 (0.04)
Average daily gain	0.10 (0.27)	0.64 (0.15)
P8 fat depth	0.82 (0.10)	0.66 (0.12)
Eye-muscle area	1.00 (0.19)	0.74 (0.10)
	Heifer Wet I vs. Heifer Dry II	
	Brahmans	Tropical Composites
Liveweight	0.99 (0.01)	0.99 (0.01)
Average daily gain	0.12 (0.30)	0.49 (0.23)
P8 fat depth	0.95 (004)	0.97 (0.03)
Eye-muscle area	0.94 (0.07)	0.98 (0.03)
	Heifer Dry II vs. Steer Feedlot Exit	
	Brahmans	Tropical Composites
Liveweight	0.37 (0.21)	0.84 (0.09)
Average daily gain	-0.01 (0.27)	0.50 (0.21)
P8 fat depth	0.67 (0.17)	0.63 (0.12)
Eye-muscle area	0.43 (0.34)	0.86 (0.11)

Southern industry herds

Research into genetic parameters for IGF-I in industry herds was undertaken in conjunction with ABGU through an MLA funded project. The plasma concentration of IGF-I was measured in 6520 seedstock Angus cattle from eastern Australia between 2002 and 2004 and used to calculate the heritability and phenotypic and genetic correlations with NFI measured on relatives and with other production traits. Concentration of IGF-I in 3792 samples taken before or at weaning was moderately heritable and had positive genetic correlations with NFI, scanned P8 and rib fat depths, scanned eye-muscle area, and was not correlated with scanned intra-muscular fat (IMF%) (Table 11). Genetic correlations with birthweight, 200-day weight and 400-day weight was significant and negative. This study showed that IGF-I is heritable and genetically correlated with important production traits. The genetic correlations indicate that selection for lower IGF-I concentration would result in cattle that have more favourable NFI, grow faster and are leaner. Being relatively easier, cheaper and quicker to measure than actual NFI, IGF-I could be used in young animals to indirectly select for NFI and potentially allow more animals to be measured. Full results are presented in Moore et al. (2005b).

Industry adoption

The blood test is conducted by the Australian company Primegro Ltd, which has the exclusive right to commercialise this Australian Intellectual Property. Being an indirect indicator for NFI, an NFI EBV computed from an IGF-I record will have lower accuracy than an NFI EBV generated from an NFI record. For example, a sire NFI

EBV with 50% accuracy could be obtained by feed intake testing 3 progeny or testing 27 progeny for IGF-I. High accuracy NFI EBV will require some animals being feed intake tested.

Tropical breeds

For the tropical breeds examined in the CRCII Northern Breeding Project (described above), IGF-I sampled at postweaning, feedlot entry and feedlot exit had a negative genetic correlation with NFI for both genotypes (Table 9) (opposite to the findings for temperate breeds; Wolcott et al. 2006). Both the timing of IGF-I sampling and the use of hormonal growth promotant may have influenced these results and are outside the current guidelines for use of this test for British breeds in southern Australia.

NFI EBVs

To be able to select bulls and cows to improve a trait, cattle breeders need to be able to compare the genetic merit of bulls. This has been achieved via BREEDPLAN's published estimated breeding values (EBV). This system was developed by the Animal Genetics and Breeding Unit, and is delivered by the Agricultural Business Research Institute (ABRI), both at the University of New England. BREEDPLAN currently delivers EBV for growth, fertility and carcass characteristics. The CRC's results confirming genetic variation in feed efficiency allowed AGBU to develop an EBV for feed efficiency. The EBV for NFI, is a world-first, and gives producers the opportunity to reduce the feed cost of beef production to improve profitability. Since 2002 the Australian Angus and Hereford breeds have had access to the NFI EBV and a number of high and low efficiency bulls in each breed have being identified. NFI EBV for other breeds will become available when sufficient number of animals have been measured for feed intake (and IGF-I) and are from several well-linked herds.

Conclusion and future directions

There was no major re-ranking of sires for liveweight and carcase traits across different market end-points, finishing systems (grain vs grass) or (in the case of tropically-adapted cattle) sub-tropical vs temperate environments. This suggests that there is no need for two separate breeding schemes for grain- and grass-finishing production systems, and for tropically adapted breeds no need for two separate breeding schemes for progeny that are to be finished in the north or in the more temperate south.

Table 11. Means, additive genetic variance (σ2A), heritability (h2) and genetic correlations (rg) for IGF-I measured before or at weaning with net feed intake (NFI), 200-d weight, and scanned P8 fat depth and intramuscular fat (IMF%) at yearling age in seedstock Angus cattle. (Adapted from Moore et al. 2005b)

Trait	Mean	σ^2_A	h^2	r_g
IGF-I (ng/mL)	291	2000	0.36	
NFI (kg/d)	-1.8	0.14	0.50	0.42
200-d weight (kg.)	227	120	0.38	-0.22
P8 fat depth	4.5	0.76	0.47	0.15
IMF%	3.4	0.44	0.30	0.07

Research has provided ample evidence for genetic variation in feed efficiency in Australian beef cattle breeds. Feed efficiency, measured as net feed intake (NFI) is moderately heritable, responds to selection and presents an opportunity to improve the feed efficiency and profitability of beef production.

There appears to be adequate knowledge of genetic correlations between NFI and test period traits and also with growth traits. There also appears to be a genetic relationship between NFI and fatness traits but additional studies are required to accurately assess the magnitude of this relationship in different breeds, sexes, ages and feeding regimes. There are gaps in our knowledge on the genetic relationships between NFI and meat quality attributes, and cow feed intake at pasture and maternal productivity. Continuing CRC research will determine the relationships with traits that affect herd productivity and profitability. In particular, carcass quality, and maternal productivity and efficiency across a range of pasture systems will be studied.

Australia is a world leader in understanding the biological basis of variation in feed efficiency and exploitation of genetic differences using BREEDPLAN NFI EBV. The unique CRC database of pedigree and performance information, and stored DNA samples, will continue to benefit the Australian beef industry, as it now provides the foundation for new CRC research in discovery of NFI genes and accelerated genetic improvement.

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Further reading

CRC Special Edition of Australian Journal of Experimental Agriculture Volume 44 Number 4-5 (2004) "Improving Efficiency of Feed Utilisation by Animals".

This special CRC edition contains 17 scientific papers on feed efficiency, including revised and updated papers presented at the CRC Feed Efficiency workshop in Armidale in 2000, plus research results from CRCI and CRCII, and two papers using the mouse as a model species tor examine the direct and correlated responses to selection for NFI.

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