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IMPROVING PRODUCTIVIY

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Improving the efficiency of feed utilization for beef production

Abstract

This Project provided targeted industry education to encourage adoption of net feed intake (NFI) technology and established an on-farm testing facility, standardised testing guidelines and an industry database to record NFI test data. Selecting high efficiency bulls can produce calves, steers and cows that are more feed efficient on pasture and in the feedlot, but possible unfavourable associations with some carcase and maternal productivity traits exist that require further research. New testing strategies, including use of the simpler, less-expensive Primegro insulin-like growth factor-I (IGF-I) blood test and two-stage selection, were developed to help identify feed efficient bulls at least cost.

Evidence for industry adoption of NFI is provided by continuing increase in numbers of seedstock cattle with estimated breeding values (EBV) for NFI. Almost 30,000 Angus animals had NFI EBV in 2006. The Hereford breeds also publish NFI EBV based on NFI test and IGF-I data. The economic benefits of adoption of NFI are substantial: $6.55 per breeding cow per year, plus $4.34 per breeding cow per year savings in feed costs in a feedlot, for British breed cattle in southern Australia. An environmental benefit is the potential reduction in greenhouse-gas emissions by more feed efficient cattle.

Subsequent to this project it has become apparent that NFI measured on young cattle postweaning and on older cattle during feedlot finishing are not genetically the same trait and the utility of the IGF-I bloodtest as now being used in seedstock herds for the purpose of genetic improvement is of less merit than it appeared during this research project. There is a fresh need to overcome barriers (mainly high cost in this time of drought) to more bulls being tested directly for NFI. This might include expediting delivery of comprehensive gene marker tests for NFI to facilitate two-stage testing, and provision of financial assistance with the high cost of NFI testing to overcome apparent market failure to reward to bull breeders who test for, and supply high-efficiency commercial bulls.

Executive Summary

Feeding cattle is a major cost of beef production. In southern Australian pasture-based systems, around 60 per cent of the variable costs of production are related to feed cost. Supplementary feeding with hay, grain and silage adds further to the cost of feeding cattle, and the cost of feed is around 70 per cent of the variable cost of operating a feedlot.

This project built on the earlier MRC/MLA DAN.075 Project, and complementary research by the Cattle and Beef CRC (CRCI) and the CRC for Cattle and Beef Quality (CRCII), that showed genetic variation in net feed intake (NFI) exists. This Project aimed to provide mechanisms for the beef industry to be able to identify and optimally utilise feed efficient bulls, and to provide knowledge of favourable and possible unfavourable associations with other economically important production traits. The project was conducted as a part of the activities of Project 2.2 of the CRC II.

The objectives of this project were:

- To utilise existing scientific information to develop NFI technology for industry application.
- To develop and implement educational and extension strategies to improve the adoption rate of NFI technology by industry.
- To evaluate key genetic relationships between NFI and other economically important traits.
- To develop lower cost methods to identify animals that are superior for NFI.
- To develop optimal breeding designs for use by industry.

The achievement milestones for all objectives of this project were met.

An on-farm testing facility and testing guidelines were devised so that cattle breeders can measure and monitor their herd with respect to NFI. An industry database to record NFI test data and process it for calculation of draft estimated breeding values (EBV) for NFI has been established. The number of animals tested for NFI annually by industry grew between the years 1997 to 2002, but has declined since 2004, with a total of 3,622 tested by industry to 2005.

Evidence for continuing industry adoption of NFI can now be provided by the continuing increase in numbers of seedstock cattle with EBV for NFI. The Primegro insulin-like growth factor-I (IGF-I) bloodspot test to identify cattle genetically superior for feed efficiency was launched November 2003. This test provides a less expensive way to find genetically superior bulls. The impact of the test was to rapidly increase the number of bulls with EBV for NFI in the Angus breed, doubling the number of animals with reportable NFI EBV in their January 2004 sire summary, and more than doubling that number again in 2005, with almost 30,000 Angus animals with NFI EBV in 2006. Hereford/Poll Hereford was the next breed in 2005 to use IGF-I data in calculating NFI EBV.

Targeted industry extension to encourage adoption of NFI technology was lead by Mr Steve Exton, Livestock Officer with NSW DPI. Steve was supported by other Livestock Officers in NSW and his counterparts in the other States, and by the research staff in the Project team. A minimum of 107 extension-related publications and field-day-type activities were held from 2000 to 2004.

This project analysed data by a number of other projects to provide evidence that selecting high efficiency bulls could produce calves, steers and cows that are more feed efficient on pasture and in the feedlot. This information has been taken up by the Australian stud cattle industry, and EBV for

NFI are now available in the Angus and Hereford Breeds to assist commercial producers introduce superior NFI-genetics into their herds.

Further, this project showed that testing of potential sires, or their progeny, for NFI is profitable despite the high cost, and provides strategies to optimise testing to ensure accurate information is obtained at least cost. This project also provides testing strategies using the simpler, less-expensive IGF-I blood test and two-stage selection to further reduce the number of cattle actually required to undergo NFI testing.

A comprehensive formal evaluation to estimate the economic, environmental and social benefits of the potential adoption of the NFI technology in the Southern Australian beef industry was undertaken by (Griffith et al. 2004). This included the impacts of the current Project, together with those from the earlier MRC/MLA DAN.075 Project, and complementary research by Beef CRCI and CRCII.

The economic benefits of the widespread adoption of NFI are substantial: $6.55 per breeding cow per year, plus $4.34 per breeding cow per year savings in feed costs in a feedlot, for a total estimated benefit of $158 million (NPV, 2004) over the period 2003-2020. These benefits are predicted on the basis of conservative estimates of industry adoption of NFI technology, and exclude benefits in northern Australian cattle that may accrue in the future. Positive potential environmental outcomes and social outcomes were also identified, including potential reduction in greenhouse-gas emissions by more feed efficient cattle.

The adoption process has commenced, although only at very modest levels to date. This project reported weak, and possibly unfavourable, associations with some carcase traits and a measure of female fertility. These antagonisms can be managed by appropriate weighting in selection indices but they have the potential to both reduce the rate of genetic improvement in NFI, and to reduce the confidence of commercial cattle producers in choosing to use a high efficiency bull. They could thereby reduce the potential economic benefit.

Further research and on-going industry education is required to ensure adoption of NFI technology. In particular there is a need to more accurately measure the associations with measures of female productivity in commercial herds. This is one of the aims of the Maternal Productivity Project in the recently established CRC for Beef Genetic Technologies.

There are currently approximately two-thousand postweaning NFI test records and three-thousand feedlot NFI-test records for Australian cattle, with only a couple of hundred of new records being added per year from research herds, and virtually nil records from private seedstock herds likely to be added over the next few years. This means that many of the phenotypic and genetic correlations between NFI for different classes of cattle, with IGF-I, and with other production traits are estimated with large error. There is a need for a co-ordinated effort to ensure at least 500 predigreed and performance animals per year are tested on an on-going basis if the accuracy of these correlations is to be both improved and for changes following selection to be better predicted.

Subsequent to this project it has become apparent that NFI measured on young cattle postweaning and on older cattle during feedlot finishing are not genetically the same trait and the utility of the IGF-I bloodtest as now being used in seedstock herds for the purpose of genetic improvement is of less merit than it appeared during this research project. There is a fresh need to overcome barriers (mainly high cost in this time of drought) to more bulls being tested directly for NFI. This might

include expediting delivery of comprehensive gene marker tests for NFI to facilitate two-stage testing, and provision of financial assistance with the high cost of NFI testing to overcome apparent market failure to reward to bull breeders who test for, and supply high-efficiency commercial bulls.

Contents

1 Background

This project was conducted as a part of the activities of Project 2.2 of the CRC for Cattle and Beef Quality. For a description, objectives, methodology and outcomes of the project, see attached document "CRC Project 2.2 Outline - 2000 to 2006". The parts to which this contract relates are:

Strategy 1 Task 1 Development and maintenance of an industry database
Strategy 1 Task 3 Extension targeted to maximise uptake of NFI technology
Strategy 1 Task 4 On-farm demonstration trials
Strategy 2 Task 1 Analysis of existing data from DAN.75, CRC I and industry herds
Strategy 2 Task 3 Evaluation of the relationship between seedstock and steer NFI with cow performance at pasture (workshop only)
Strategy 3 Task 5 Design of breeding schemes to optimise the use of direct and indirect selection for feed efficiency in industry

2 Project Objectives

As per CRC Project 2.2 Outline – 2001 to 2006 (Appendix 1) the objectives of this project were:

- To utilise existing scientific information to develop NFI technology for industry application.
- To develop and implement educational and extension strategies to improve the adoption rate of NFI technology by industry.
- To evaluate key genetic relationships between NFI and other economically important traits.
- To develop lower cost methods to identify animals that are superior for NFI.
- To develop optimal breeding designs for use by industry.

3 Methodology

As per CRC Project 2.2 Outline – 2001 to 2006 (see Appendix 1).

Strategy 1 was to foster the roll-out of net feed efficiency technology to industry in its current state, and to keep industry abreast of improvements in the technology which will arise from further research.

Strategy 2 was to involve the assessment of genetic relationships identified as being key pieces of information required. This involved analysis of existing data and collection of new data where required.

Strategy 3 was to focus on finding better and more cost-effective ways of implementing NFI technology in industry. Three approaches were explored, being an investigation of ways to reduce the cost of measurement, a search for indirect selection criteria (including genetic and non-genetic markers), and modelling work to examine the optimal design of breeding schemes and provide

recommendations to industry as to how (and on what animals) the technology should be implemented.

4 Results and Discussion

Strategy 1 Task 1 ~ Development and maintenance of an industry database

A database to accept and process feed intake and weight data collected by industry has been developed by the CRC for Cattle and Beef Quality. The database now accepts data from NFI tests conducted by industry, summarises the information and sends it for loading onto the National Beef Recording Scheme (NBRS) database maintained by the Agricultural Business Research Institute. Specifications for data to be loaded onto the NBRS database were developed by Jack Allen (ABRI), Hans Graser (AGBU) and Jason Archer (NSW DPI).

The relational database is written in Informix and held on a secure NSW DPI server located in Orange. The Input specifications for industry data have been written and incorporated into the Standards Manual outlining required test procedures for measuring Net Feed Intake (Exton 2001) (copy in Appendix 4). Before the milestone achievement date, industry test data from a commercial NFI test conducted at the Pastoral and Veterinary Institute, Hamilton, was been successfully loaded onto the database, processed and sent to ABRI. Data integrity and processing of industry NFI test data continues to be performed by NSW DPI, by Karen Dibley at the Trangie ARC.

Strategy 1 Task 3 ~ Extension targeted to maximise uptake of NFI technology

Targeted industry extension was lead by Mr Steve Exton, Livestock Officer with NSW DPI, based at the Trangie Agricultural Research Centre, and later in the project at the Wagga Wagga Agricultural Institute. Steve was supported by other Livestock Officers in NSW and his counterparts in the other States, and by the research staff in the Project team. A minimum of 107 extension-related publications and field-day-type activities were held from 2000 to 2004. A list of these is attached in Appendix 2.

The number of animals tested by industry was 546 in 2003 (the final year for this activity in this Project), bringing to 2,910 animals tested by industry to date. The number of cattle being tested appears to have plateaued (Figure 1). NFI test data for industry cattle continued to be submitted to NSW DPI at Trangie. The data collected during NFI tests is checked and processed, with summarised information sent to clients and to ABRI for loading on the NBRS database. The number of animals tested by industry was 163 in 2005, bringing to 3,622 animals tested by industry to date. Factors contributing to this less than anticipated level of animal testing have previously included the restricted test facility capacity available for private testing, the strong spring/autumn calving in southern Australian herds and the impact of drought on money available to spend on private testing.

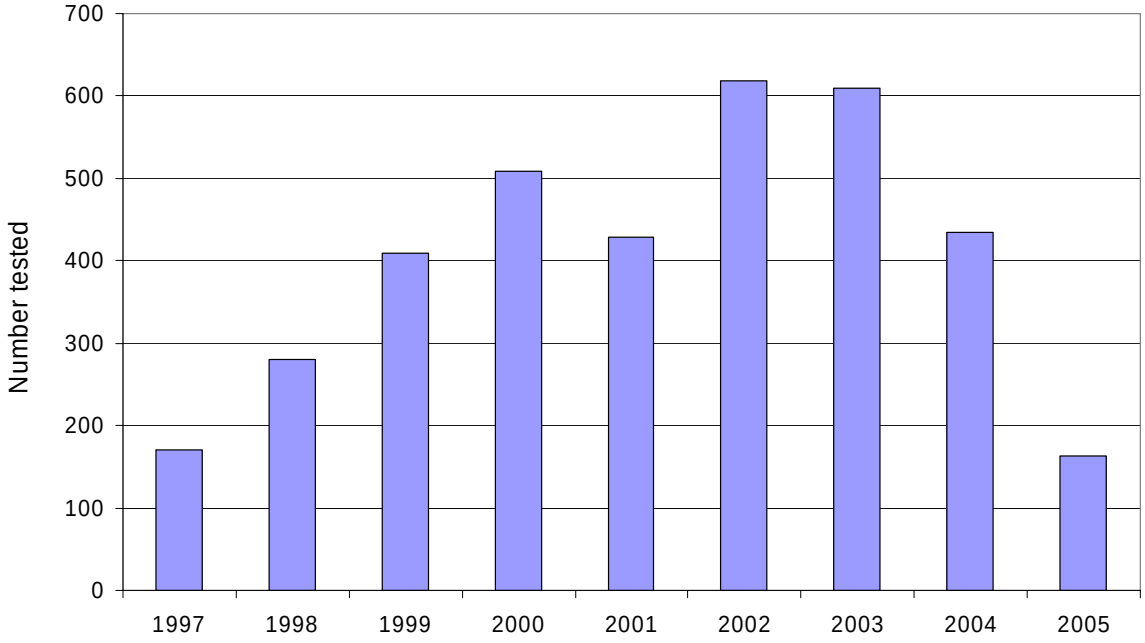

Figure 1. Numbers of cattle tested for net feed intake by industry to 2005

The Primegro insulin-like growth factor-I (IGF-I) bloodspot test to identify cattle genetically superior for feed efficiency was launched November 2003. This test provided a less expensive way to find genetically superior bulls. The impact of the test was to rapidly increase the number of bulls with EBV for NFI in the Angus breed, doubling the number of animals with reportable NFI EBV in their January 2004 sire summary, and more than doubling that number again in 2005 (Figure 2). Hereford/Poll Hereford was the next breed in 2005 to use IGF-I data in calculating NFI EBV.

Evidence for industry adoption of NFI can now be provided by looking at the increase in numbers of seedstock cattle with EBV for NFI as shown in Figure 2.

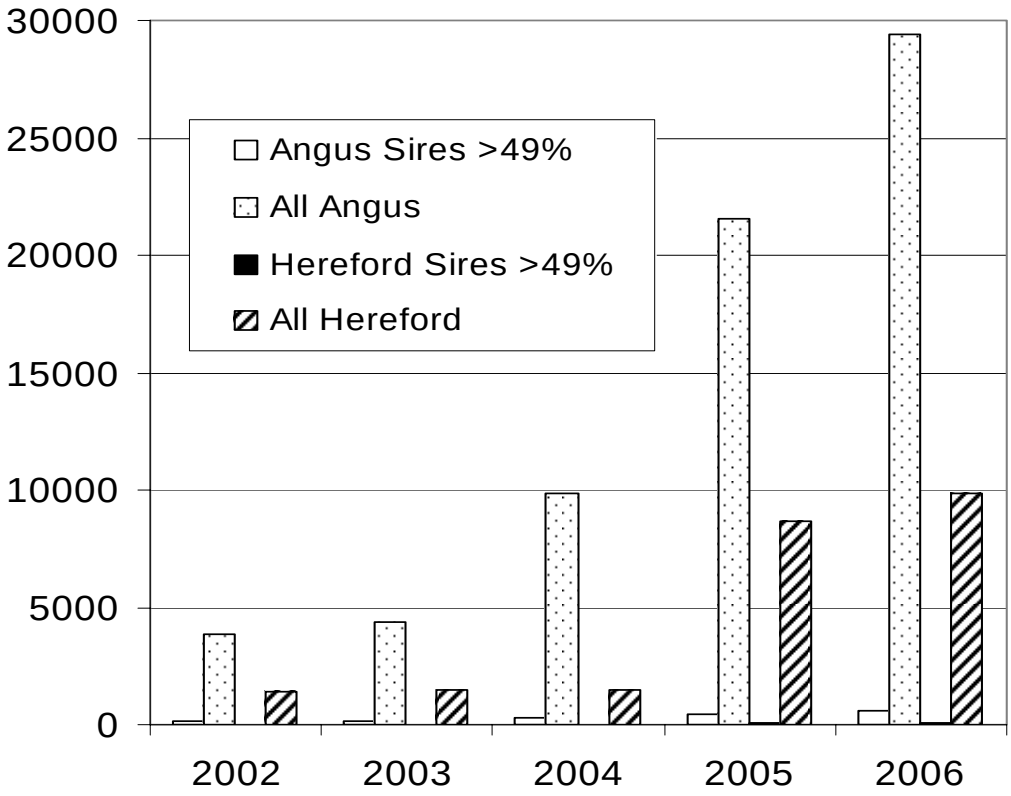

Figure 2. EBV for NFI for all Angus and Hereford cattle (accuracy >19%) and for sires (accuracy >49%). IGF-I data was first used for EBV published for Angus in 2004 and for Hereford in 2005.

Angus and Hereford/Poll Hereford remain the only breeds to publish NFI EBV. Over the same period the number of new animals with NFI test data has declined (Figure 1). However, IGF-I data alone cannot produce an accuracy of 50% or better: this being the level required for a sire EBV to be published in Breedplan. Feed intake and NFI records on individual sires and/or relatives are still required if higher accuracy EBV are to be produced.

Strategy 1 Task 4 ~ On-farm demonstration trials

The original proposal to purchase two Ruddweigh Feed Intake Recorders in early 2000 to enable testing to begin 2000/2001 was severely delayed by complications with signing of the contract. Two Feed Intake Recorders were purchased in January 2001 and seedstock breeders that had expressed interest in collaborating were contacted.

The earliest any of these herds would have bulls ready for testing was Spring 2001. The 1st on-farm demonstration trial was conducted from September to December 2001, at Toolangatta Herefords, Tambar Springs, with 11 bulls completing the test and having Trial EBVs for NFI calculated.

Three further trials were confirmed to be conducted from December 2001 to March 2002, April to July 2002 and September to December 2002. The 2nd trial began at Injemira Herefords, Holbrook in

January 2002, but was discontinued within two weeks due to a significant number of the bulls contracting pneumonia. The rapid change in diet and the unusually dry, dusty and windy seasonal conditions are suspected to have pre-disposed the bulls to infection. A 2nd trial at Toolangatta was conducted between March and May 2002, with 18 bulls completing the test. The 3rd trial was commenced at Kenny's Creek Angus, Boorowa, in June, and completed in September 2002, with 19 bulls completing the test.

Since the 4th trial it was not possible to find clients prepared to conduct a test on their property. Early in 2003 approximately 60 NSW Angus and Hereford/Poll Hereford studs were individually contacted. Nine expressed interest in conducting a test in the next 18 months. Five eventually declined due to drought, labour restrictions, time, etc. Each of the final 4 clients scheduled to conduct tests withdrew at short notice and it was not been possible to find alternate clients. The reason given was that they will use the new, cheaper IGF-I test and do not wish to spend the time and money to conduct the NFI tests.

Our extension team, particularly Mr Steve Exton, has spent a considerable amount of time and energy in trying to facilitate these tests. Four of the eight on-farm tests that were to be conducted as part of BFGEN005 were completed. In hindsight, it was clear that a combination of drought, the strong spring and autumn calving pattern in southern Australian herds and the large amount of time required to be committed by a bull owner to conduct an on-farm test, and then the imminent availability of the less-expensive IGF-I bloodtest, all unforeseen, lead to the remaining four tests not being conducted. Funds allocated for these tests were re-allocated within CRC Project 2.2 to facilitate collection of large numbers of bloodspot cards from cattle in research and industry herds. This provided additional data for the development of the IGF-I test and demonstration to industry of the method of collecting bloodspot cards.

Strategy 2 Task 1 ~ Analysis of existing data from DAN.75, CRC I and industry herds

The analysis was completed and submitted to AGBU for incorporation into BREEDPLAN. A scientific paper on the results was published in the *Journal of Animal Science*, entitled "Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle" (Arthur, Archer et al. 2001). An abstract on the results is provided below, and a copy of the full paper is in Appendix 4.

ABSTRACT: 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 d at the start of the performance test, which comprised 21-d adjustment and 70-d test periods. Traits studied included 200-d weight, 400-d weight, scrotal circumference, ultrasonic measurements of rib and rump fat depths and longissimus muscle area, ADG, metabolic weight, daily feed intake, feed conversion ratio, and residual feed intake. For all traits except the last five, additional data from the Angus Society of Australia pedigree and performance database were included, which increased the number of animals to 27,229. Genetic (co)variances were estimated by REML using animal models. Direct heritability estimates for 200-d weight, 400-d weight, rib fat depth, ADG, feed conversion, and residual feed intake were 0.17 ± 0.03, 0.27 ± 0.03, 0.35 ± 0.04, 0.28 ± 0.04, 0.29 ± 0.04, and 0.39 ± 0.03, respectively. Feed conversion ratio was genetically (r_g = 0.66) and phenotypically (r_p = 0.53) correlated with residual feed intake. Feed conversion ratio was correlated (r_g = –0.62, r_p = –0.74) with ADG, whereas residual feed intake was not (r_g = –0.04, r_p = –0.06). Genetically, both residual feed intake and feed conversion ratio were negatively correlated with direct effects of 200-d weight (r_g = –0.45 and –0.21) and 400-d weight (r_g = –0.26 and –0.09). The correlations between the remaining traits and the feed efficiency traits were near zero, except between feed intake and feed conversion ratio (r_g = 0.31, r_p = 0.23), feed intake and residual feed intake (r_g = 0.69, r_p = 0.72), and rib fat depth and residual feed intake (r_g = 0.17, r_p = 0.14). These results indicate that genetic improvement in feed efficiency can be achieved through selection and, in general, correlated responses in growth and the other postweaning traits will be minimal.

from (Arthur, Archer et al. 2001)

Milestone 10. Analysis of steer feedlot NFI data from CRC-I together with industry data on BREEDPLAN traits collected on young animals completed.

The analysis was completed and submitted to AGBU for incorporation into BREEDPLAN. A scientific paper on the Beef CRC-I results was published in the *Livestock Production Science* (Robinson and Oddy 2004). An abstract from the paper is provided below, and a copy of the full paper is in Appendix 4. Additional analysis of this data is reported by (Robinson 2005; Robinson 2005).

Heritabilities for feed intake traits related to feed efficiency were lowly to moderately heritable and sufficient genetic variation exists to expect reasonable genetic progress will be made through selection. The amount of genetic variation for NFI from the Beef CRC's progeny test in steers and heifers at Tullimba is similar to that reported from young bulls in a performance test at Trangie, suggesting that both progeny tests and performance tests will yield similar genetic progress.

Net feed intake was not phenotypically correlated with liveweight maintained or average daily gain over the feedlot test period (as expected by definition of NFI). However, NFI was negatively genetically correlated with liveweight maintained. Daily feed intake was positively correlated with average daily gain and also with NFI. This suggests that selection reducing NFI (ie. improving efficiency) will result in a genetic reduction of daily feed intake, but with no correlated change in average daily gain over the period in the feedlot. The relationships between daily feed intake and NFI with carcase attributes show that measures of feed intake were positively correlated with fatness traits and negatively correlated with retail beef yield percentage, meaning that favourable responses in NFI (ie. decreased feed intakes) were associated with reduced subcutaneous fat cover and marbling and increased retail beef yield percentage. The estimates suggest that selection for increased DFI will result in genetically faster growing, heavier and fatter animals whilst selection for reduced NFI will result in genetically leaner, more muscular, and heavier animals.

The correlated responses in feedlot performance of steers from lines selected for high and low NFI from the Trangie feed efficiency herd were reported by (Herd, Archer et al. 2003). The summary from that publication is provided below, and a copy of the full paper is in Appendix 4. Results confirmed that selection for low NFI produced steers that ate less per unit gain, with no adverse effects on growth and retail beef yield. Feeding low-NFI steers for slaughter should therefore be more profitable than feeding high-NFI steers.

For breeders of cattle finished in feedlots, the improvement in feed efficiency is desirable. The genetic associations of NFI with subcutaneous fatness, eye-muscle area, dressing percentage and intramuscular fat percentage (marbling) suggest these traits should be monitored to ensure that selection for NFI does not have an undesired negative impact on meeting market specifications for these carcase traits.

Abstract

Feed intake (FI), weight gain (WG), metabolic weight (MW), feed conversion ratio (FCR), residual feed intake calculated by regression (RFI) and feeding standards formulae (RFIS) were recorded on 1481 steers and heifers of tropically adapted and temperate breeds of cattle feedlot finished on a grain based diet for the domestic (liveweight 400 kg), Korean (520 kg) or Japanese (steers only; 600 kg liveweight) markets. Also measured were subcutaneous fat at the rump (P8) and 12/13 rib sites, 12/13 rib eye muscle area and intra-muscular fat (IMF%), time spent eating, eating rate and number of meals per day. Estimated heritabilities of FI, MW, WG, FCR, RFI and RFIS were 0.27, 0.41, 0.23, 0.06, 0.18 and 0.13. RFI and RFIS had very high genetic (0.98) and phenotypic (0.94) correlations, suggesting that they represent very similar traits. RFI had relatively high genetic correlations with rump and rib fat (0.72 and 0.48 adjusted for age; 0.79 and 0.58 adjusted for carcase weight), but lower correlations with IMF% (0.22 and 0.25 adjusted for age and carcase weight, respectively). Selection for lower RFI is therefore possible in feedlot finished cattle, but fatness will also decrease. In this study, selection for reduced fatness was predicted to reduce RFI by more than direct selection. When appropriate, multivariate selection is therefore recommended to achieve increased feed efficiency together with the desired level of fatness, using an index including RFI, on-test weight gain and fat measurements.

There were large breed differences for number of meals 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 meals per day.

from (Robinson and Oddy 2004)

SUMMARY

This experiment investigated whether divergent selection on postweaning residual feed intake (RFI) resulted in differences in steer growth, feed intake and feed efficiency over a 70-day test period in the feedlot, and in carcass attributes at slaughter. Selection for low postweaning RFI (high efficiency line, HE) produced steer progeny that ate less per unit liveweight gain compared to steers from high RFI (low efficiency line, LE) parents, with no adverse effects on growth. The HE steers tended to have lower feed conversion ratio (feed:gain; FCR) than the LE steers (7.6 *v* 8.2 kg/kg; P<0.1) and had lower RFI (-0.12 *v* 0.10kg/day; P<0.05). Significant positive regressions of FCR and RFI with mid-parent estimated breeding value for RFI (EBV_{RFI}) provided further evidence for favourable genetic associations with postweaning RFI. Ultrasound measurement before slaughter showed that HE steers had less depth of fat over their rib and rump and a smaller cross-sectional area of the eye-muscle than LE steers (10.2 *v* 11.6mm, 13.1 *v* 14.8mm, 66.9 *v* 70.6cm^2; all P<0.05). The HE 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 mid-parent EBV_{RFI} provided additional evidence of genetic association. There were no differences (P>0.05) between HE and LE steer progeny in hot carcass weight or in predicted retail beef yield.

from (Herd, Archer et al. 2003)

Milestone11. Analysis of relationships between NFI and cow performance using data from Trangie and industry completed

The analysis has been completed and submitted to AGBU for incorporation into BREEDPLAN. The results have been published in one conference paper (Archer, Reverter et al. 2002) and one journal (Arthur, Herd et al. 2005). The abstracts of the two published papers appear below and the full papers are in Appendix 4.

A summary of the results of these analyses follows:

Analyses were conducted to examine the genetics of cow performance, including feed intake, efficiency, weight, fertility and milk production, and the relationship of these traits with post-weaning performance including net feed intake and related traits. Records of mature cow weight from industry Angus herds extracted from the NBRS database were also used in the analyses to account for sampling of sires within the experiment. Results from the analyses showed that:

- Considerable genetic variation in net feed intake of mature cows exists.
- There is a strong genetic correlation between post weaning net feed intake and the feed intake and efficiency of cows, such that selection for improved efficiency (ie. lower postweaning net feed intake) will lead to correlated improvements in efficiency of the breeding herd.
- Selection for lower post-weaning net feed intake will lead to slightly heavier cows which eat less, and are also *slightly* leaner (as assessed by subcutaneous fat depths). The correlation with fat depth is low (around 0.2), and so ample scope exists to select efficient cows with adequate fat

coverage. There is no relationship between post-weaning net feed intake and eye muscle area of cows.

- Selection for lower net feed intake post-weaning may have a small unfavourable effect upon fertility (as assessed by the trait "days to calving"), but too little data is available to draw a firm conclusion, and more data collection is required.

- Selection for lower postweaning net feed intake does not appear associated with weight or calf born per cow exposed, milk production of cows or weight of calf weaned. Milk production was assessed by the weigh-suckle-weigh method, which measures how much milk a calf suckles from its dam. These relationships need to be further monitored because there appears to exist a weak genetic correlation (approximately 0.25) between postweaning net feed intake and the maternal component of weaning weight. Again, the weak correlation implies scope exists to select cattle which break this relationship.

- It is proposed that the data be re-analysed using recent statistical genetic methodologies for estimation of genetic parameters and the results published in a scientific journal.

CONCLUSION

There appears to be a strong genetic relationship between intake-related traits from shortly after weaning to maturity, indicating that some biological processes with genetic variation regulating intake and efficiency post-weaning are similar to processes regulating intake of adult animals. This is consistent with the observation that feed intake matures at a faster rate than bodyweight (Taylor *et al.* 1986). These strong relationships present the opportunity to utilise selection to improve feed efficiency of growing animals and mature cows simultaneously, based on measurements taken post-weaning prior to selection decisions being made.

from (Archer, Reverter et al. 2002)

Abstract. Data on 185 Angus cows were used to study the effect of divergent selection for residual feed intake 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 estimated breeding value for residual feed intake 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 ± 0.4 *v.* 9.3 ± 0.4 mm), 2001 (11.3 ± 0.4 *v.* 9.8 ± 0.4 mm) and 2002 (7.0 ± 0.5 *v.* 5.7 ± 0.5 mm) 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 658 kg. 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). The study indicates that after 1.5 generations of divergent selection for residual feed intake there are no significant selection line differences for maternal productivity traits.

from (Arthur, Herd et al. 2005)

Strategy 2 Task 3 ~ Evaluation of the relationship between seedstock and steer NFI with cow performance at pasture (workshop only)

Milestone 12. Workshop on measurement of feed intake at pasture completed and recommendations for future research determined

A workshop to examine techniques for measuring intake at pasture was held in Armidale on 25th and 26th October 2000. The proceedings of the workshop and recommendations for further research and development of this technology (Herd 2000) is attached in Appendix 3. The meeting identified several opportunities for further improvement of technology for measuring intake at pasture, particularly where the technology was to be used as a research tool.

Possible application of the technology were to be considered by the CRC when developing operational plans for the coming years, in particular its application to assessing whether groups of animals with low EBVs for net feed intake use feed more efficiently at pasture compared to their contemporaries with high EBVs. Subsequently alkanes released by intra-ruminal controlled-release devices were used in such studies, reported by (Herd 2002; Herd 2004). However, the workshop participants agreed that, within the life of the current CRC, the technology for measuring pasture intake was unlikely to be developed to sufficient accuracy to be used as a routine measure for genetic evaluation of individual animals.

Strategy 3 Task 5 ~ Design of breeding schemes to optimise the use of direct and indirect selection for feed efficiency in industry
The work proposed consisted of modelling work to investigate the best use of resources by industry for genetic improvement, including measurements of feed intake and correlated traits. Issues which needed to be determined included the use of progeny testing versus measuring the seedstock trait on bulls, the potential impact of genetic and non-genetic markers for feed efficiency, and the use of reproductive technologies to maximise the benefits obtained from genetic improvement. Funds were used to support a PhD student (Ben Wood at UNE) to work on design and economic assessment of breeding programs incorporating new quantitative traits which are expensive or difficult to measure (eg. feed intake) and gene markers.

Milestone 13. Economic analysis of breeding programs incorporating feed intake measurements at the industry level using Zplan model completed.

Zplan is a model of investment in breeding programs which operates at an industry level (ie. across seedstock and commercial breeding sectors). Investment in measurement is compared to returns generated after genetic gain (based on multiple trait indices) and flow of superior genetics into commercial populations have been calculated. The model has been previously used to assess the value of incorporating ultra-sound scanning and reproductive measures into BREEDPLAN (Graser, Nitter et al. 1994).

The Zplan model was used for three major studies, being:

1. Evaluation of performance testing of young bulls for feed intake.
2. Comparing performance testing of bulls with a combination of performance and progeny testing, including feed intake measurement.
3. Evaluation of IGF-1 as a potential indirect selection criterion to improve feed efficiency, with and without direct measurement of feed intake.

These studies have been written up for publication in Australian Journal of Experimental Agriculture (Archer *et al.* 2004), the Association for Advancement of Animal Breeding and Genetics 2001 Conference proceedings (Archer and Barwick 2001), and the 7th World Congress on Genetics Applied to Livestock Production (August 2002; Wood *et al.* 2002) respectively. The abstracts of these papers appear below and copies of the full publications are attached in Appendix 4.

The main recommendations arising from the work were:

1. Performance testing of bulls for feed intake is profitable when between 10 and 25% of bulls are selected for measurement of intake, based on information available at weaning.
2. Bulls to be tested for feed intake should be in the top 25% of the breed, and be a potential seedstock sire. For measuring feed intake to be economically viable, animals identified as superior (for a multiple trait index including feed intake) should be used as sires in seedstock herds to disseminate the improved genetics as widely as possible.
3. Using a combination of performance and progeny testing is not as profitable as performance testing alone, as evaluated using Zplan. However, progeny-testing including feed intake measurement was more profitable than schemes without feed intake measurement, and other considerations (such as the need for high accuracy breeding values on AI sires) might mean that progeny testing is still justified.
4. IGF-1 shows considerable potential as a useful indirect selection criterion to improve feed efficiency and fatness traits. It will be most profitably used in combination with direct measurement of feed intake, but will significantly reduce the number of bulls which should be tested to generate maximum profit.

Subsequent to this project it has become apparent that NFI measured on young cattle postweaning and on older cattle during feedlot finishing are not genetically the same trait and the utility of the IGF-I bloodtest as now being used in seedstock herds for the purpose of genetic improvement is of less merit than it appeared during this research project (Johnston 2007). There is a fresh need to overcome barriers (mainly high cost in this time of drought) to more bulls being tested directly for NFI. This might include expediting delivery of comprehensive gene marker tests for NFI to facilitate two-stage testing, and provision of financial assistance with the high cost of NFI testing to overcome apparent market failure to reward to bull breeders who test for, and supply high-efficiency commercial bulls.

Abstract. A model beef cattle breeding scheme consisting of a breeding unit and a commercial unit was used to evaluate the impact on genetic gain and profitability of incorporating feed intake measurements as an additional selection criterion in breeding programmes. Costs incurred by the breeding unit were compared with returns generated in the commercial unit, with bulls from the breeding unit being used as sires in the commercial unit. Two different market objectives were considered — a grass-fed product for the Australian domestic market, and a grain-fed product for the Japanese market. Breeding units utilising either artificial insemination or natural service were also considered. A base scenario was modelled incorporating a range of criteria available to Australian cattle breeders. A second scenario incorporated selection of sires for the breeding unit using a 2-stage selection process, with a proportion of bulls selected after weaning for measurement of (residual) feed intake. Measurement of feed intake of bulls improved accuracy of breeding unit sire selection by 14–50% over the equivalent base scenario, and genetic gain in the breeding objective was improved for all scenarios, with gains ranging from 8 to 38% over the base scenario. After accounting for the cost of measuring feed intake ($150–450), additional profit was generated from inclusion of feed intake measurement on a proportion of bulls for all breeding schemes considered. Profit was generally maximised where 10–20% of bulls were selected at weaning for measurement of intake, with improvement in profit ranging from 9 to 33% when optimal numbers of bulls were selected for intake measurement.

from (Archer *et al.* 2004)

SUMMARY

Investment in breeding programs incorporating two-stage selection and measurement of net feed intake (NFI) was assessed for designs using performance test information only, or including information from progeny tests. Both designs were profitable relative to a performance test scenario without NFI measurement. Profit from optimally designed performance tests (where 5% to 30% of candidate sires for the breeding unit were performance tested for NFI) was higher than profit from optimal progeny test designs (2% to 5% of candidate sires progeny tested). This suggests that progeny testing may not be justified when analysed at an industry-wide level. However, accuracy of selection and genetic gain were greater from progeny testing. Accounting for risk/return relationships and market share might mean that progeny testing is justified at the level of an individual business.

from (Archer and Barwick 2001)

CONCLUSION

The implication from this study is that IGF-1 can be best used as a screening test in a two-stage selection policy to identify animals to be placed into RFI trials. The profitability of the selection is increased in three ways : a decrease in the number of animals placed into the feeding trials, returns from lower feeding costs and lastly improvements in marble score. The number of animals measured in RFI tests will depend on the cost of the trial but less costly trials also affect accuracy of the test. Scenarios 4-6 demonstrated that just using IGF-1 without further RFI measurements would also raise profit of the breeding scheme. Cost of IGF-1 had little impact on profit and its implementation as an indirect selection criterion. Generally, the more animals measured for IGF-1 the more profit but some strategies with limited investment gave a better return per dollar spent.

from (Wood, Archer et al. 2002)

Milestone 14. Framework for simulation studies to assess breeding program design and investment using phenotypic trait measurements developed. Alternate breeding program designs incorporating measurement of feed intake evaluated.

In the report against milestone 13 above we described progress and publications on our use of the Zplan model to assess the value of performance testing bulls with a combination of performance and progeny testing, and to evaluate IGF-I as a potential indirect selection criterion to improve feed efficiency.

Zplan is a very useful, deterministic model of investment in breeding programs but does not account for risk or for inbreeding. To redress this deficiency, CRC PhD student Ben Wood developed a stochastic model to account for risk and inbreeding which he then used to evaluate alternate breeding program designs incorporating measurement of feed intake and the use of IGF-1 as an indirect selection trait. Ben also added a multi-trait selection index selection program concurrently with the stochastic program to consider selection criteria measurement. He concluded that response at the asymptote rather than the response in the first generation should be considered when assessing breeding programs and programs used earlier such as Z-plan while not incorrect might have overestimated the possible gains achievable without taking into account decreases in variance due to selection.

This evaluation was subsequently redone using updated parameter estimates for IGF-I with other traits, and a much more comprehensive journal paper prepared for submission by end 2002 (Wood, Archer et al. 2004). The abstract of this paper appears below and a copy of the full paper is in Appendix 4.

The primary outcomes were that IGF-I continues to show potential as a useful indirect marker for feed efficiency and fatness traits. It is recommended that IGF-I be used as a first-stage selection criterion to reduce the number of animal required for feed intake testing. The number of bulls required to be tested could be reduced from 20% down to 5% to still have accurate selection and gains in NFI.

Improvements in profitability resulting from IGF-I testing came from a decrease in the number of animals needing to be placed into feed tests, increased returns from lower feed costs and improvements in carcass characteristics in the case of the Japanese market objective. In contrast, its impact on profitability for the Domestic objective did not come from decreased first-stage selection percentages, but from increased profitability through higher accuracy of first and second-stage selection. Improvements in NFI traits and the growth and sale weight traits resulting from the use of IGF-I also increased overall profitability. The optimal scenario for both objectives was the use of IGF-I as a first-stage selection criterion to screen animals for further feed intake tests.

Abstract

In this study various scenarios of selection in beef cattle using the physiological marker insulin-like growth factor (IGF-1) were investigated. Previous research shows that IGF-1 has favourable correlations with a number of important traits in beef cattle including residual feed intake (RFI), carcass fatness, average daily gain, live weight and carcass weight. The aim of this study was to compare the genetic response and profit to varying selection strategies that used direct selection for RFI and indirect selection with IGF-1 in association with other traits. Two breeding objectives for Australian producers were assessed relating to the high value Japanese export market, of which marbling is paid a premium, and the Australian domestic market. Selection for IGF-1 proved profitable in all scenarios for an export objective with the most optimal use as a first-stage selection tool before a feed intake trial for young bulls. Benefits of selection for IGF-1 with the domestic objective were similar to the export objective but increases in profit were marginal when used without feed intake information.

from (Wood, Archer et al. 2004)

Milestone 15. Framework for evaluating QTL in breeding programs developed. Alternative breeding programs incorporating existing or potential gene-markers for feed intake and other traits evaluated.

Using modified gene flow principle the value of existing gene markers was evaluated with respect to commercial breeders. GeneSTAR Marbling and GeneSTAR Tenderness are both currently commercially available so the value to a commercial breeder was assessed. Two breeding schemes were analysed, one for the producer using bulls as terminal sires and, more importantly, bulls being used in a self-replacing herd. Benefits using GeneSTAR Marbling were quantified and ranged from $200-$500 depending on the on the initial gene frequencies assumed. At frequencies consistent with those found in the Australian Angus population benefits are in the higher range.

A journal paper quantifying the benefits to the Australian producer was published in the Australian Journal of Agricultural Research (Wood, van der Werf et al. 2004). See abstract below, copy of the paper is appended.

Abstract. This paper quantifies the benefits of using a sire genotyped for a single recessive gene in a commercial beef herd. A modified gene-flow method was used to account for changing allele frequency over time. The benefits to a commercial breeder of using a genotyped sire were highest when initial allele frequency was moderate and when the sire was used in a self-replacing herd that had increased allele frequency over time. An example of the thyroglobulin gene affecting marbling in beef cattle was used. The value to a self-replacing herd of a sire homozygous for the favourable allele of the thyroglobulin gene was shown to be up to $338 more than of an ungenotyped sire, in a population where the initial gene frequency was 0.3 and the genotype accounted for 0.5 standard deviations of phenotypic variation.

from (Wood, van der Werf et al. 2004)

This framework then allowed the value of potential gene markers for NFI to be modelled (see next Milestone).

Milestone 16. Framework for decision criteria and tactical decision-making concerning trait measurement and genotyping developed. General recommendations for breeding program design in beef cattle populations formulated.

This work mainly consisted of the deterministic model in development and the analysis of various trait and genotype measurement scenarios. With this framework the value of potential gene markers for NFI was modelled. The use of markers for NFI is attractive due to the high cost of NFI measurement of individual animals. A number of assumptions were considered such as the mode of inheritance and gene frequencies in modelling the value an NFI QTL.

This study showed the potential to increase the selection response by using marker-assisted selection and by selecting more young sires on an index not containing all potential phenotypic measures. Annual response was decreased by between 6.3%-10.8% if delaying sire selection until after two years of age and the benefits of marker-assisted selection were decreased even more if early sire selection was not practiced. The study was reported to the 2005 Conference of the Association for Advancement of Animal Breeding and Genetics (Wood, van der Werf et al. 2005). The summary of that paper appears below, and the full paper is in the appendix.

SUMMARY

A pseudo-BLUP index was used to evaluate the selection response from using a quantitative trait locus (QTL) for residual feed intake (RFI). The index included phenotypic information on the individual, sire, dam, half-sibs and progeny. To compare with marker-assisted selection (MAS), a single locus was assumed to be genotyped that explained a proportion of the variance for RFI and this was included in the selection index. Two breeding objectives were examined with a different relative economic value for RFI, one targeting the Australian domestic market and one targeting a high value Japanese export market. The selection response and optimal age structure altered with the inclusion of genotype information. Response was increased because the pre-selection accuracy, before RFI measurement, was improved. Genotyping increased the earlier selection of sires and decreased the optimum generation interval of sires; consequently, this increased the annual selection response. With a QTL that explained 0.33 phenotypic standard deviations of variance, response was shown to increase by up to 11% when both sexes were genotyped and 7.6% when only males were genotyped. When sire selection was delayed until after 2 years of age, the increase in response from genotyping was 8.1% and 5.1%, respectively. If the QTL explained a relatively large part of the breeding objective, the locus was rapidly fixed resulting in rapid early gains.

from (Wood, van der Werf et al. 2005)

A prototype of selection index in visual basic has been completed and will be further developed to include genetic markers. This is available from Dr Julius van der Werf through his website: www-personal.une.edu.au/~jvanderw/

5 Success in Achieving Objectives

The achievement milestones for all objectives of this project were met.

This project built on the earlier MRC/MLA DAN.075 Project, and complementary research by the Cattle and Beef CRC and the CRC for Cattle and beef Quality. The project was conducted as a part of the activities of Project 2.2 of the CRC for Cattle and Beef Quality which consistently ranked among the top achieving projects judged at the annual external scientific and industry reviews conduced by the CRC.

An on-farm testing facility and testing guidelines were devised so that cattle breeders can measure and monitor their herd with respect to NFI. An industry database to record NFI test data and process it for calculation of draft EBV for NFI has been established. The number of animals tested for NFI annually by industry grew between the years 1997 to 2002, but has declined since 2004, with a total of 3,622 tested by industry to 2005.

Evidence for continuing industry adoption of NFI can now be provided by continuing increase in numbers of seedstock cattle with EBV for NFI. The Primegro insulin-like growth factor-I (IGF-I) bloodspot test to identify cattle genetically superior for feed efficiency was launched November 2003. This test provided a less expensive way to find genetically superior bulls. The impact of the test was to rapidly increase the number of bulls with EBV for NFI in the Angus breed, doubling the number of animals with reportable NFI EBV in their January 2004 sire summary, and more than doubling that number again in 2005, with also 30,000 Angus animals with NFI EBV in 2006. Hereford/Poll Hereford was the next breed in 2005 to use IGF-I data in calculating NFI EBV.

Targeted industry extension to encourage adoption of NFI technology was lead by Mr Steve Exton, Livestock Officer with NSW DPI, based at the Trangie Agricultural Research Centre, and later in the project at the Wagga Wagga Agricultural Institute. Steve was supported by other Livestock Officers in NSW and his counterparts in the other States, and by the research staff in the Project team. A minimum of 107 extension-related publications and field-day-type activities were held from 2000 to 2004.

This project analysed data by a number of other projects to provide the evidence that selecting high efficiency bulls could produce calves, steers and cows that are more feed efficient on pasture and in the feedlot. This information has been taken up by the Australian stud cattle industry, and estimated breeding values for NFI are now available in some breed societies to assist commercial producers introduce NFI-superior genetics into their herds.

Further, this project showed that testing of potential sires, or their progeny, for NFI is profitable despite the high cost, and provides strategies to optimise testing to ensure accurate information is obtained at least cost. This project also provides testing strategies using the simpler, less-expensive IGF-I blood test, and two-stage selection to further reduce the number of cattle actually required for NFI testing.

A comprehensive formal evaluation of the economic benefits of the widespread adoption of NFI showed them to be substantial: $6.55 per breeding cow per year, plus $4.34 per breeding cow per

year savings in feed costs in a feedlot, for a total estimated benefit of $158 million (NPV, 2004) over the period 2003-2020. These benefits are predicted on the basis of conservative estimates of industry adoption of NFI technology, and exclude benefits in northern Australian cattle that may accrue in the future. Positive potential environmental outcomes and social outcomes were also identified, including potential reduction in greenhouse-gas emissions.

6 Impact on Meat and Livestock Industry – now & in five years time

Feeding cattle is a major cost of beef production. In southern Australian pasture-based systems, around 60 per cent of the variable costs of production are related to feed cost. Supplementary feeding with hay, grain and silage adds further to the cost of feeding cattle, and the cost of feed is around 70 per cent of the variable cost of operating a feedlot.

The scenario for the cattle industry without access to the NFI technology would be that productivity gains would improve based on past and easily forecast rates of genetic gain. The NFI technology is taken to provide an additional improvement above that already filtering through from past R,D&E.

This project brought together results from previous projects and provided new research and extension efforts that have laid the foundation for industry adoption of NFI. Adoption has commenced and it is expected that the rate of adoption will increase with the availability of gene markers and new knowledge of associations with carcase traits and maternal productivity from on-going Beef CRC research.

A comprehensive formal evaluation to estimate the economic, environmental and social benefits of the potential adoption of the NFI technology in the Southern Australian beef industry was undertaken by (Griffith, Alford et al. 2004). This included the impacts of the current Project, together with those from the earlier MRC/MLA DAN.075 Project, and complementary research by the Cattle and Beef CRC (CRCI) and the CRC for Cattle and beef Quality (CRCII).

The main outcomes of this research, development and extension (R,D&E) effort to date have been economic. Genetic variation in net feed intake exists, the trait is moderately heritable (around 0.4), and selecting high efficiency bulls will produce calves, steers and cows that are more feed efficient on pasture and in the feedlot. Further, where it has been formally measured, there does not seem to be significant adverse implications for other traits of commercial importance. Thus breeders can select for NFI and growth and meat quality and not have to make any significant tradeoffs.

This information has been taken up by the Australian stud cattle industry, and NFI EBV have been made available in some breed societies to assist commercial producers introduce superior NFI-genetics into their herds. The adoption process has commenced, although only at very modest levels to date.

An on-farm testing facility and testing guidelines have been devised so that cattle breeders can measure and monitor their herd with respect to NFI. Unfortunately, such a facility is costly to purchase and there is a high opportunity cost in allocating breeding stock to intensive feeding trials. However, the simpler IGF-I blood test provides a way of differentiating between NFI efficient and inefficient breeding stock.

The economic benefits of the widespread adoption of this technology throughout the southern Australian cattle herd was estimated to be an improvement in cow/calf productivity of $6.55 (net present value (NPV) in 2004) per breeding cow per year over the base herd, evaluated at a discount rate of 4 per cent. This per cow benefit was multiplied by the number of breeding cows in the

southern Australian beef herd, and then by the assumed adoption rate of the technology to generate an aggregate value of $128.6 million for the cow-calf component of the southern herd.

For the feedlot sector, it was estimated that the savings in feed costs in a feedlot in southern Australia due to the introduction of NFI efficient cattle would be $4.34 per breeding cow per year, or an aggregate value of $29.4 million.

Adding these components together, the total estimated benefits from the adoption of the NFI technology were calculated to be $158 million (NPV, 2004) over the period 2003-2020. Of course not all this benefit can be ascribed to the current project alone.

Contributors to the cost of this R,D&E included NSW Agriculture/NSW Department of Primary Industries (NSW DPI), MRC/MLA, the Commonwealth Government and Industry partners through the Beef CRCs and a number of breed societies. The total cost of all inputs was $20.6 million (NPV in 2004) using a 4 percent real discount rate. The total cost of NSW DPI inputs was estimated as $13.9 million, on a similar basis, this being 67.5 per cent, or more than two-thirds.

Comparing the benefits to all recipients in southern Australia relative to the costs incurred by all R,D&E suppliers resulted in a NPV of $137.4 million, an internal rate of return of 13 per cent and a benefit cost ratio of 7.7. These benefits are predicted on the basis of conservative estimates of industry adoption of NFI technology, and exclude benefits in northern Australian cattle that may accrue in the future.

In addition, the NFI technology has some quite positive potential environmental outcomes. If a cattle producer introduces genetics with superior NFI, then over time the herd will require less feed to maintain the same herd size and farm income. This may result in a lower stocking rate and may provide some environmental benefits to the farm in terms of better ground cover, greater water holding capability and less grazing pressure on preferred pasture species. Superior NFI cattle will also produce less manure and urea and more easily cope with drought conditions. More promising though is the potential reduction in greenhouse-gas (GHG) emissions from more feed efficient cattle. Selecting for improved NFI will reduce GHG.

Social outcomes are more difficult to identify and to quantify. Because the technology has been developed in Australia, the beef industry will be less dependent on imported genetics. This may result in more vibrant breed societies and industry organizations, and perhaps greater export opportunities. Since cattle selected for NFI can cope more readily with dry conditions, the beef industry would not be as adversely affected by droughts and this may provide some social benefits during such times.

7 Conclusions and Recommendations

This project built on the earlier MRC/MLA DAN.075 Project, and complementary research by the Cattle and Beef CRC and the CRC for Cattle and Beef Quality. This other research showed that genetic variation in net feed intake exists, that the trait is moderately heritable (around 0.4), and that selecting high efficiency bulls had the potential to produce calves, steers and cows that are more feed efficient on pasture and in the feedlot. This project aimed to provide mechanisms for the beef industry to be able to identify and optimal utilise feed efficient bulls, and knowledge of favourable and possible unfavourable associations with other economically important production traits.

An on-farm testing facility and testing guidelines were devised so that cattle breeders can measure and monitor their herd with respect to NFI. An industry database to record NFI test data and process it for calculation of draft EBV for NFI has been established. Unfortunately, NFI testing is costly and there is a high opportunity cost in allocating breeding stock to intensive feeding trials.

This project has shown that testing of potential sires, or their progeny, for NFI is profitable despite the high cost, and provides strategies to optimise testing to ensure accurate information is obtained at least cost. This project also provides testing strategies using the simpler, less-expensive IGF-I blood test, and two-stage selection to further reduce the number of cattle actually required for NFI testing.

Further, this project analysed data by a number of other projects to provide the evidence that selecting high efficiency bulls could produce calves, steers and cows that are more feed efficient on pasture and in the feedlot. This information has been taken up by the Australian stud cattle industry, and NFI EBV have been made available in some breed societies to assist commercial producers introduce NFI-superior genetics into their herds.

The economic benefits of the widespread adoption of NFI are substantial: $6.55 per breeding cow per year, plus $4.34 per breeding cow per year savings in feed costs in a feedlot, for a total estimated benefit of $158 million (NPV, 2004) over the period 2003-2020. These benefits are predicted on the basis of conservative estimates of industry adoption of NFI technology, and exclude benefits in northern Australian cattle that may accrue in the future.

The adoption process has commenced, although only at very modest levels to date. This project reported weak, and possibly unfavourable, associations with some carcase traits and a measure of female fertility. These antagonisms can be managed by appropriate weighting in selection indices but they have to potential to both reduce the rate of genetic improvement in NFI, and to reduce the confidence of commercial cattle producers to choosing to use a high efficiency bull. They could thereby reduce the potential economic benefit.

The rate of adoption is expected to increase with the availability of gene markers and new knowledge of associations with carcase traits and maternal productivity from on-going Beef CRC research.

The IGF-I test was developed as a more convenient, less expensive method to screen young cattle in a two-stage selection process to reduce the number of animals required to undergo the more

expensive NFI test. More recently it has been used as an indirect physiological marker to calculate EBV for NFI, albeit less accurately then using actual NFI test data. This use has resulted in an exponential increase in the number of cattle with NFI EBV in the Angus and Hereford breeds which have approved its use for this purpose.

There are currently approximately two-thousand postweaning NFI test records and three-thousand feedlot NFI-test records for Australian cattle, with only a couple of hundred of new records per year from research herds, and virtually nil records from private seedstock herds likely to be added over the next few years. This means that many of the phenotypic and genetic correlations between NFI of different classes of cattle, with IGF-I, and with other production traits are estimated with large error. There is a need for a co-ordinated effort to ensure at least 500 predigreed and performance animals per year are tested on an on-going basis, to ensure the accuracy of these correlations is both improved and change following selection is better predicted.

NFI technology has some quite positive potential environmental outcome and no negative social outcomes:

- a lower stocking rate leading to better ground cover, greater water holding capability and less grazing pressure on preferred pasture species
- cattle that produce less manure and urea and more easily cope with drought conditions
- potential reduction in greenhouse-gas emissions.

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Subsequent to this project it has become apparent that NFI measured on young cattle postweaning and on older cattle during feedlot finishing are not genetically the same trait and the utility of the IGF-I bloodtest as now being used in seedstock herds for the purpose of genetic improvement is of less merit than it appeared during this research project. There is a fresh need to overcome barriers (mainly high cost in this time of drought) to more bulls being tested directly for NFI. This might include expediting delivery of comprehensive gene marker tests for NFI to facilitate two-stage testing, and provision of financial assistance with the high cost of NFI testing to overcome apparent market failure to reward to bull breeders who test for, and supply high-efficiency commercial bulls.

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9 Appendices

9.1 Appendix 1

CRC Project 2.2 Outline - 2000 to 2006

Improving the Efficiency of Feed Utilisation for Beef Production

EXECUTIVE SUMMARY

The activities planned for CRC Project 2.2 reflect the agreed priorities set at a CRC-sponsored workshop on feed efficiency held on 23rd and 24th May 2000. The activities encompass research, industry development and extension aimed to assist the beef industry to adopt selection for improved feed efficiency of cattle. The major strategies and tasks are:

Strategy 2.2.1 Development and extension of net feed efficiency technology to industry
This strategy aims to foster the roll-out of net feed efficiency technology to industry in its current state, and to keep industry abreast of improvements in the technology which will arise from further research. The tasks listed under this strategy include:

- Task 1 - Development and maintenance of an industry database
- Task 2 - Production of BreedPlan EBVs for NFI and incorporation into BreedObject
- Task 3 – Extension targeted to maximise uptake of NFI technology
- Task 4 - On-farm demonstration trials

Strategy 2.2.2 Evaluation of key genetic relationships between net feed intake and other economically important traits for beef production.
This strategy will involve the assessment of genetic relationships identified as being key pieces of information required. This will involve analysis of existing data and collection of new data where required. As part of this, the animal resource and measurements of feed intake and efficiency required for strategy 3 will also be provided. The tasks for strategy 2.2.2 are:

- Task 1 - Analysis of existing data from DAN.75, CRC I and industry herds.
- Task 2 - Create a cattle resource with measurements of feed intake to estimate the correlation between the seedstock and steer measures of feed efficiency, and to provide the resource population for other tasks within strategies 2 and 3.
- Task 3 - Evaluation of the relationship between seedstock and steer NFI with cow performance at pasture.
- Task 4 - Objective and sensory evaluation of meat from high and low NFI steers.

Strategy 2.2.3 Cost-effective ways to identify animals genetically superior for NFI.

This strategy will focus on finding better and more cost-effective ways of implementing NFI technology in industry. Three approaches will be explored, being an investigation of ways to reduce the cost of measurement, a search for indirect selection criteria (including genetic and non-genetic markers), and modelling work to examine the optimal design of breeding schemes and provide recommendations to industry as to how (and on what animals) the technology should be implemented. The tasks within strategy 2.2.3 are:

- Task 1 - Reducing the cost of measuring feed intake and efficiency by using automated weighing systems.
- Task 2 - Genetic markers for feed efficiency (linked to CRC Project 2.1).
- Task 3 - Evaluation of the IGF axis as an indirect marker for feed efficiency.
- Task 4 - Evaluation of hind-gut fermentation and faecal NIR technology as sources of variation in feed efficiency of steers in feedlots.
- Task 5 - Design of breeding schemes to optimise the use of direct and indirect selection for feed efficiency in industry.

PROJECT OUTLINE

Project Leader: Dr Jason Archer (NSW Agriculture)

Mission
To reduce the cost of beef production through genetic improvement in efficiency of feed utilisation.

Background
Feed costs are a major part of total production costs for the Australian Beef Industry. The poultry and pork industries have made significant gains in feed efficiency over 30 years. The beef industry has made far less genetic progress than the intensive monogastric industries.

Net feed intake (NFI) refers to the variation in feed intake of animals after accounting for the requirements for growth and maintenance of body tissue. It is a useful way of assessing variation in feed efficiency that is independent of (ie. net of) size and growth rate. NFI is defined as actual feed intake minus expected feed intake calculated based on body weight and average daily gain.

The outcomes from feed efficiency research by the former CRC for the Cattle and Beef Industry and by NSW Agriculture and the MLA at Trangie has proved the important principles that:

- there is large variation among individuals and among sire progeny groups for NFI measured post-weaning and during feedlot finishing
- NFI is moderately heritable, and
- NFI responds to selection, with demonstrated improvement in feedlot feed efficiency.

A workshop on feed efficiency was held in May 2000 at Robb College, University of New England, under the auspices of the Cattle and Beef Quality CRC. The objectives of the workshop were i) to review information on feed efficiency in beef cattle as well as other species that is available world-wide and ii) to make recommendations on areas of research, development and extension that are required for an effective industry application. It was attended by 35 leading national and international scientists with expertise in the area, representing the scientific disciplines of genetics, nutrition and physiology. Proceedings of the workshop are available through the CRC secretariat.

The portfolio of this project has thus been developed to reflect the recommendations of the workshop.

Objectives

The objectives of Project 2.2 are:

- To utilise existing scientific information to develop the NFI technology for industry application.
- To develop and implement educational and extension strategies to improve the adoption rate of NFI technology by industry.
- To evaluate key genetic relationships between NFI and other economically important traits.
- To develop lower cost methods to identify animals that are superior for NFI.
- To develop optimal breeding designs for use by industry.

Linkages with other Projects

This project is operationally linked to Program 2 project on Genetic Markers (Project 2.1), the Northern Australia project (Project 2.3) and Program 1 Project 1.1 (Biophysical mechanisms that affect eating quality of beef).

Strategy 2.2.1 ~ Development and Extension of NFE Technology to Industry

Economic analyses indicate that the southern Australian beef industry stands to reap financial benefits from genetic improvement of NFI. This benefit will be captured through the use of cattle with superior genetics for NFI, which will be produced by the seedstock sector. It has been planned that delivery of the technology to industry will be through BreedPlan and BreedObject. Trial EBVs (estimated breeding values) are currently being produced for cattle tested for NFI in Australia. It is planned that BreedPlan EBVs for this trait will be developed, and the trait incorporated into BreedObject.

The research and development program will be supported by a comprehensive national extension program, aimed at fostering industry testing of sufficient numbers of animals with adequate genetic linkages to enable the development and subsequent industry adoption of BREEDPLAN EBVs for NFI. Seedstock breeders, the commercial sector and the feedlot industry will require specific educational programs to enable NFI technology to be utilised in profitable beef production systems.

Strategy 2.2.1 will aim to achieve a 2% per annum adoption rate across the industry in southern Australia. This aim can be objectively quantified as the number of calves born in seedstock herds which are by sires with EBVs for NFI published. Thus the specific aim is that by 2007, 14% of the calves registered in southern British-breed seedstock herds will be by sires with published NFI EBVs. As these sires will likely be AI sires, achieving this aim will represent a significant proportion of the potential genetic gain available under the current industry structure.

Task 1 ~ Development and maintenance of industry database

The data generated from industry testing will need to be stored in a central database, and processed to provide a summarised performance record for each animal for loading on the breed society's national database held at ABRI. This record will then be used to calculate BreedPlan EBVs. An appropriate database will be created and maintained (by NSW Agriculture) for the first 4 years, after which the arrangements will be reviewed in consultation with all relevant parties.

Task 2 ~ Production of BreedPlan EBVs for NFI and incorporation into BreedObject

An essential part of the strategy for implementing selection for NFI in the industry is to incorporate facilities to calculate and publish an EBV for NFI in Breedplan, and to expand BreedObject software to incorporate the new EBV. This task will be managed separately by the Animal Genetics and Breeding Unit and will not form part of the CRC budget, but is included in the operational plan for project 2.2 as it forms the central part of the strategy for industry implementation.

Task 3 ~ Extension targeted to maximise uptake of NFI technology

An extension program targeted to maximise the uptake of NFI technology will be conducted, with technical input from staff of relevant institutions including NSW Agriculture, Beef CRC, Agriculture WA, Agriculture Victoria, ABRI, AGBU and Breed Societies currently enrolled in GROUP BREEDPLAN. The program will support the implementation of NFI technology, while maintaining the perspective that NFI is one of several traits for consideration in balanced breeding programs. The program will:

- Ensure significant adoption of NFI testing by influential seedstock breeders, through continued education and support programs, including assistance with technical issues concerning measurement of the trait and use of the data.
- Facilitate increased use of NFI-tested bulls by the commercial breeding sector.
- Provide revised protocols for implementation of NFI by industry, including test protocol, accreditation programs and auditing procedures to ensure the integrity of data generated and increased industry adoption.
- Integrate appropriate information on NFI technology into existing education programs supported by the Beef CRC and other education programs concerned with cattle selection and breeding.
- Provide support programs for client education for seedstock breeders who implement NFI measurement in their herds, including client awareness days for producers measuring NFI on-farm.
- Increase industry access to latest results by establishing a NFI web-site to augment the existing extension publications.
- Ensure that appropriate staff from appropriate organisations involved in advancing NFI technology are suitably trained to support increased industry adoption.

Task 4 ~ On-farm Demonstration Trials

Develop on-farm demonstration trials of testing for NFI utilising commercially developed testing units. In order to implement testing procedures at least cost and maximum flexibility within their breeding programs, several seedstock producers have expressed interest in evaluating the commercially available on-farm NFI testing units. To date, these units have been used under research conditions at existing Government facilities. They have not been evaluated "on-farm", and

the practicalities of establishing these units and managing the program for the duration of the test are not known.

Therefore, two Ruddweigh Feed Intake Recorders and weighing systems will be purchased and tests will be conducted at 3 influential British breed studs each year. At the completion of each of these tests, we would conduct a field day aimed at education of both commercial and seedstock producers regarding testing for NFI, and subsequent development and use of EBVs generated from this testing.

Outcomes (Strategy 2.2.1)

- Systems for implementing NFI technology in industry established (by June 2001).
- Breedplan EBVs for NFI published (by date set in AGBU workplan).
- NFI incorporated into BreedObject (by date set in AGBU workplan).
- Seedstock and commercial breeders educated as to how to implement NFI technology and interpret results (ongoing until June 2004).
- Seedstock breeders using on-farm and off-farm facilities to measure NFI (ongoing until June 2003).
- By 2007, 14% of calves born in southern British-breed seedstock herds will be sired by bulls with published EBVs for NFI.

Resources

Physical Computer facilities at NSW Agriculture and AGBU, Trangie Research Centre, Rutherglen Research Institute, PVI Hamilton and Vasse Research Institute.

Human Jason Archer, Paul Arthur, Karen Dibley, Steve Exton, Brian Sundstrom, Brian Cumming, David Burton (NSW Agriculture), Hans Graser, David Johnston, Steve Barwick (AGBU), Geoff Tudor (Agriculture WA), Extension Officers from Vic, SA and WA, breed society technical staff.

Strategy 2.2.2 Evaluation of key genetic relationships between net feed intake and other economically important traits for beef production.

Beef producers and seedstock breeders investing in genetic improvement programs must know and understand the impact of their selection decisions on the traits which economically influence beef production. Whilst work to date has provided a good basis of information, there are still several gaps in knowledge of the full genetic parameter matrix required. Of these gaps, key pieces of information have been identified, following the CRC Feed Efficiency Workshop held in May 2000, as a priority for further research. This information is required for a number of reasons. Firstly, the information will be used to better understand and predict correlated responses to selection, thereby improving industry (and scientific) confidence in the value of including net feed intake as a selection criterion. Secondly, knowledge of the full genetic relationship matrix is required to derive economically optimal

selection indices (such as those provided by BreedObject) and to determine appropriate balances between individual traits in selection programs. Thirdly, in some cases, knowledge of relationships between traits is required as an input for the prediction of breeding values from more than one source of information. Specifically, combining information on feed intake and efficiency from seedstock tests and steer progeny tests to produce an EBV requires knowledge of the genetic relationships between these traits. Finally, as genetic improvements in feed efficiency for animals fed on pasture will never be directly observed by producers, there is a real need for clear, unequivocal evidence that the improvement claimed is real and of economic significance not only for feedlot cattle but also for cattle on pasture.

Strategy 2 will focus on providing information on relationships identified at the Feed Efficiency Workshop as being key ones. Existing data from CRC-I and DAN.75 projects will be used to estimate relationships where possible, but collection of additional data will be required to estimate particular relationships. Additional data on the relationship between the seedstock measure of NFI with feed intake and performance of steers in feedlots is required. The second area requiring additional data are the relationships between NFI of young animals (seedstock and steer feedlot) with feed intake, maternal and reproductive performance of cows on pasture. Other information for relationships of lesser importance will be able to be estimated from data collected by industry over time.

Task 1 ~ Analysis of data from DAN.75, CRC I and industry herds.
Analysis of existing data from DAN.75, CRC I and industry herds will be required to investigate associations between feed efficiency and other traits related to whole-herd productivity. Traits will be analysed where sufficient data already exists to allow at least preliminary estimates to be calculated (eg. carcase and meat quality traits, female reproductive and maternal performance) and as additional data are obtained from tasks 2 and 3.

Outcomes

- Knowledge of phenotypic and genetic relationships of feed efficiency with other traits.

Resources

Physical:	AGBU computing facilities, Trangie, CRC-I and industry databases.
Human:	Jason Archer, Paul Arthur, Robert Herd (NSW Agriculture), David Johnston, Dorothy Robinson (AGBU)

Task 2 ~ Create a cattle resource with measurements of feed intake to estimate the correlation between the seedstock and steer measures of feed efficiency, and to provide the resource population for other tasks within strategies 2 and 3.

Design requirements: A core cattle resource is required to 1) estimate the correlation between the seedstock and steer measures of feed efficiency; and 2) Provide the animals with intake measurements essential to the tasks within strategies 2 and 3, including the search for cheaper tests and alternative selection criteria. To estimate the relationship between seedstock and steer feed efficiency, sires are required with progeny measured using the seedstock test and progeny measured for the required traits during finishing in feedlots. Approximately 1000 seedstock and 1000 steer progeny are required, with around 15 progeny per sire. Current plans are to continue to use the population at Trangie which has the most extensive records on the seedstock measure, and

to generate steers to provide information on steer efficiency. Existing data on steers which fit these criteria include 150 steers measured as part of CRC-I, and 200 steers bred at Trangie and currently being measured at Tullimba feedlot. It is planned that the additional data will be obtained by 1) Using bulls over Trangie cows to produce progeny which will be tested for the seedstock trait, and the same bulls will also be used over Hamilton and Struan cows to produce steers which will be tested for NFI and other traits during feedlot finishing; and 2) Using steers from existing industry progeny testing programs which are by sires which also have progeny measured using the seedstock test, where available. The cost-effectiveness and feasibility of these two data sources will be assessed to determine the optimum design.

Outcomes

- Knowledge of genetic relationship between seedstock NFI measure and steer feedlot performance by June 2006.
- Animals with phenotypic data and pedigree structure required to evaluate genetic and non-genetic markers for feed efficiency under strategy 3.

Resources

Physical:	Cow herds and facilities at Trangie, Hamilton and Struan, Facilities for intake measurement at Trangie, Tullimba, Rutherglen and Struan.
Human:	Jason Archer, Paul Arthur, Robert Herd (NSW Agriculture), Bruce Knee, Brendan Tatham (DNRE), Peter Speck, Mick Deland (SARDI), John Thompson (UNE).

Task 3 ~ Evaluation of relationship between seedstock and steer NFI with cow performance at pasture.

Design requirements: Data already collected at Trangie includes records on feed intake of 800 dry, non-pregnant cows fed on a pelleted ration using an automated feed intake recording system. Extra information required includes an estimate of appropriate variances for feed intake of cows at pasture (ideally over a complete production cycle), along with convincing evidence to demonstrate that selection on NFI will alter the feed requirements of cows at pasture.

A major limitation in this area is the technology for measuring intake at pasture. Existing controlled release device (CRD) technology suffers from problems with variation in release rates of chromium or alkane markers, leading to inaccuracies of the assessments for individual animal intakes at pasture. Moreover, the CRDs only provide an estimate of intake over 10-14 days, while analyses from data at Trangie show that even with accurate measurement of intake (using an automated feeding system), approximately 35 days are required to obtain a stable estimate of individual intake. DNRE has shown that it may be possible to accurately deliver known doses of marker to cattle over extended periods using automated self-feeders located in the field. Use of such a system potentially provides a way of overcoming the two deficiencies of the existing CRD technology, and may mean that more accurate measurement of intake at pasture over longer periods may be possible.

A preliminary study to determine the feasibility of this alternative approach to delivery of markers in being conducted by QDPI in Rockhampton, and will be completed in June 2000, and a report written

by July 2000. In August a meeting of project members will be held to determine whether the approach is promising and further technique development should continue in this area. Subject to a positive recommendation from this meeting, work for the remainder of the financial year will focus on further refinement of the marker delivery system.

The refined marker technology will be used in future years to estimate pasture intake of cows at Trangie and provide the critical information required to demonstrate the benefits of selection for NFI to the breeding herd. The exact approach and design for cow pasture intake studies will be dependant upon the refined marker delivery technology and the animal resources available.

Outcomes (these outcomes are contingent upon obtaining accurate methodology for measuring feed intake at pasture)

- Improved technology for measurement of pasture intake (for research purposes).
- Knowledge of variances associated with intake of cows at pasture.
- Unequivocal evidence to demonstrate the benefits of selection for NFI on feed requirements of the cow herd to seedstock and commercial breeders.

Resources

Physical:	Facilities at Tropical Beef Centre and Brian Pastures, Pastoral and Veterinary Institute Hamilton
Human:	Rod Hill, Ron Hendricksen (QDPI), Bruce Knee (DNRE), Robert Herd, Roger Hegarty (NSW Agriculture)

Task 4 ~ Objective and sensory evaluation of meat from high and low NFI steers

Previous results have suggested that a relationship between NFI and product quality might exist, but the outcomes have been inconclusive. Further data is required to determine whether selection to improve NFI may be associated with changes in the objective and sensory attributes of meat quality, and with changes in meat yield that might affect their commercial value of heavy feedlot steers. It is proposed that yield, and objective and sensory assessment of meat samples, be done for 124 Trangie-bred HE and LE steers due to complete a feedlot NFI test in July 2000 and which will meet heavy export market specifications. Meat samples will be taken from these animals at slaughter, and objective measurements of meat quality will be performed as well as evaluations under the MSA grading system.

Outcomes

- Knowledge of possible associations (if any) between improved NFI and meat quality assessed using objective measurements and consumer evaluations (by June 2001).

Resources

Physical:	124 steers on feed at Tullimba, laboratory facilities at Armidale.
Human:	Robert Herd (NSW Agriculture), Kerynn Zirkler (CSIRO)

Strategy 2.2.3 Cost-effective ways to identify animals genetically superior for NFI.

Economic analyses have indicated that at the current cost of measuring NFI the technology is economically viable for some situations, particularly for high-value markets with animals are fed for

long periods. However, the cost of testing bulls or steers for NFI is high, and the cost and lack of other suitable indirect selection criteria remains a significant barrier to adoption of the technology by industry. Strategy 2.2.3 will focus on improving the cost effectiveness of implementing the technology in the beef industry. Three approaches will be explored, being an investigation of ways to reduce the cost of measurement, a search for indirect selection criteria (including genetic and non-genetic markers), and modelling work to examine the optimal design of breeding schemes and provide recommendations to industry as to how (and on what animals) the technology should be implemented.

Task 1 ~ Reducing the cost of measuring feed intake and efficiency.

Design requirements: The use of automatic scales to weigh animals in front of feeders is a possible way to reduce test length, and hence cost. To date, preliminary investigations undertaken by DNRE and NSW Agriculture indicate that the use of automatic weighing could reduce the length of NFI test. However, to properly assess the potential for this, and to determine appropriate regression equations to calculate NFI under this system, data on at least 600 animals with an appropriate pedigree structure to estimate variance components are required. This data can be collected from both research animals and animals tested by industry. Since the success of this task will greatly reduce the cost of testing, it is worth completing this task as soon as possible to enhance industry adoption. Therefore it is proposed that measurements on research animals be taken and combined with data on animals tested by industry to produce an outcome in as short a time as possible.

Outcomes

- Revised recommendations for test duration implemented (and appropriate regression equations estimated) for measurement systems incorporating automated daily measurement of animal liveweight (for seedstock tests by December 2003, and for steer tests by December 2005).

Resources

Physical: Feed intake measurement facilities at Trangie, Struan, Pastoral and Veterinary Institute, Hamilton and Rutherglen

Human: Jason Archer, Paul Arthur, (NSW Agriculture), Bruce Knee, John Graham, Brendan Tatham (DNRE), Peter Speck, Mick Deland (SARDI).

Task 2 ~ Genetic markers for feed efficiency.

Design requirements: Regions containing genetic markers for feed efficiency will be obtained from Limousin x Jersey cattle used in the University of Adelaide project under Project 2.1. These markers will then need to be evaluated in a population which is industry-relevant to verify that markers found are useful in the straight-breeding populations where they will be applied. With the correct design, a genome scan for QTL for feed efficiency in straight-breeding populations may also detect additional regions not detected in the previous study. Project 2.2 will provide the phenotypic measurements, the pedigree and DNA samples to be used by Project 2.1 for work in this area. The design of such a population will be agreed between staff in both projects, and will endeavour to provide the most efficient use of available cattle resources for multiple tasks in project 2.2 and 2.1.

Outcome

- DNA database of animals with pedigree and phenotypic records available for use by CRC Project 2.1 (by December 2003).

Resources

Physical: Cattle and feed intake measurement facilities at Trangie, Laboratory facilities for DNA extraction and storage at CSIRO, Brisbane

Human: Jason Archer, (NSW Agriculture), Blair Harrison (CSIRO)

Task 3 ~ Evaluation of the IGF axis as an indirect marker for feed efficiency.

Design requirements: The IGF axis has been identified as a marker for feed efficiency in pigs, and is the subject of a patent. Project 2.2 will estimate the genetic correlations between IGF and feed efficiency in cattle to verify whether IGF has merit as an indirect selection criterion for feed efficiency in cattle. Data requirements for such a study include measures of IGF (taken at an appropriate time in the animal's lifetime) which are collected on cattle which also have phenotypic and pedigree information on feed efficiency, with a minimum of 1000 animals needed to provide estimates of the genetic correlations required. The animals used will be obtained from the cattle resource generated by strategy 2.2.2 task 2.

Outcome

- Knowledge of the genetic association between IGF-1 and feed efficiency, and it's potential as a biochemical marker for indirect selection to improve feed efficiency.

Resources

Physical: Cattle and feed intake measurement facilities at Trangie, Hamilton, Struan and Rutherglen, Laboratory facilities for IGF assays at Armidale, cattle from Project 2.3.

Human: Robert Herd, Jason Archer (NSW Agriculture), Kerynn Zirkler, Heather Burrow (CSIRO), Sean Clearkin (PrimeGro), Brian Luxford (Bunge Meat Industries), Hans Graser (AGBU).

Task 4 ~ Evaluation of hind-gut fermentation and faecal NIR technology as sources of variation in feed efficiency of steers in feedlots.

Design requirements: Individual animals may vary in the site of digestion of starch, and hence in their susceptibility to acidosis when fed high-grain rations. This variation might provide a potential mechanism which influences feed efficiency of steers in feedlots. To test this hypothesis, measurements of relevant traits including faecal pH and faecal NIR measurements should be made on steers from an appropriate pedigree structure while being fed high-energy rations in feedlots. Similar design requirements to task 3 apply, with maximum information being gained from using the same animal population as other components of Project 2.2.

Outcome

- Knowledge of variation between individuals in site of starch absorption, and its associations with acidosis of cattle fed high-grain diets.

Resources

Physical: Cattle and feed intake measurement facilities at Tullimba, Struan and Rutherglen, Laboratory facilities at Armidale.

Human: James Rowe, Andrew Channon (CRC Scholarship), Wendy Brown, Bronwyn Schwartz (UNE).

Task 5 ~ Design of breeding schemes to optimise the use of direct and indirect selection for feed efficiency in industry.

Requirements: The work proposed in this area consists of modelling work to investigate the best use of resources by industry for genetic improvement, including measurements of feed intake and correlated traits. Issues which need to be determined include the use of progeny testing versus measuring the seedstock trait on bulls, the potential impact of genetic and non-genetic markers for feed efficiency, and the use of reproductive technologies to maximise the benefits obtained from genetic improvement. Funds will be used to support a PhD student (scholarship and operating) to work on design and economic assessment of breeding programs incorporating new quantitative traits which are expensive or difficult to measure (eg. feed intake), gene markers and reproductive technologies.

Outcomes

- Recommendations to industry regarding the design of breeding programs incorporating the strategic use of measurement (including NFI) on seedstock animals and progeny-test animals to optimise profitability (by December 2003).
- Economic evaluation of genetic and non-genetic (eg. IGF-1) markers for feed efficiency in selection programs (by December 2003).

Resources

Physical: Office and facilities at UNE

Human: Jason Archer (NSW Agriculture), Hans Graser, Steve Barwick (AGBU), Julius van der Werf (UNE), Peter Parnell (Angus Society), PhD Student (to be appointed).

Cattle Resource base

A core population of research cattle with phenotypic measurements on the seedstock measure of NFI, and a deep pedigree with extensive records on the trait, is currently being maintained at Trangie. Selection for high or low feed efficiency will be practiced within the herd to increase the power of the population for studies involving gene markers and cow intake at pasture. Cow resources at Hamilton and Struan will also be used by natural mating following an AI program for project 3.3. Bulls used in the population at Trangie will also be used to breed steer progeny at Hamilton and Struan, which will then be finished in research feedlots at Rutherglen and Struan with feed intake information collected. Additional cattle from industry progeny testing programs will be used to supplement cattle numbers from the base resource if suitable cattle with appropriate structure and measurements can be identified.

Genetic correlations between the seedstock NFI measure and steer feedlot efficiency would use data from bulls and heifers at Trangie and steers bred at Struan and Hamilton, and animals from industry progeny testing programs where suitable. (Strategy 2.2.2 Task 2). Cow pasture intake

would utilise cows from Trangie (Strategy 2.2.2 Task 3). Studies to reduce the cost of measuring NFI would involve data collected using automatic weigh platforms from Hamilton, Rutherglen and Trangie and would include research and industry animals (Strategy 2.2.3 Task 1). The search for genetic markers for feed efficiency would be based on the population at Trangie, with additional data on steers by the same sires available from Struan and Hamilton if required (Strategy 2.2.3 Task 2). The use of these research cattle will depend on the simulation study to be done by Project 2.1 in 2000/01 and the cost of alternative designs to achieve the same power. IGF measurements taken on animals at Trangie, Struan and Hamilton would be used to estimate genetic correlations with other production traits (Strategy 2.2.3 Task 3. Faecal samples from steers at Rutherglen and Struan, and other industry progeny-testing programs if required, would be used to investigate genetic variation in susceptibility to acidosis and possible links (ie. genetic correlations) with feedlot performance (Strategy 2.2.3 Task 4).

Following the Feed Efficiency workshop in May 2000, the design of the animal resource is currently being re-examined to determine whether it is still the optimal design to address the priority issues identified at the workshop (see milestone under strategy 2.2.2).

9.2 Appendix 2

Extension-related publications and field-day-type activities from 2000 to 2004

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9.3 Appendix 3

MEASURING PASTURE INTAKE BY BEEF CATTLE

Report on Beef Quality CRC Project 2.2 Team Meeting
25-26 October 2000
Armidale

Meeting participants: Robert Herd (Convenor: NSWAg, Armidale), Greg Lee (NSWAg, Orange), Hugh Dove (CSIRO, Canberra), Bruce Knee (DNRE, Hamilton), Roger Hegarty (NSWAg, Armidale), Rod Hill and Ron Hendricksen (QDPI Rockhampton), Jason Archer and Paul Arthur (NSWAg, Trangie).

Funds to convene this meeting were provided to the CRC by Meat and Livestock Australia. This was the third in this series of meetings and the participants wish to record their appreciation to MLA for their ongoing support of this area of research.

Report prepared by Robert Herd 30 November 2000.

SUMMARY

1. Since 1996 the use of synthetic alkanes administered by controlled-release devices (CRDs), analysed together with complementary alkanes present naturally in herbage, has become the internationally accepted method to measure pasture intake in free-ranging sheep and cattle (approximately 1,600 sheep and 1,300 cattle CRDs are sold annually). Alkanes have also been used to successfully measure supplement intake by sheep and dairy cows, and in studies of diet selection and of diet composition by sheep and undomesticated herbivores.

2. Our confidence in using this methodology has matured over the past 4 years. We have learnt that the discrepancy between estimated and actual fed intake (FI) can be reduced by using better estimates of recovery, and by better understanding of the consequences of faecal sampling routine and of implications of errors in recovery. The emphasis in research has shifted from technique development to application in agricultural systems *eg* studying phosphorus and nitrogen cycling in pasture ecosystems; diet selection and understanding the basis thereof.

3. Actual intake can be estimated without bias (*ie* the mean of the estimated FIs = the mean of the actual FIs) but errors from various sources can result in small discrepancies between estimated and actual FIs. The meeting concentrated on the technology-based sources of error, being the ones that the researcher has some power to control, and excerpts from several presentations are appended to this report. The technology-based sources of variation discussed included:

- variation in dosing of synthetic alkanes
- errors in estimation of recovery of alkanes
- schedule of faecal sampling
- sample preparation
- lab analytical technique
- statistical procedures used to estimate diet composition.

Of these areas, estimation of alkane recovery and understanding the biological factors associated with recovery were perceived to be particularly important for increased precision of future pasture intake assessment.

1. Within CRC projects, alkane CRDs could be used in projects that need to measure pasture intake by groups of cattle. Examples might include demonstration of the correlated response in pasture intake and efficiency of cattle with high and low EBVs for net feed intake, and measurement of intake and hence cost and efficiency of pasture usage in different management systems, or by different genotypes, or by cattle with different previous growth paths. There are many issues of experimental design that need to be considered.

2. For the purpose of genetic improvement the meeting concluded that, within the life of the current CRC, the current alkane-CRD and possible new marker delivery systems were unlikely to deliver a system with sufficient accuracy for individual animal evaluation of feed intake and efficiency on pasture.

3. The importance of determining diet composition for accurate calculation of feed intake, and in applications studying diet selection and nutrient cycling, now drives a need for research into:
   - a better understanding of the biological basis of incomplete recoveries of alkanes
   - evaluation of other, complementary plant markers
   - better statistical methods to resolve diet composition.

   This is a major deficiency in our knowledge and must be addressed for both temperate and tropical pastures.

4. Alternate marker delivery systems, used with a feed supplement with a distinct marker pattern as a natural marker, particularly impressed the meeting with their potential utility for measuring pasture intake over longer time periods than is currently possible with CRDs. Further development of this method is strongly recommended for research projects requiring measurement of pasture intake.

Objectives

1. To review progress in the measurement of pasture intake by ruminants using dosed alkanes since the CRC alkane workshop held in 1996.
2. To review the magnitude and sources of variation contributing to discrepancy between estimated and actual feed intake (FI), and to decide how precision can be further improved.

1. To review whether a longer-life alkane controlled-release device (CRD), or other alkane delivery system, could improve precision and/or increase the utility of this technique.
2. To identify areas of strategic research into improving the precision and utility of the technique with beef cattle.
3. To make recommendations on possible application of this technology to Beef CRC research projects.

Discussion of each objective

1. Review of progress in the measurement of pasture intake by ruminants

By 1996 experiments had shown use of alkanes could reliably produce unbiased estimates of actual feed intake. Most of this developmental research used penned sheep, penned beef cattle and dairy cows where once or twice daily dosing with synthetic alkanes in gelatine capsules could be routinely performed.

Since 1996 the use of synthetic alkanes administered by CRDs, analysed together with complementary alkanes present naturally in herbage, has become the internationally accepted method to measure pasture intake in free-ranging sheep and cattle (approximately 1,600 sheep and 1,300 cattle CRDs are sold annually). Alkanes are also being used to successfully measure supplement intake by sheep and dairy cows, and in studies of diet selection and of diet composition by sheep and undomesticated herbivores.

Two key elements to the successful application of this technique are firstly, a constant, known daily dose of synthetic alkane, and secondly, knowledge of the alkane profile of the diet consumed. The latter can be complicated in the pasture situation where an animal may choose to eat plant species and their parts in different proportions to those present. Fortunately many plants have characteristic alkane signatures that allow estimation of their contribution to the diet to be made and from this, the alkane content of the diet consumed calculated. The calculation of diet composition based on faecal alkane profiles requires knowledge of the extent of the relative recovery in faeces of alkanes present in the diet. Absolute recoveries are not needed, though they clearly would be the ideal.

Our confidence in using this methodology has matured over the past 4 years. We have learnt that, when the natural alkane profile in the consumed diet is calculated from estimated diet composition, the discrepancy between estimated and actual FI can be reduced by using better estimates of recovery and better understanding of the consequences of faecal sampling routine and the implications of errors in recovery. Further, we have learnt that the recovery curves for individual animals are similar in shape and that this is satisfactory for ratio estimates of FI and for diet composition, because relative recoveries are what is used: small systematic variation in absolute recoveries is not important. The emphasis in research has shifted from technique development to application in agricultural systems *eg* studying phosphorus and nitrogen cycling in pasture ecosystems; diet selection and understanding the basis thereof. Nevertheless, new opportunities exist for making the techniques even more useful, especially in the area of estimating diet composition.

This methodology was developed in temperate regions, using sheep and cattle grazing or being fed a monoculture or simple grass/legume mix. It has been repeatedly shown to work very well in estimating FI, supplement intake and diet composition under these conditions. Several Australian experiments have been conducted with sheep and cattle consuming such diverse diets as complex temperate pasture, high-digestibility forage, feedlot grain-ration and tropical grasses. It should not have been surprising that, for example, at the 1996 meeting we identified situations where our application of this methodology produced unusual or unexpected results. Experience has shown that if differences in alkane recoveries can be quantified then unbiased (and believable) estimates of FI obtained.

2. Precision in estimating feed intake

As mentioned above, actual intakes can be estimated without bias (*ie*. the mean of the estimated FIs = the mean of the actual FIs) but errors from various sources can result in small discrepancies between estimated and actual FIs.

Where do the errors come from:

1. Some are due to animal and plant factors that are intrinsic to the animal and production system under study, would be difficult to reduce (and perhaps should not be if a normal part of the production system under study), or are of interest themselves:
   i. Intake of food and water is not constant and can result in dilution in the rumen of the dosed alkane marker. Such inconstant intake generates diurnal variation in alkane excretion patterns of dosed compared to natural marker.
   ii. Mixing of food, water and alkane marker in rumen contents may be incomplete.
   iii. Variation between animals in diet selection, digestion, breakdown and absorption of feed and alkanes.
   iv. Variation between and within, and over time (days), in herbage alkane content, digestibility and faecal recovery of alkanes.

2. Technology-based sources of variation include:
   i. Variation in dosing of synthetic alkanes.
   ii. Errors in estimation of recovery of alkanes.
   iii. Schedule of faecal sampling is inappropriate with respect to patterns of variation in alkane marker concentration in faeces.
   iv. Sample preparation.
   v. Lab analytical technique.
   vi. Statistical procedures used to estimate diet composition.

The meeting concentrated on the technology-based sources of error, and excerpts from several presentations are appended to this report.

<u>The alkane-CRD</u>

- In extensive grazing systems, CRDs have become the preferred method for administering the synthetic alkane dose. They reduce the frequency of mustering, and hence reduce the disruption to animals' normal grazing behaviour, and also reduce the labour requirement (and hence cost) of the experiment.

- The release rate of alkane dose from the CRDs has been found to be linear in numerous studies with sheep and cattle, but the rate of release can vary slightly between diets (eg. grain-based *v* pasture) and with level of intake (*eg* maintenance *v ad libitum*). In experiments where unbiased estimates of intake are required (rather than just a ranking), the implication is that the manufacturer's stated release rate should be checked under the conditions of the specific experiment (this is also recommended by the manufacturer).

- In sheep at least, multiple CRDs in the rumen do not appear to interfere with the release rate of each other. Further, if handled with care, calibration of release rate by periodic withdrawal from the rumen of fistulated sheep and measurement of rate of plunger travel yields the same dose rate as determined from the alkane content of faeces from penned, normal (ie. non-fistulated) sheep. Thus, measurement of rate of plunger travel for multiple CRDs in the rumen of a fistulated animal (as is currently performed by the manufacturer to calibrate the devices) provides a reliable method of measuring alkane dose rate in a specific experiment. A corollary is that sequential or multiple dosing with CRDs is plausible, providing distress to the animal is avoided.

- The release rate of each CRD within a manufacturing batch is very similar, but not identical. The CV of the release rate of the same batch of CRD, measured across sheep, is typically 3%, and lower than that for cattle CRDs, typically 5%: range 3 to 9%. This CV for any given batch of CRDs is supplied by the manufacturer.

- The alkane-CRD is a commercial product resulting from a decade of research by CSIRO and Captec and is manufactured to strict QA standards. Redesign would be expensive and the likelihood of further reduction in between-device variation in a comparably priced product is probably low.

<u>Incomplete recovery of alkanes</u>

- Estimation of diet composition using alkanes is not always needed to calculate FI. In situations where the herbage being consumed is known (*eg* monoculture pasture or forage) or can be estimated (*eg* from samples of pasture being consumed by oesophageal-fistulated animals or plucked samples of pasture observed to being eaten), the alkane content of this herbage can be used in the calculation of FI.

- In more complex situations it may be useful to estimate diet composition using the alkane signatures of plants present. To facilitate this, adjustment of faecal concentrations of the different chain-length alkanes for differences in their recovery in faeces is theoretically required, though may not always be required in practice.

- Recovery in faeces of dosed and herbage alkanes increases with increasing carbon-chain lengths from about C23 to C31, then plateaus, and in beef cattle at least, perhaps begin to decline for alkanes C36 and longer. There are also at least 2 data sets with sheep indicating 'lower-than-expected' recoveries for C38 alkane. These patterns were summarised by G.Lee in 1996.

Because recovery of alkanes in the region of interest *ie* C31 to C33, and possibly C36, have plateaued, it can be possible in a "monoculture" situation (*eg* a vegetative

- winter wheat) to ignore diet composition and recoveries, and just use the ratios to estimate FI.

- Since 1996 the trend for lower and more variable recoveries of alkanes in cattle, compared to sheep, continues to be reported. Hugh Dove cautions on the use of C36 and longer alkanes in cattle studies until we understand the basis for their apparent lower and variable recovery.

- Recovery of C32 is often a little higher than expected: expected being midway between recoveries for C31 and C33. It is often closer to that for C33 and estimates of intake based on the C33:C32 pair are often more accurate than those based on the C31:C32 pair.

- Where recoveries for alkanes for a particular diet (and perhaps between animals consuming the same diet) appear a little higher or lower than expected, the recoveries for all the alkanes consumed appear to increase or decrease together. This has at least two benefits: firstly, as absolute recoveries are not needed to calculate FI, then even if recovery of both alkanes in the C33:C32 pair increase, their ratio will still yield an unbiased estimate of FI; and secondly, if you can calculate the recovery of one alkane then it may be possible to extrapolate from the form of usual recovery curve to get recovery values for the other alkanes.

Faecal sampling and sample preparation

- The importance of faecal sampling and sample preparation to the final value for alkane concentration reported has been established for a number of years but should not be overlooked.

- Diurnal patterns in the concentration of dosed alkane marker in faeces have been reported when marker dosing has been one or twice daily dosing. Such variation is much reduced using CRDs, but can still be present due to patterns of feed ingestion and water consumption. Herbage and faecal sample preparation can affect the measured alkane concentrations *eg* freeze-drying versus various oven-drying treatments, fineness of grinding especially for micro-analysis of alkanes.

Lab analytical technique

- The analytical method developed by Mayes and Dove, and now widely used, was designed for samples with alkane contents typical of temperate pasture species. It is possible that some samples containing much higher alkane loads may fail to have their alkanes completely extracted and as a consequence their content of alkane may be underestimated. This could be a problem with some tropical pasture species, and requires exploration.

- Hugh Dove suggested that it is generally good practice to analyse feed samples first, before faecal samples, as problems *eg* alkenes, contaminants, unusual concentrations of particular alkanes, often first become apparent in the feed samples. Moreover, preliminary analyses of herbage samples without the addition of internal standard can alert the analyst to situations in which the intended internal standard is naturally present in appreciable quantities in the sample (eg, unexpectedly high levels of C34 in tropical pasture species).

Statistical procedures used to calculate diet composition

- In situations where many pasture species are present it is legitimate to use any information that allows particular species to be excluded (*eg* known to be unpalatable or observed not to be grazed), or to place bounds on its dietary contribution (*eg* observed to be highly-preferred, perhaps at least 50% of DM consumed).

- There can be variation between sites, between plants within a site, within parts of a plant, and within plants over time (days). The strategy for sampling pasture will be important.

- Care is required when using shorter-chain alkanes in estimating diet composition because errors in correcting for differences in recovery are likely to be greater than for longer-chain alkanes. Avoid using herbage alkanes present at less than 10ppm in faeces as their values can have large CVs about them, and recoveries calculated for them can be very imprecise.

- There is a folklore, based on a comment in a single publication, about not using herbage alkanes present at less than 50ppm in calculations for FI, but Hugh Dove assured the meeting that this belief is wrong and that alkanes present at lower concentrations can be used and have been used in the estimation of intake.

- When it is considered necessary to estimate diet composition using alkane signatures Hugh Dove cautions that the diet should be estimated both before (without) and then after (with) adjustment for alkane recoveries to examine the sensitivity of the estimated diet composition to the use of specific values for recoveries.

- The statistical procedures commonly used to calculate diet composition are insufficient. They: (i) can fail to find unique or even sensible solutions, and (ii) the "sum-of-squares of residuals" used to measure "goodness-of-fit" is not a good enough measure of the actual error term associated with the estimate of diet composition. Better statistical methods and understanding, such as better knowledge of the factors contributing to components of variance in alkane concentrations, canonical variates or similar methods of grouping species of like alkane profiles, and understanding of error structures are needed to resolve diet composition. This is especially true if there is an intent to use data from more than one kind of wax marker, or more than one method, to estimate diet composition (see below).

- When there are more wax markers than diet components the main issue is to devise an accepted, non-arbitrary procedure for identifying which markers to use in computations.

- When there are more diet components than markers the main issues are first, the definition of error structures involved to improve techniques for combining species in groups, and second, further development of a new wax-based markers. Long chain alcohols show great promise.

- Resolution of these issues should allow us to move from measuring "diet composition" to studying "diet selection". Further, the need for and use of oesophageal-fistulated animals will be reduced.

Improving precision

- Actual intakes can be estimated without bias (*ie*. the mean of the estimated FIs = the mean of the actual FIs) but errors from various sources can result in small discrepancies between estimated and actual FIs of individual animals. Improving precision refers to reducing the errors from various sources that result in small discrepancies between estimated and actual FIs.

- In 1996 Robert Herd suggested that the CV of the difference between estimated and actual FIs was about 10% in cattle, and still believes this is about right. He suggests about half is due to the CV of 5% for alkane release rate from cattle CRDs (factor 2i above), and perhaps half from factors 2ii to 2vi above.

- If correct, the above implies that the advent of a novel marker delivery device, that could be produced in quantity to deliver an identical and known linear release rate, might reduce the CV of the discrepancy in cattle to perhaps 5%. Further reduction would require reduction in variation due to factors 2ii to 2vi.

- Hugh Dove claims the CV for this discrepancy in sheep is a little lower (5 to 10%), perhaps not surprising given that sheep CRDs typically have a lower CV in release rate (~3%). Hugh reported on an experiment he recently completed that tried to quantify the contributions to variation in estimated FI made by many of the above factors – this should be in print soon.

1. Alternate alkane delivery systems to improve precision and/or increase utility

- The following attributes for alternate alkane delivery systems were sought:
  - Longer life to facilitate measurement of feed intake over longer periods.
  - Very low, ideally zero, variation between devices.

- The currently available Captec cattle CRDs release alkane markers over 20 to 21 days. FI is typically estimated from faecal samples taken 2 or 3 times a week for two weeks, starting about one week after insertion of the CRD. Therefore FI is estimated on 4 to 6 occasions over two weeks, from the alkane content of faecal grab samples. As described above, the between-device variation in release rate has a CV of about 5%, and estimates of the discrepancy between estimated FI compared to actual FI have a CV of up to 10% in cattle.

- Captec advise that they could make a longer-life CRD: perhaps twice as long as the current devices, even longer if the daily release rate (dose) of alkane was reduced. But at a greater cost (both of the CRD and from the additional pasture and faecal samples to be analysed) and Captec emphasises that calibration and checking of the performance of such novel devices (*eg* linearity over time) would be the responsibility of the user.

- In principle, the same result *ie* a longer period of alkane dosing, could be achieved by sequential dosing with the existing CRDs. Again, at a greater cost and with greater potential for loss of data, through increased risk to the animal and from capsule failures.

- An additional concern over a longer-life CRC includes abuse through use in "changeover" experiments (*eg* used to measure FI on pasture and then on grain) can result in loss of linearity or complete failure of the capsule, giving the CRDs a bad name.

- Whilst not tested, it is difficult to envisage that use of these "longer-life" CRDs would yield estimates of FI that have less variation from actual FI than the current CRDs.

- Alternate alkane delivery systems were presented:

  - Bruce Knee described how a modified "Bunge" pig feeder had been used to accurately meter out daily small (2kg) amounts of feed pellets to cattle grazing pastures. This machine is being commercialised by a Queensland company called Agricultural Requirements, and is sold as an "Electronic Feeder".

  - Potentially naturally occurring alkanes present in the supplement could be used with diet composition methods to estimate what portion of each animal's diet consisted of these pellets. Since the quantity of pellets consumed is already known, intake of the remainder of the diet could be calculated. Depending upon the alkane profiles of the pellets and the pasture, the pellets may not need to contain synthetic alkanes. This approach has been evaluated by Hugh Dove and Bob Mayes using existing data sets, but has yet to be explicitly tested.

  - Rod Hill described an experiment that confirmed the potential for a molasses mixture to deliver synthetic alkanes to cattle. A suitable delivery system to meter out this mixture to cattle in the paddock is still to be developed.

  - The impact of the proportion of the diet that the supplement formed on the error in FI estimation, and of consequences to grazing behaviour, need to be examined.

  - Until the systems are fully developed and tested it cannot be concluded if either will offer an improvement in precision over the existing CRDs. However, if they can more accurately deliver the alkane dose/supplement to each animal, than the current CRDs, then potentially their use would yield estimates of FI that have less variation from actual FI, perhaps with a discrepancy CV closer to 5% than the 10% with the current CRDs.

  - Alternate marker delivery systems, used with a feed supplement with a distinct marker pattern as a natural marker, particularly impressed the meeting with their potential utility for measuring pasture intake over longer time periods than is currently possible with CRDs,. Further development of this method is strongly recommended for research projects requiring measurement of pasture intake.

4. Strategic research to improve precision and utility

- **A better understanding of the biological basis of incomplete recoveries of alkanes** is now needed because of their central importance for determining diet composition to accurate calculation of feed intake, and in applications studying diet selection and nutrient. Use of "generic" recovery values based on "old" recovery curves is no longer good enough. This is a major deficiency in our knowledge and must be addressed for both temperate and tropical pastures. It was clear that there is much to be learnt from conducting parallel experiments of temperate and tropical pastures.

- **Other plant markers**, especially alkenes, alcohols and fatty acids, require research and are needed because of the central importance of determining diet composition. These markers would not necessarily replace alkanes but would rather complement them.

- **Better statistical methods to resolve diet composition** are needed, such as use of variance components and canonical variates, together with a better understanding of the consequences of error structures. Resolution of these issues should allow us to move from measuring "diet composition" to studying "diet selection".

- **The use of a feed supplement as a marker**, perhaps without the need for synthetic alkanes (*eg* C32, C36), has been proposed by Bob Mayes of the UK. The principle has been shown to work in studies with penned animals. Intake of the supplement could be measured by machines as described by Bruce Knee or by inclusion of an intake marker (*eg* lithium). There will be a need to consider the amount of supplement fed relative to the amount of base diet consumed, because of possible changes to intake of the base diet (substitution; with less supplement being preferable) and consideration of errors that might increase as the amount of supplement given is reduced. On the other hand, one great value of the approach would actually be to measure substitution routinely (since it involves the estimation of both supplement and herbage intake).

- **Alternate marker delivery systems**, used with a feed supplement with a distinct marker pattern as a natural marker, particularly impressed the meeting with their potential utility for measuring pasture intake over longer time periods than is currently possible with CRDs. Further development of this method is strongly recommended for research projects requiring measurement of pasture intake.

5. Application of this technology to Beef CRC research projects

<u>Within Project 2.2 – Improving the efficiency of feed utilization</u>

The application is in genetic improvement:

i. Demonstration of the correlated benefit.
ii. Individual animal evaluation and improvement

For (i), advances in our understanding and use of alkanes CRDs mean that it should be possible to do a better job, than in CRC1, in measuring differences in pasture intake between groups of animals. One application might be demonstration of the correlated response in pasture intake and efficiency of cattle with high and low EBVs for net feed intake.

For (ii), the current alkane CRD technology is neither sufficiently accurate nor estimates FI over a sufficiently long period. Whether development of new systems that deliver marker/supplement over longer periods will also be more accurate remains to be tested. For the purpose of genetic improvement the meeting concluded that, within the life of the current CRC, the current alkane-CRD and possible new marker delivery systems were unlikely to deliver a system with sufficient accuracy for individual animal evaluation of feed intake and efficiency on pasture.

Consideration to both the size of the expected difference in mean intake between the groups evaluated as well as to the sample size of the groups will be important (*ie* the power of proposed experiments to detect a minimum difference in FI should be checked). Issues of choice of pasture, pasture and faecal sampling, diet composition, CRD calibration, recovery values, lab and data analyses will need to be addressed.

Within other CRC projects

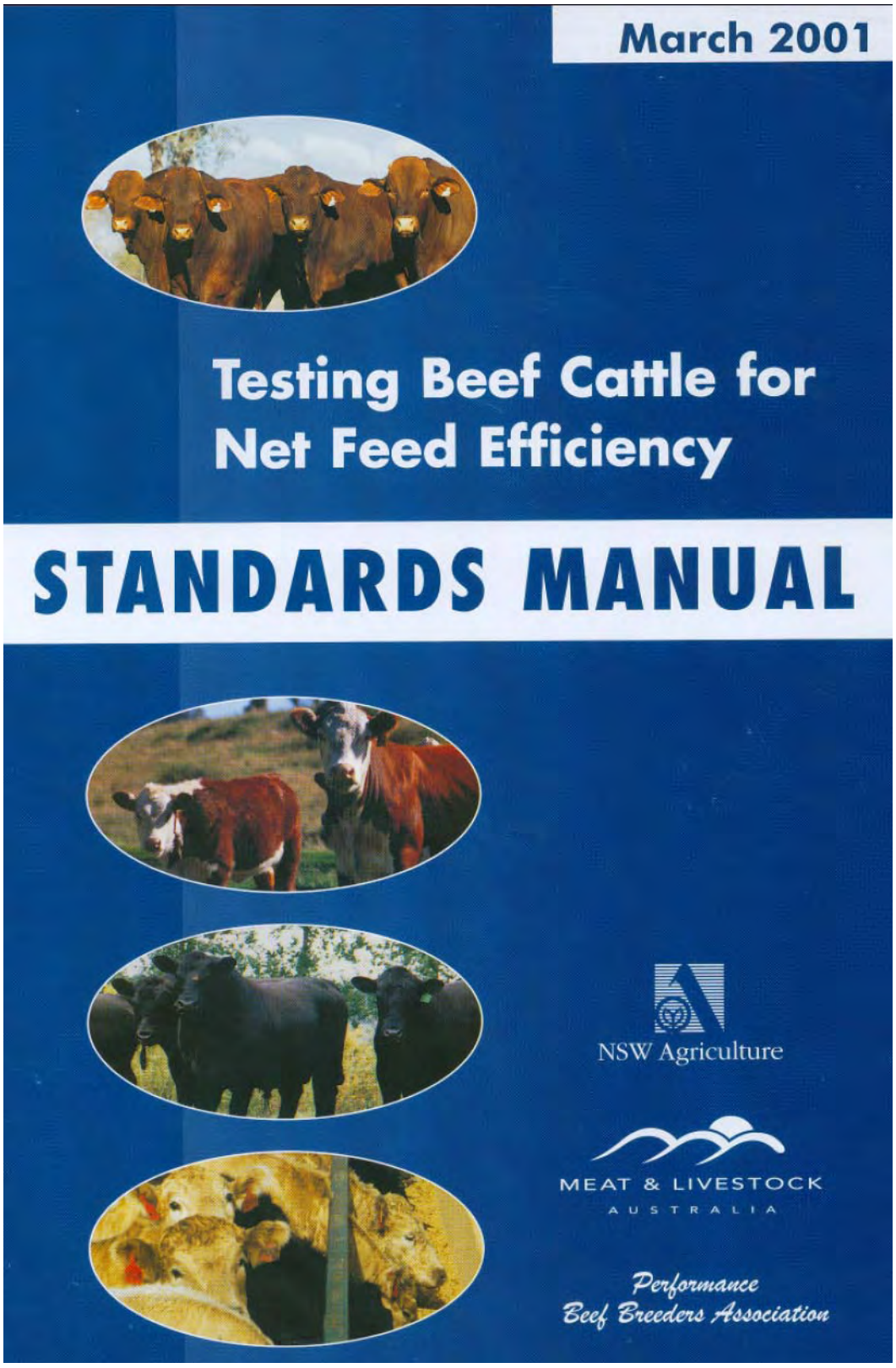
Alkane CRDs could be used in projects that need to measure pasture intake by groups of cattle. Examples might include measurement of intake and hence cost and efficiency of pasture usage in different management systems, or by different genotypes, or by cattle with different previous growth paths. The same precautions on experimental design as given above in Project 2.2 (ii) would apply.

Attachments

- Meeting program
- Presenter's overheads and slides.

- -

9.4 Appendix 4 Significant research publications


March 2001
Testing Beef Cattle for Net Feed Efficiency
STANDARDS MANUAL
NSW Agriculture
MEAT & LIVESTOCK AUSTRALIA
Performance Beef Breeders Association

Testing Beef Cattle for
NET FEED EFFICIENCY

- Standards Manual -

Steve Exton
NSW Agriculture, Trangie

This manual has been developed in conjunction with research project DAN.75, funded jointly by NSW Agriculture and Meat and Livestock Australia and conducted at Trangie Agricultural Research Centre; Research conducted by the Co-operative Research Centre for the Cattle and Beef Industry (Meat Quality) at Armidale; and a series of workshops involving key representatives from the Australian beef cattle industry.
These workshops, held at Armidale and Trangie, included representatives from:

NSW Agriculture
Performance Beef Breeders Association
Animal Genetics and Breeding Unit
Agricultural Business Research Institute
CRC for the Cattle and Beef Industry
Meat Research Corporation
Agriculture Victoria
Agriculture Western Australia
Queensland Dept. of Primary Industries
University of New England
University of Adelaide
South Australian Research & Development Institute
Angus Society of Australia
Australian Hereford Society Ltd.
Australian Poll Hereford Society Ltd.
Australian Limousin Breeders Society Ltd.
Murray Grey Beef Cattle Society Inc.
Santa Gertrudis Breeders Association
Shorthorn Society of Australia
Seedstock sector of industry
Lotfeeding sector of industry
Commercial sector of industry

Performance Beef Breeders Association

NSW Agriculture

MEAT & LIVESTOCK AUSTRALIA

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Disclaimer
The information contained in this publication is based on knowledge and understanding at the time of writing (March 2001). However, because of advances in knowledge, users are reminded to ensure that information upon which they rely is up to date and to check currency of the information with the appropriate representative of their State Department of Agriculture, the Performance Beef Breeders Association or Breed Society.

Testing Beef Cattle for NET FEED EFFICIENCY

- Standards Manual -

FOREWORD

This manual outlines the standards required for accreditation by the Performance Beef Breeders Association (PBBA) as a testing facility eligible to submit data to breed society databases for the purpose of generating BREEDPLAN Estimated Breeding Values (EBVs) for Net Feed Efficiency (NFE).

Testing animals for NFE allows for comparison of individual animals within a test group. The main objective, however, is to generate EBVs of potential sires by removing non-genetic variation as much as possible. Ideally, data from all NFE tests within and between locations should be able to be pooled for the estimation of EBVs for as many sires as possible. Standardising the test procedures within and between locations reduces non-genetic variation, and with adequate genetic linkages between tests, data from different tests can be used for estimating EBVs.

This manual contains descriptions of the various components of testing for NFE, and in many cases outlines recommendations or alternatives to the systems available. Each of the points listed as the Code of Practice for that particular section is mandatory, and must be included in the testing procedures.

It is expected that NFE tests will be conducted either "on-farm", where all animals originate from the same property, or at a "central-test" facility where animals from a number of origins are assembled at a designated location for testing under uniform conditions. The recommendations and requirements provided apply to both types of testing unless otherwise stated.

GLOSSARY OF TERMS

Accreditation	Following a successful audit in accordance with this manual, data submitted to BREEDPLAN will be accepted for calculation of EBVs.
ABRI	Agricultural Business Research Institute at University of New England (UNE) Armidale. Is responsible for data processing and commercial operation of BREEDPLAN.
AGBU	Animal Genetics and Breeding Unit at joint institute of NSW Agriculture and UNE. Is responsible for research, development and management of BREEDPLAN.
Application for accreditation	Application to PBBA to be accredited as a testing facility, accepting the requirements of the Standards Manual and outlining the procedures adopted to meet those requirements.
BREEDPLAN	The Australian genetic evaluation system for Beef Cattle. BREEDPLAN is overseen by a management committee representing Breed Societies, State Government and research bodies.
Code of Practice	The minimum requirements that have to be met in each case to achieve accreditation.
CRC	Co-operative Research Centre for the Cattle and Beef Industry (Meat Quality) with head office based at UNE and the Tropical Beef Centre at Rockhampton Queensland.
EBV	Estimated Breeding Value. A measure of an animals genetic merit for a given trait provided by BREEDPLAN.
GROUP BREEDPLAN	System providing genetic analysis and comparison across herds within a breed.
NFE	Net Feed Efficiency. Refers to the difference in animals feed intake independent of requirements for growth rate and body weight.
NFI	Net Feed Intake. The trait calculated by phenotypic adjustment of feed intake for body weight and growth as a measure of NFE.
PBBA	Performance Beef Breeders Association. A technical committee representing each of the Breed Societies that conduct annual GROUP BREEDPLAN analyses.
Test	Measurement and recording of individual animals feed intake and body weight over a specified period for the purpose of determining NFI.

CONTENTS

1. ACCREDITATION OF TESTING FACILITIES

Persons or companies wishing to gain accreditation as either an "on-farm" or "central" test facility should:

a) Notify the PBBA and the relevant Breed society or societies of their intent.

b) Complete and submit to PBBA an "Application for Accreditation" (available from PBBA or breed societies), agreeing to abide by the requirements of this manual, and outlining intended procedures in accordance with these requirements.

Acceptance of this application and subsequent accreditation as a testing facility will be at the discretion of the PBBA.

The PBBA Secretariat is currently care of the Australian Limousin Breeders Society Ltd, PO Box 262, Armidale, NSW 2350. Ph: (02) 67711648, fax: (02) 67729364. E-mail: limo@northnet.com.au.

With ongoing development of testing procedures and NFE research, periodic changes to the Standards Manual may be made. In the case of significant changes being made, an amended edition of the Standards manual will be issued to all accredited facilities. In the case of minor changes, all accredited facilities will be notified of that change. It remains the responsibility of individual managers of testing facilities to ensure that the current edition of the Standards Manual is addressed in their application for accreditation.

The purpose of the application for accreditation is to describe the system developed at that testing facility to satisfy the requirements of the Standards Manual to achieve accreditation. It is expected that the application will address the procedures, systems, resources and responsibilities that are, or will be, utilised to satisfy the accreditation requirements.

Once a facility is accredited, if changes to the testing procedures are proposed, an amended application for accreditation must be submitted to the PBBA for approval before data generated from the modified system can be accepted for BREEDPLAN analysis.

Code of Practice:

Each testing facility will submit an application for accreditation that acknowledges the requirements of this manual and outlines procedures or systems in place to satisfy each of the requirements of the Standards Manual, and which must be approved by the PBBA prior to accreditation.

The relevant sections of the application for accreditation must be assessed following notification of any changes to the Standards manual, and appropriate modifications made to the application and to testing procedures. Each modification to the application shall be recorded and an amended copy submitted to the PBBA.

2. ENVIRONMENTAL AND LEGAL RESPONSIBILITIES

Development and establishment of testing facilities may require development consent under the particular State Environmental Planning and Assessment (EP&A) Acts. Each State has different requirements and different consent authorities for different levels of development. These requirements should be available through that States Department of Agriculture or Primary Industries.

Testing facilities may be regarded as legally constituting feedlots. The National Guidelines for Beef Cattle Feedlots in Australia define a feedlot as "a confined yard area with watering and feeding facilities where cattle are completely hand or mechanically fed for the purpose of production".

Further requirements for feedlots, such as environmental protection and animal welfare are detailed in the National Guidelines for Beef Cattle Feedlots in Australia, published by the Standing Committee on Agriculture and Resource Management. Specific requirements regarding animal welfare, the Australian Code of Practice for Welfare of Cattle in Beef Feedlots, are outlined as an appendix in this document, which is available from CSIRO Publishing, PO Box 1139, Collingwood, Vic. 3066.

3. ELIGIBILITY OF ANIMALS FOR TESTING

3.1 Age

Animals can be tested from immediately post weaning until the later stages of their growth phase, usually less than two years of age. It is strongly recommended that during the initial years, tests should be conducted post-weaning, as more data is currently available and the development of EBVs will be more rapid. The range in age within a contemporary group must not exceed 60 days. (see 3.3)

3.2 Sex

Bulls, steers or heifers can be tested. Due to management difficulties with testing of mixed sex groups, and the fact that genetic improvement can be achieved faster through appropriate bull selection, it is recommended that bulls only should be tested, especially at Central Test facilities.

3.3 Contemporary Groups

Animals must be tested in contemporary groups to ensure that comparisons are made between animals which have been run under identical conditions, both for traits measured before and during the NFE test. The largest practical number of animals in a contemporary group is recommended as it will provide more comparative information per animal. In the event of an animal being withdrawn from a contemporary group after commencement of the test, data from the remaining animals should still be submitted.

Code of Practice:

A contemporary group shall consist of a minimum of four animals bred from a minimum of two sires with a minimum of two progeny per sire.

The contemporary group must adhere to the BREEDPLAN specifications provided for the trait of 400 day weight, ie: the maximum range in age is 60 days, same herd, same sex and same management since birth.

3.4 Genetic Links

Comparison between contemporary groups is based on genetic links. To ensure that adequate linkage is available between contemporary groups it is recommended that each contemporary group should include the progeny of at least one link sire. A link sire is defined as any sire which has had progeny tested for NFE in another contemporary group.

Central test facilities and/or Breed Societies should provide a list of all previously represented sires at all test stations which can be used to create linkages.

For breeds where no sires have been previously represented in a test, it is recommended that a sire represented in the CRC project be used. It is also recommended that bulls selected for testing have well balanced EBVs to increase the desirability of usage in AI programs and to therefore increase and improve linkages.

3.5 Animal Health

Health requirements are the responsibility of individual test managers and shall be specified for entry to each location in the case of Central Test facilities.

The purpose of specifying mandatory health treatments is to ensure that all animals have the ability to achieve their potential growth performance, and all animals are assessed on an equal basis.

Code of Practice:

Within a test all animals shall be subjected to identical health treatments.

All animals entering a test will have received standard health treatments that allow each animal to achieve potential growth performance in that environment.

Records of any remedial health treatments administered to individual animals must be maintained.

3.6 Mandatory Background Information

Specific background information must be recorded for all animals entering a test for data to be accepted by BREEDPLAN.

It is recommended that twins not be tested, as they must form a separate contemporary group from single born animals, as specified for BREEDPLAN contemporary groups.

Within one week of beginning testing, and before removing test animals from existing contemporary groups, the weights of all animals in that group should be recorded.

Code of Practice:

The following information will be recorded for all animals entering a test:

- *Individual animal identification*
- *Sire and Dam identification*
- *Date of Birth*
- *Whether single or twin birth*
- *Breed*
- *Sex*
- *Property of birth identification*
- *Weights of all animals from contemporary group test animal originated from.*

All animals must be recorded on BREEDPLAN, with at least a 200 day weight record available. Performance data on all animals from the same herd as the tested animals must be available so as to account for effects of prior selection of animals entering the test.

4. CONDUCT OF TEST

4.1 Allocation of Animals to Groups

A "group" may consist of any number of animals in individual pens, providing those pens are adjacent to each other and are of a similar structure, size and physical environment. In the case of the use of semi or fully automatic feeding systems, large groups may need to be sub-divided into smaller groups and placed in group pens. The allocation of individuals to group pens should be random and must be recorded.

Code of Practice:

All animals in the same group must be fed and maintained under similar physical conditions, and must be fed a ration containing ingredients from the same batch.

Bulls must be tested separately to steers and heifers. Where animals need to be fed in more than one group, they must be allocated to groups at random within age and/or weight classes, to minimise bullying when randomising animals. Contemporary groups existing prior to the test must be maintained.

4.2 Feeding System

The greatest variation across testing facilities will be in the use of alternate feeding systems. The simplest and cheapest system to develop and use is to hand feed a manually weighed ration to animals in individual pens. Alternately, different levels of automation may be incorporated, up to fully automatic and computer recorded weighing and dispensing of feed to electronically identified animals run in group pens.

Commercial feeding units that automatically weigh, dispense and record intake of individually electronically identified animals are currently being developed for purchase for "on-farm"

testing. Details on availability and suitability of these units can be obtained from Breed Societies or State Departments of Agriculture or Primary Industries Extension staff.

Cattle should have constant access to feed. In the event of a mechanical breakdown or disruption to the feeding system, strategies must be in place to enable all cattle to have access to their normal ration within 24 hours. If this feed cannot be accurately weighed or recorded to each individual animal, that days data must be excluded from the weekly feed intake summary, and this event recorded.

Code of Practice

The feeding system used must incorporate accurate measurement and recording of daily individual animal feed intake. Provision must be made to have available sufficient back-up facilities, resources, equipment and personnel to ensure that interruptions to feeding systems are minimised.

Feeding must be ad libitum throughout the test, with animals having constant 24 hour access to feed.

If changes to the feeding system prevent accurate measurement of individual feed intake for any period, for the duration of that period any data generated must be excluded from weekly feed intake summaries, and this event recorded.

4.3 Animal Identification

The animal identification system adopted must be appropriate for the feeding system used. An adequate identification system is essential to allow individual animal feed intake to be recorded and data submitted to BREEDPLAN.

Commercially available automatic feeding systems require the use of a compatible electronic animal identification system, with details available from the manufacturer.

Code of Practice

Individual animal identification in accordance with BREEDPLAN requirements must be utilised.

4.4 Ration

The ration offered must be balanced for all essential nutrients and be of suitable energy and protein levels so as not to inhibit potential animal performance and must be delivered in a format that minimises ingredient selection.

Feeding of a supplementary roughage such as straw is not a requirement, but may be provided to aid rumen function. If it is used, it must be available to all animals (free choice) at an average of not more than 0.5 kg per day per head.

Commercially available feed additives or supplements may be included in a ration to minimise health risks, to provide essential nutrients lacking in the base ration, or to ensure that the ration meets the minimum standards for metabolisable energy and crude protein, provided they are included within the manufacturers recommendations or to accepted industry standards.

Code of Practice:

The ration must be analysed for level of metabolisable energy (MJ ME/kg dry matter) and crude protein (%) by a licensed feed analysis service prior to testing and whenever there are major changes in ingredient source to ensure it falls within the acceptable range. During the test, a sample of the feed must be taken at least weekly and weekly samples bulked. The bulked samples must be analysed following the test to determine average feed composition.

Feed additives or supplements included in the ration must be recorded.

If supplementary straw is provided, it must be analysed prior to and following the test.

The ration must consist of a minimum of 9.0 MJ metabolisable energy (ME) per kg dry matter (DM), and a minimum of 14% crude protein (CP) per kg dry matter (DM).

Minimum levels for ME and CP are stipulated in the Code of Practice to ensure that potential growth rates are not restricted. It is recommended that for a postweaning test operators aim to provide a ration as close to 10 MJ ME/kg DM as possible, and for progeny tests or animals during the finishing phase, as close to 12 MJ/kg DM as possible. This will help to ensure rations used in different tests are as similar as possible, and non-genetic variation is minimised.

Care should be taken to ensure the ration is suitable for the class of stock. Young growing animals should not be fed rations containing excessive levels of energy. If a high energy finishing ration is fed for a specific test, and is achieved by inclusion of a substantial grain component (>40%), it is recommended that buffers be included in the ration and progressive increases from low to high grain content during the pre-test period be adopted.

It is strongly recommended that feed analyses performed before the commencement of test are conducted in sufficient time to modify the intended ration if there is a risk that the ration could fall outside the stipulated levels and cause data generated to be rejected.

4.5 Pre-test Adjustment Period

An adjustment period is necessary to allow all animals in the test to adjust to the ration and the environment prior to commencement of the test. Assessments should be made during this period to monitor individual feed intakes and acceptance of the diet.

If shy feeders are detected during this phase, it is recommended that they be separated from the rest of the group during the pre-test adjustment period. If substantially more than 21 days is required to ensure all animals have achieved satisfactory levels of feed intake, caution must be used to ensure that no animals reach an age unacceptable for the intended test prior to commencement of the test.

Shy feeders or poor performers may have to be excluded before the test commences.

Code of Practice:

A minimum of 21 days adjustment period will be adopted.

4.6 Test Protocol

Net Feed Intake is the trait which will be calculated by phenotypically adjusting feed intake for liveweight and gain. As such, within the duration of the test, each animal is weighed at

regular intervals to provide an average liveweight for the test and liveweight gain during the test, and the total feed intake by each animal is measured for the duration of the test.

Animals may be removed in groups from the pens where they are maintained for the purpose of conducting fortnightly weighing. All animals must be treated in a similar manner and denied access to any feed during this time.

Automatic feeding systems may incorporate automatic (continuous) weighing procedures. If these are employed, an average daily weight for the first, and each subsequent 14th day is recorded and submitted following the test. Weight records for all days should be retained for the possibility of further analysis being required.

During the test period, it is strongly recommended that animal performance be monitored by way of regular checks. Sick animals may have to be removed from the test.

Faulty equipment, causing loss of reliable data, such as feeding units, scales or identification systems may also be detected in time to allow repairs before the test is invalidated. It is strongly recommended that a back-up power source and spare or reserve weighing, recording and computing requirements are available for emergency use.

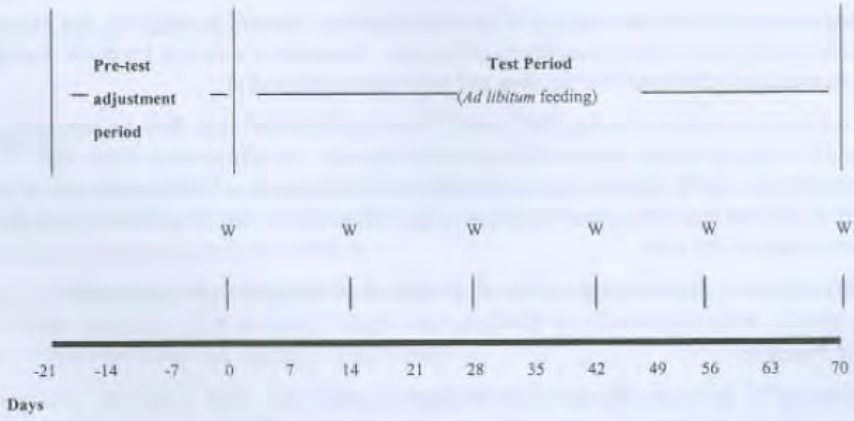
Code of Practice:

The duration of the test must be for a minimum of 70 days on a constant ration. A maximum total of 7 days when data is not recorded within a maximum 77 day period is allowable for the duration of the test.

Animals must be weighed at the start of the test and at least every fortnight thereafter. Animals must not be fasted before weighing.

Figure 1: Time Scale for NFE Test

*(**W** represents days on which animals are weighed)*



4.7 Data Collection and Recording

Records must be taken and stored in a format appropriate to the individual tests.

Code of Practice:

Provision must be made to have available adequate back-up facilities or resources to ensure that interruptions to data collection or recording are minimised.

The following records are required for each animal:

- *Mandatory background information specified previously.*
- *Weighing dates and individual animal weights as specified. If automatic (continuous) weighing is used, an average daily weight for each of the fortnightly weight dates (section 5.6) need to be recorded.*
- *Feed intake data (including supplementary roughage where applicable). Minimum requirement is total feed intake per animal per week.*
- *Feed analysis results - including date of analysis, laboratory, ME, CP and roughage as specified previously.*
- *Feed additives or supplements included in the ration.*
- *Details of interruptions to data collection or recording.*
- *All health treatments administered, and details of sick animals.*
- *Individual pen or group pen for each animal.*

5. DATA INPUT SPECIFICATIONS

To calculate NFI, and ultimately BREEDPLAN EBVs for NFI, data must be loaded onto centralised databases. This will happen in a two-step process.

1. Detailed data from a feed intake test will be loaded onto a database maintained by NSW Agriculture at Trangie. The data will be checked for compliance to test requirements, and will be processed into a summarised form. Reports of results from individual animals will be produced, and sent to the test station submitting the data.

2. A summarised form of the feed intake result will be sent to ABRI for loading onto the NBRS database. This data will be used to calculate BREEDPLAN EBVs for NFI when these become available.

Code of Practice:

Only data submitted electronically in a specified format will be accepted for loading onto the Trangie database. Files should be submitted in a spreadsheet format compatible with Microsoft Excel 97. Most spreadsheet packages are able to save files in a format able to be read by Excel. If this is not possible, data should be saved in a "comma separated variable" format (filename.csv), where columns are delimited by commas. Four sheets must be submitted, named "test", "animal", "intake" and "weight". Where possible, these sheets should be contained within a single workbook, and the file should be named by the test station code - year - test number combination (ie. the first 3 fields of the test sheet).

Once in the correct format, the data file should be sent on disc (PC format) to NFI Testing, NSW Agriculture, PMB 19, Trangie NSW 2823 or e-mailed to nfi@agric.nsw.gov.au *with subject heading "NFI data". A copy of the ration analysis report should be sent or faxed to*

02 6888 7201. Data will not be processed until the ration analysis report is received. Contact details should be supplied so that receipt of the data and ration analysis report can be acknowledged.

The formats for the four sheets are described below. Example sheets containing data in the correct format for submission are also given. The data used in the example have been altered for demonstration purposes in some instances.

NSW Agriculture will endeavour to process the data within a maximum of 10 working days of receiving the data in the correct format. The processed data will be forwarded to ABRI for loading on the NBRS database. As with other data submitted to BREEDPLAN, a charge will apply for loading onto the NBRS database, and ABRI will invoice the breeder or test station manager for this work. NSW Agriculture will notify the test station manager once the data has been sent to ABRI, and a report on phenotypic performance of the animals will be sent.

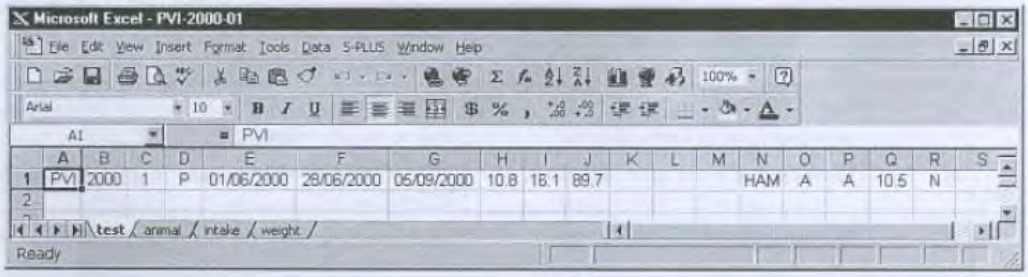
5.1 Test Sheet

This sheet contains information specific to each test (defined as a group of animals fed using the same ration and feeding system at the same time). The sheet should contain one row of information laid out as follows.

Column	Field Name	Format	Description
A	Test Station	3 Character code (Upper Case). Eg "PVI"	Code assigned to the test station at which the test was conducted. This code will be supplied when accreditation is gained.
B	Test Year	Integer. Eg. "2000"	Year in which the test started.
C	Test Number	Integer. Eg. "1"	Number of the test started that year (1 to 99, assigned by station manager). The columns Test Station, Year and Number combined must define a unique test.
D	Test Type	1 Character. Eg. "P"	P = post-weaning (generally used for bulls on lower energy diets); or F = finishing (generally used for steers measured on feed-lot rations).
E	Pre-test Date	dd/mm/yyyy Eg. 01/06/2000	Date animals entered test facility and started pre-test adjustment period.
F	Start Date	dd/mm/yyyy	Date the test period started.
G	End Date	dd/mm/yyyy	Date the test period finished.
H	Ration ME	Number rounded to 1 decimal place. Eg. "10.8"	Metabolisable Energy content of the test ration (in MJ ME/kg Dry Matter).
I	Ration Protein	Number rounded to 1 decimal place. Eg "16.1"	Protein content of the test ration (in %)
J	Ration Dry Matter	Number rounded to 1 decimal place. Eg "89.7"	Dry Matter content of the ration (in %)
K	Supplement Quantity	Optional. Number rounded to 1 decimal place. Eg "0.5"	Quantity of supplement (eg. straw) fed to maintain rumen function (kg per head per day). Can be left blank if no supplement fed.

L	Supplement ME	Optional. Number rounded to 1 decimal place. Eg. "5.1"	Metabolisable energy content of the supplement (MJ ME/kg DM). Can be left blank if no supplement fed.
M	Supplement Dry Matter	Optional. Number rounded to 1 decimal place. Eg "98.7"	Dry Matter of the supplement (%). Can be left blank if no supplement fed.
N	Laboratory Code	3 Character code (Upper Case). Eg "HAM"	Code for laboratory providing ration analysis. HAM = Feedtest, Hamilton, Victoria; AGT = Agritech, Toowoomba, Queensland.
O	Method for Intakes	1 Character. Eg "A"	A = Automated measurement; M = Manual Measurement.
P	Method for weights	1 Character. Eg "A"	A = Automated measurement; M = Manual Measurement.
Q	Animals per pen	Number to 1 decimal place. Eg "10.5"	Average number of animals per pen.
R	Combine Pens for analysis	1 Character. Eg "Y"	Whether test manager believes that animals can be compared across pens (Y=Yes; N=No).

The *test* sheet should look something like this:



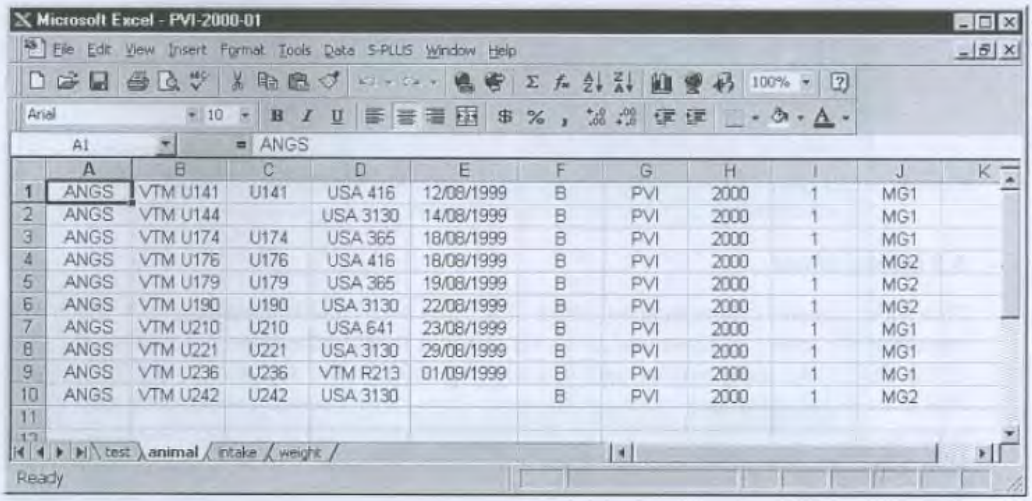
Note that where optional data is not given (eg. For fields describing the supplementary ration, where no supplementary ration was fed), the relevant column is left empty.

5.2 Animal Sheet

This sheet contains information specific to each animal within the test. Each animal should be represented by one row.

Column	Information	Format	Description
A	Breed	Up to 5 Characters (upper case). Eg "ANGS"	Code to describe breed society the animal is registered by. The code must match codes used by the NBRS database (see table below).
B	Ident	Up to 19 characters (upper case). Eg "VTM U141"	The Breed Society ident of the animal. This *must match exactly* the ident of the animal on the NBRS database (including spaces) if present, so that BREEDPLAN can match the record with other performance and pedigree information. Breed and Ident columns together define a unique animal.
C	Tag	Optional. Up to 20 characters. Eg "U141"	A tag or name to refer to the animal – useful for telephone queries regarding animal where Breed Society uses a numerical ident system.
D	Sire Ident	Optional. Up to 19 characters (upper case). Eg "USA 416"	The Breed Society ident of the animal's sire (used to verify animal identification on NBRS database).
E	Birthdate	Optional. dd/mm/yyyy Eg "12/08/1999"	Date of birth of the animal (Optional – used to verify animal identification on NBRS database).
F	Sex	1 Character. Eg "B"	B=Bull; H=Heifer; S=Steer
G	Test Station	3 Character code (Upper Case). Eg "PVI"	3 Character test station code, matches to test station field in *test* information.
H	Test Year	Integer. Eg. "2000"	Year at start of test, matches to year field in *test* information.
I	Test Number	Integer. Eg. "1"	Number of test, matches to test number field in *test* information.
J	Management Group	3 Character description of management groups. Eg "MG1"	Field used by test station manager to identify separate management groups *during* the test which are treated differently and shouldn't be directly compared. Management groups imposed prior to the test will be determined by BREEDPLAN using contemporary group information on the most recent weight prior to entering the test.

The *animal* sheet should look something like:



	A	B	C	D	E	F	G	H	I	J
1	ANGS	VTM U141	U141	USA 416	12/08/1999	B	PVI	2000	1	MG1
2	ANGS	VTM U144		USA 3130	14/08/1999	B	PVI	2000	1	MG1
3	ANGS	VTM U174	U174	USA 365	18/08/1999	B	PVI	2000	1	MG1
4	ANGS	VTM U176	U176	USA 416	18/08/1999	B	PVI	2000	1	MG2
5	ANGS	VTM U179	U179	USA 365	19/08/1999	B	PVI	2000	1	MG2
6	ANGS	VTM U190	U190	USA 3130	22/08/1999	B	PVI	2000	1	MG2
7	ANGS	VTM U210	U210	USA 641	23/08/1999	B	PVI	2000	1	MG1
8	ANGS	VTM U221	U221	USA 3130	29/08/1999	B	PVI	2000	1	MG1
9	ANGS	VTM U236	U236	VTM R213	01/09/1999	B	PVI	2000	1	MG1
10	ANGS	VTM U242	U242	USA 3130		B	PVI	2000	1	MG2
11										
12										

Table 1. Breed Society Codes

Australian Societies

ABBA	Brahman	ABS	Braford
ADA	Dexter	AHS	Hereford
ANGS	Angus	APHS	Poll Hereford
ARPS	Red Poll	ASBA	Simmental
BDAQ	Blonde d'Aquitaine	BELG	Belgian Blue
BORA	Boran	BR	Belmont Red
BSSA	Beef Shorthorn	CHAR	Charolais
CHIA	Chianina	DEVN	Devon
DSBS	Droughtmaster	GCSA	Galloway
GELB	Gelbvieh	LIMO	Limousin
LOWL	Lowline	MA	Maine Anjou
MG	Murray Grey	OSBA	Braunvieh
PIED	Piedmontese	QBRA	Brangus
RANG	Red Angus	RBS	Romagnola
SALR	Salers	SANTA	Santa Gertrudis
SDEV	South Devon	SSA	Shorthorn
TULI	Tuli	WAGY	Wagyu

New Zealand Societies

NZAA	Angus	NZHA	Hereford
NZLM	Limousin	NZMA	Maine Anjou
NZMG	Murray Grey	NSAL	Salers
NZSD	South Devon	NZSH	Shorthorn
NZSM	Simmental		

Contact ABRI (02 6773 3555) if you need a code for a Society that is not listed.

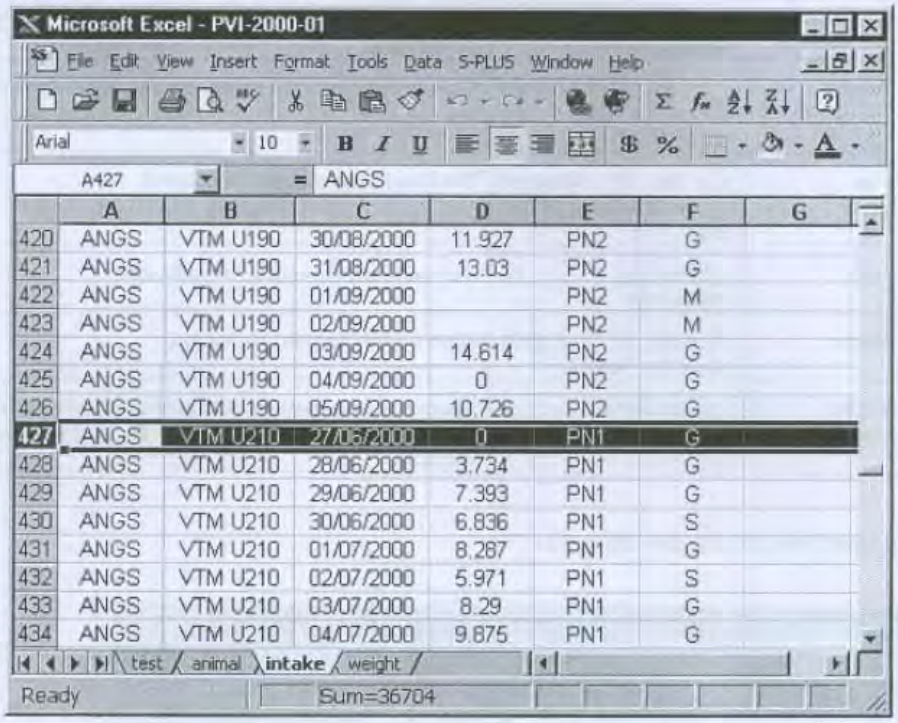
5.3 Intake Sheet

This sheet contains information on intake of animals over periods during the test. Each row represents the intake of the animal since the previous intake information. To define the start of the first intake measurement period, a row representing the day prior to the test starting should be included for each animal, with intake set to zero. A code accompanying each intake must be submitted to indicate whether the data is good, suspect or missing (due to problems with data collection). Only periods where information is "good" will be analysed. However it is important that a row is submitted even for instances where the information is suspect or missing, so that this period of time can be excluded when average daily intake of the animal is calculated. Zero intakes should be examined and given a code for "good" if the animal genuinely did not eat for that period, or a code for "missing" should be assigned if the animal did eat but data was lost.

Intakes can be submitted as frequently as daily (1 day periods), or as infrequently as fortnightly (14 day periods). Where possible, data should be submitted in shorter periods (ideally daily), so that suspect or missing data for an animal on one day does not lead to unusable data for the animal for a whole fortnight.

Column	Information	Format	Description
A	Breed	Up to 5 Characters (upper case). Eg "ANGS"	Code to describe breed society the animal is registered by.
B	Ident	Up to 19 characters (upper case). Eg "VTM U210"	The Breed Society ident of the animal.
C	Date	dd/mm/yyyy Eg 28/06/2000	Date at the end of the intake period.
D	Intake	Number to 3 decimals. Eg "3.734"	Intake of the animal (kg feed freshweight). Can be set to zero or left blank if data is missing for a period, but a row should still be loaded for the period.
E	Pen Number	3 Characters. Eg "PN1"	Optional. Number of the pen the animal was in.
F	Data Quality	1 Character. Eg "G"	Code to describe data quality. G = Good data; S = Suspect data; M = Missing data.

The *Intake* sheet should look something like:



	A	B	C	D	E	F	G
420	ANGS	VTM U190	30/08/2000	11.927	PN2	G	
421	ANGS	VTM U190	31/08/2000	13.03	PN2	G	
422	ANGS	VTM U190	01/09/2000		PN2	M	
423	ANGS	VTM U190	02/09/2000		PN2	M	
424	ANGS	VTM U190	03/09/2000	14.614	PN2	G	
425	ANGS	VTM U190	04/09/2000	0	PN2	G	
426	ANGS	VTM U190	05/09/2000	10.726	PN2	G	
427	ANGS	VTM U210	27/06/2000	0	PN1	G	
428	ANGS	VTM U210	28/06/2000	3.734	PN1	G	
429	ANGS	VTM U210	29/06/2000	7.393	PN1	G	
430	ANGS	VTM U210	30/06/2000	6.836	PN1	S	
431	ANGS	VTM U210	01/07/2000	8.287	PN1	G	
432	ANGS	VTM U210	02/07/2000	5.971	PN1	S	
433	ANGS	VTM U210	03/07/2000	8.29	PN1	G	
434	ANGS	VTM U210	04/07/2000	9.875	PN1	G	

Note that intake on day before the first test day is set to zero. This will be interpreted as stating that the first data collection period started at the end of 27/06/2000. The next row (row 428) therefore is interpreted as stating that the intake of VTM U210 from 27/06/2000 to 28/06/2000 (ie. one day) was 3.734 kg.

Data from periods where the quality code (column F) is "S" or "M" will not be used when the overall intake is calculated, but must still be included so that the correct daily intake can be calculated. For example, the data from VTM U210 on 30/06/2000 (row 430) will not be used to calculate intake, but must still be included so that the period for the subsequent row of data will be correctly calculated as 1 day. If row 430 was omitted, the calculation would (incorrectly) assume that the next intake (8.287 kg) was the intake from 29.06/2000 to 01/07/2000, a period of 2 days.

For days where an animal genuinely had zero intake, this should be recorded as zero (not left blank), and the data quality code set to "G" to indicate that the zero is the correct intake. For example, see the intake for VTM U190 on 04/09/2000 (row 425) in the sheet above.

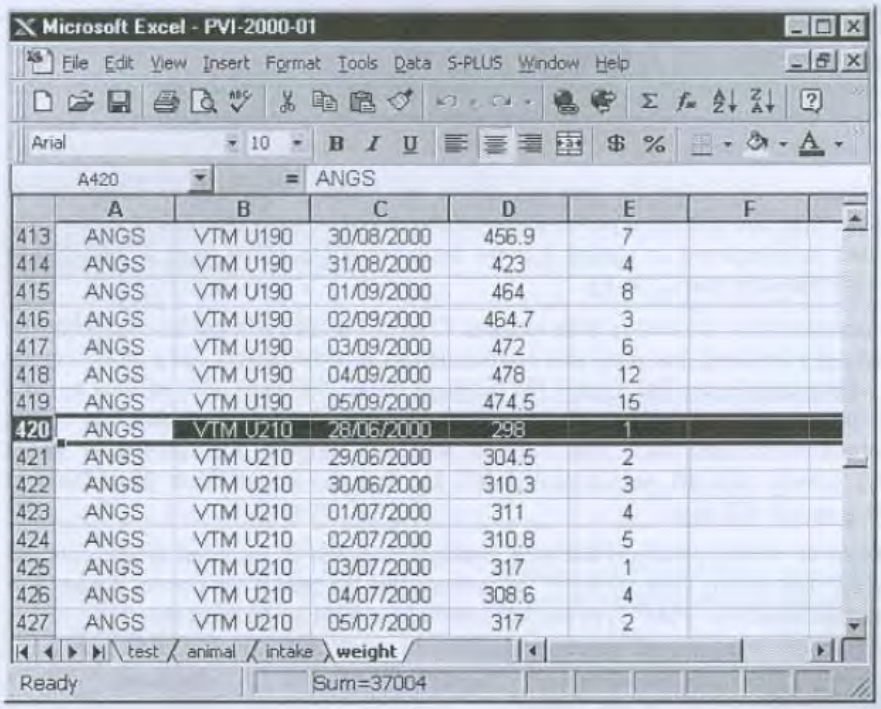
5.4 Weight Sheet

This sheet contains information on liveweight of the animal. Daily. weekly or fortnightly weights can be submitted. Where weights are collected automatically and several weights are available for each day, the mean weight for each day should be submitted, along with how

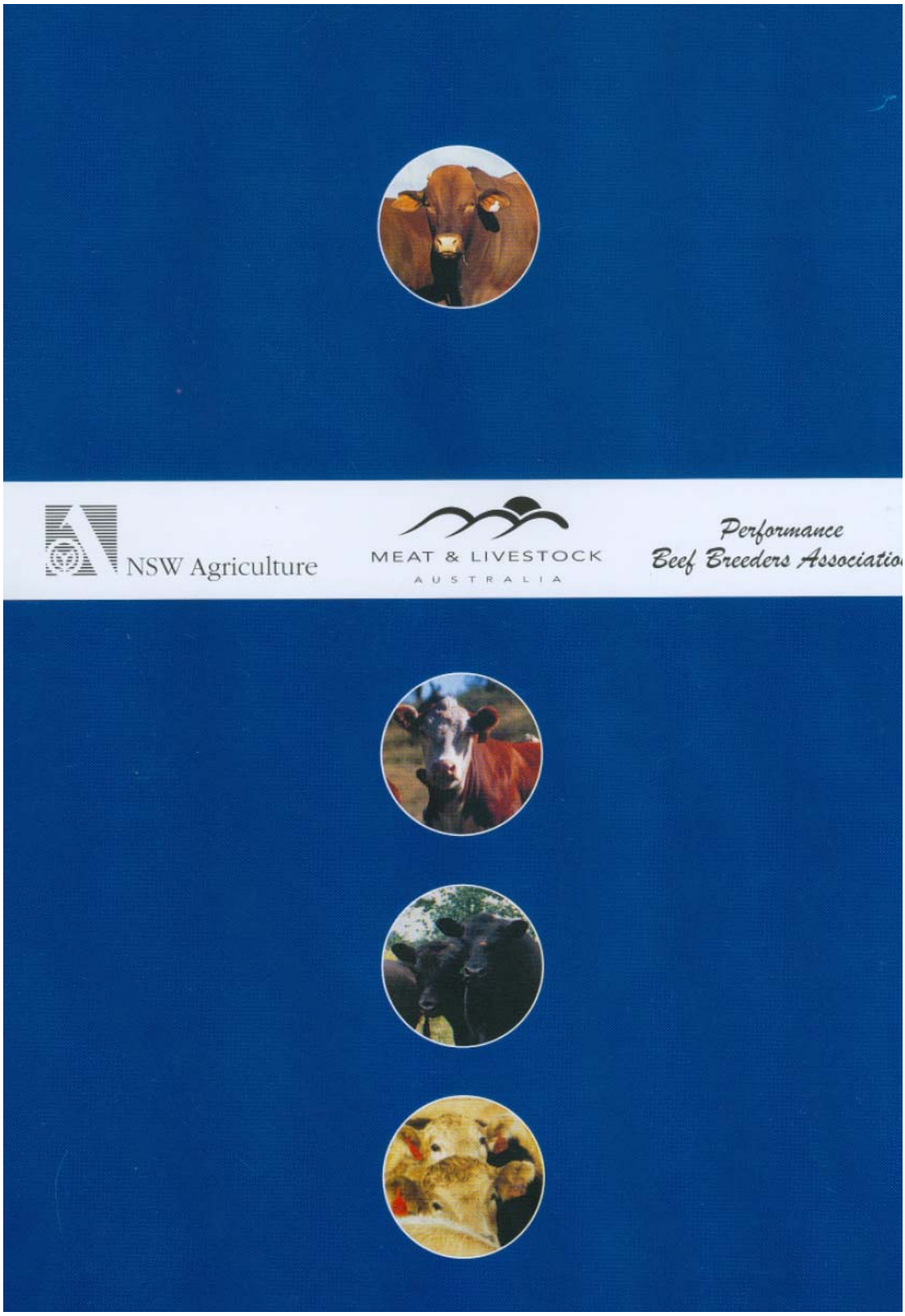
many individual weights the mean represents. If a weight is missing, no row should be submitted for that animal on that day.

Column	Information	Format	Description
A	Breed	Up to 5 Characters (upper case). Eg "ANGS"	Code to describe breed society the animal is registered by.
B	Ident	Up to 19 characters (upper case). Eg "VTM 210"	The Breed Society ident of the animal.
C	Date	dd/mm/yyyy Eg 29/06/2000	Date on which the weight was collected.
D	Weight	Number to 1 decimal place. Eg "304.5"	Mean weight of animal on that date.
E	Number of Records	Integer. Eg "2"	Number of individual weights used to calculate mean weight. Set to "1" where animals are weighed once manually.

The *weight* sheet should look something like:



	A	B	C	D	E	F
413	ANGS	VTM U190	30/08/2000	456.9	7	
414	ANGS	VTM U190	31/08/2000	423	4	
415	ANGS	VTM U190	01/09/2000	464	8	
416	ANGS	VTM U190	02/09/2000	464.7	3	
417	ANGS	VTM U190	03/09/2000	472	6	
418	ANGS	VTM U190	04/09/2000	478	12	
419	ANGS	VTM U190	05/09/2000	474.5	15	
420	ANGS	VTM U210	28/06/2000	298	1	
421	ANGS	VTM U210	29/06/2000	304.5	2	
422	ANGS	VTM U210	30/06/2000	310.3	3	
423	ANGS	VTM U210	01/07/2000	311	4	
424	ANGS	VTM U210	02/07/2000	310.8	5	
425	ANGS	VTM U210	03/07/2000	317	1	
426	ANGS	VTM U210	04/07/2000	308.6	4	
427	ANGS	VTM U210	05/07/2000	317	2	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Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle[1,2]

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ABSTRACT: 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 d at the start of the performance test, which comprised 21-d adjustment and 70-d test periods. Traits studied included 200-d weight, 400-d weight, scrotal circumference, ultrasonic measurements of rib and rump fat depths and longissimus muscle area, ADG, metabolic weight, daily feed intake, feed conversion ratio, and residual feed intake. For all traits except the last five, additional data from the Angus Society of Australia pedigree and performance database were included, which increased the number of animals to 27,229. Genetic (co)variances were estimated by REML using animal models. Direct heritability estimates for 200-d weight, 400-d weight, rib fat depth, ADG, feed conversion, and residual feed intake were 0.17 ± 0.03, 0.27 ± 0.03, 0.35 ± 0.04, 0.28 ± 0.04, 0.29 ± 0.04, and 0.39 ± 0.03, respectively. Feed conversion ratio was genetically (r_g = 0.66) and phenotypically (r_p = 0.53) correlated with residual feed intake. Feed conversion ratio was correlated (r_g = –0.62, r_p = –0.74) with ADG, whereas residual feed intake was not (r_g = –0.04, r_p = –0.06). Genetically, both residual feed intake and feed conversion ratio were negatively correlated with direct effects of 200-d weight (r_g = –0.45 and –0.21) and 400-d weight (r_g = –0.26 and –0.09). The correlations between the remaining traits and the feed efficiency traits were near zero, except between feed intake and feed conversion ratio (r_g = 0.31, r_p = 0.23), feed intake and residual feed intake (r_g = 0.69, r_p = 0.72), and rib fat depth and residual feed intake (r_g = 0.17, r_p = 0.14). These results indicate that genetic improvement in feed efficiency can be achieved through selection and, in general, correlated responses in growth and the other postweaning traits will be minimal.

Key Words: Beef Cattle, Feed Conversion Efficiency, Genetic Parameters, Growth

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Introduction

Profitability of beef production depends on both inputs and outputs. In the past, genetic improvement has been aimed mainly at output traits such as fertility and live weight, and more recently carcass and meat quality traits, with little emphasis placed on reducing inputs. Providing feed to cattle is the single largest expense in most commercial beef production enterprises, and thus any effort at improving the efficiency of feed use will help reduce input costs. In beef cattle, attempts at genetic improvement of feed use have been based on feed conversion ratio, which is the amount of feed consumed divided by live weight gain. Although there are a number of published studies on feed conversion ratio, those that deal with the genetics of the trait are limited and are based on relatively small numbers of animals. Koots et al. (1994a,b) summarized the published estimates.

Feed cost for maintenance is estimated to represent at least 60 to 65% of the total feed requirements for the cowherd, with considerable variation among individual animals independent of their body size (Montaño-Bermudez et al., 1990; Parnell et al., 1994). Koch et al. (1963) proposed residual (net) feed intake as an alter-

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nate measure of feed efficiency. It is the difference between actual feed intake and the expected feed requirements for maintenance of body weight and some measure of production (such as growth in beef cattle or milk production in dairy cattle). There is some evidence of genetic variation in residual feed intake, as indicated in the review by Archer et al. (1999). However, the evidence is also based on few studies, most of which had relatively small numbers of animals.

The objective of this study was to provide genetic and phenotypic variance and covariance estimates for feed intake, feed efficiency, and other postweaning traits and to examine the interrelationships among these traits in young Angus cattle.

Materials and Methods

Animals, Management, and Test Protocols

In 1993, a research project was begun at the Agricultural Research Centre, Trangie, NSW, Australia to investigate the potential for genetic improvement in postweaning feed efficiency as a means of improving whole beef production system efficiency in feed utilization. The design of the main project was described in detail by Arthur et al. (1996). In this study, a total of 1,180 animals from nine groups tested for postweaning feed efficiency were used. Animals from groups 1, 3, 5, and 7 consisted of bulls and heifers that were progeny of the Angus cowherd at the research center, with the majority (all of groups 1 and 3 and most of group 5 and 7) sired by Angus bulls obtained from the industry. The Angus cowherd had been selected over 17 yr for growth (Parnell et al., 1997) and cows from only the control and high growth rate lines were used. The animals tested were born in winter/spring of 1993 to 1996 and were tested for feed efficiency in the autumn of the following year. Some animals in groups 5 and 7 were sired by bulls selected for high or low residual feed intake. Animals from groups 8 and 9 were also born at the research center and consisted of Angus bulls and heifers and were progeny of sires that had been divergently selected for high or low residual feed intake and females, some of which had been selected for residual feed intake. These animals were born in the winter/spring of 1997 and 1998 and were tested for efficiency in the autumn the following year. All the animals born at Trangie were managed as similarly as possible, except the 1996-born calves that were raised from birth to weaning in three separate management groups (mgt group). Animals from groups 2, 4, and 6 were all heifers that were purchased from industry herds after weaning. These animals were fully pedigreed and approximately seven progeny per sire were purchased. They were born in the autumn of 1994 to 1996 and were brought to Trangie and tested in spring the same year.

Feed intake was measured for each animal using an automated feeding system, developed and located at the research center. The feeding system is housed in a shed with the long (east and west) sides open, to provide access to 10 feeding stalls on each side, where the animals were kept in large outdoor pens. Each animal was fitted with an electronic ear tag (transponder) and animals on either side of the shed (maximum 100 animals per side) had access to any of 10 feeding stalls. The animals were brought to the testing facility a few weeks (generally 4 to 6 wk) after weaning. At the testing facility, a pretest adjustment period of at least 21 d was allowed for the animals to adapt to the feeding system and diet. The average age at the start of test was 268 d (± 23 d, SD). For test groups 1 to 7, the adjustment period was followed by a 120-d test. Based on the recommendations by Archer et al. (1997), a 70-d test was instituted for groups 8 and 9. For this study, the efficiency test traits for all groups have been recalculated using only data from the first 70 d of the test.

During the test, animals had ad libitum access to a pelleted diet composed of 70% alfalfa hay and 30% wheat plus monensin, vitamins, and mineral supplements. This diet had an average energy content of 10.5 MJ metabolizable energy (ME) per kilogram dry matter and 15 to 17% crude protein. Straw was provided at an average of 0.5 kg per animal per day. All animals were weighed weekly, and ultrasonic measurement of 12/13th rib fat depth, P8 fat depth, and area of the longissimus muscle between the 12th and 13th ribs were taken at the start and end of test. Measurement of fat depth at the P8 site is a common practice in Australia. The P8 site is located at the intersection of an imaginary line drawn from the dorsal tuberosity (*tuber ischii*) parallel to the sawn chine and another imaginary line drawn at 90° to it, starting at the spinus process of the third sacral vertebra (Arthur et al., 1995). The scrotal circumference of bulls was measured near the end of the test.

Traits Studied

The traits studied were 200-d weight, 400-d weight, scrotal circumference for bulls, ultrasound measurements of 12/13th rib fat depth, P8 fat depth, longissimus muscle area, ADG during the test period, metabolic weight at the midpoint of the test period, daily feed intake, feed conversion ratio, and residual feed intake. The growth of each animal during the test was modeled by linear regression of weight on time (d) using SPLUS (MathSoft, Seattle, WA), and the regression estimates were used to calculate ADG (the regression coefficient) and weight at start and end of test. The mean weight (**MWT**) of an animal during the test was computed as the average of the start and end of test weights. Metabolic body weight was calculated as $MWT^{0.73}$. Feed intake was calculated by adding the daily energy intake of the pelleted ration and straw and then adjusted to a common concentration of 10 MJ ME/kg dry matter. Feed conversion ratio was calculated as feed intake divided by ADG. Using SPLUS, a linear regression model of feed intake on metabolic weight and ADG,

with test group and sex included as class variables, was fitted to data for groups 1 to 7. The regression coefficients from this model were used to predict feed intake of all animals, including groups 8 and 9. Residual feed intake was calculated as the actual (measured) feed intake minus that predicted using the regression equation.

Additional performance and pedigree data from the Angus Society of Australia's pedigree and performance database were used in the genetic parameter estimation. The additional data were included to account for any selection based on estimated breeding values (EBV) that may have occurred in the sampling of sires used to generate progeny for feed intake measurements. To restrict the amount of this data, only performance records from herds that had ultrasound scan records and large contemporary groups (greater than 15 records for 400-d weight) were used. In addition, only two generations of pedigree for each animal with a record were used.

Statistical Analyses

Genetic variances and covariances were estimated by REML using VCE4.2.5 (Groeneveld and Garcia-Cortes, 1998) and ASREML (Gilmour et al., 1996). Data were analyzed in a series of trivariate animal models and 400-d weight was always included as one of the three traits. The first series of trivariate analyses included each pairwise combination of the five feed intake-related traits (feed intake, feed conversion, residual feed intake, ADG, and metabolic weight). The model included fixed contemporary group effect, random additive genetic and residual effects, and linear covariate for age. In all analyses, 400-d weight was included as the third trait and was modeled with a random additive genetic and residual component and a fixed contemporary group effect. All 400-d weight records were preadjusted for age and age of dam, using standard BREEDPLAN (Graser et al., 1995) adjustments. For the feed intake traits, contemporary group was defined as all animals from the same herd‖sex‖test group‖mgt group subclass. Contemporary group for 400-d weight for animals from the feed intake group was defined as above. However, for the 400-d weight records from the Angus Society database, the contemporary group was as defined for a BREEDPLAN analysis (Graser et al., 1995).

The second series of trivariate analyses included pairwise combinations of feed intake, feed conversion ratio, and residual feed intake with the other production traits (scrotal circumference, rib fat depth, P8 fat depth, and longissimus muscle area). Fixed effects for feed intake, feed conversion ratio, and residual feed intake were as modeled previously. The production traits included a fixed contemporary group effect and were preadjusted for age and age of dam (Howarth and Johnston, 1995). The third trait included in all analyses was 400-d weight and was modeled with a random genetic additive and residual component and a fixed contemporary group effect. All 400-d weight records were preadjusted for age and age of dam.

The third series of trivariate analyses included pairwise combinations of feed intake, feed conversion ratio, and residual feed intake with 200-d weight and 400-d weight when it was necessary to construct different random effects to model direct (-d) and maternal (-m) effects. The random effects included were sire × herd interaction and additive genetic, additive maternal, and permanent environmental variances for both 200-d weight and 400-d weight. The sire × herd interaction was included based on studies by Robinson (1996) and Meyer (1997) that showed the importance of this effect on maternally influenced traits.

Table 1. Number of animals with records, mean, and standard deviation (SD) of the traits studied

Trait				
Full name	Abbreviation	Number	Mean	SD
200-d weight, kg	200dWT	26,030	241.71	37.46
400-d weight, kg	400dWT	27,229	370.36	71.08
Scrotal circumference, cm	SC	7,260	35.15	2.87
12/13th rib fat depth, mm	RIBFAT	26,892	4.15	2.16
Rump P8 fat depth, mm	P8FAT	27,010	5.44	3.02
Longissimus muscle area, cm^2	EMA	26,791	67.59	13.74
Average daily gain, kg d	ADG	1,180	1.26	0.24
Metabolic mid-weight, kg	MMWT	1,180	68.77	8.18
Daily feed intake, kg	FI	1,180	9.65	1.33
Feed conversion ratio	FCR	1,180	7.79	1.35
Residual feed intake, kg d	RFI	1,177	0.05	0.74

Results

Descriptive statistics of the traits studied are presented in Table 1. It should be noted that for feed conversion ratio and residual feed intake lower values indicate greater efficiency. The additive genetic variances and heritability estimates of the traits are presented in Table 2. The minimum and maximum values for the series of trivariate analyses indicate that, for a particular trait, the additive variances were relatively stable from one analysis to the other. Direct heritability estimates for all the traits were moderate and ranged from 0.17 for 200-d weight to 0.43 for scrotal circumference. Maternal heritability estimates were 0.13 and 0.04 for 200-d weight and 400-d weight, respectively.

Genetic and phenotypic correlations among feed efficiency and their component traits are presented in Table 3. Metabolic body weight and ADG were correlated with each other and with feed intake, both genetically (r_g) and phenotypically (r_p). Feed intake was correlated with both feed efficiency traits but was more strongly correlated with residual feed intake (r_g = 0.69) than with feed conversion ratio (r_g = 0.31). By definition, residual feed intake should not be phenotypically correlated with its component traits, and the results confirmed this. In addition, the results show that residual

Table 2. Additive variance and heritability (± SE) for postweaning traits

	Additive variance[b]			
Trait[a]	Mean	Minimum	Maximum	Heritability
200dWT-d	70.9	69.0	72.2	0.17 ± 0.03
200dWT-m	54.9	53.1	55.7	0.13 ± 0.02
400dWT-d	211.5	207.4	216.5	0.27 ± 0.03
400dWT-m	30.8	28.6	32.9	0.04 ± 0.01
SC	2.00	1.99	2.01	0.43 ± 0.06
RIBFAT	0.47	0.47	0.47	0.35 ± 0.04
P8FAT	1.04	1.04	1.04	0.38 ± 0.03
EMA	8.61	8.59	8.64	0.27 ± 0.04
ADG	0.0076	0.0075	0.0076	0.28 ± 0.04
MMWT	5.11	5.09	5.12	0.40 ± 0.02
FI	0.275	0.274	0.282	0.39 ± 0.03
FCR	0.267	0.260	0.282	0.29 ± 0.04
RFI	0.149	0.147	0.151	0.39 ± 0.03

[a]Trait abbreviations: 200dWT-d = direct effect of 200-d weight; 200dWT-m = maternal effect of 200-d weight; 400dWT-d = direct effect of 400-d weight; 400dWT-m = maternal effect of 400-d weight; SC = scrotal circumference; RIBFAT = 12/13th rib fat depth; P8FAT = rump P8 fat depth; EMA = longissimus muscle area; ADG = average daily gain; MMWT = metabolic mid-weight; FI = daily feed intake; FCR = feed conversion ratio; RFI = residual feed intake.
[b]Mean and range from different trivariate analyses.

feed intake was genetically independent of the component traits (r_g = –0.04 and –0.06). This implies that selection against residual feed intake is not likely to result in changes in the two component traits. However, a negative correlation was observed between feed conversion ratio and its component trait, ADG. This indicates that faster-growing animals tended to have improved (lower) feed conversion ratios and that selection against this ratio is likely to result in faster-growing cattle. Positive correlations (r_g = 0.66, r_p = 0.53) were obtained between the two feed efficiency traits.

Genetic and phenotypic correlations for feed intake, feed conversion ratio, and residual feed intake with other postweaning traits are presented in Tables 4 and 5. The genetic correlations among the 200-d and 400-d weights were in general agreement with published estimates (e.g., Koch et al., 1973; Meyer, 1995). Parameter estimates for these weights have been the subject of a few reviews (e.g., Mohiuddin, 1993; Koots et al., 1994a,b) and so will not be discussed in detail.

Feed intake was positively correlated with all the postweaning traits (Tables 4 and 5), with the strongest genetic correlation being with direct effects on 400-d weight. The correlations between feed conversion ratio and other postweaning traits (Tables 4 and 5) were generally weak. The exceptions to this general trend were those between feed conversion ratio and direct effects on 200-d weight, which was negative and moderate, and between feed conversion ratio and maternal effects on 200-d weight, which was positive and moderate, but all with large SE. For residual feed intake, its correlations with scrotal circumference, P8 fat depth, and longissimus muscle area were close to zero, whereas those with rib fat depth (Table 4) and with the postweaning weight traits (Table 5) were different from zero. Residual feed intake was negatively correlated with the direct effects and positively correlated (but with large SE) with the maternal effects of 200- and 400-d weight.

Discussion

There are a number of published estimates of heritability for most growth traits in beef cattle. The most recent review (Koots et al., 1994a) of these estimates for growth indicates that they are all moderately heritable, with weighted heritability estimates of 0.33 and 0.31 for yearling weight and postweaning gain, respectively.

Table 3. Genetic (above diagonal, ± SE) and phenotypic correlations for growth and feed efficiency traits during the test period

Trait[a]	ADG	MMWT	FI	FCR	RFI
ADG		0.53 ± 0.07	0.54 ± 0.06	–0.62 ± 0.06	–0.04 ± 0.08
MMWT	0.24		0.65 ± 0.03	–0.01 ± 0.07	–0.06 ± 0.06
FI	0.41	0.63		0.31 ± 0.07	0.69 ± 0.03
FCR	–0.74	0.16	0.23		0.66 ± 0.05
RFI	–0.06	0.02	0.72	0.53	

[a]Trait abbreviations: ADG = average daily gain; MMWT = metabolic mid-weight; FI = daily feed intake; FCR = feed conversion ratio; RFI = residual feed intake.

Table 4. Genetic (± SE) and phenotypic correlations between feed efficiency traits and postweaning traits

	FI		FCR		RFI	
Trait[a]	Genetic	Phenotypic	Genetic	Phenotypic	Genetic	Phenotypic
SC	0.21 ± 0.09	0.28	−0.10 ± 0.13	0.00	−0.03 ± 0.11	0.10
RIBFAT	0.27 ± 0.05	0.23	0.03 ± 0.06	0.08	0.17 ± 0.05	0.14
P8FAT	0.14 ± 0.05	0.16	−0.04 ± 0.07	0.07	0.06 ± 0.06	0.11
EMA	0.43 ± 0.07	0.33	−0.12 ± 0.11	0.03	0.09 ± 0.09	0.06

[a]Trait abbreviations: SC = scrotal circumference; RIBFAT = 12/13th rib fat depth; P8FAT = rump P8 fat depth; EMA = longissimus muscle area; FI = daily feed intake; FCR = feed conversion ratio; RFI = residual feed intake.

Relatively fewer heritability estimates are available in the literature for feed efficiency traits in beef cattle, with most of the estimates being for feed intake, feed conversion ratio, and more recently residual feed intake. Estimates for these traits, included in the reviews by Koots et al. (1994a) and Archer et al. (1999), range from low to moderate heritability, with most of the values falling in the moderate range. Recent heritability estimates for these three traits by Robinson et al. (1999), Herd and Bishop (2000), and Arthur et al. (2001a) also fall into the moderate range.

There are very few reports in the literature on genetic and phenotypic correlations among different estimates of feed efficiency, but those available are in general agreement with the findings of this study. Koots et al. (1994b) summarized available estimates between feed intake and feed conversion ratio to be 0.71 and 0.75 for the genetic and phenotypic correlations, respectively. Fan et al. (1995) reported a genetic correlation between residual feed intake (calculated from feeding standards formula) and feed conversion ratio of 0.90 and 1.00 for Angus and Hereford bulls, respectively, and phenotypic correlations of 0.91 and 0.97, respectively. Herd and Bishop (2000) reported phenotypic correlations for residual feed intake and the following traits to be 0.64 with feed intake and 0.70 with feed conversion ratio for British Hereford cattle. Corresponding genetic correlation coefficients reported by Arthur et al. (2001a) were 0.79 and 0.85 for Charolais bulls.

The correlations between the ultrasound measures of fat depth and feed conversion ratio or residual feed intake obtained in this study were low (Table 4). We are not aware of any published studies using ultrasound fat measurement, for comparison. However, Jensen et al. (1992) reported a genetic correlation of –0.13 ± 0.34 between residual feed intake and carcass fat percentage for animals of an age similar to that of animals used in this study. Genetic correlation between feed conversion ratio (r_g = –0.32, Koots et al., 1994b) or residual feed intake (r_g = 0.17 ± 0.32, Jensen et al., 1992; r_g = –0.47 ± 0.23, Herd and Bishop, 2000) and carcass lean percentage have also been reported. The SE associated with the genetic correlations reported by Jensen et al. (1992) for residual feed intake and either percentage of carcass fat or lean indicate that those estimates may not be different from zero. However, the estimates by Koots et al. (1994b) and Herd and Bishop (2000) imply some relationship between feed conversion ratio or residual feed intake and fatness. In a study by Richardson et al. (1999) that used animals generated through this project, the chemical composition of carcasses from high- (low residual feed intake) and low- (high residual feed intake) efficiency steers was assessed. The results showed that differences in fatness accounted for only a small proportion of the variation in feed efficiency and that other biological mechanisms could be involved.

Maternal effects are known to influence weaning weight. Therefore, when the data structure allows, variation in weight around weaning should be partitioned into additive direct and additive maternal effects, as done in this study. A weak to moderate genetic correlation between residual feed intake (r_g = 0.22) or feed

Table 5. Heritability (diagonal) and genetic (above diagonal) correlations (± SE) for feed efficiency traits and the direct and maternal effects of growth traits

Trait[a]	FI	FCR	RFI	200dWT-d	400dWT-d	200dWT-m	400dWT-m
FI	0.37 ± 0.05	0.31 ± 0.07	0.69 ± 0.03	0.28 ± 0.15	0.56 ± 0.09	0.45 ± 0.16	0.46 ± 0.20
FCR		0.32 ± 0.06	0.66 ± 0.05	−0.21 ± 0.20	−0.09 ± 0.15	0.39 ± 0.41	0.08 ± 0.25
RFI			0.38 ± 0.06	−0.45 ± 0.17	−0.26 ± 0.13	0.22 ± 0.20	0.14 ± 0.25
200dWT-d				0.17 ± 0.03	0.88 ± 0.03	−0.17 ± 0.12	−0.14 ± 0.17
400dWT-d					0.28 ± 0.03	0.13 ± 0.10	0.18 ± 0.17
200dWT-m						0.13 ± 0.02	0.99 ± 0.05
400dWT-m							0.04 ± 0.01

[a]Trait abbreviations: 200dWT-d = direct effect of 200-d weight; 200dWT-m = maternal effect of 200-d weight; 400dWT-d = direct effect of 400-d weight; 400dWT-m = maternal effect of 400-d weight; FI = daily feed intake; FCR = feed conversion ratio; RFI = residual feed intake.

conversion ratio ($r_g = 0.39$) and maternal effects on 200-d weight was obtained. The SE associated with the correlations involving maternal effects were large, and thus due care should be taken in forecasting the correlated response to selection on these maternal effects. Some studies have reported the correlation between weaning weight direct and feed conversion ratio, as presented in the review by Koots et al. (1994b). However, we did not find any studies reporting the correlation between weaning weight maternal and feed conversion ratio or residual feed intake. Across-breed studies suggest that efficiency of feed use for maintenance is associated with lower milk production (Taylor et al., 1986; Solis et al., 1988; Montaño-Bermudez et al., 1990). However, the genetic correlations of –0.07 to –0.10, reported by Nieuwhof et al. (1992), between residual feed intake in the growing dairy heifer and milk yield (fat and protein corrected) in the lactating heifer suggest that this relationship may be different within breed or different in dairy cattle.

The computation of residual feed intake requires the estimation of expected feed intake, which can be obtained through regression, as was the case in this study, or can be obtained through the use of feeding standards formula. When expected feed intake is obtained by regression, the residual feed intake calculated is expected to be phenotypically independent of the component production traits used, thus allowing for comparison of animals differing in the level of these production traits. Residual feed intake with expected feed intake calculated from feeding standards formula however, is not automatically independent of production and is usually correlated with these traits, as observed in the studies by Fan et al. (1995) and Arthur et al. (2001a). Kennedy et al. (1993) intimated that even with residual feed intake calculated by regression (as in this study), there is no guarantee that its genetic correlations with these production traits will be close to zero. In this study, both metabolic body weight and ADG were phenotypically and genetically independent of residual feed intake (Table 3). However, direct effects on 200-d and 400-d weight were genetically correlated with residual feed intake (Table 5). Jensen et al. (1992) obtained genetic correlations between residual feed intake and ADG of 0.32 and –0.24 for two different test periods. Herd and Bishop (2000) reported genetic correlations between residual feed intake and yearling weight of 0.15. Arthur et al. (2001a) obtained a genetic correlation of 0.32 between residual feed intake and 15-mo weight. The computation of residual feed intake from genetic regression, (i.e., using genetic variance - covariances) is genetically independent of the production traits and was suggested by Kennedy et al. (1993) as an alternative for genetic improvement purposes. Archer et al. (1998), using a subset of the data used in this study, reported a high correlation between residual feed intake estimates using phenotypic and genetic regressions, although component traits were not partitioned into direct and maternal effects in that study.

The review by Archer et al. (1999) indicated that genetic variation in feed efficiency exists for growing cattle and for cattle at maintenance. Measures of feed efficiency that incorporate both live weight and ADG seek to capture some of the underlying variation in feed used for both growth and maintenance. The expectation is that when such a trait is used for selection the resultant progeny will be efficient as steers for slaughter as well as mature cows in the breeding herd where growth has virtually ceased and efficiency of feed use for maintenance is of prime importance. In a study reported by Arthur et al. (2001b), feed conversion ratio and residual feed intake were measured in young Charolais bulls as weaners (274 d of age), as in this study, and again as yearlings (430 d of age). The phenotypic and genetic correlations between feed conversion ratios in weaners and in yearlings were 0.06 and 0.42, respectively. The corresponding values for residual feed intake were 0.43 and 0.75. Although the ages of the bulls at the start of test for the two measurement periods were only 166 d apart, the genetic correlations indicate that, of the two traits measured in weaners, residual feed intake is the one most likely to be correlated with efficiency later in life.

Feed conversion ratio is expressed as a ratio, whereas residual feed intake is a linear index. The use of ratio traits for genetic selection presents problems relating to prediction of the change in the component traits in future generations. This is due to the disproportionate fashion by which selection pressure is exerted on the component traits. A linear index, however, places a predetermined amount of selection pressure on the traits and thus results in a predictable amount of genetic change. Gunsett (1984) compared the efficiency of direct selection for a two-component trait with a linear index trait derived from the same two components. It was concluded that the use of a linear index increases selection responses as compared with direct selection on the ratio trait. For residual feed intake, the weights of the component traits in the index are determined by only biological variances. However, profitability will be maximized when index weights on feed intake (or residual feed intake), growth, and other traits are determined by both biological and economic parameters, as used in economic selection indices (Simm et al., 1987).

This study considered feed efficiency and growth in the young growing animal; therefore, the conclusions and implications apply to the postweaning phase of production. However, it is important to assess the relationships between these traits and those measured later in life as they affect whole production system efficiency. The relationships between the growth traits and some of the traits measured later in life, such as reproduction and maternal traits, have been studied and summarized in the review by Koots et al. (1994b). However, there are very few research endeavors worldwide that are looking at measures of feed efficiency in the young animal and its relationship with traits measured later in life, such as reproduction and mature cow effi-

ciency. Reproduction and other breeding herd records are currently being collected on the females involved in this study. These females are also being evaluated for feed efficiency as 4 yr old cows and the results will be published later.

Implications

Existence of both phenotypic and genetic variation in feed efficiency in beef cattle and the associated moderate heritability for both feed conversion ratio and residual feed intake imply that genetic improvement can be made through selection. The expected correlated responses in most of the traits studied to selection for more efficient animals are minimal. Given the associated problem with selection for ratio traits and the fact that residual feed intake is strongly correlated with feed conversion ratio, residual feed intake should be the preferred trait for genetic improvement of postweaning feed efficiency.

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Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle

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Abstract

Feed intake (FI), weight gain (WG), metabolic weight (MW), feed conversion ratio (FCR), residual feed intake calculated by regression (RFI) and feeding standards formulae (RFIS) were recorded on 1481 steers and heifers of tropically adapted and temperate breeds of cattle feedlot finished on a grain based diet for the domestic (liveweight 400 kg), Korean (520 kg) or Japanese (steers only; 600 kg liveweight) markets. Also measured were subcutaneous fat at the rump (P8) and 12/13 rib sites, 12/13 rib eye muscle area and intra-muscular fat (IMF%), time spent eating, eating rate and number of meals per day. Estimated heritabilities of FI, MW, WG, FCR, RFI and RFIS were 0.27, 0.41, 0.23, 0.06, 0.18 and 0.13. RFI and RFIS had very high genetic (0.98) and phenotypic (0.94) correlations, suggesting that they represent very similar traits. RFI had relatively high genetic correlations with rump and rib fat (0.72 and 0.48 adjusted for age; 0.79 and 0.58 adjusted for carcase weight), but lower correlations with IMF% (0.22 and 0.25 adjusted for age and carcase weight, respectively). Selection for lower RFI is therefore possible in feedlot finished cattle, but fatness will also decrease. In this study, selection for reduced fatness was predicted to reduce RFI by more than direct selection. When appropriate, multivariate selection is therefore recommended to achieve increased feed efficiency together with the desired level of fatness, using an index including RFI, on-test weight gain and fat measurements.

There were large breed differences for number of meals 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 meals per day.

Keywords: Beef cattle; Feed intake; Weight gain; Feed efficiency; Residual feed intake; Fatness

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1. Introduction

Feed is a major cost in the production of beef cattle. For example, based on an estimated 650,000 cattle in Australian feedlots at any one time on feed (Foster, 2001; Graham, 2001), feed costs of $200 per tonne and mean feed consumption of 12.5 kg/head/day, a 10% reduction in feed intake (FI) could save the Australian feedlot industry $59 million per year. One way to reduce feed costs is through genetic selection of more efficient animals.

A commonly used measure of efficiency is feed conversion ratio (FCR=FI/estimated weight gain. However, Bishop et al. (1991) carried out a genetic selection experiment for improved FCR and reported that progeny of selected lines had higher weight gain but no reduction in FI. Another experiment (Mrode et al., 1990) created two selection lines of cattle—one for increased lean growth rate (LGR) and another for reduced (FI/LGR), named "lean FCR." REML estimates of (co)variances showed the LGR line had a correlated response of −0.14 (kg food/kg lean gain), *better* than the direct response of −0.12 (kg food/kg lean gain) in those actually selected for lean FCR. This prompted Cameron (1998) to suggest that measuring FI was not cost effective; selecting for LGR improved efficiency more than direct selection, without the substantial expense of recording FI and growth for several weeks.

Luiting et al. (1994) and Parnell et al. (1995) also highlighted potential difficulties associated with the relationship between FCR and growth, suggesting that it may be more desirable to select for a trait such as residual feed intake (RFI), defined as the amount of feed eaten by an animal less what would be expected from the animal's growth rate and body weight. Use of RFI may also help avoid the problem of inaccurate estimates of weight gain causing skewness in the distribution of FCR, potentially biasing estimates of heritability and breeding values, unless transformations are applied.

Despite the pioneering work of Koch et al. (1963), there are few published studies of genetic parameters for RFI based on more than 1000 cattle. Arthur et al. (2001a) reported genetic parameters for RFI, feed intake, weight, weight gain and fatness estimated from 1180 young Angus bulls and heifers (mean age 303 days) on a pelleted 70% alfalfa 30% wheat diet. However, efficiency in young animals may differ from efficiency of older, fatter cattle (near market endpoints) on a high-energy feedlot diet. This study investigated the efficiency of 1481 feedlot finished cattle, with mean on-test age of 629 days and mean weight of 502 kg. Results are presented for FI, weight and weight gain, RFI, FCR, subcutaneous and intramuscular fat, *longissimus* muscle area, number of feeding sessions, time spent eating and eating rate. Genetic and phenotypic parameters from this study are compared with other published results, and the consequences of selection discussed, especially effects on fatness.

2. Materials and methods

2.1. Animals and Feed Management

Cattle in this study were part of the Cattle and Beef Industry Cooperative Research Centre (CRC) research herd. The experimental protocol, cattle, feed management and automatic feed recording system were described by Robinson (submitted for publication). Briefly, cattle were feedlot finished for the domestic (D, 400 kg liveweight at slaughter), Korean (K, 520 kg) or Japanese (J, steers only; 600 kg liveweight) markets. Feed intake measurements were available on 524 steers and 172 heifers of tropically adapted breeds and 785 steers of temperate breeds feedlot finished at the University of New England's beef cattle research facility (Tullimba, near Armidale, northern New South Wales (NSW), Australia) between February 1996 and January 2000.

Weaners of tropically adapted breeds were supplied by four Brahman, three Belmont Red and four Santa Gertrudis herds in Queensland. After a short period at a research station in central Queensland, the tropically adapted cattle were transferred south to northern NSW where they were grown out on pasture and then finished in the feedlot. Weaner steers from 10 Angus, 6 Hereford, 2 Murray Grey and 3 Shorthorn herds were grown out, sometimes under three or four different grow-out nutritional treatments in northern NSW (see Dicker et al., 2001), then finished at Tullimba.

When the average weight of each group of cattle reached feedlot entry weight (300 kg for domestic

market groups; 400 kg for Korean and Japanese groups), cattle were transferred to the feedlot. Cattle were placed in pens of approximately 50×40 m with a water trough and feed bunk. During a 2-week introductory period, the proportion of dry rolled barley grain in the diet was increased from 40% to 75% (w/w) and roughage reduced from 50% to 10% (w/w). Animals were then offered a standard finisher ration of (by weight) 75% dry rolled barley grain, 10.5% milled sorghum hay, 5% pelletted cottonseed meal, 8% Molafos ® (Ridley, Wacol, Qld, Australia, contributing 0.8% urea and 25 mg/kg Monensin sodium, trace minerals and vitamins to the final ration), 1% finely ground limestone and 0.5% ammonium sulphate. The estimated nutrient density was 12.1 MJ ME with a minimum of 150 g crude protein (Kjeldahl nitrogen ×6.25) per kg dry matter (DM); DM content was 88%.

Feed intake (FI) was measured in special automatic feeder (AF) pens. Cattle in the AF pens were normally weighed weekly, with fortnightly weighings at other times. Domestic and Korean animals spent an average of 53 and 57 days, respectively, in the AF pens, entering them on average 21 and 29 days after their first weighing at Tullimba. Japanese market steers entered the AF pens, on average, 65 days (range 15–112 days) after their first weighing at Tullimba and spent an average of 74 days using the automatic feeders. FI measurements of Japanese steers were delayed until space was available in the AF pens, often at the exit of Korean animals in the same cohort. Mean ages at the midpoint of the FI test were 477, 640 and 673 days for domestic, Korean and Japanese animals; means on-test weights were 377, 490 and 548 kg.

Data from the AF recorders were summarised into daily totals for amount of feed eaten, time spent eating and number of feeding sessions. For the latter, a second session by the same animal within 2 min of the end of the previous feeding session was considered as part of the previous session.

2.2. Estimation of weight gains

The calculation of residual feed intake (RFI) requires an estimate of weight gain over the period for which FI was measured. Robinson (submitted for publication) showed the best estimate of an animal's weight gain (WG) for the relatively short period in the AF pens was, in fact, weight gain for the entire time spent in the feedlot (from a linear model of weight over time, fitted to all weights in the feedlot). Estimates were transformed to the correct mean for each test group by:

$$\mathrm{WG} = \mathrm{Flgain} - \mathrm{mean}(\mathrm{FLgain}) + \mathrm{mean}(\mathrm{AFgain}) \quad (1)$$

where means are for each test group; FLgain and AFgain are estimates of weight gain (kg/day) for the entire time in the feedlot and for the period in the AF pens, respectively.

2.3. Modelling the relationship between feed intake, weight and weight gain

The relationship between feed intake, weight and weight gain was modelled (using ASREML software, Gilmour et al., 1998) by fitting:

$$\mathrm{FI}_a = \mathrm{constant} + \alpha^{*}\mathrm{age}_a + (\beta_{wo} + \beta_{wm} + \beta_{wt})^{*}\mathrm{MW}_a + (\beta_{go} + \beta_{gm} + \beta_{gmb})^{*}\mathrm{WG}_a + (\text{other factors})_a \quad (2)$$

where, for animal a, FI_a is mean feed intake (kg/day); age_a=age of animal a; MW_a=metabolic weight (expected to be proportional to maintenance requirements), i.e. mean(weight$^{0.73}$) for all weights of animal a recorded in the AF pens; WG_a=weight gain (Eq. (1)). Age, MW and WG were standardised to have mean zero by subtracting the mean (of the entire dataset) from each observation. The coefficients α, β_{wo} and β_{go} represent fixed overall relationships with age, MW and WG, respectively. β_{wm} and β_{wt} represent random departures (for each market and test group) from the overall relationship for MW; β_{gm} and β_{gmb} random departures (by market and market×breed type) from the overall relationship for WG.

Other factors, all fitted as random, were breed type (temperate or tropically adapted breeds); breed (Angus, Hereford, Murray Grey, Shorthorn, Brahman, Belmont Red or Santa Gertrudis, nested within breed type), birth herd (each herd supplied only one breed of cattle, so herds were nested within breeds); destination market (domestic, Korean or Japanese), sex (heifer or steer); test group (36 levels, one for each group tested,

nested within sex, market and breed type) plus genetic effects of animal. The latter were fitted by a relationship matrix including identifiers of sires (n=313), dams (from commercial herds, usually with very little pedigree information, but some dams were used more than once), parents, grandparents and great-grandparents of sires. Only the terms listed above were fitted; estimated variation of other factors was negligible.

The underlying biological processes of using feed eaten to grow and maintain fat and lean tissue are believed to be similar for all breeds. Thus, the fitted relationships between FI, MW and WG should be consistent, perhaps with some variation as animals mature and due to local environmental factors. Fitting separate regression relationships for all 36 test groups would have led to substantial variation in fitted slopes, because of sampling variation and the relatively small numbers per group. The random regression techniques used here enabled variation (with market and other factors) to be quantified, allowing for genuine variation, without additional variation and inconsistencies from fitting a different regression relationship for each test group. Other factors were fitted as random for similar reasons (see, e.g. Robinson, 1987).

All outliers (>3 S.D. from the fitted values) were checked carefully. Those considered due to data recording errors were omitted. However, those considered to represent valid data were retained, including those with unusually low growth rate or FI. Animals with low growth help reduce the confounding of weight and weight gain, so that estimates of partial regression coefficients should correspond more closely to the true parameters.

2.4. Calculation of residual feed intake

For each animal a, RFI was calculated as:

$$RFI_a = FI_a - \beta^*_w MW_a - \beta^*_g WG_a \quad (3)$$

where FI_a, MW_a and WG_a are as defined in Eq. (2), $\beta_w=(\beta_{wo}+\beta_{wm}+\beta_{wt})$ and $\beta_g=(\beta_{go}+\beta_{gm}+\beta_{gmb})$ are the partial regression coefficients from Eq. (2) for MW and WG, depending on the animal's market, breed type and test group. Intercepts were not included in Eq. (3) (even though β_w and β_g were estimated from Eq. (2), which contained intercepts), because RFI was calculated for a genetic analysis that fitted and removed all fixed effects. Estimated genetic parameters would therefore be identical whether or not Eq. (3) contained intercepts.

2.5. SCA reference equations for feed intake and weight gain

The Standing Committee on Agriculture (SCA, 1990) published generalised equations relating amounts of feed eaten for cattle of different breeds and sexes to energy requirements for maintenance and weight gain over a wide range of weights, weight gains and feed energy densities. To evaluate the usefulness of these generalised equations and compare the results with RFI from Eq. (2), SCA residual feed intake (RFIS) was also calculated as the difference between FI of each animal and its requirement estimated by a modified version of SCA (1990, see Appendix A).

Various other methods of calculating RFI were considered, such as a linear version of the SCA equations, adjusting for bias of regression coefficients, and calculating RFI from estimated weight gain in the AF pens. Genetic and phenotypic correlations between the different measures of RFI were very high. Therefore, for brevity, results are presented here for just RFI and RIFS.

2.6. Measurement of other traits

Subcutaneous fat depth at the P8 rump and 12/13 rib sites and 12/13 *longissimus* muscle area were measured by ultrasound scanning (Robinson et al., 1992) approximately 1 week before transport to the abattoir to ensure minimum disturbance of animals before slaughter. Carcase intra-muscular fat percent (IMF%) was measured on a sample of *M. longissimus* close to the 12/13th rib site using near infrared spectroscopy (Technicon Infralyser 450, Bran and Luebbe, Australia) calibrated against soxhlet extraction of fat in boiling chloroform for 24 h. The calibration equation explained 96% of variation in measured IMF% (Perry et al., 2001).

2.7. Estimation of genetic parameters

Genetic variances, covariances and heritabilities were estimated by REML using VCE software

(Groeneveld and García-Cortés, 1998). For all traits, additive genetic effects were fitted, plus a fixed effects model including test group, birth herd, age at measurement, previous grow-out nutrition treatment (if applied, see Section 2.1) and (for traits where the entire test group was not measured on the same day) day of measurement. The model was simpler than Eq. (2) so that several traits could be analysed at the same time. Here, systematic effects were considered as nuisance parameters simply to be estimated and removed. Thus, there was no need to estimate or partition variances to determine effects of market, sex, breed or other factors.

Nine animals included in the analysis to fit Eq. (2) were omitted from the genetic analysis. These animals were identified as outliers with extremely low growth rates (<0.3 kg/day), or inconsistent eating patterns associated with failure to gain weight for part of their time in the AF pens, suggesting they may have been sick. Because weight gain was not measured for the same time period as FI, data for such animals may have been subject to biases compared with healthy animals. Furthermore, the presence of even a small number of outliers can have considerable influence on estimates of genetic parameters, so it was considered advisable to remove such data from the genetic parameter analysis. The genetic analysis was therefore based on 1472 animals. Pedigree information was as described for Eq. (2). Traits analysed included FI, MW, WG, RFI, RFIS, feed conversion ratio (FCR), as well as IMF%, rump (P8) and 12/13 rib fat, 12/13 *longissimus* (eye) muscle area (EMA), time spent eating (min/day), eating rate (g/min) and number of feeding sessions per day. Multivariate analyses were carried out for up to six traits at a time, then results averaged over all runs that converged satisfactorily (i.e. VCE status 1).

A separate analysis was also carried out of rump, rib and intra-muscular fat, fitting carcase weight as a covariate in the model, to adjust fat measurements to 300 kg carcase weight and determine the relationship of fatness with RFI independently of any effects caused by differences in carcase weight.

2.8. Response to single-trait selection

The estimated response was calculated to one generation of phenotypic single-trait selection, assuming 50% of females and 10% of males were selected in a large herd or breeding population. Two scenarios were considered: (a) the effect (and correlated response in RFI) to single-trait selection to increase each of the traits analysed; and (b) the correlated responses in the traits analysed to single-trait selection to reduce RFI. For any two traits, s and t, the indirect or correlated response, Rs, in trait s to single-trait selection for trait t as described above was estimated as: $Rs=i^*r_g h_s h_t \sigma_{Ps}$, where r_g is the genetic correlation between traits s and t, h_s and h_t are square roots of the estimated heritabilities of traits s and t, σ_{Ps} is the phenotypic standard deviation of trait s, and i is the average selection intensity, in this case 1.2765 (Falconer, 1989).

3. Results and discussion

3.1. Means and variability of measurements

Mean age (at the midpoint of the feed intake test), feed intake (FI), weight and weight gain by market (D, K, J), breed type and sex are shown in Table 1. Means for time spent eating, numbers of eating sessions, eating rate, intra-muscular fat, scanned rump, rib fat and eye muscle area are shown in Table 2. Weight gain (kg/day for animals in the AF pens) generally decreased with age. Domestic market animals (mean age 477 days) grew fastest; Korean market animals (mean 640 days) were intermediate, with Japanese market steers (mean 673 days) lowest. FI tended to be highest for Koreans; domestic market groups averaged 0.6–1.1 kg/day less FI than Koreans; Japanese steers 0.4–1.0 kg/day less. Domestic groups had highest mean weight gains but moderate FI hence the lowest mean FCR; Koreans were intermediate; Japanese groups had the highest mean FCR (Table 1).

3.2. Variation of partial regression coefficients with sex and market

Table 3 shows the partial regression coefficients, β_w and β_g, for MW and WG from Eq. (2). Variation in β_w was relatively small; Japanese groups generally had lowest values, with Koreans marginally higher and

Table 1
Numbers of animals and groups; means (±S.D.) for age, weight, weight gain, feed intake and efficiency

Market and sex[a]	Number of animals	Number of groups tested	Mean age in AF pens (days)[b]	Mean daily feed intake (kg, as fed)	Mean $wt^{0.73}$ during test $(kg)^{0.73}$	Mean weight gain[b] (kg/day)	RFI[b] (kg as fed/day)	RFIS[b] (kg as fed/day)	FCR[b] (kg as fed/kg)
Temperate breeds (steers only)									
D	75	1	459±32	12.1±1.6	79.7±5.7	1.73±0.26	−2.7±1.0	0.5±1.1	7.1±0.9
K	401	7	583±67	13.1±1.6	94.1±6.4	1.45±0.25	−2.3±1.0	1.3±1.1	9.4±1.6
J	309	6	627±72	12.7±1.7	103.0±6.7	1.18±0.19	−3.4±0.9	1.6±1.0	11.2±1.6
Tropically adapted breeds									
D, H	69	2	504±44	11.4±1.9	74.8±7.6	1.58±0.33	−2.3±0.8	0.6±0.9	7.7±2.0
D, S	63	2	468±42	11.2±1.7	76.6±8.3	1.45±0.33	−1.1±0.8	1.4±0.9	8.0±1.5
K, H	103	3	719±45	12.0±1.5	90.6±6.4	1.34±0.30	−2.8±0.7	1.1±0.9	9.6±1.7
K, S	244	8	699±67	12.3±2.0	92.0±8.3	1.35±0.32	−2.5±0.9	1.6±1.0	9.5±1.6
J, S	217	7	737±80	11.3±1.9	97.7±8.8	1.15±0.29	−2.8±0.8	1.1±0.9	10.3±2.1

[a] D=Domestic; K=Korean, J=Japanese markets; H=Heifer, S=Steer.
[b] For age, S.D.=population S.D. (for each category); for other traits, S.D.s were calculated for each test group and then pooled; means for weight gain (Eq. (1)) are for the period in the AF pens; RFI=Residual Feed Intake from Eq. (3), which ignores intercepts so mean values are not expected to be zero; RFIS=Residual Feed Intake based on the SCA equations (see Section 2.5); FCR=feed conversion ratio=(mean daily intake, kg/day)/(mean weight gain, kg/day).

domestic groups generally highest. Somewhat lower β_w were expected for fatter Japanese animals nearing maturity, because 1 kg body fat generates less heat than 1 kg of lean tissue (Webster, 1985).

Variation in β_g was greater than β_w, especially by market, with minor differences between temperate (D 2.80; K 3.02; J 4.02) and tropically adapted breeds (D 2.79; K 3.15; J 3.49). Depositing 1 kg of fat requires more energy than 1 kg of lean tissue (SCA, 1990), so higher β_g were expected for older, heavier Japanese market animals, depositing a higher proportion of fat.

Table 3 also shows the implied relationship from the SCA equations (Appendix A). The SCA equations, based on mean(weight$^{0.75}$), were re-expressed in terms of mean(weight$^{0.73}$) to allow comparison with results from Eq. (2). β_w was on average 210–235% higher from Eq. (2) than SCA. In contrast, β_g from Eq. (2) averaged only 64–85% of the SCA values.

A crude estimate of the percentage of feed devoted to maintenance implied by these equations is: $100*\beta_w*MW/(\beta_w*MW+\beta_g*WG)$. Somewhat diffe-

Table 2
Means±S.D. for eating time, feeding sessions, eating rate, fatness and longissimus (eye) muscle area

Market and sex	Time spent eating (min/day)	Number of eating sessions (no./day)	Eating rate (g/min)	Carcase intra-muscular fat (%)	Pre-slaughter ultrasound scan		
					P8 rump fat (mm)	12/13 rib fat (mm)	Eye muscle area (cm^2)
Temperate breeds (steers only)							
Domestic	105±20	7.9±2.6	131±26	3.7±1.3	8.1±2.0	6.8±2.2	57.5±6.2
Korean	98±18	8.0±2.8	142±30	5.3±1.6	12.7±3.1	10.2±2.8	66.3±6.6
Japanese	92±15	9.5±3.8	144±26	7.0±2.0	16.4±4.1	13.4±3.7	77.0±7.1
Tropically adapted breeds							
Domestic—heifer	89±27	18.1±7.3	141±36	3.0±0.8	9.1±3.0	5.8±1.9	56.5±6.8
Domestic—steer	96±26	15.9±5.2	126±32	2.3±0.7	7.9±2.6	5.1±1.4	58.5±6.2
Korean—heifer	93±23	18.8±7.9	142±46	3.6±1.1	15.6±5.0	9.6±3.5	70.8±6.0
Korean—steer	86±20	14.4±4.8	154±34	3.6±1.1	10.6±3.5	7.0±2.6	67.8±7.1
Japanese—steer	77±19	15.5±5.5	158±37	4.4±1.4	12.3±4.5	8.6±3.5	76.3±7.6

Carcase intra-muscular fat and muscle area were measured on the longissimus (eye) muscle, 12/13 rib; S.D.s were calculated for each test group and then pooled.

Table 3
Partial regression coefficients for metabolic weight (β_w) and weight gain (β_g) used to calculate RFI and the implied percentage of intake required for maintenance

Market and sex	RFI[a] (means±S.E.)		RFIS[b] (means±S.D.)		% of intake for maintenance	
	β_w	β_g	β_w	β_g	RFI[c]	SCA[c]
Temperate breeds (steers only)						
Domestic	0.125±0.015[a]	2.80±0.54	0.054±0.000[b]	4.20±0.21	67	38
Korean	0.119±0.009	3.02±0.52	0.054±0.000	4.58±0.15	72	44
Japanese	0.113±0.009	4.02±0.53	0.054±0.000	4.72±0.10	71	50
Tropically adapted breeds						
Domestic—heifer	0.120±0.012	2.79±0.53	0.051±0.002	4.37±0.25	68	36
Domestic—steer	0.114±0.012	2.79±0.53	0.051±0.002	4.06±0.33	67	41
Korean—heifer	0.116±0.011	3.15±0.51	0.050±0.001	4.74±0.10	72	43
Korean—steer	0.115±0.009	3.15±0.51	0.050±0.002	4.51±0.21	72	44
Japanese—steer	0.107±0.009	3.49±0.52	0.050±0.002	4.62±0.17	72	49

[a] Means±S.E. from fitting Eq. (2).
[b] For RFIS: means+pooled within group S.D. NB, RFIS was calculated for each animal according to its weight, sex, age and breed type (see Appendix A). Thus, β_w and β_g for RFIS: means ± pooled within group S.D.
[c] Crude estimate, calculated as: $100*\beta_w*MW/(\beta_w*MW+\beta_g*WG)$—i.e. ignoring intercepts.

rent answers are obtained for the two methods—36–50% for the modified SCA equations, and 67–72% from fitting Eq. (2). The latter proportion seems somewhat high. As discussed by Robinson (submitted for publication), errors in estimated weight gain cause downward bias in estimates of β_g and compensatory upward bias in estimates of β_w. This may partly explain the lower estimates of β_g and higher β_w from Eq. (2) than SCA. However, the full random regression model including overall slopes, and random deviations (by market and other factors) for β_w and β_g, plus animals, herds, breeds, markets, sex and their interactions, produced estimates of β_w and β_g closer to the SCA equations than fixed effects models fitted to individual test groups (Robinson, submitted for publication). This suggests that, as discussed in Section 2.3, using random regression techniques to estimate and allow for observed variation, instead of fitting separate regression relationship for each test group, may provide better estimates.

Means for RFIS (feed intake less expected values calculated by the modified SCA equations) are shown in Table 1. All means were positive, implying that the modified SCA equations tended to under-estimate the amount of feed eaten. A major difference between the equations used here and those used by Robinson et al. (1999) was that the former used general estimates of the efficiencies of feed utilisation for maintenance, K_m, and weight gain, K_g, viz. K_m=0.7 and K_g=0.4. In contrast, estimates of K_g and K_m in the modified equations (Appendix A) were based on the energy density of dry feed, resulting K_m=0.742 and K_g=0.5203. Although they were based on standard equations, the resulting values seem somewhat high, which may explain the under-estimation of feed intake.

In contrast, RFI calculated from Eq. (3) was generally negative, because the (generally negative) intercepts fitted in Eq. (2) were omitted from Eq. (3). The values are, however, quite close to zero (the hypothetical limit for zero weight and weight gain). This suggests that the relationships had a substantial linear component, low metabolic weights and weight gains corresponding to low FI.

3.3. Heritabilities, genetic variances and correlations

3.3.1. Feed intake (FI), metabolic weight, weight gain and feed efficiency (RFI, RFIS, FCR)

FI had high estimated genetic correlations with feedlot gain ($\hat{r}_g$=0.87) and metabolic weight (0.76). Environmental correlations were slightly lower ($\hat{r}_e$=0.68 and 0.69 respectively). The high genetic correlations show that a considerable proportion (78%) of genetic variation in FI is associated with genetic variation in weight and weight gain. Thus, the

remainder (i.e. independent variation in feed efficiency) represents only a small proportion of total variation. Here, estimated genetic variation was 0.64 $(kg/day)^2$ for FI, compared to 0.139 $(kg/day)^2$ for RFI (Table 4).

Nonetheless, the genetic S.D. for RFI (0.37 kg/day) represents useful variation to enable feed efficiency to be improved. A 10% reduction in the amount of feed consumed in feedlots (estimated to save $59 million annually—see Section 1), corresponds to 3.3 genetic standard deviations, which, especially if feed efficiency is combined with other traits in the breeding objective, may take some generations of selection to achieve.

RFIS (feed efficiency from the modified SCA equations) had a different emphasis on MW and WG. However, RFI and RFIS had $\hat{r}_g$=0.98 and $\hat{r}_e$=0.94, implying that they are almost the same trait (Table 5), partly because $\hat{r}_g$ of MW and WG was high (0.77). RFI tended to be more heritable (18% vs. 13%) with marginally higher genetic variation (0.139 vs. 0.116), so may be a more useful trait for selection given data similar to ours. Estimated genetic correlations of RFI with WG and MW were 0.09 and −0.20, respectively, but with large S.E. of 0.20 and 0.16, suggesting that selection for reduced RFI ignoring other traits will have no clear effect on weight or WG.

In contrast, FCR had very low estimated heritability (6%), and strong negative genetic correlations with WG (−0.86), metabolic weight (−0.62) and FI (−0.49). The low estimated heritability of FCR implies that direct selection to increase WG would reduce FCR by more (−0.19) than direct selection (−0.11, Table 4), consistent with the results of Mrode et al. (1990). Inaccuracies in estimated WG may cause skewness in FCR, which can cause problems for the estimation of variance components and heritability. Sample skewness of FCR in our data was 1.28 indicating the distribution was not symmetric. Thus, if estimates of FCR are needed, it may be desirable to base them on more accurate estimates of WG or transform the data to reduce skewness.

3.3.2. Feed intake, RFI and fatness traits

For FI and fat measurements, $\hat{r}_g$ ranged from 0.39 to 0.61; $\hat{r}_e$ from 0.12 to 0.18. A partial explanation is that heavier animals generally eat more, and feed intake in excess of requirements can lead to increased fat deposition.

Estimated genetic correlations of RFI with rump (0.72) and rib fat (0.48) were similar in magnitude to those of FI with the same traits (0.59 and 0.61). For RFI and IMF%, $\hat{r}_g$ was 0.22, with S.E. of 0.17. Estimated environmental correlations of RFI were −0.11, 0.01 and 0.09 with P8 fat, rib fat and IMF%, respectively. Thus, selection for lower RFI is likely to reduce subcutaneous fat. Intra-muscular

Table 4
Overall means, estimates of phenotypic and genetic variances, heritabilities, direct and indirect responses to selection

	FI	WG	MW	RFI	RFIS	FCR	Feed time	Eat sess	Eat rate	IMF%	P8 fat		Rib fat		EMA
											Adj age	Adj wt[a]	Adj age	Adj wt[a]	
Overall mean	12.34	1.347	93.5	−2.63	1.32	9.69	91.4	12.0	145	4.79	12.67		9.49		69.42
Phenotypic variance	2.35	0.056	32.4	0.767	0.882	2.09	339	21.6	1046	1.89	12.39	11.54	8.01	7.20	41.29
Genetic variance	0.64	0.013	13.4	0.139	0.116	0.13	120	9.5	531	0.63	5.30	4.99	3.61	3.06	5.33
Heritability (%)	*27*	*23*	*41*	18	*13*	*6*	*36*	*44*	*51*	*33*	*43*	43	*45*	42	*13*
S.E. Heritability (%)	*6*	*6*	*7*	6	*5*	*4*	*5*	*7*	*6*	*6*	*6*	6	*6*	7	*5*
Dir. response: select ↑[b]	0.53	0.07	3.00	0.20	0.16	0.11	8.35	2.60	21.0	0.58	1.92	1.88	1.63	1.46	1.06
Indir. response in RFI[c]	0.11	0.02	−0.06	0.20	0.17	0.05	0.10	0.14	−0.02	0.06	0.23	0.25	0.15	0.18	−0.04
Indir. response to RFI ↓[d]	0.19	−0.01	0.40	−0.20	−0.18	−0.08	−2.10	−0.72	0.84	−0.09	−0.90	−0.95	−0.50	−0.55	0.30

[a] Rump (P8) and rib fat adjusted to 300 kg carcase weight.
[b] Direct response=response to one generation of phenotypic selection (10% of males, 50% of females) to increase the trait.
[c] Indirect response in RFI to selection for the trait as described.
[d] Indirect response=estimate of correlated response to single trait phenotypic selection (10% of males, 50% of females) for reduced RFI.
Trait abbreviations: FI=mean feed intake (kg/day); WG=weight gain (Eq. (1)); MW=metabolic weight, i.e. mean(weight$^{0.73}$); FCR=feed conversion ratio (kg/kg); Feed time=time spent eating (min/day); Eat sess=number of eating sessions (number/day); Eat rate=eating rate (g/min); IMF%=intra-muscular fat percent.

Table 5
Estimated genetic correlations (% below diagonal, S.E. underneath) and phenotypic correlations (% above diagonal[a], environmental correlations underneath) (%)

	FI	WG	MW	RFI	RFIS	FCR	Feed time	Eat sess	Eat rate	IMF %	P8 fat	Rib fat	EMA
Feed intake (FI; kg/day)		73	71	57	42	−14	30	18	26	20	28	32	30
		(68)	(69)	(62)	(45)	(−8)	(43)	(20)	(23)	(12)	(13)	(18)	(33)
Wt gain (WG kg/day)	87		57	−1	−26	−8	23	13	18	13	19	23	29
	(5)		(49)	(−3)	(−29)	(−67)	(44)	(18)	(1)	(12)	(19)	(15)	(33)
Metabolic weight ($kg^{0.73}$)	76	77		−1	−1	−14	20	2	20	14	27	31	41
	(7)	(8)		(7)	(8)	(−3)	(38)	(12)	(11)	(−1)	(23)	(23)	(41)
RFI (kg/day)	43	9	−20		94	45	16	18	14	12	11	13	−3
	(15)	(20)	(16)		(94)	(47)	(11)	(10)	(25)	(9)	(−11)	(1)	(0)
RFIS (kg/day)	32	−14	−26	98		63	10	13	11	10	10	11	−5
	(20)	(24)	(18)	(3)		(63)	(3)	(5)	(24)	(5)	(−12)	(0)	(−4)
FCR (kg/kg)	−49	−86	−62	41	69		−5	−8	−5	−2	−5	−5	−14
	(22)	(10)	(18)	(32)	(27)		(−19)	(−20)	(12)	(−4)	(−15)	(−15)	(−17)
Feeding time (min/day)	3	−30	−7	35	39	78		−1	−77	8	9	11	12
	(13)	(19)	(11)	(17)	(16)	(16)		(4)	(−66)	(24)	(14)	(20)	(7)
Number of eating sessions/day	16	2	−12	43	40	49	−8		14	0	3	−1	5
	(10)	(10)	(12)	(11)	(14)	(25)	(12)		(23)	(−10)	(3)	(6)	(19)
Eating rate (g/min)	33	53	29	−7	−17	−83	−92	4		4	8	7	7
	(10)	(14)	(10)	(17)	(18)	(14)	(3)	(11)		(−16)	(−4)	(−7)	(25)
Intra-musc fat (IMF%)	39	17	41	22	31	8	−25	16	32		19	21	2
	(14)	(12)	(9)	(17)	(20)	(28)	(12)	(11)	(14)		(1)	(6)	(15)
P8 fat (mm)	59	21	33	72	87	40	0	2	20	48		68	11
	(10)	(10)	(11)	(17)	(21)	(33)	(9)	(8)	(8)	(11)		(66)	(19)
Rib fat (mm)	61	40	41	48	50	38	−1	−10	22	45	72		13
	(11)	(13)	(10)	(12)	(18)	(32)	(10)	(9)	(8)	(10)	(5)		(24)
EMA (cm^2)	23	14	50	−24	−15	20	30	−32	−39	−44	−8	−14	
	(16)	(22)	(16)	(26)	(22)	(42)	(16)	(15)	(21)	(20)	(17)	(18)	

See footnote to Table 4 (or text) for list of trait abbreviations.
[a] Phenotypic correlations (%) have S.E.=3.

fat may also be reduced, though the evidence is not quite as strong as for subcutaneous fat.

The main statistical analysis in this study fitted age but not weight as a covariate. Because, even at the same age, heavier animals tend to have more kg fat, estimated genetic correlations of MW with rump, rib and intra-muscular fat were all positive (0.33, 0.41 and 0.41, respectively). To confirm the association of RFI and fatness ($\hat{r}_g$=0.72 (rump) and 0.48 (rib)) was unrelated to weight, a second analysis was carried out fitting carcase weight as a covariate. Estimated genetic correlations of RFI with rump, rib and intra-muscular fat, adjusted to constant carcase weight were 0.79±0.16, 0.58±0.14 and 0.25±0.17, respectively, marginally higher than the age-adjusted estimates. This implies that selection for reduced RFI is likely to decrease both subcutaneous and intra-muscular fatness at both constant weight and constant age. In fact, for RFI and weight-adjusted rump fat, $\hat{r}_g$ was 0.79, marginally higher than for rump and rib fat ($\hat{r}_g$=0.72, or 0.70 adjusted to constant carcase weight). The strong genetic correlation between RFI and rump fat and higher heritability of fatness than RFI implies that, for our data, single-trait phenotypic selection to reduce weight-adjusted rump fat would reduce RFI more (0.25 kg/day) than direct selection for lower RFI (0.20 kg/day, Table 4).

Thus, if the main economic goal were to improve feedlot efficiency in terms of either (a) reduced FCR or (b) lower RFI, our data suggest this may be achieved without the expense of directly measuring FI) by (a) selecting for WG or (b) selecting against weight-adjusted P8 fat. However, if other traits, or efficiency in other circumstances (e.g. mature cows, or pasture-finished cattle), are also important, the most cost-effective strategy is usually to define the breeding

objective, consider what traits to measure, the optimal age at measurement and the optimal time interval to record data, and so determine the most profitable way of achieving the all desired goals.

3.3.3. RFI, time spent eating, number of eating sessions and eating rates

Estimated genetic correlations of RFI with number of eating sessions (NES) and time spent eating were positive (0.43 and 0.35), but feed intake was not genetically related to either trait. However, NES was markedly affected by breed type. Temperate breed steers ate on average 8–9 times per day, compared to 14–19 times for tropically adapted breed steers and heifers (Table 2). To quantify these effects, NES was modelled (using ASREML software, Gilmour et al., 1998) fitting random effects for breed, sex (of tropically adapted breeds), market, birth herd and test group. This showed that Brahmans ate about 4 more meals per day than Belmont Reds and Santa Gertrudis, which in turn ate 5 to 6 more meals than temperate breeds. Heifers of tropically adapted breeds averaged 2.5 more meals per day than steers. Thus, within breeds, more efficient animals tended to have fewer meals ($\hat{r}_g$=0.43 for RFI and NES). In contrast, breeds adapted to harsher tropical conditions ate more meals per day.

3.4. Comparison with other studies

3.4.1. Feed intake (FI) and RFI

This study shows that, as for younger cattle, RFI is heritable. Genetic progress can be made to reduce RFI of cattle with ad libitum access to a feedlot ration. Our cattle were finished for three different markets, so the range of weights was much greater than other published work (Arthur et al., 2001a,b,c; Herd and Bishop, 2000) and measurements recorded on several breeds of temperate and tropically adapted cattle. The cattle in our study were generally older, heavier (and therefore fatter) with serial, but unrestricted, access to a typical high-energy feedlot diet.

After accounting for age, breed, birth herd, grow-out nutrition and test group, our phenotypic variation ($\hat{\sigma}^2_P$) in FI was 2.35 (kg/day)^2. This is higher than corresponding values of 1.23 and 1.90 (kg/day)^2 for weaner and yearling Charolais bulls (mean on-test ages 344 and 500 days) on a pelleted diet of 57% alfalfa hay and 37% corn (Arthur et al., 2001c). Our phenotypic variation in FI was three times greater than the Trangie post-weaning efficiency test ($\hat{\sigma}^2_P$=0.705 (kg/day)^2), where heifers and bulls (mean on-test age 303 days) had FI measured for 70 days on a pelleted ration (10.5 MJ ME per kg DM and 15–17% crude protein) of 70% alfalfa hay, 30% wheat, and vitamin/mineral supplements (Arthur et al., 2001a).

For RFI, our $\hat{\sigma}^2_P$ of 0.767 was broadly comparable to estimates of 0.583 and 1.097 for weaner and yearling Charolais bulls (Arthur et al., 2001c), but twice as high as the Trangie post-weaning test (0.38; Arthur et al., 2001a). Despite the higher $\hat{\sigma}^2_P$, estimated genetic variation of RFI from our study ($\hat{\sigma}^2_g$=0.139) was little different from that at Trangie (0.149; Arthur et al., 2001a) and lower than for weaner and yearling Charolais bulls (0.186 and 0.274, Arthur et al., 2001c). Our estimated heritability (0.18) was substantially less than at Trangie (0.39), or the weaner and yearling Charolais bulls (0.32 and 0.25). As noted, some groups of animals could be tested for only 50 days, so our measurements of weight gain were less accurate. Moreover, weight gain was not estimated over the same period that feed intake was measured, so genotype×environment interactions for the three different markets may have contributed to a reduced estimate of heritability.

However, if the trait of interest is overall efficiency in the feedlot, all important markets should be considered. About 240,000 of the 650,000 animals on feed in Australia are destined for the domestic market (Foster, 2001), so considerations of efficiency may need to include the domestic as well as export markets, even if efficiency over a broad age range is less heritable than for a small age range.

3.4.2. RFI and fatness

Our older animals on a high-energy feedlot diet were fatter than seedstock cattle. Scan rump and rib fat averaged 12.7 and 9.5 mm, compared to 5.3 and 3.8 mm for bulls and heifers aged 300–600 days from seedstock herds (Robinson et al., 1993) or 5.4 and 4.2 mm and for similarly aged seedstock cattle (Arthur et al., 2001a). The high-energy environment allowed genetic differences in fatness to be expressed. Our genetic variances were 5.3 and 3.6 mm^2, compared to 1.37 and 0.45 (Robinson et al., 1993) and 1.04 and 0.47 mm^2 (Arthur et al., 2001a).

The greater total variation in fatness was accompanied by moderate to high genetic correlations with RFI, e.g. $\hat{r}_g$=0.79 (0.58) for rump (rib) fat adjusted for carcase weight. As noted, depositing 1 kg of fat requires more energy than 1 kg of lean tissue (SCA, 1990), so animals gaining proportionately more fat (than the average of their group) are likely to have higher RFI. Arthur et al. (2001a) reported much lower $\hat{r}_g$ of 0.06 and 0.17 for rump and rib fat (of cattle in seedstock herds) with RFI from the Trangie post-weaning test. Herd and Bishop (2000) found a moderate association between RFI and leanness, $\hat{r}_g$ for RFI with carcase lean content and lean growth rate were −0.43 and −0.47.

Although Arthur et al. (2001a) reported very low $\hat{r}_g$ for RFI and fatness, when progeny from Trangie were feedlot finished at Tullimba, offspring of low RFI parents had lower rib fat (9.2 vs. 10.1 mm, $P<0.05$) and rump fat (11.5 vs. 12.1 mm, $P=0.1$) than high RFI parents, though there was no difference in marbling (McDonagh et al., 2001).

Indeed, after approximately two generations of selection, Arthur et al. (submitted for publication) reported that, at Trangie, 1999-born progeny from the low RFI line had similar 365-day weights to the high RFI line (384 vs. 381 kg), similar weight gains (1.44 vs. 1.40 kg/day), reduced FI (9.4 vs. 10.6 kg/day) and lower rump (6.7 vs. 8.8 mm) and rib fat (5.3 vs. 7.2 mm, at average age of 338 days). Based on realized differences in fat measurements, realized genetic correlations between RFI and rump/rib fat were estimated to be 0.71 and 0.68, respectively (Arthur et al., submitted for publication), similar to the results of our study, rather than the estimates of Arthur et al. (2001a).

Based on the genetic parameters in Tables 4 and 5, one generation of phenotypic selection for lower RFI, keeping 10% of males and 50% of females, is expected to decrease RFI by 0.20 kg/day, and rump and rib fat by 0.90 and 0.50 mm (Table 4). So, for older, feedlot finished animals, correlated responses to single-trait selection for lower RFI would result in a smaller response in RFI, but greater reductions in fatness than realized by the Trangie selection lines. Our calculations (Table 4) imply that selection to reduce weight-adjusted P8 fatness would result in a greater reduction in RFI (0.25 kg/day) than direct selection (0.20 kg/day).

However, both feed composition and timing of the FI test may influence relationships with fatness. The positive association between RFI and fatness is likely to occur only when RFI is measured during the growing and especially the fattening phase. In mature animals, increased fat percentage is usually associated with lower maintenance requirements (Webster, 1985). So, contrary to what was found for growing animals, increased fatness in mature animals may be associated with lower RFI. This was true for adult mice (Bünger et al., 1998); fatness was increased by selection for lower FI (adjusted for weight). In contrast, Archer et al. (1998) reported $\hat{r}_g$ of 0.17 between mature fat proportion and RFI in young mice (mean age 35 days). This suggests that selection for reduced postweaning RFI in mice may, if anything, slightly decrease fatness. Thus, selection from tests of growing animals may lead to decreased fat deposition leading to decreased fatness at maturity, but selection from tests of mature animals may (as was found for mice) increase fatness.

RFI of mature animals may therefore be a different, but related, trait to that in growing ones. Archer et al. (1998) reported a genetic correlation between RFI measured in post-weaning and mature mice of 0.6. For cattle, Arthur et al. (2001c) reported a genetic correlation of 0.75 between post-weaning and yearling measures of RFI in bulls. Though our results for feedlot finished cattle suggest that selection for reduced P8 fat would reduce RFI more than direct selection, tackling this single aspect of efficiency (reducing P8 fat) may not improve the efficiency of mature cows or produce worthwhile benefits for young growing animals.

In other species, the calculation of RFI may include changes in body composition (Luiting and Urff, 1987; de Haer et al., 1993). However, in cattle, it is more practical to measure subcutaneous and intra-muscular fat on entire seedstock herds by ultrasound scanning (Graser et al., 1998), resulting in accurate estimated breeding values (EBVs) for fatness. Unless RFI is also measured on the entire seedstock herd, EBVs for RFI will have lower accuracy. Multi-trait selection, using EBVs for RFI derived by a procedure such as Eq. (2), and EBVs for fatness from scanning large numbers of animals in the seedstock herd, therefore, offers a better way to select animals for reduced RFI and the desired level of

fatness. Where there is a clearly defined breeding objective, EBVs may be appropriately weighted to produce optimal response in the objective.

Such analyses require good estimates of genetic correlations. If, as suggested by the discrepancy in estimates from Trangie and Tullimba data, genetic correlations between RFI and fatness depend on diet, sex, or maturity of the animals, genetic analyses need to allow for this. Changes in fatness should therefore be monitored and consideration given to most appropriate age at which cattle should be tested for feed efficiency.

Several factors affect feed efficiency, including activity levels, visceral mass, efficiency of digestion, rates of protein turnover, as well as fatness. Differences in RFI in Trangie data cannot be explained entirely by differences in body composition. Richardson et al. (1999) indicated that steer progeny of the first generation (G1) of Trangie low-RFI parents had proportionately larger differences in heat production than body composition. McDonagh et al. (2001) found offspring of G1 low-RFI parents had more calpain system protease inhibitor calpastatin in muscle; this is expected to lead to reduced protein turnover.

3.4.3. Subcutaneous and intra-muscular fat

Our estimated genetic correlations of subcutaneous and intra-muscular fat (0.48 and 0.45 for rump and rib fat with IMF%) are consistent with literature estimates for feedlot-finished animals. For example, Gregory et al. (1995) reported genetic correlations of 0.64 and 0.66 for IMF% and marbling with fat trim percentage; 0.33 and 0.44 for IMF% and marbling with adjusted rib fat. Estimates of genetic correlations from data including pasture finished animals may be lower because of genotype×environment interactions. For example, for the entire CRC dataset of feedlot and pasture finished animals of tropically adapted and temperate breeds, Reverter et al. (2002) reported estimates ranging from 0.20 to 0.34 for $\hat{r}_g$ between IMF% and rump/rib fat.

3.4.4. RFI and feed intake pattern

In laying hens, physical activity was shown to be highly correlated with RFI (Luiting et al., 1991; Braastad and Katle, 1989), and to differ between genotypes (Luiting et al., 1994). In pigs, it is recognised that heat production due to activity can account for as much as a third of total heat production. Indeed, variation in feeding activity (number of visits to feeders and daily eating time) accounted for 44% of the phenotypic variation of RFI in pigs (de Haer et al., 1993). RFI had phenotypic correlations of 0.64, 0.45 and 0.51 with time spent eating, number of meals per day and visits to the feeder. The higher correlation for number of visits than number of meals suggests that this effect might be related in some way to activity.

Because of energy costs associated with grazing and ruminating, activity may account for an even greater proportion of energy expenditure of grazing ruminants than poultry or pigs. Although, in a feedlot environment, activity is expected to represent a smaller proportion of total energy expenditure, differences in feeding behaviour may still contribute to variation in RFI. Richardson et al. (1999) found that bulls from a low RFI line were less active (as assessed by pedometer) than bulls from a high RFI line. In our data, RFI had estimated genetic and phenotypic correlations of 0.43 and 0.18 with the number of feeding sessions and 0.35 and 0.16 with time spent eating. Thus, consistent with the phenotypic correlations observed in pigs, within breeds, lower RFI in our cattle was genetically associated with having few meals per day and spending less time eating. However, breed and sex were also important.

Genetic and phenotypic correlations of FI and number of meals per day were 0.16 and 0.18, suggesting that the genetic association of RFI with number of meals per day is not explained simply by differences in FI. Estimated genetic correlations of eating rate with WG (0.53), FI (0.33), MW (0.29), IMF% (0.32), rump fat (0.20) and rib fat (0.22) were all positive. Phenotypic correlations were 0.18, 0.26, 0.20, 0.04, 0.08 and 0.07. Genetic and phenotypic correlations of eating rate with RFI were −0.07 and 0.14. Thus, slow eating had an association with lower growth in the feedlot, eating less, lower weight, and perhaps reduced fatness. Phenotypic correlations for three of the above (between slow eating and lower feed intake, reduced fatness and lower growth) were also noted by de Haer et al. (1993) for pigs. In pigs, eating rate and RFI were unrelated (de Haer et al., 1993).

Time spent eating was not genetically associated with FI, but $\hat{r}_e$ was 0.43 (Table 5). Phenotypic

correlations of time spent eating were 0.30 with FI and 0.16 with RFI. In some countries, time spent eating has been used as an estimate of FI (Engellandt, personal communication). However, these results suggest that it would not provide a particularly good phenotypic estimate of FI in our data, nor would eating rate (phenotypic correlation 0.26, Table 5), though faster eaters tended to eat more. In pigs, de Haer et al. (1993) reported higher phenotypic correlations of time spent eating with feed intake (0.55) and RFI (0.64). Thus, though phenotypic correlations were in the same direction for cattle and pigs, the correlations in our study were lower.

3.5. Variation in β_w and β_g by test group and season

Evidence presented here suggests that β_w and β_g may depend on age or maturity of the animal, and perhaps other factors, e.g. seasonal conditions or diet. We did not find large or significant variation of β_w and β_g with test group. However, cyclical variation in FI of cattle has been noted (Stroup et al., 1987; Wynn et al., 2001) and also seasonal variation (Mossberg and Jönsson, 1996). In Australia, FI has been observed to vary in a cyclical manner by as much as two-fold at certain times; periods of elevated FI coincided for all the cattle tested (Perry, personal communication). This suggests that β_w and β_g may differ according to time of year, maturity or fatness. Variation in β_w and β_g should therefore be monitored and, if necessary, appropriate adjustments made. If β_w and β_g are calculated by regression, a model such as Eq. (2) could be fitted to all relevant data, allowing adjustment factors to vary with age and maturity of the animals.

Estimates of RFI will have maximum robustness if β_w and β_g reflect the true amounts of food needed for these activities. The differences between SCA (1990) and estimates from Eq. (2) (Table 3) have not yet been fully resolved. However, the greatest differences will occur in animals whose growth in the AF pens differs from what might be expected from prior growth. For example, Fig. 1 shows data for a group of tropically adapted Japanese market steers with mean gain of 1.4 kg/day. Weight and FI were strongly correlated (r=0.82), with FI of two steers noticeably below the general trend. Both animals had quite low estimated growth rates (0.26 and 0.78 kg/day in the AF pens) but higher estimates (0.47 and 1.06) for the entire time in the feedlot. They had no noted problems or illness, were not identified as outliers in models of weight over time (Robinson, submitted for publication), and the two estimates of gain were within 1.5 S.D. of each other for the first and 1.8 S.D. for the second steer. However, there is some concern that the low RFI of these two steers was due to their low growth in the AF pens. The first steer was omitted from the genetic parameter analysis (because of its low growth); the EBV for RFI of the second steer may over-estimate its true genetic potential.

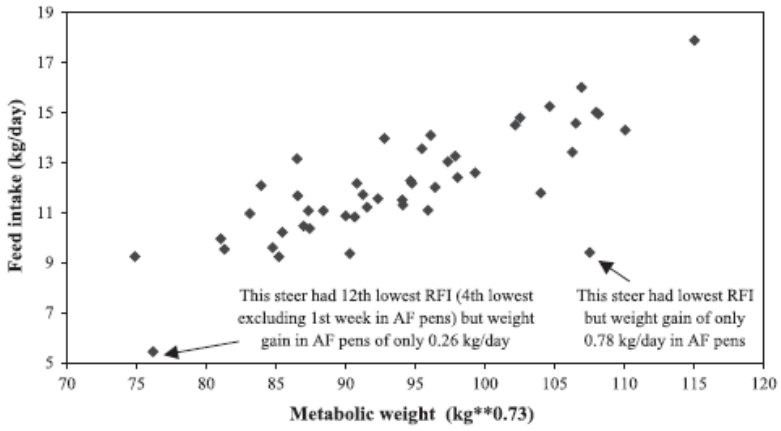

Fig. 1. Relationship between feed intake and metabolic weight for a group of tropically adapted steers finished for the Japanese market.

3.6. Practical implications for selection strategies

Some care may therefore be required if, due to the high cost of measuring FI, small numbers of animals (e.g. seedstock bulls raised in diverse backgrounds) are tested in a central unit. A fast growing, temperamental bull may perform well when undisturbed on open pasture, but fail to settle when transported to a FI test unit. Even without signs of clinical sickness, it may eat little and have inferior growth during the test. There is a danger this animal could be considered exceptionally efficient, unless β_w and β_g represent the true amounts of feed needed for growth and maintenance.

If only a small proportion of the herd is tested, a bull's EBV for FI will rely heavily on its own record, but that for weight and WG will be influenced by data from all relatives. Thus, a bull with good genes for growth, but unsettled behaviour and low phenotypic growth in the AF pens, may have favourable EBVs for weight and growth because of relatives, but a low FI EBV due mainly to unsettled on-test behaviour. An unduly favourable EBV for RFI may result, unless RFI is calculated from actual weight gain in the AF pens, using adjustments for weight and gain that reflect the true amounts of energy required for maintenance and growth.

Further work may help reconcile the discrepancies between SCA and regression estimates of β_w and β_g and so determine the best possible adjustments. Meanwhile, FI tests should be long enough to provide accurate estimates of weight gain. In addition, S.E. of WG estimates should be recorded along with other details, so the consequences of inaccuracy can be assessed. Automatic weighing equipment may help improve accuracy of WG. Consideration could also be given to including on-test WG as a trait in the genetic analysis and treating with caution any animals with low phenotypic on-test growth.

Biases will be much lower in other circumstances, such as whole-herd testing of feed efficiency fitting a model including on-test weight gain. With whole-herd testing, information from relatives helps minimise problems of bias in EBVs, especially given the high genetic correlation between RFI and RFIS in our data. In these circumstances, the recommendation of Kennedy et al. (1993) to use a selection index of weight and FI EBVs may also prove effective.

4. Conclusion

These, and other, analyses have shown that feed efficiency is heritable and genetic improvement is possible. Some consideration needs to be given to the optimal age for measurement, the desired level of fatness and the effect of changes in RFI on fatness. Multi-trait selection is recommended to ensure that selected animals have appropriate EBVs for RFI, weight gain during the feed efficiency test, and desired amounts of subcutaneous and intra-muscular fat and other economically important traits.

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Appendix A. Equations used to calculate energetic requirements for maintenance of weight and weight gain (based on a variant of the formula published by SCA, 1990)

Energy required for gain (MJ/day),

$$\text{Egain} = \text{EBG}^*((20.3 - R)/(1 + \exp(2.4 - 6P) + 6.7 + R)/K_g$$

where: EBG=Empty body gain=0.92*liveweight gain (kg/day); SRWT=Standard Reference Weight=550 kg for heifers and 660 kg for steers; R=250*EBG/(SRWT$^{0.75}$)−1; ALWT=average on-test liveweight; P=ALWT/SRWT; K_g=efficiency of ME use for gain=0.043*MD=0.5203; MD=dry matter feed energy density=12.1 MJ/kg DM.

Energy required for maintenance (MJ/day),

$$\text{Emaint} = K^*0.28^*\text{ALWT}^{0.75}*\exp(-0.03A)/K_m + 0.1^*(\text{Egain})$$

where: K=1.4 for *Bos taurus*, 1.3 for Belmont Red and Santa Gertrudis, 1.2 for Brahmans; A = age in years; K_m = efficiency of ME use for maintenance = 0.5+0.02MD = 0.742.

Energy requirements were converted into kg of feed (as fed) using an average energy value of 10.63 MJ/kg for the feed used. Residual feed intake based on SCA equations for each animal (RFIS) was the difference between feed eaten per day (kg, as fed) and predicted values for maintenance and gain according to these equations.

Note: these equations differ from those of Robinson et al. (1999) in that the efficiencies of ME use, K_m and K_g, here are based on the energy density of dry feed, whereas Robinson et al. (1999) used general estimates, viz. K_m=0.7 and K_g=0.4. In addition, the equation for Emaint has been altered to include a term for age and 0.1*(Egain) has been used in place of the 0.09*(MJ eaten) in the work of Robinson et al. (1999). Most of the difference between the above equations and those of Robinson et al. (1999) relates to the revised values for K_g and K_m, rather than the small changes in the calculation of Emaint.

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Feed Efficiency

SELECTION FOR LOW POSTWEANING RESIDUAL FEED INTAKE IMPROVES FEED EFFICIENCY OF STEERS IN THE FEEDLOT

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SUMMARY
This experiment investigated whether divergent selection on postweaning residual feed intake (RFI) resulted in differences in steer growth, feed intake and feed efficiency over a 70-day test period in the feedlot, and in carcass attributes at slaughter. Selection for low postweaning RFI (high efficiency line, HE) produced steer progeny that ate less per unit liveweight gain compared to steers from high RFI (low efficiency line, LE) parents, with no adverse effects on growth. The HE steers tended to have lower feed conversion ratio (feed:gain; FCR) than the LE steers (7.6 *v* 8.2 kg/kg; $P<0.1$) and had lower RFI (-0.12 *v* 0.10kg/day; $P<0.05$). Significant positive regressions of FCR and RFI with mid-parent estimated breeding value for RFI (EBV_{RFI}) provided further evidence for favourable genetic associations with postweaning RFI. Ultrasound measurement before slaughter showed that HE steers had less depth of fat over their rib and rump and a smaller cross-sectional area of the eye-muscle than LE steers (10.2 *v* 11.6mm, 13.1 *v* 14.8mm, 66.9 *v* 70.6cm^2; all $P<0.05$). The HE 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 mid-parent EBV_{RFI} provided additional evidence of genetic association. There were no differences ($P>0.05$) between HE and LE steer progeny in hot carcass weight or in predicted retail beef yield.
Keywords: beef cattle, feed intake, feed efficiency, selection, carcass

INTRODUCTION
Feeding cattle is a major cost of beef production. Residual (or net) feed intake (RFI) has been proposed as a measure of feed efficiency that is independent of liveweight (LW) and growth rate. It is calculated as the amount of feed consumed net of that predicted based on LW and growth rate. Cattle with low RFI eat less than expected for their LW and growth rate and are therefore more efficient than cattle with high RFI. Postweaning tests of young bulls and heifers from a number of British beef breeds have shown RFI to be heritable (Arthur *et al.* 2001a) and to respond to selection (Arthur *et al.* 2001b). This experiment investigated whether divergent selection on postweaning RFI resulted in differences in steer growth, feed intake and feed efficiency in the feedlot, and in carcass attributes at slaughter.

MATERIALS AND METHODS
Cattle breeding. Cattle breeding and postweaning tests for RFI were undertaken at the NSW Agriculture Research Centre, Trangie, NSW, Australia. Briefly, RFI tests were conducted each year for Trangie-bred Angus bulls and heifers and for Angus, Shorthorn, Hereford and Poll Hereford

heifers purchased from industry herds. Details of the postweaning test procedure are given in Arthur *et al.* (2001a) and establishment of divergent selection lines by Arthur *at al.* (2001b). Male progeny of the matings of Trangie bulls to industry-bred heifers were castrated for subsequent evaluation as steers. The steers were weaned at about seven months of age and then grown on pasture and finished in a feedlot for slaughter. Progeny used in this experiment were born in 1997, 1998 and 1999 and were fed for slaughter at light, heavy and medium LW respectively. The 1997-born steers entered the CRC for Cattle & Beef Quality "Tullimba" Research Feedlot (Armidale, NSW) when they were approximately 13 months old and weighed on average 314kg. The steers born in 1998 entered the feedlot when they were approximately 24 months old and weighed 502kg. The 1999-born steers entered the feedlot at approximately 15 months of age, weighing 338kg.

Measurements in the feedlot. The steers were fed a standard finishing ration that consisted of approximately 75% grain, 10% sorghum hay, 5% protein pellets, plus molasses and vitamin and mineral additives (fresh weight basis). To standardise feed intakes for small differences in metabolizable energy (ME) content between years, daily feed intakes were calculated as kilograms per day of a ration equivalent to 12MJ ME/kg dry matter (DM). Individual feed intakes were recorded by automated feeders (Ruddweigh, Guyra, NSW) for approximately 70 days. Start-of-test, mid-test and end-of-test LW, and average daily gain (ADG) for each steer were calculated from the linear regression of its weekly (year 1) or fortnightly (years 2 and 3) LW against time. At their final weighing the steers had subcutaneous fat depth at the rib (12/13th) and rump (P8 site), and eye-muscle area, measured using an Aloka 500 ultrasound scanner. In year 1, sufficient feedlot yards with individual feed-intake recorders were only available to accommodate the Angus portion of the steers.

Carcass measurements. The weight of the "hot" carcass and depth of fat at the P8 site was recorded before being chilled overnight. Next morning, individual weights of selected, trimmed primal cuts from the left side of each carcass were recorded for subsequent use in prediction of beef yield. Difference in the depth of fat trim by the abattoir in year1 compared to years 2 and 3 required that the predictive equation of Reverter *et al.* (1999) be used for the year 1 steers and the temperate feedlot cattle equation of Reverter *et al.* (2001) for year 2 and 3 steers.

Data analysis. The data set analysed contained 144 low-RFI (HE) line steers and 165 high-RFI (LE) line steers. They were the progeny of 14 HE sires and 15 LE sires, each of which had at least five progeny (mean 10.5 per HE sire; 11.0 per LE sire). Each year, RFI for each animal was calculated as the residual from the regression of individual feed intake on mid-test $LW^{0.75}$ and ADG. Feed conversion ratio was calculated as DM-intake:ADG. Differences in the means for the HE and LE lines were tested within a general linear model. Included in the model were the fixed effects of year, breed, age of dam and selection line, calf age at weaning as a covariate, and line-by-breed and line-by-year interactions. Preliminary analyses showed that age of dam and line-by-breed and line-by-year interactions were not significant ($P>0.05$) and they were dropped from the final model. Since the management of animals in the two selection lines was identical, any observed differences in mean performance of the lines were attributed to genetic selection. In addition, regressions were determined of traits measured on the steers on the mid-value of their sire and dam estimated breeding value for postweaning RFI (EBV_{RFI}). These EBVs were calculated for each parent based on its

performance in postweaning RFI tests conducted at the Trangie Agricultural Research Centre and genetic parameters reported by Arthur *et al.* (2001a). Sire EBV_{RFI} ranged from -0.50 to +1.15kg/day and dam EBV_{RFI} from -0.63 to +0.67 kg/day. Regression coefficients were determined within a model that included year, breed, age of steer and mid-parent EBV_{RFI}. Regression coefficients significantly different from zero were presumed to provide evidence for genetic association.

RESULTS AND DISCUSSION

Performance over feedlot RFI test. Phenotypic correlations for RFI with LW (start-of test and end-of-test LW) and ADG were non-significant ($P>0.05$), as expected given that RFI is calculated to be independent of them. Phenotypic correlations of RFI with actual feed intake ($r=0.50$, $P<0.001$) and FCR ($r=0.27$, $P<0.001$) showed that steers with lower RFI in the feedlot also had a lower feed intake and more favourable FCR. There was no difference between HE and LE progeny in LW at the start of the RFI-test period, in ADG over the test, or in LW at the end of the test (Table 1). Daily feed intake did not differ between the selection lines. However, HE steers tended ($P<0.1$) to have lower FCR than the LE steers and had significantly lower RFI. A generation of divergent selection resulted in a 0.22kg DM/day difference in RFI or 6% better FCR by the HE steers, with no compromise in growth performance. Significant regressions of steer ADG, FCR and RFI on mid-parent EBV_{RFI} provided additional evidence for favourable genetic associations between postweaning RFI of the parents with the growth and efficiency of their progeny in the feedlot.

Body composition and carcass traits. There were significant differences between HE and LE steers in the body composition traits measured by ultrasound before slaughter. The HE steers had less depth of fat over their rib and rump and a smaller cross-sectional area of eye-muscle than LE steers. There was no difference between the HE and LE steers in hot carcass weight. The HE steers had less fat depth at the rump site on the hot carcass and there was a small difference in dressing percentage. There was no difference between HE and LE steers in predicted retail beef yield. There were significant regressions of the three subcutaneous fat measurements, eye-muscle area and dressing percentage on mid-parent EBV_{RFI}, providing evidence for genetic associations.

Reduced fatness accompanying selection for low RFI might be expected from the small but significant genetic correlations reported at the end of postweaning tests (Arthur *et al.* 2001a). Phenotypic correlations for the scanned and carcass measurements with RFI in the feedlot were not significant ($P>0.05$) indicating that these measurements of body composition were not associated with variation in RFI in this experiment. Richardson *et al.* (2001) found that variation in body composition explained only a very small portion of variation in RFI in beef steers.

Selection for low RFI produced steers that ate less per unit gain, with no adverse effects on growth and retail beef yield. Feeding low-RFI steers for slaughter should therefore be more profitable than feeding high-RFI steers. The genetic correlations of postweaning RFI with feedlot RFI and FCR are at present unknown but the regressions reported above indicate that both will be non-zero and positive. The genetic associations of RFI with subcutaneous fatness, eye-muscle area and dressing percentage suggest these traits should be monitored in association with on-going selection for RFI.

Table 1. Feedlot performance and carcass charcteristics of steer progeny from parents selected for low postweaning residual feed intake (RFI: high efficiency) or high RFI (low efficiency), and regression coefficients with mid-parent EBV for postweaning RFI

	Selection line[A]			Regression on
	High efficiency	Low efficiency	P	parental EBV_{RFI}
Feedlot performance				
Number of animals	144	165		
Start of test weight, kg	480 ± 9	490 ± 9		-7.5 ± 7.4
Average daily gain, kg/day	1.53 ± 0.03	1.49 ± 0.02		-0.09 ± 0.05*
End of test weight, kg	586 ±10	593 ± 10		-14 ± 9
Daily feed intake, kg DM/day[A]	12.3 ± 0.2	12.5 ± 0.1		0.04 ± 0.26
Feed conversion ratio, kg/kg[A]	7.6 ± 0.2	8.2 ± 0.2	†	0.59 ± 0.33†
Residual feed intake, kg DM/day[A]	-0.12 ± 0.08	0.10 ± 0.07	*	0.42 ± 0.16*
Preslaughter fat depth over ribs, mm	10.2 ± 0.3	11.6 ± 0.3	*	1.8 ± 0.5*
Preslaughter fat depth over rump, mm	13.1 ± 0.4	14.8 ± 0.4	*	2.4 ± 0.7*
Preslaughter eye-muscle area, cm^2	66.9 ± 0.9	70.6 ± 0.9	*	3.6 ± 1.0*
Carcass				
Hot carcass weight, kg	306 ± 6	314 ± 6		-1.1 ± 5.0
Dressing percentage	52.1 ± 0.3	52.9 ± 0.2	*	1.3 ± 0.5*
Rump fat depth on hot carcass, mm	14.9 ± 0.5	16.5 ± 0.5	*	1.5 ± 0.7*
Predicted retail beef yield, %	67.5 ± 0.3	67.3 ± 0.2		-.27 ± 0.51

P: Probability values: †<0.1; *<0.05. Values are means and regression coefficients ±standard error for Angus and Angus-crossbred steers born in 1987, 1998 and 1999.
[A]Individual feed intakes were recorded on 102 high and 130 low efficiency line steers.

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GENETIC VARIATION IN FEED INTAKE AND EFFICIENCY OF MATURE BEEF COWS AND RELATIONSHIPS WITH POSTWEANING MEASUREMENTS

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INTRODUCTION

Providing feed to animals is a major cost to beef production, and so improving the efficiency with which feed is utilised is an important goal to cattle breeders. In many beef production systems, a large proportion of the feed used is consumed by the cow breeding herd, while young growing animals consume feed which is often of higher value. A review of the literature showed that genetic variation in feed efficiency of younger animals exists, but there is little information available on the relationships of feed intake and efficiency measured post-weaning with these traits in mature breeding cows (Archer *et al*. 1999). This paper reports results from a study examining feed intake and efficiency traits of beef cows and their relationship to similar measurements taken post-weaning.

MATERIALS AND METHODS

Data used in this study were part of a larger project described by Arthur *et al.* (2001). A total of 1781 young bulls and heifers were tested in 10 groups for feed intake, growth and efficiency at Trangie Agricultural Research Centre shortly after weaning at approximately 7 to 9 months. The bulls and some of the heifers were bred using a range of Angus sires from industry over the spring calving Angus cow herd at the Agricultural Research Centre. Other heifers were sourced from industry autumn calving herds with sire identified, and included Angus, Hereford, Poll Hereford and Shorthorn breeds. The test consisted of a 21 day introductory period, followed by a 70 day test period, and animals were fed a pelleted ration with approximately 10 MJ ME/kg dry matter (range was 9.7 to 10.5) and 16 to 18% protein, in an automated feed intake recording facility. Further details on the post-weaning test and experimental design are given by Arthur *et al.* (2001).

Following the post-weaning test, all heifers entered the cow herd (spring or autumn calving) and were given at least two opportunities to calve. Cows were only culled after two consecutive failures to calve. 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 in the automated feeding facility. Data on 751 cows tested in 7 groups was available. The test was conducted in a similar manner to the post-weaning tests, with a 14 to 21 day introductory period and a 70 day test period. The mature cow test used the same pelleted ration as the post-weaning test, and the cows had *ad libitum* access to feed.

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Definition of traits. The same procedures were used to define similar traits for the post-weaning and mature cow tests. Trait abbreviations have been given subscripts of "pw" and "cow" to distinguish measurements taken post-weaning and on mature cows respectively. The average daily feed intake (DFI) of the animals was adjusted to 10 MJ ME/kg dry matter. Weight of individual animals (measured weekly) were regressed against time on test and the regression coefficients used to calculate average daily gain (ADG) over the test period, and mid-weight (average of the start and end weights) raised to the power of 0.73 ($MidWt^{0.73}$). Residual feed intake (RFI) was calculated as actual (daily) feed intake minus feed intake predicted based on ADG and $MidWt^{0.73}$. The equations used to predict feed intake were developed by regression using data from the first seven post-weaning tests (separate equations for bulls and heifers were used) or from all of the mature cow tests. Feed conversion ratio (FCR) was calculated as DFI divided by ADG.

Statistical analyses. Genetic parameters were estimated by REML procedures using the VCE 4.2.5 software (Groeneveld and Garcia-Cortes, 1998). Previous experience analysing post-weaning data from this experiment showed that sampling of sires had created inflated genetic variances for weight traits (Arthur *et al.* 2001). To account for this, records on weight of cows at the weaning of their second calf were extracted from the national Angus and Hereford databases (3630 records from 807 sires) and the experimental dataset (843 cow weight records from 171 sires). This trait was included in all analyses which were conducted as tri-variate analyses, with the other two traits being formed from pair-wise combinations of the traits examined. All traits were analysed using an animal model with a random term for direct additive effect, a fixed effect describing contemporary groups and age as a covariate.

RESULTS AND DISCUSSION

Mature cows during the test were on *ad libitum* intake, and consumed an average of 15.7 kg/day and gained 1.19 kg/day bodyweight. These levels of intake and gain are considerably higher than might be expected from typical pasture-based cattle production systems in Australia. This, together with the fact that the cows were neither pregnant nor lactating during the test, means that caution should be used when extrapolating the results (particularly the variances) to pasture-based production systems. Alternative measures of feed intake at pasture or efficiency at maintenance feeding levels are not readily available for application to a significant number of animals, and so the results from *ad libitum* intake tests remain the best available indication of mature cow efficiency in this context.

Genetic parameters for the mature cow test traits are given in Table 1. All traits were moderately to highly heritable. The heritability of $MidWt^{0.73}_{cow}$ was higher than might be expected from other estimates of mature cow weight, indicating that inclusion of cow-weight in tri-variate analyses did not completely account for inflated genetic variance for growth traits which is a feature of this data set. However, the main focus of this study are the genetic relationships between traits, which are unlikely to be strongly influenced by this problem. Importantly, the results indicate that there is significant genetic variation in DFI_{cow} and the two measures of cow efficiency, RFI_{cow} and FCR_{cow}. Additive variances for these traits were markedly greater compared to those for the same trait measured post-weaning (Arthur *et al.* 2001). Moreover, DFI_{cow} was strongly related to RFI_{cow} at both phenotypic and genetic levels.

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The phenotypic and genetic relationships between traits measured during the post-weaning and mature cow tests are presented in Table 2. At the phenotypic level, most traits (with the exception of $MidWt^{0.73}$) were only moderately correlated from post-weaning 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 post-weaning and mature DFI and RFI were strong, with the genetic correlations approaching unity. These correlations are high, but are consistent with other analyses of this data using alternative approaches.

Table 1. Genetic parameter estimates among traits measured on mature cows. Heritabilities[A] are given on the diagonal, with genetic and phenotypic correlations given above and below the diagonal respectively

	DFI_{cow}	ADG_{cow}	$MidWt^{0.73}_{cow}$	RFI_{cow}	FCR_{cow}
Mean	15.7 kg/d	1.19 kg/d	110 $kg^{0.73}$	-0.54 kg/d	14.3 kg/kg
SD[b]	1.7	0.26	6	1.42	4.4
DFI_{cow}	**0.28**	0.57	0.45	0.71	-0.57
ADG_{cow}	0.42	**0.33**	0.37	0.02	-0.87
$MidWt^{0.73}_{cow}$	0.41	0.21	**0.71**	-0.21	-0.12
RFI_{cow}	0.88	0.04	0.07	**0.23**	-0.21
FCR_{cow}	-0.04	-0.73	0.01	0.23	**0.26**

[A] Heritabilities and additive variances are average results from 19 tri-variate analyses including traits in this study as well as other traits not reported here. [B]Phenotypic standard deviation.

The results show that selection for lower RFI_{pw} (a measure of feed efficiency which accounts for both maintenance and growth requirements) measured postweaning will lead to a reduction in the intake of cows together with a slight increase in cow weight ($MidWt^{0.73}$), thus improving the efficiency of the cow herd. Selection to improve FCR_{pw} (a "gross" measure of feed efficiency) will cause an increase in cow weight, with little change in cow intake. However, selection on a multi-trait index including information on feed intake (irrespective of what form feed intake is expressed in) will allow the balance between increasing growth and decreasing cow intake to be economically optimised. More importantly, the results indicate that strong genetic relationships exist between feed intake and efficiency measured post-weaning and these traits in the breeding herd.

The genetic correlations of feed intake and residual feed intake from young growing animals to mature adults have few counterparts for comparison. Niewhof *et al.* (1992) found a genetic correlation between RFI of heifers measured post-weaning and during first lactation of 0.58. Archer *et al.* (1998) found a genetic correlation between RFI of mice post-weaning and at maturity of 0.60.

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Table 2. Phenotypic and genetic relationships between traits measured post-weaning and on mature cows

	Mature cow traits				
Post-weaning traits	DFI_{cow}	ADG_{cow}	$MidWt^{0.73}_{cow}$	RFI_{cow}	FCR_{cow}
Phenotypic correlations					
DFI_{pw}	0.51	0.24	0.60	0.34	0.03
ADG_{pw}	0.33	0.28	0.61	0.09	-0.07
$MidWt^{0.73}_{pw}$	0.34	0.18	0.70	0.10	0.02
RFI_{pw}	0.34	0.06	-0.02	0.40	0.06
FCR_{pw}	0.09	-0.11	-0.13	0.20	0.10
Genetic correlations					
DFI_{pw}	0.94	0.67	0.69	0.69	-0.12
ADG_{pw}	0.73	0.72	0.91	0.20	-0.30
$MidWt^{0.73}_{pw}$	0.51	0.39	0.82	0.06	0.05
RFI_{pw}	0.64	0.22	-0.22	0.98	-0.06
FCR_{pw}	0.15	-0.33	-0.54	0.75	0.20

CONCLUSION

There appears to be a strong genetic relationship between intake-related traits from shortly after weaning to maturity, indicating that some biological processes with genetic variation regulating intake and efficiency post-weaning are similar to processes regulating intake of adult animals. This is consistent with the observation that feed intake matures at a faster rate than bodyweight (Taylor *et al.* 1986). These strong relationships present the opportunity to utilise selection to improve feed efficiency of growing animals and mature cows simultaneously, based on measurements taken post-weaning prior to selection decisions being made.

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Maternal productivity of Angus cows divergently selected for post-weaning residual feed intake

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Abstract. Data on 185 Angus cows were used to study the effect of divergent selection for residual feed intake 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 estimated breeding value for residual feed intake 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 ± 0.4 *v.* 9.3 ± 0.4 mm), 2001 (11.3 ± 0.4 *v.* 9.8 ± 0.4 mm) and 2002 (7.0 ± 0.5 *v.* 5.7 ± 0.5 mm) 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 658 kg. 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). The study indicates that after 1.5 generations of divergent selection for residual feed intake there are no significant selection line differences for maternal productivity traits.

Introduction

Providing feed for cattle is the single largest input cost in most beef production enterprises. Therefore, genetic improvement in the efficiency of feed utilisation could help in reducing the cost of production. In recent years there has been renewed interest in research in this area, and several reviews have been published (Archer *et al*. 1999; Arthur *et al*. 2004; Herd *et al*. 2003).

Feed cost for maintenance is estimated to represent at least 60–65% of the total feed requirements of the cow herd, with considerable variation among individual animals, independent of their liveweight (Montaño-Bermudez and Nielsen 1990; Parnell *et al*. 1994). Residual feed intake (RFI) is a measure of feed efficiency that seeks to capture some of this variation in maintenance requirements (Herd *et al*. 2003). Residual feed intake is the difference between actual feed intake and the expected feed requirements for maintenance of liveweight and some measure of production (such as growth in beef cattle). Therefore animals with lower RFI values are more efficient in feed utilisation than those with higher RFI values. Residual feed intake is sometimes referred to as net feed intake (NFI). Since 2002, the BREEDPLAN beef genetic improvement system routinely publishes NFI estimated breeding values (EBV) for Angus and Hereford–Polled Hereford breeds. The NFI EBV with minimum accuracy of 50% for each breed can be viewed at http://breedplan.une.edu.au/.

A review of recent studies conducted by Herd *et al*. (2003) indicates that feed costs can be reduced in the slaughter generation with little impact on growth through selection for RFI. The review also indicated that selection for post-weaning RFI may lead to substantial savings in feed cost in the cow herd. However, there is currently no substantive information on the impact of selection for RFI on the productivity of the breeding herd females. The objective of this study was to evaluate the maternal productivity of Angus cows divergently selected for post-weaning RFI, by examining: (i) the changes in size and body composition of cows; (ii) reproductive performance and productivity of cows; and (iii) preweaning growth of the progeny of the cows.

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Materials and methods

Feed efficiency selection lines

Starting with the 1993-born Angus cattle at the Agricultural Research Centre, Trangie, NSW, Australia, a post-weaning feed intake and efficiency test was conducted each year using an automated feeding system which delivers and records individual animal feed intake. The test period was for 70 days, after a 21-day adjustment period. It was conducted during the post-weaning period, at an average start of test age of 268 (s.d. = 23) days. Creation of the RFI selection lines commenced in 1994 with the establishment of high and low feed efficiency selection lines. The 1993- and 1994-born cattle formed the foundation herd. After completion of the feed efficiency testing of the 1993-born animals in 1994, the females were allocated to the selection lines based on their individual RFI values. Females with low RFI values (<0) are more efficient (consume less feed than that predicted for growth and maintenance) and were allocated to the low RFI line, and those with high RFI values (≥0) were allocated to the high RFI line. The 3 most efficient bulls born in 1993 were allocated to the low RFI line and the 3 least efficient bulls to the high RFI line. A similar breeding design was followed in subsequent years up to the 1998 matings. Throughout this period the sole selection criterion for all replacement bulls and heifers in the high and low lines was individual post-weaning RFI. There was very little selection in the females due to limited numbers. In the males however, 3–6 bulls were selected per line each year, depending on the number of females available to be mated. The first progeny of selected parents were born in 1995 and the last in 1999.

For the computation of RFI, the growth of each animal during the 70-day test was modelled by linear regression of weight (measured weekly) on time (days), and the regression coefficient represented average daily gain (ADG). Start and end of test weights were also computed from the regression parameters. The mean weight (MWT) of an animal during the test was computed as the average of the start and end of test weights. Metabolic liveweight (MMWT) was calculated as MWT^{73}, and feed intake (FI) was standardised to a concentration of 10 MJ ME/kg dry matter. A linear regression model of FI on MMWT and ADG, with test group and sex included as class variables, was fitted to the data. The regression coefficients from this model (coefficient of determination = 0.69) were used to obtain expected feed intake of all animals based on ADG and MMWT. Residual feed intake was calculated as the actual (measured) FI minus that predicted using the regression equation.

The divergence of the selection lines is presented in Figure 1, using the estimated breeding values for post-weaning RFI of selection line progeny across years (Arthur *et al.* 2001*a*). This breeding design was chosen to provide a rapid divergence in RFI between the high and low selection lines. Additional information on the creation of the lines and response to selection can be obtained from Arthur *et al.* (2001*a*, 2001*b*).

Breeding herd management

The study covered 3 mating seasons, beginning with the 2000 matings, which commenced in September of that year. The study concluded at the weaning of the 3rd cohort of calves, in March 2004. During this period, there were about 450 females in the breeding herd each year, but not all were involved in this study. The breeding herd was managed as one unit all year round, except during the mating season where the females were split into mating groups. Table 1 provides an outline of activities and measurements taken in one breeding cycle.

The females were on pasture all year round. Perennial pastures included windmill grass (*Chloris truncata*), spear grass (*Stipa* spp.), and wallaby grass (*Danthonia* sp.). Annuals were primarily barley grass (*Hordeum leporinum*), rats-tail fescue (*Vulpia myuros*), burr-medic (*Medicago* spp.) and crowsfoot (*Erodium* sp.). Much of the summer feed consisted of dry residue from winter annuals. Pasture quality and quantity was influenced by rainfall. The annual rainfall at the research centre is 480 mm and is distributed evenly across the year with no distinct peak periods. The rainfall during the period of study and the long-term average rainfall is presented in Figure 2. In general, rainfall during the period of study was lower than the long-term average, with the period between March 2002 and February 2003 recording only 49% of the expected long-term average. The conditions at the Trangie area met the official drought declarations criteria from June 2002 to August 2003, and again from February 2004 to March 2004. Supplementary feeding of hay and grains were provided when necessary to minimise the effect of drought.

The 2000 matings were by natural service. Heifers (1999-born) were exposed to bulls in single sire mating groups starting in September, for 9 weeks at about 14 months of age. Cows were exposed to bulls in single sire mating groups for 9 weeks, starting 3 weeks after the commencement of matings in the heifers. Bulls from the RFI selection lines were used for the matings at a ratio of 30 females per bull. At that stage matings were designed to continue divergent selection based on RFI, but also to set up a control line with random mating. Hence, about 80% of females allocated to each bull were from the same RFI selection line as the bull while the remainder were from the other selection line. For the 2001 and 2002 matings a small number of randomly selected females were exposed to bulls right from the beginning of the mating season in October. These females were not involved in this study. Most of the females, however, were mated by

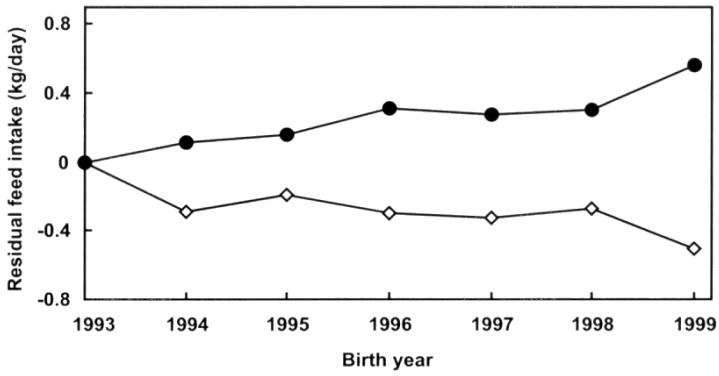

Figure 1. Trends in estimated breeding values for post-weaning residual feed intake (RFI) for the low (◇) and high (●) RFI selection lines.

Table 1. Outline of activities and measurements taken in one breeding cycle

Stage in breeding cycle	Month	Activity or measurement	Comments
Pre-mating	Early September	Weight and ultrasound fat depth measurements of heifers taken Start of mating season	Heifers only
	Late September	Weight and ultrasound fat depth measurements of cows taken Start of mating season Weight of calves taken	Cows only
Post-mating	December	Weight of heifers taken and end of mating season (in November) Weight of cows taken and end of mating season Weight of calves taken	All breeding herd females
Pregnancy test	January–February	Pregnancy testing by ultrasound	All breeding herd females
Weaning	March	Weaning of calves Weight and height of calves taken Weight and ultrasound fat depth measurements of cows taken	All breeding herd females
Pre-calving	June	Weight of cows taken	
Calving	July–September	Weight and body measurements of calves taken	Heifers
	August–September	Weight and body measurements of calves taken	Cows

2 rounds of artificial insemination (AI) followed by cover bulls. Semen from 10 Angus bulls from industry herds were used for the AI each year. A total of 3 Angus bulls from industry herds were used each year as cover bulls. Males (semen and bulls) were randomly allocated to cows.

The AI was conducted by a commercial artificial breeding company, using standard protocols. The total number of cows programmed for insemination was split among 3 (approximately equal sized) groups, commencing the synchrony protocol on 3 consecutive days. The cows were synchronised for AI using a protocol which combines the use of progesterone via a slow release intravaginal device (EAZI-BREED CIDR, Pfizer Australia Pty Ltd, West Ryde, NSW), administered for 8 days, with an initial injection of oestradiol benzoate (ODB, 2 mL Cidirol, Pharmacia Inc., Pfizer Australia Ltd) at the time of CIDR insertion, an injection of prostaglandin (2 mL Juramate, Jurox Pty Ltd, Rutherford, NSW) given at the time of CIDR removal, and a second injection of ODB (1 mL Cidirol) given 24 h after CIDR removal. Heat detection devices (KMAR Heatmount detectors, Kamar Inc., Steamboat Springs, CO) were applied to the cows 24 h after CIDR removal. A day later, cows were inspected to determine those in oestrus, and these were inseminated first, after which the rest of the cows were also inseminated. Following insemination, the groups were prepared for re-synchrony of those returning to service. CIDR devices (washed and re-cycled from the first administration) were re-inserted into these cows 15 days after initial device removal, and they were given ODB injections (1 mL Cidirol) at the same time. The devices were then removed 8 days later and heat detectors applied. Cows returning to service were detected on heat and presented for insemination as above. After that a cover bull was allocated to each of the groups of cows from early November to mid-December.

All females were tested for pregnancy by ultrasound in late January or early February each year. The calving season spanned from July to September, with most calves born in August. At calving, assistance was given only after prolonged labour. Calves were tagged and

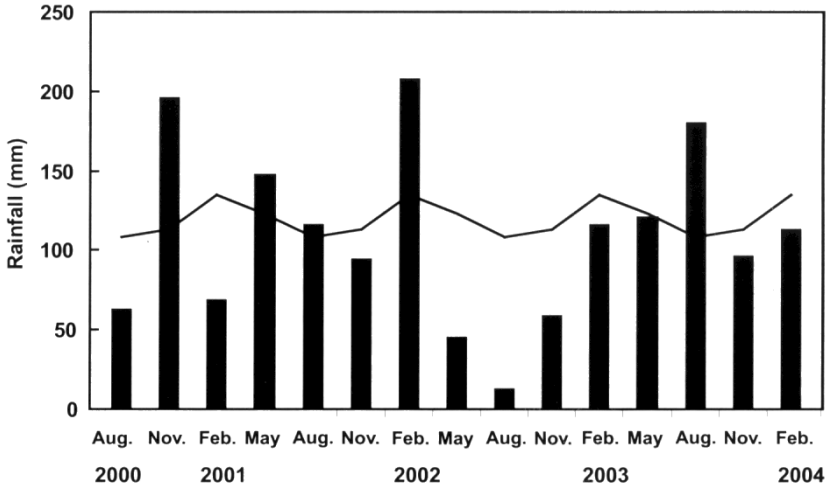

Figure 2. Quarterly rainfall during the period of the study (bars) and quarterly long-term (1887–2003) average rainfall (line) at the Agricultural Research Centre, Trangie. Data represents the total rainfall, or the long-term average rainfall, for the quarter ending in the month indicated.

measurement of liveweight and size (height, length and girth) recorded at birth. For the 2002- and 2003-born calves, which resulted from AI plus cover sire matings, parentage was confirmed through DNA fingerprinting. Calves nursed their dams until they were weaned at about 225 (s.d. = 17) days of age. During the period of this study, all males were castrated at about 3 months of age.

Milk production by cows was measured during their second lactation by the weigh–suckle–weigh method (Totusek *et al*. 1973). The 1997-, 1998- and 1999-born cows were therefore measured in 2000, 2001 and 2002, respectively. Each year a date was chosen, based on calving dates, such that cows would be measured in early lactation (at an average of 60 days post-partum). Thus cows with very young calves (less than 25 days old) and those more than 85 days post-partum were not measured. The total number of cows measured was 122, with a mean of 58 (s.d. = 11) days post-partum. At 1100 hours on the day of the milk yield determination, calves were separated from their dams. At 1500 hours calves were taken to their dams to suckle and each calf was observed to have suckled by 1530 hours, after which cows and calves were separated. At 0730 hours the next day, calves were weighed, allowed to suckle their dams and re-weighed. The difference in the weight of calves represented the overnight milk production of their dams from 1530 hours the previous day. A 6 h separation of cows and calves was effected immediately until 1330 hours, after which calves were weighed, allowed to suckle their dams, then re-weighed to determine the 6 h milk production. The sum of the overnight and 6 h milk production values, which represented production over a 22 h period, was then proportionally corrected to 24 h production, and is referred to as 'milk yield' in this study.

Animals and traits studied

For this study, records on all Angus heifers and cows generated in the last three years of the high and low RFI selection were used. These were the 1997-, 1998- and 1999-born females, and there were 184 for the 2000 matings. These females were the result of 1.5 generations of selection, on average. There was a sizeable degree of divergence between the selection lines, with the mean estimated breeding values for RFI for the high and low RFI females being 0.5 kg/day and –0.3 kg/day, respectively. Due to pressure to reduce stock numbers at the research centre, females that failed to calve were culled. A total of 9 sets of twins were born during the study, and records on the twin calves and their dams were not included. Coupled with a few deaths and culling for physical injury, the number of females available for the 2001 and 2002 matings were 153 and 132, respectively.

Traits studied included the weight and subcutaneous fat depth measured by ultrasound at the 12th/13th rib (rib fat) and on the rump (P8 fat) of the cows at different stages during the 3 breeding cycles of this study. The stages in the breeding cycle and the months in which the records were taken are outlined in Table 1. Calf traits studied included birth weight, age-corrected weaning weight and preweaning ADG. Weaning weight of calves were corrected to 220 days of age and is referred to as 220-day weight. Reproductive performance of females was assessed by pregnancy rate, calving rate and weaning rate, all expressed per cow exposed to a bull, either by AI or natural service. These rates were coded as binomial traits (1, yes; 0, no). For example, a cow that is tested pregnant received a code of 1, while a cow that is tested non-pregnant received a code of 0. The 2001 and 2002 mating seasons involved 2 rounds of AI followed by natural service cover bulls. To determine the percentage of cows calving to the natural service cover bulls, the calving data were coded as binomial trait, with those calvings resulting from AI sires coded as 0 and those from the natural service bulls coded as 1. Calving date was also studied as one of the reproductive performance traits, and was coded as the number of days from 1 January of the calving year. Cow productivity traits studied included milk yield, and weight of calf born or weaned per cow exposed to bull.

Statistical analyses

For cow weights, fat depths and milk yield, the general linear model (GLM) procedure of SAS (1989) was used. The model used included the fixed effects of selection line (Selnline; low or high line), age of cow at the start of the study (Agecow; 1, 2 and 3 years of age), their interaction (Selnline × Agecow), sire of cow (n = 30) nested within Selnline × Agecow [Sire(Selnline × Agecow)] and random error. Although the Selnline × Agecow effect was not significant, it was left in the model, due to the nested Sire effect. The Sire(Selnline × Agecow) effect was used as the error term for testing for the significance of the effects of Selnline, Agecow and Selnline × Agecow interaction.

For cow productivity traits a full model that included the fixed effects of Selnline, Agecow, mating year (Mateyear; 2000, 2001 or 2002), their 2-way interactions, Sire(Selnline × Agecow) and random error, was used in a preliminary analysis using the GLM procedure in SAS (SAS Institute, Cary, NC). In another preliminary analysis rib fat depth at pre-mating in 2000 was used as a covariate in the above model, but was found to be non significant. After removing non-significant (P>0.05) interaction terms (except Selnline × Agecow) and the covariate, the final model used included Selnline, Agecow, Mateyear, Selnline × Agecow, Sire(Selection × Agecow) and the random error. Although the Selnline × Agecow effect was not significant, it was left in the model, due to the nested Sire effect. The Sire(Selnline × Agecow) effect was used as the error term for testing for the significance of the effects of Selnline, Agecow and Selnline × Agecow interaction. All other terms in the model were tested against the random error. Correlation analysis, using the CORR procedure in SAS, was run with rib fat depth at pre-mating and the cow reproduction and productivity traits.

For calf growth traits, the model used included the fixed effects of Selnline (of dam), Sire of dam nested within Selnline [Sire(Selnline)], age of dam (Agedam; 2, 3, 4 or over 4 years), sex of calf (male or female) and the random effects of sire of calf (n = 42) and error. Age of dam was the age (in years) of the calf's dam at calving. However, due to low numbers in the 6-year olds, this group was combined with the 5-year olds and referred to as 5^+ year group. In a preliminary analysis it was found that Agedam and Year of birth of calf could not be fitted simultaneously in the above model due to confounding between the 2 effects. The Year of birth effect was therefore dropped from the model. The Sire(Selnline) effect was used as the error term for testing for the significance of the effect of Selnline. All other terms in the model were tested against the random error.

The binomial data (pregnancy, calving and weaning rates and the percentage of calves born by cover bulls) were analysed using the generalised linear model (GENMOD) procedure of SAS with a logit link function. The model fitted included the fixed effects of Selnline, Agecow and Mateyear. Interactions were omitted from the model because preliminary analysis indicated that the interaction effects were not significant. Significance test for effects were based on the Wald chi-square statistic.

Results and discussion

Effect of RFI selection line

The changes in liveweight and rib fat depth of low and high RFI cows over three breeding cycles are presented in Figure 3. Rib fat depths were about 25% less than P8 fat depths. However, the effects of selection line and other factors on the 2 measures of fat depth were similar so only the results for rib fat depth are reported. Mean rib fat depth was lowest (6.1 mm) at the 2003 weaning (March) and highest (17.2 mm) at the beginning of the mating season (September) in 2003. For each breeding cycle (September–September), rib fat was highest at the beginning

of the mating season (September) and lowest at the weaning of their calves (March). This period of decline in fat corresponds to the lactation period, suggesting that there is mobilisation of body fat for lactation. This is followed by a period of fat deposition (March–September), with the exception of 2002 where fat deposition after weaning did not occur. These changes in rib fat depth across the breeding cycles were also observed in liveweight, however, they were not as pronounced. The growth of cows was characterised by a period of weight stasis or weight loss from the beginning of mating to weaning (September–March) followed by 6 months of weight gain. The exception was for 3 months after March 2002, where cows lost weight instead of gaining weight. Rainfall for the period between March 2002 and February 2003 was only 49% of the expected long-term average (Fig. 2). This means that during this period pasture quality and quantity was limiting. This explains why the typical pattern in growth and fat deposition was not observed during this period. The provision of supplementary feed might only have helped in moderating the impact of this severe drought.

The authors are not aware of any other selection experiments for RFI in beef cattle with which to compare results, except one in France where selection was based on an index that combined final weight and RFI (Renand *et al.* 1998). The formula used in the computation of RFI in the French experiment is slightly different from that used in this study; hence the 2 sets of results might not be directly comparable. Inferences will, therefore, be made using appropriate genetic correlations in beef cattle, where

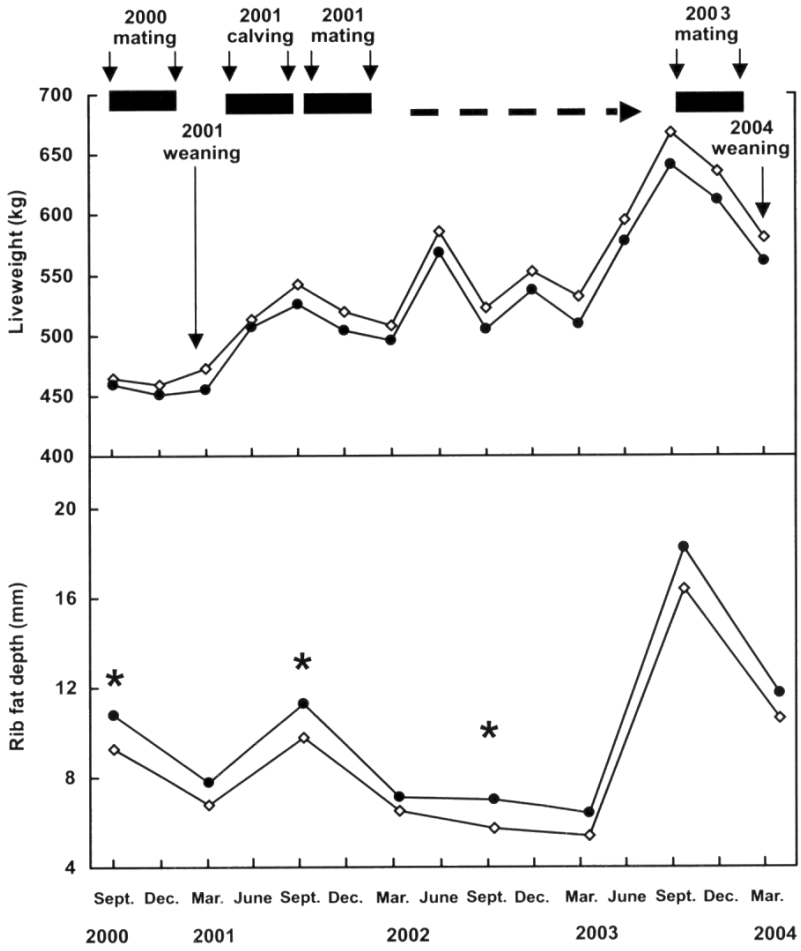

Figure 3. Liveweights and rib fat depths measured over 3 breeding cycles in cows divergently selected for low (◇) and high (●) post-weaning residual feed intake. Significant selection line differences are indicated by * ($P<0.05$).

available, as well as results from selection experiments in other species.

High RFI line cows were generally fatter than low RFI cows (Fig. 3), however, the differences in fatness were significant only at the point in the breeding cycle where the fatness of the cows was at its highest (beginning of the mating seasons in September). The mean rib fat depth for the high RFI *v.* low RFI cows were 10.8 ± 0.4 *v.* 9.3 ± 0.4 mm, 11.3 ± 0.4 *v.* 9.8 ± 0.4 mm and 7.0 ± 0.5 *v.* 5.7 ± 0.5 mm at the beginning of the 2000, 2001 and 2002 mating seasons, respectively. The exception to this general trend was the mean rib fat at beginning of the mating season (September) in 2003, where no significant differences were obtained between the selection lines. Arthur *et al*. (2001*b*) reported a low genetic correlation (0.17 ± 0.5) between post-weaning RFI and post-weaning rib fat depth. The data used by Arthur *et al*. (2001*b*) included records on the females in this study (collected when they were younger), and on their male siblings. The low magnitude of the differences in rib fat depth between the high RFI and low RFI cows in this study and the inconsistency of the statistical significance of the differences is therefore not unexpected, given the low genetic correlation reported for the post-weaning period (Arthur *et al*. 2001*b*).

The low RFI cows were heavier than high RFI cows, however, the differences were not significant ($P>0.05$) at any stage in the breeding cycle (Fig. 3). By definition, RFI should be phenotypically independent of liveweight and this has been shown to be the case in studies where the liveweights were measured at an age comparable to that at which RFI was measured (Arthur *et al*. 2001*b*, 2001*c*; Schenkel *et al*. 2004). The results of this study indicate firstly, that the relationship goes from post-weaning, through to maturity. Second, that the relationship was not only phenotypic, but was expressed at the genetic level, through the selection lines.

Predicted means for reproductive performance (pregnancy, calving and weaning rates) are presented in Table 2. There were no significant ($P>0.05$) selection line differences in any of the reproductive performance traits. Least squares means for calving date, milk yield and cow productivity traits are presented in Table 3. Selection line differences in milk yield were also not significant. Studies by Totusek *et al*. (1973) and Jenkins and Ferrell (1984, 1992) indicate that in beef cattle peak lactation is achieved between 7 and 11 weeks post-partum and, thus, the milk yield measured in this study (average of 60 days post-partum) was close to peak lactation. Mean milk yield obtained in this study (7.7 kg/day) is similar to that (8.0 kg/day) reported by Arthur *et al*. (1997) in crossbred beef cows on medium quality pasture, also measured close to peak lactation. Cow productivity is a composite index that incorporates reproductive performance of the cow, mothering ability and growth of her calves during the period of nursing. Selection line differences in the cow productivity traits were also not significant.

There was no significant ($P>0.05$) selection line difference in calving date (Table 3), however, there was a trend ($P<0.10$) towards low RFI cows calving later (mean of 5 days) than high RFI cows. This trend is not a cause for concern as it did not affect reproductive performance (i.e. pregnancy, calving and weaning rates). However, it needs to be monitored, as there is the possibility that it could be significant after more generations of selection and further divergence of the selection lines. This caution is based on reported associations between RFI and reproductive rate in some studies on multiparous animals. Hagger (1994) reported an unfavourable association between egg number and RFI in poultry, while Hughes and Pitchford (2004) reported a weak but unfavourable correlation between litter size and RFI in mice. Nielsen *et al*. (1997) also reported an unfavourable response to 15 generations of selection for heat loss in mice. The effect of selection for heat loss is expected to be similar to that of selection for RFI.

The correlation coefficients between rib fat depth at pre-mating and the reproductive traits including calving date ranged from 0.002 to 0.03, and were not significantly different from 0. As well, pre-mating rib fat depth was not a significant covariate for these traits. Although there were

Table 2. Predicted means (± s.e.) for transformed (T) and untransformed (UT) values for maternal productivity traits of cows divergently selected for residual feed intake (RFI)

The number of cows exposed to a bull was 222 for low RFI and 247 for high RFI

Trait	Data type	Selection line		Level of significance
		Low RFI	High RFI	
Pregnancy rate (%)[A]	T	2.38 ± 0.40	2.35 ± 0.40	n.s.
Pregnancy rate (%)[A]	UT	90.5	90.2	
Calving rate (%)[A]	T	2.19 ± 0.37	2.09 ± 0.36	n.s.
Calving rate (%)[A]	UT	89.2	88.3	
Weaning rate (%)[A]	T	1.52 ± 0.29	1.44 ± 0.29	n.s.
Weaning rate (%)[A]	UT	81.5	80.2	

[A]Per cow exposed to bull through natural service or artificial insemination.

Table 3. Least squares means (± s.e.) for maternal productivity traits of cows divergently selected for residual feed intake (RFI)

The number of cows exposed to a bull was 222 for low RFI and 247 for high RFI

Trait	Selection line		Level of significance
	Low RFI	High RFI	
Calving day[A]	215 ± 2	210 ± 1	$P = 0.07$
Milk yield (kg/day)[B]	7.5 ± 0.3	7.8 ± 0.3	n.s.
Weight of calf born per cow exposed (kg)	33.6 ± 1.1	31.8 ± 1.0	n.s.
Weight of calf weaned per cow exposed (kg)	191.3 ± 8.4	198.4 ± 7.7	n.s.

[A]1 January is day 1 each calving year.
[B]The number measured for milk yield was 56 and 66 for low and high RFI cows, respectively.

significant differences between the low RFI and high RFI cows in pre-mating rib fat depth, these results suggest that, in this study, the differences in fatness were not related to reproductive performance and the trend in calving date. For each of the 3 calving seasons, there were a few (1–4%) low RFI cows that were yet to calve after all the high RFI cows had finished calving. Differences in calving date can be due to differences in gestation length or differences in how early in the mating season the cow became pregnant. The latter is influenced by the earliness with which cows resume normal oestrus activity during the post-partum period. The 2 rounds of AI followed by natural service cover bulls employed during the 2001 and 2002 matings, resulting in the 2002 and 2003 calvings. Examination of the parentage of the 2002- and 2003-born calves indicate that 22% of the calves born to the low RFI cows were by the natural service cover sires provided late in the mating season, compared with 13% in the high RFI cows. While this difference is not significant ($P = 0.07$), it points to the fact that there is the need to monitor the differences in how early after calving that cows resume their normal oestrus activity.

The least squares means for the effect of the cow's selection line on the preweaning growth performance of her calf is presented in Table 4. The birth weight, preweaning ADG and 220-day weight of calves were not significantly ($P>0.05$) influenced by the selection line of her dam. The sires used on the cows to produce these calves were from the RFI selection lines for the 2000 matings and from the industry herds for the 2001 and 2002 matings. A random effect of calf's sire was also fitted in the model for the analysis. The cow's selection line effect on calf performance is therefore not confounded with sire effect, and the results are as expected: that, selection for RFI should not have a significant effect on calf performance.

Effect of other factors

Age of cow had a significant ($P<0.05$) effect on liveweight of the cows from the beginning of the study (September 2000 pre-mating weight) up to the December 2002, post-joining weights. The oldest (1997-born) cows were the heaviest while the youngest (1999-born) cows were the lightest. The age of cow effect was not significant after December 2002, and this is a reflection of the fact that as the cows approached maturity, it is expected that age effect on weight will be minimal. A similar pattern was observed for rib fat depth where the age of cow effect was significant ($P<0.05$) from the beginning of the study to the September 2002 measurement taken at the beginning of the mating season. The oldest (1997-born) cows were significantly ($P<0.05$) fatter than the 2 younger cohorts (1998- and 1999-born cows). The differences in fatness between the 1998- and 1999-born cows were not significant except at the 2001 (March) weaning, at which the 1999-born cows were significantly fatter. The age of cow effect on rib fat depth was not significant from the March 2003 measurement to the end of the study. Age cow at the start of the study had a significant ($P<0.05$) effect on weaning rate. The youngest cows (1999-born) had significantly lower rate (73.7%) than that for 1998 (84.0%)- and 1997 (84.8%)-born cows.

Age of dam had a significant ($P<0.05$) effect on preweaning ADG and 220-day weight. Both traits showed a general linear trend, with mean values increasing with

Table 4. Least squares means (± s.e.) for preweaning growth of calves from cows divergently selected for residual feed intake (RFI)

The number of calves was 198 for low RFI and 217 for high RFI

Trait	Selection line of dam		Level of significance
	Low RFI	High RFI	
Birth weight (kg)	36.9 ± 0.5	36.2 ± 0.5	n.s.
Preweaning average daily gain (kg/day)	0.88 ± 0.01	0.89 ± 0.01	n.s.
220-day weight (kg)	230.8 ± 2.7	230.6 ± 2.6	n.s.

increasing age of dam. Means for ADG were 0.75 ± 0.04 kg/day, 0.85 ± 0.02 kg/day, 0.93 ± 0.01 kg/day and 1.01 ± 0.02 kg/day for calves with 2, 3, 4 and ≥5-year-old dams, respectively. The corresponding values for 220-day weight were 197.5 ± 8.2 kg, 223.3 ± 4.3 kg, 240.5 ± 2.2 kg and 261.3 ± 5.2 kg, respectively. Although the effect of age of dam on calf birth weight was not significant ($P = 0.09$), there was a general linear trend in mean values (33.9 ± 1.4 kg, 36.3 ± 0.8 kg, 37.2 ± 0.4 kg and 38.8 ± 0.9 kg) similar to those of ADG and 220-day weight. These results are in general agreement with the well-established principle that preweaning growth increases with increase in age of dam, reaching a peak when dam age is about 6–8 years of age (Ahunu *et al*. 1993; Cundiff *et al*. 1966; Pell and Thayne 1978).

Sex of calf effect on preweaning growth was significant ($P<0.05$). Male calves were 8.5% heavier (38.2 ± 0.4 *v.* 35.2 ± 0.4 kg) at birth and had 9.2% higher (0.95 ± 0.01 *v.* 0.87 ± 0.01 kg/day) preweaning ADG, resulting in 9.3% higher (248.0 ± 2.1 *v.* 226.6 ± 1.9 kg) 220-day weight, relative to female calves. These results are in agreement with the well-established effect that male calves are generally heavier and grow faster than their female contemporaries (Anderson and Wilham 1978; Bailey *et al*. 1975).

Year of mating effect was significant ($P<0.05$) for pregnancy rate and calving rate, with the 2002 matings resulting in significantly lower rates compared with the 2000 and 2001 matings. Mean pregnancy rates for 2000, 2001 and 2002 matings were 95.1, 90.8 and 83.3%, respectively. Corresponding values for calving rates were 92.9, 89.5 and 81.8%, respectively. The 2002 mating season (October–December) and the 6 months preceding the mating season was characterised by drought (Fig. 2), resulting in drastically reduced pasture quantity and quality. As indicated earlier, the cows were expected to deposit fat at this time of year but that did not happen (Fig. 3).

It is acknowledged that the limited period of this study (3 breeding cycles), and the disposal of non-pregnant females each year limits the inferences that can be made in relation to other aspects of maternal productivity such as longevity and lifetime productivity.

Beef cattle breeding herds are generally composed of overlapping generations of cows. In the RFI selection lines, the foundation animals are classified as generation 0. The cows used in this study ranged from generation 1 to generation 2.5, with a mean of 1.5 generations, and were the results of 5 years of selection. In industry herds, it will take longer to achieve such divergence due to the fact that selection will likely be in males only (as evidenced by the low number of industry heifers tested for RFI to date; K. Dibley pers. comm.), the unidirectional nature of selection in industry herds (selection only for high efficiency), and the generally higher generation interval (average of 5 years) in industry females. This is in contrast with the selection lines in this study where, selection was in both sexes, was divergent (high and low RFI), and the generation interval in the females was 3 years.

Conclusions

The results of this study indicate that 5 years of divergent selection for RFI did not have any significant effect on measures of maternal productivity in cows differing in RFI EBV by 0.8 kg/day. Although feed intake was not measured on the cows in this study, earlier results would suggest that the low RFI (high efficiency) cows consumed less feed than high RFI (low efficiency) cows (Archer *et al*. 2002) for the same level of maternal productivity.

The non-significant selection line by mating year interaction suggests that maternal productivity in the 2 lines were similar under either a natural service or an artificial insemination breeding system. In addition, it appears that although the drought of 2002 reduced fat levels and reproductive rates, its effect on the 2 selection lines were of the same magnitude.

In this study the cows were managed in one environment and under one level of nutrition. Experiments with crossbred and purebred cattle under different levels of nutrition have shown significant interactions between the effects of genotype and level of nutrition on reproductive performance (e.g. Barlow *et al*. 1994; Jenkins and Ferrell 1992). Hence, the extrapolation of the results of this study, beyond that of a temperate environment with a moderate level of nutrition, should be made with caution. Further research in this area is required.

It is suggested that in current and future research with RFI females, traits and indices relating to age at puberty and how early females resume oestrus activity after calving need to be recorded. Evaluation of such data will be critical in developing strategies to minimise any potential reduction in reproductive performance of low RFI (high efficiency) cows, should the trend ($P<0.10$) in calving day become significant ($P<0.05$) after more generations of selection in the cows, and/or under different environmental or nutritional management.

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Economic evaluation of beef cattle breeding schemes incorporating performance testing of young bulls for feed intake

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Abstract. A model beef cattle breeding scheme consisting of a breeding unit and a commercial unit was used to evaluate the impact on genetic gain and profitability of incorporating feed intake measurements as an additional selection criterion in breeding programmes. Costs incurred by the breeding unit were compared with returns generated in the commercial unit, with bulls from the breeding unit being used as sires in the commercial unit. Two different market objectives were considered — a grass-fed product for the Australian domestic market, and a grain-fed product for the Japanese market. Breeding units utilising either artificial insemination or natural service were also considered. A base scenario was modelled incorporating a range of criteria available to Australian cattle breeders. A second scenario incorporated selection of sires for the breeding unit using a 2-stage selection process, with a proportion of bulls selected after weaning for measurement of (residual) feed intake. Measurement of feed intake of bulls improved accuracy of breeding unit sire selection by 14–50% over the equivalent base scenario, and genetic gain in the breeding objective was improved for all scenarios, with gains ranging from 8 to 38% over the base scenario. After accounting for the cost of measuring feed intake ($150–450), additional profit was generated from inclusion of feed intake measurement on a proportion of bulls for all breeding schemes considered. Profit was generally maximised where 10–20% of bulls were selected at weaning for measurement of intake, with improvement in profit ranging from 9 to 33% when optimal numbers of bulls were selected for intake measurement.

Introduction

Studies reviewed by Archer *et al.* (1999) and recent reports by Arthur *et al.* (2001), Herd and Bishop (2000) and Robinson *et al.* (1999) have shown substantial genetic variation in feed efficiency of cattle. The potential exists to exploit this variation to improve profitability and there is considerable interest in the idea of incorporating feed intake measurement as an additional selection criterion in beef cattle breeding programmes. However, collecting the information is expensive, with the cost of measurement at least an order of magnitude greater than the cost of the most expensive phenotypic measurement currently used routinely for beef cattle genetic evaluation in Australia. Therefore, it is important that any investment made to collect feed intake data for inclusion as selection criteria is justified by the economic returns generated. As it is unlikely that routine measurement of feed intake on all selection candidates is justified, consideration needs to be given to breeding programmes that record feed intake for only a proportion of the selection candidates.

This paper presents an analysis of investment in breeding programmes for beef cattle production in temperate Australia. The analysis considered a breeding programme incorporating most information sources currently used in beef cattle genetic evaluation in Australia, and compared it with a programme that included measurement of feed intake at the second stage of a 2-stage selection process. The analysis sought to provide information: (i) to evaluate the impact on genetic gain and profitability of incorporating feed intake measurements of young bulls as an additional selection criterion in breeding programmes; and (ii) to give recommendations as to how best to utilise feed intake measurements in breeding programmes.

Materials and methods

The 'ZPLAN' programme of Karras *et al.* (1997) was used to model an industry breeding structure. ZPLAN is a deterministic model of investment in performance recording in the seedstock population(s) and uses a multiple trait selection index approach to predict genetic progress for a specified breeding objective, given certain trait measurements. The flow of genes from the seedstock breeding sector through to the commercial production sector is described, and the increase in economic return due to selection (discounted over a specified investment horizon) is calculated and compared to the cost of investment in the breeding programme. The procedures used by ZPLAN have been described by Nitter *et al.* (1994).

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For the analysis described, 2 modifications to the ZPLAN code were made. The index subroutine of Künzi (1976) used by ZPLAN to calculate selection indices for selection groups was modified to accept information from 2 different sources of the same relationship type (e.g. groups of half-sibs with different information recorded). Also, the ZPLAN subroutine for calculating response from 2-stage selection based on the approximation described by Niebel and Fewson (1976) was replaced with a subroutine which used an iterative process to arrive at a solution, based on methods described by Wade and James (1996).

Population structure

The structure of the breeding population modelled was similar to that described by Nitter *et al.* (1994) and Graser *et al.* (1994). A total population of 200000 breeding cows was considered, with 10000 of these cows forming the breeding unit where measurement and selection occurs and genetic improvement is generated, and the remaining 190000 cows in the commercial beef production unit. The breeding unit formed a closed structure with all replacement bulls and females sourced from within the unit and selected on appropriate indices including all available information at the time of selection. A proportion of bulls was selected for measurement of feed intake based on an index incorporating information available at weaning. Bulls to be used as sires in the breeding unit were then selected from this subset in a 2-stage selection process. All heifers suitable as replacements in the breeding unit were joined, and selection decisions on replacement cows were made after their first calves were born, but before they were mated a second time.

Bulls not selected for use in the breeding unit were available for use in the commercial unit. Ninety-nine percent of bulls used in the commercial unit were sourced from the breeding unit. The remaining 1% were sourced from within the commercial unit but selected on an index not correlated with the breeding objective and so did not contribute to generating genetic gain and economic returns. (The proportion of bulls from the commercial unit was set to a low value, so the model represented the proportion of the industry which actively uses improved genetics; this value is likely to be greater than 1% when taken over the whole industry.) Replacement cows for the commercial unit were selected from heifers within the unit, based on an index not correlated with the breeding objective.

The population structure modelled resulted in the following 10 selection groups:

Group 1 — bulls from the breeding unit selected for a post-weaning feed intake test;

Groups 2 and 4 — sires from the breeding unit to breed sires (2) and dams (4) for the breeding unit (selected from bulls in selection group 1);

Groups 3 and 5 — dams from the breeding unit to breed sires (3) and dams (5) for the breeding unit;

Groups 6 and 8 — sires from the breeding unit to breed sires (6) and dams (8) for the commercial unit;

Groups 7 and 10 — dams from the commercial unit to breed sires (7) and dams (10) for the commercial unit; and

Group 9 — sires from the commercial unit to breed dams for the commercial unit.

Various biological and technical parameters describing the population structure are given in Table 1.

Breeding objective

Breeding objectives for 2 production systems were considered, chosen to represent 2 diverse target markets and finishing regimes used in beef production systems in southern Australia. Both systems consisted of self-replacing cow herds, and would typically be based on British breeds of cattle. The first breeding objective described a system targeting the domestic Australian market where steers are finished on pasture and slaughtered at a fixed age with a target slaughter weight of 400 kg liveweight. Marbling was assumed to have no value for this market. The second breeding objective described the production of steers for the high quality Japanese market, where marbling has a high value. Steers for this market are finished on concentrate rations in feedlots for 210 days and slaughtered at a target weight of 650 kg

Table 1. Biological and technical parameters describing the modelled herd structure and recording costs

Parameter	Value
Age when first progeny born (years)	
Sires in breeding unit (groups 2 and 4)	2.5
Sires in commercial unit (groups 6 and 8)	3
Home-bred sires in commercial unit (group 9)	2.5
Dams in breeding unit (groups 3 and 5)	2
Dams in commercial unit (groups 7 and 10)	2
Productive lifetime (years)	
Sires in breeding unit	2.5
Sires in commercial unit	3
Home-bred sires in commercial unit	2.5
Dams in breeding unit	4.5
Dams in commercial unit	5.5
Survival rate (including deaths and culling)	
Bulls (annual)	0.8
Cows (annual)	0.9
Calf survival from birth to 200 days	0.97
Calf survival from birth to 400 days	0.96
Reproductive parameters	
Calving rate in breeding unit	0.88
Calving rate in commercial unit	0.88
Proportion of males fit for breeding	0.8
Proportion of females fit for breeding	0.9
Proportion of females kept as potential replacements	0.75
Number of new sires selected for breeding unit per year[A]	20, 100
Number of females per male in breeding unit[A,B]	200, 40
Number of females per male in commercial unit	40
AI conception rate	0.55
Number of rounds of AI used[A]	3, 0
Investment parameters	
Investment period (years)	25
Discount rate for returns	0.08
Discount rate for costs	0.06
Breeding unit costs per even, with age when occurring shown in parentheses (year)	
Fixed costs per cow in breeding unit	$10.00 (2)
Birth weight and calving difficulty score	$3.00 (0)
200-day weight	$1.00 (0.55)
400-day weight	$1.50 (1.1)
600-day weight	$1.50 (1.65)
Scrotal size	$2.00 (1.1)
Days to calving	$0.50 (2)
Ultrasound scanning	$13.50 (1.1)
Cow weight	$1.00 (2.5)
Feed intake	$150–450 (1.1)
Artificial insemination cost (per cow)	$30.00 (1.3)

[A]Alternatives correspond to breeding units using AI or natural mating.
[B]Number of females per male calculated as number of cows in breeding unit/(number of new sires per year × average productive lifetime of sires).

Table 2. Summary description of breeding objective cases where production is for Japanese or domestic markets from straight-breeding herds

Details	Japanese	Domestic
Product		
Steer sale liveweight (kg)	650	400
Slaughter age (m)	25	17
P8 fat depth (mm)	20	8
Base steer price (c/kg liveweight)	150	140
Cow price (c/kg liveweight)	93	90
Environment and herd performance		
No. months of surplus feed[A]	2	3
Young feed cost ($/t DM)	146	105
Young feed quality (MJ/kg DM)	10	10
Cow feed cost ($/t DM)[B]	100	100
Cow feed quality (MJ/kg DM)[B]	10	10
Other costs per steer ($)	67	62
Other (annual) costs per cow ($)	174	176
Cow weight (kg)	450	450
Probability of calving difficulty in heifers (%)	15	15
Annual cow weaning rate (%)	88	88
Unfinished steers at finished sale (%)	Nil	6

[A]For management close to optimal and an average year.
[B]Cow feed cost equivalent to supplying 7 MJ/kg DM silage at $70/t.

liveweight. Summary descriptors of the production systems considered are given in Table 2.

The traits in the breeding objective reflected the traits of economic importance in the production systems. They included sale liveweight (direct and maternal, SWd and SWm), dressing percent (DP), saleable meat percent (SMP), fat depth at the Australian P8 site over the rump (FD), Australian marbling score (MS), cow weaning rate (CWR), cow survival rate (CSR), cow weight (CW), calving ease (direct and maternal, CEd and CEm) and residual feed intake of cows (CRFI) and of young animals (YRFI). The economic values for these traits were derived with BreedObject software according to methods described by Barwick *et al*. (1999) and are presented in Table 3. A profit-per cow basis was used to derive the breeding objectives.

The economic values for SWd, SWm, CWR, CSR, and CW include an account of changes in predicted feed costs associated with these traits. The remaining variation in feed costs, i.e. those occurring beyond that expected due to body size and growth rate, were included as residual traits, in a similar manner to that used by Koots and Gibson (1998). Those residual feed requirements were described by 2 traits in the breeding objective, 1 for intake of young animals during growth and finishing and the other to describe intake of mature cows in the breeding herd. The economic value of feed for a young animal was calculated as the cost of increasing residual feed intake by 1 kg/day, on a per cow per year basis, weighted for the number of animal days spent consuming pasture and concentrate rations.

Selection criteria and information sources

Selection criteria were chosen to represent the criteria recorded and included in version 4.1 of BREEDPLAN (Johnston *et al*. 1999), the national genetic evaluation system for beef cattle in Australia. The criteria included measurements of liveweight at birth, 200, 400 and 600 days (with direct and maternal components for weight at 200 days; Bwt, Wt200d, Wt200m, Wt400 and Wt600), ultrasound scanning traits measured on the live animal (fat depth between 12th/13th rib and on the rump (P8 site), eye muscle area and intra-muscular fat percent; RIB, P8, EMA and IMF), scrotal circumference (SC), days to calving (DC) and weight of mature cows at weaning of their calves (MCW). Scanning measurements recorded on bulls and heifers were treated as separate correlated criteria (denoted by a 'b' or 'h' following the abbreviation). A new criterion of residual feed intake (RFI) measured during a post-weaning performance test of bulls was also included. Whether feed intake is expressed as actual or residual for inclusion in selection indices has no impact on the outcome for a given breeding objective, provided appropriate genetic parameters are used (Kennedy *et al*. 1993).

Two scenarios were modelled, in the 'base' scenario all criteria excluding RFI were measured within the breeding unit. The various information sources available (Table 4) were chosen to represent the likely information available for a breeding enterprise measuring these criteria. Where an information source represents a group of animals, the number of animals in the group was calculated from the herd structure parameters given in Table 1, and discounted by 0.7 to account for lower

Table 3. Traits in the breeding objective, their abbreviations, definitions and economic value assigned for two different production systems

Trait	Abbreviation	Unit	Economic value ($ per unit)			
			Japanese	Japanese (feed costs × 1.15)	Japanese (feed costs × 1.30)	Domestic
Sale liveweight — direct[A]	SWd	kg	0.655	0.608	0.560	0.813
Sale liveweight — maternal[A]	SWm	kg	0.655	0.608	0.560	0.813
Dressing %	DP	%	11.07	11.07	11.07	6.39
Saleable meat %	SMP	%	9.04	9.04	9.04	5.03
Fat depth (rump)	FD	mm	0	0	0	0.741
Marbling score	MS	score	56.28	56.28	56.28	0
Cow weaning rate[A]	CWR	%	3.53	2.62	1.71	0.934
Cow survival rate[A]	CSR	%	4.69	4.48	4.28	3.73
Cow weight[A]	CW	kg	–0.189	–0.244	–0.299	–0.152
Calving ease — direct	CEd	%	0.671	0.671	0.671	0.647
Calving ease — maternal	CEm	%	0.426	0.426	0.426	0.426
Cow residual feed intake	CRFI	kg/day[B]	–30.50	–35.08	–39.65	–27.50
Young residual feed intake	YRFI	kg/day[B]	–52.61	–60.54	–68.47	–20.64

[A]Predicted feed requirements accounted for in the calculation of economic values.
[B]At a feed value of 10 MJ ME/kg DM.

effective numbers with the animals managed in different contemporary groups (after Graser *et al.* 1994). All selection groups included information contributed from records on the sire, dam and male and female half-sibs of the sire and dam. The information available on the individual and paternal half-sibs differed for the selection groups, reflecting the different ages at which selection decisions are made for each group. The base scenario utilised 2-stage selection routines to ensure that consistent computational processes were used. However, the proportion of bulls selected in the first stage was set to 99.9%, and so effectively modelled a 1-stage selection process.

The second scenario (+RFI) included all the information available for the base scenario, with the addition of RFI using a 2-stage selection process. After weaning, a proportion of young bulls from the breeding unit was selected (based on information available at weaning) and measured for RFI and other criteria. The sires for the breeding unit were chosen from this group and then the sires for the commercial unit were chosen from the remaining bulls. Information for this latter selection decision did not include RFI measurements, as only a subset of these bulls had RFI measured under this structure. Information on RFI of the sire was included for relevant selection groups, as it was assumed that breeding unit sires had been previously selected under the same structure.

Genetic parameters

Genetic and phenotypic parameters used were based on estimates for *Bos Taurus* breeds (mostly Angus) used in BREEDPLAN (Johnston *et al.* 1999) at the time the analysis was conducted, as well as from literature estimates (e.g. Koots *et al.* 1994*a*, 1994*b*), as used by Barwick *et al.* (1999). Parameters involving residual feed intake were obtained from Arthur *et al.* (2001) and from analyses of data from 2 Australian projects investigating this trait (unpublished data). Genetic, phenotypic and residual variance/covariance matrices were checked for usual permissability criteria. Where necessary a bending routine was used to produce a permissible matrix close to the initial values. The parameters used are given in Tables 5, 6 and 7.

Variations and parameter sensitivity analyses

To examine the sensitivity of the results, and to find breeding structures close to optimal for the situation, a number of parameters considered likely to be critical to the outcomes were varied. These parameters generally described the investment in measurement of

Table 4. Information sources for indices used to select sires and dams for the breeding unit and sires for the commercial unit

Selection criteria recorded include weight at birth, 200, 400 and 600 days (BWt, Wt200, Wt400, Wt600 respectively), ultrasound scan measurements, scrotal circumference (SC), days to calving (DC), weight of cows at weaning of their calves (MCW) and residual feed intake of bulls measured post-weaning (RFIpw)

Selection group and information source	No. of contributing animals[A]	Selection criteria recorded								
		BWt	Wt200	Wt400	Wt600	Scan[B]	SC	DC	MCW	RFIpw[C]
(1) Bulls for RFI test										
Individual	1	✓	✓							
Paternal half sibs — all males	59, 12	✓	✓	✓	✓	b	✓			
Paternal half sibs — all females	59, 12	✓	✓	✓	✓	h				
(2 & 4) Sires for breeding unit										
Individual	1	✓	✓	✓	✓	b	✓			✓
Paternal half sibs — all males	59, 12	✓	✓	✓	✓	b	✓			
Paternal half sibs — all females	59, 12	✓	✓	✓	✓	h				
(3 & 5) Dams for breeding unit										
Individual	1	✓	✓	✓	✓	h		✓		
Paternal half sibs — all males	59, 12	✓	✓	✓	✓	b	✓			
Paternal half sibs — females, not replacement	15, 3	✓	✓	✓	✓	h				
Paternal half sibs — females, replacement	44, 9	✓	✓	✓	✓	h		✓		
(6 & 8) Sires for commercial herd										
Individual	1	✓	✓	✓	✓	b	✓			
Paternal half sibs — all males	59, 12	✓	✓	✓	✓	b	✓			
Paternal half sibs — all females	59, 12	✓	✓	✓	✓	h				
Plus (for all selection groups above)										
Sire	1	✓	✓	✓	✓	b	✓			✓
Dam	1	✓	✓	✓	✓	h		✓	✓	
Half sibs of sire — all males	106, 21	✓	✓	✓	✓	b	✓			
Half sibs of sire — females, not replacement	26, 5	✓	✓	✓	✓	h				
Half sibs of sire — females replacement	80, 16	✓	✓	✓	✓	h		✓	✓	
Half sibs of dam — all males	106, 21	✓	✓	✓	✓	b	✓			
Half sibs of dam — females, not replacement	26, 5	✓	✓	✓	✓	h				
Half sibs of dam — females replacement	80, 16	✓	✓	✓	✓	h		✓	✓	

[A]Where 2 numbers are given, the first corresponds to the scenario where AI is used, while the second corresponds to natural service mating.
[B]Measurements taken using ultrasound scanning, including fat depth at 12th/13th rib, rump (P8), eye muscle area and percent intra-muscular fat. Measurements on bulls and heifers were treated as separate traits, and are denoted by 'b' and 'h', respectively.
[C]RFIpw measurements apply only to the +RFI scenarios. All other criteria were measured in both the base and +RFI scenarios.

Table 5. Assumed phenotypic standard deviations, heritabilities, genetic (above diagonal) and phenotypic (below diagonal) correlations between selection criteria (see Table 4 for trait abbreviations)

	BWt	Wt200	Wt400	Wt600	P8h	P8b	RIBh	RIBb	EMAh	EMAb	IMFh	IMFb	SC	DC	MCW	RFIpw	Wt200m
Phenotypic s.d.	3.808	22.36	30.89	34.64	1.975	1.581	1.378	1.049	5.254	6.671	1.000	0.8944	2.049	23.39	46.90	0.6181	—
h^2	0.39	0.18	0.25	0.31	0.41	0.28	0.34	0.23	0.26	0.27	0.25	0.12	0.39	0.07	0.41	0.39	0.10
Units	kg	kg	kg	kg	mm	mm	mm	mm	cm^2	cm^2	%	%	cm	days	kg	kg/day	kg
BWt		0.66	0.53	0.56	–0.05	–0.05	–0.05	–0.05	0.15	0.15	0	0	0.10	0	0.35	–0.05	0
Wt200	0.35		0.74	0.69	0.05	0.05	0.05	0.04	0.21	0.21	–0.05	–0.06	0.10	0	0.40	–0.30	0
Wt400	0.30	0.54		0.81	0.05	0.05	0.10	0.10	0.39	0.39	–0.15	–0.15	0.15	0	0.49	–0.15	0
Wt600	0.31	0.51	0.68		0.05	0.05	0.10	0.11	0.38	0.39	–0.19	–0.19	0.15	0	0.72	–0.15	0
P8h	–0.04	0.13	0.20	0.20		0.75	0.85	0.65	0.29	0.30	0.30	0.10	0	0	0.10	0.25	0
P8b	–0.04	0.14	0.22	0.22	—		0.65	0.85	0.20	0.10	0.10	0.10	0	0	0.10	0.10	0
RIBh	–0.04	0.14	0.22	0.23	0.89	—		0.75	0.20	0.20	0.30	0.10	0	0	0.10	0.30	0
RIBb	–0.04	0.15	0.23	0.24	—	0.90	—		0.19	0.09	0.10	0.10	0	0	0.09	0.20	0
EMAh	0.07	0.21	0.34	0.36	0.21	—	0.19	—		0.80	–0.01	–0.01	0.05	0	0.21	–0.10	0
EMAb	0.07	0.21	0.34	0.36	—	0.15	—	0.17	—		–0.10	–0.01	0.05	0	0.21	–0.05	0
IMFh	0	–0.01	–0.04	–0.06	0.10	—	0.09	—	0	—		0.65	0	0	–0.01	0.20	0
IMFb	0	–0.01	–0.03	–0.04	—	0.02	—	0.02	—	0	—		0	0	–0.01	0.20	0
SC	0.04	0.33	0.21	0.20	—	0	—	0	—	0.08	—	0		–0.28	0.05	–0.03	0
DC	0	–0.04	–0.05	0	0	—	0	—	0	—	0	—	—		0	0.07	0
MCW	0.20	0.30	0.50	0.63	0.10	—	0.10	—	0.20	—	0	—	—	0.07		–0.34	0
RFIpw	0	0	0	0	0.11	0.11	0.14	0.14	0.06	0.06	0	0	0.10	0	–0.07		0.10

intake, the value of intake in the breeding objective, and the efficiency of the breeding scheme in selecting and disseminating superior genes. As already described, 2 breeding objectives were considered to represent beef production systems used in southern Australia. As well, 2 breeding structures, representing (i) mating predominantly by artificial insemination (AI), and (ii) natural mating were modelled by setting the number of new bulls entering the breeding unit per year at 20 (equivalent to 200 cows per sire per year serviced) or 100 (40 cows per sire per year serviced) respectively. This contrast was included to investigate possible interactions between the inclusion of a high-cost measurement of intake and the efficiency of the breeding structure in utilising superior genetics. Where a breeding unit utilising AI was modelled, the number of inseminations was calculated from the conception rate to AI (55%) and the number of rounds of AI used (3). This figure was incorporated in the cost structure for the breeding unit at $30 per insemination. The combination of market objective and type of service used in the breeding unit (AI *v.* natural service) defined the different 'breeding schemes' considered.

Under the +RFI scenario, the impact of proportion of bulls selected for RFI measurement and the cost of RFI measurement were examined. The proportion of bulls entering for the second selection stage for RFI measurement was varied from 2 to 99.9% of bulls available. To examine the sensitivity of the analysis to the cost of measuring RFI, alternative costs were used ($150, $300 or $450 per animal). This range was based on the current cost of testing cattle in a commercially operated facility in Australia which is up to $500 per animal. The commercial price of testing includes the cost of feed (about $200), of which at least part should be excluded from the measurement cost. On-farm tests might be considerably cheaper.

Sensitivity of the analysis to the assumed cost of feed was also considered. The cost of feed was increased above the base assumption by 15 and 30%, and the breeding objective for the Japanese market

Table 6. Assumed genetic correlations between selection criteria and traits in the breeding objective (see Tables 3 and 4 for trait abbreviations)

	SWd	SWm	DP	SMP	FD	MS	CWR	CSR	CW	CEd	CEm	CRFI	YRFI
BWt	0.50	0	0	0	–0.05	0	–0.03	–0.02	0.32	–0.40	0.15	–0.10	–0.10
Wt200	0.62	0	–0.05	–0.06	0.04	–0.05	0	0	0.36	–0.19	0.10	–0.30	–0.30
Wt400	0.73	0	–0.05	–0.04	0.06	–0.15	0	0	0.45	–0.16	0	–0.15	–0.15
Wt600	0.90	0	–0.05	–0.04	0.06	–0.20	0	0	0.70	–0.17	0	–0.15	–0.15
P8h	0.05	0	0.15	–0.52	0.85	0.23	0	0	0.04	0	0	0.25	0.25
P8b	0.05	0	0.15	–0.53	0.64	0.15	0	0	0.04	0	0	0.10	0.10
RIBh	0.09	0	0.15	–0.53	0.72	0.23	0	0	0.04	0	0	0.30	0.30
RIBb	0.09	0	0.15	–0.52	0.55	0.15	0.00	0.00	0.04	0.00	0	0.20	0.20
EMAh	0.35	0	0.20	0.33	0.28	–0.14	0.00	0.00	0.20	–0.09	0	–0.10	–0.10
EMAb	0.36	0	0.20	0.34	0.29	–0.15	0.00	0.00	0.20	–0.10	0	–0.05	–0.05
IMFh	–0.20	0	0.10	–0.25	0.26	0.60	0	0	–0.20	0	0	0.20	0.20
IMFb	–0.20	0	0.10	–0.07	0.10	0.53	0	0	–0.20	0	0	0.20	0.20
SC	0.14	0	0	0	0	0	0.20	0	0.25	–0.04	0	–0.03	–0.03
DC	0	0	0	0	0	0	–0.65	0	0	–0.07	–0.20	0.33	0.07
MCW	0.69	0	–0.05	–0.01	0.09	–0.18	0	0	0.89	–0.22	0	–0.34	–0.34
RFIpw	–0.15	0.07	0	–0.40	0.15	0.15	–0.05	0	–0.30	0	0	0.50	0.75
Wt200m	0	0.61	0	0	0	0	–0.05	–0.15	0	0	–0.10	0.10	0.10

re-calculated using these values. The resulting breeding objectives are given in Table 3.

Results and discussion

Accuracy of selection and genetic gains

Table 8 shows the accuracy of selection for the various selection groups for each of the breeding schemes examined. Measurement of RFI on a proportion of bulls significantly improved the accuracy of selection of sires for the breeding unit for all breeding schemes, with improvements for the +RFI scenario over the base scenario ranging from 14 to 50%. Small improvements were also achieved in the accuracy of selection of dams for the breeding unit and sires for the commercial unit, through information on RFI of the sires of these animals. The +RFI scenario did not include potential information on RFI of a proportion of half-sib brothers for any of the selection groups, or individual RFI information on a proportion of individuals when selecting sires for the commercial unit. These information sources were omitted due to limitations of the model, which did not allow for unequal information on animals of a selection group. A slight improvement in selection accuracy (and consequently genetic gains and profit) might be expected were this information included. A greater improvement would be expected if a higher proportion of bulls were measured for RFI, and thus the model slightly underestimated both profit and the optimum proportion of bulls to select for RFI measurement.

Table 8 also shows the relative contribution of the selection groups towards generating economic returns. Where the breeding unit used AI, selection of sires for the breeding unit was 4–5 times more important, in terms of the contribution towards generating economic returns, than selection of breeding unit dams and commercial sires (which were about equal in all circumstances). Where natural service was used, selection of breeding unit sires was 3–4 times as important as the other selection groups. This indicates that to generate economic returns, most emphasis should be placed on the selection of sires for the breeding unit, and that the selection of sires to disseminate genetic gains to the commercial sector, while still significant, is relatively less important. The relative significance of sire selection for the breeding and commercial units would vary with the proportion of the total population recorded in the breeding unit. However, the situation modelled (5% of cows in the breeding unit) meant that 46% of available bulls were selected for use in the commercial unit, and is a reasonable reflection of industry practice. Where criteria such as RFI are too expensive to profitably measure on all selection candidates, targeted measurement of these criteria on the selection group(s) with the largest influence over total returns is important to maximise benefits from the breeding scheme.

Genetic gains in the breeding objective for different breeding schemes modelled are presented in Figure 1. Genetic gain for the base scenario varied between different breeding schemes. Gains for the Japanese market objective were higher than for the Australian domestic market objective, as the production system for the Japanese market is based on a higher value of inputs and outputs relative to the Australian domestic market objective. Similarly, gains for breeding schemes using AI were higher than those using natural service matings. This is mainly a result of the higher selection intensity available when AI is used, but is also a consequence of more information available on half-sib relatives acting to slightly increase accuracy of selection (see Table 8). Additional genetic gain was generated for each scenario through inclusion of RFI as a criterion measured in the breeding programme. As the proportion of bulls selected for RFI measurement increased, the magnitude of the improvement in genetic gain followed a pattern of

Table 7. Assumed phenotypic standard deviation, heritability and genetic correlations between traits in the breeding objective (see Table 3 for trait abbreviations)

	SWd	SWm	DP	SMP	FD	MS	CWR	CSR	CW	CEd	CEm	CRFI	YRFI
Phenotypic s.d.	34.64	—	1.800	2.000	1.975	0.707	32.50	9.950	46.90	20.30	—	0.618	0.618
h^2	0.31	0.04	0.33	0.56	0.41	0.38	0.05	0.03	0.41	0.10	0.10	0.39	0.39
SWd		0	–0.06	–0.03	0.06	–0.05	0	0	0.73	–0.17	0	–0.15	–0.15
SWm			0	0	0	0	0	0	0	0	0	0.07	0.07
DP				0.10	0.17	0.10	0	0	–0.05	–0.06	0	0	0.00
SMP					–0.63	–0.20	0	0	0	–0.01	0	–0.40	–0.40
FD						0.15	0	0	0.10	–0.01	0	0.30	0.30
MS							0	0	–0.20	0	0	0.20	0.20
CWR								–0.10	0	0.07	0.20	–0.21	–0.05
CSR									0	0.04	0.25	0	0
CW										–0.25	0	–0.30	–0.30
CEd											–0.50	0	0
CEm												0	0
CRFI													0.65

Table 8. Accuracy of selection (correlation between index and breeding values) and relative contribution to returns of the major selection groups for the four breeding schemes

Selection group	Scenario	Breeding scheme			
		Japanese objective		Domestic objective	
		AI	Natural service	AI	Natural service
		Accuracy			
Bulls for RFI measurement[A]	+ RFI	0.31	0.27	0.46	0.43
Sires for breeding unit	Base	0.30	0.26	0.49	0.46
Sires for breeding unit	+ RFI	0.41	0.39	0.56	0.55
Dams for breeding unit	Base	0.33	0.29	0.51	0.48
Dams for breeding unit	+ RFI	0.35	0.32	0.52	0.50
Sires for commercial unit	Base	0.30	0.26	0.48	0.45
Sires for commercial unit	+ RFI	0.32	0.29	0.49	0.47
		Return[B]			
Sires for breeding unit	Base	67%	62%	68%	63%
Sires for breeding unit	+ RFI	71–73%	63–69%	70–71%	62–66%
Dams for breeding unit	Base	16%	19%	15%	18%
Dams for breeding unit	+ RFI	13–14%	15–18%	14–15%	16–18%
Sires for commercial unit	Base	16%	19%	16%	19%
Sires for commercial unit	+ RFI	14–15%	16–19%	15%	17–19%

[A]This selection group does not exist in the base scenario where selection of bulls for the breeding unit occurs in one step.
[B]Percentage of total economic return generated by each selection group. Where varying proportions of bulls were selected for RFI measurement, the relative contributions varied within the ranges reported (higher numbers of bulls selected for RFI measurement led to higher % returns for sires for breeding unit, and lower % returns for other selection groups).

diminishing returns. With the information sources modelled, the accuracy of selection of sires for the breeding unit was independent of the proportion of sires measured for RFI, and so the increase in genetic gain with more bulls tested was solely a function of the increased selection intensity applied. Improvements in genetic gain diminished faster in scenarios using AI compared to those using natural service, as fewer sires were required for selection.

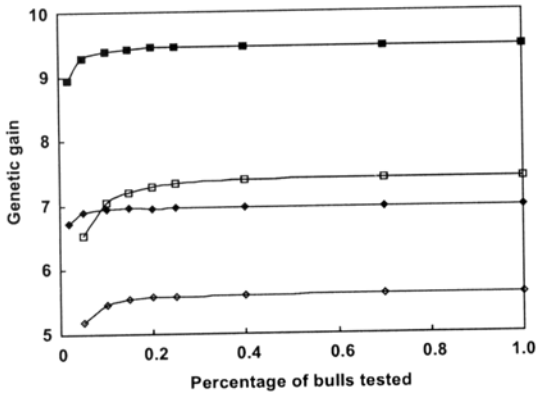

Figure 1. Genetic gain in the breeding objective from 4 breeding schemes with RFI measured on a proportion of bulls. Genetic gains from the equivalent base scenarios (no RFI measurement) were: Japanese objective, AI (■) gain — \$7.40; Japanese objective, natural service (□) gain — \$5.36; domestic objective, AI (◆) gain — \$6.15; and domestic objective, natural service (◇) gain — \$4.81.

Profit and returns from breeding schemes

Figure 2 shows the profit per cow generated from one round of measurement and selection. Profit was calculated after discounting costs and returns, and represents the net present value of investment in the breeding scheme. Profit for the base scenario varied between different breeding schemes, and there was an evident interaction between the market targeted and the type of mating system used in the breeding unit. Under natural service, profit when targeting the Japanese market objective was only 6% higher than when targeting the Australian domestic market objective. When AI was used, profit for the Japanese market objective was 15% higher than for the domestic objective. For both Japanese and domestic market objectives, use of AI in the breeding unit (after accounting for an additional cost of \$30 per insemination) generated significant additional profit compared to natural service mating.

Figure 2 also presents the profit from scenarios including RFI measurement in a 2-stage selection scheme at different measurement costs. Profit from inclusion of RFI as an additional selection criterion should be assessed relative to the profit generated from the base scenario. Where all bulls are measured for RFI (i.e. 99.9% selected for second stage), significant additional profit (over the base scenario) is generated where the Japanese market objective is targeted

and cost of RFI measurement is as high as $450 per animal. However, where the Australian domestic market is targeted, measuring RFI on all bulls was only more profitable than the base scenario where the measurement cost was $150 per animal.

Measurement of RFI on a proportion of candidate bulls in a 2-stage selection process was more profitable than measuring all animals, and generated positive returns for all breeding schemes modelled, even when the cost of RFI measurement was $450. The optimal proportion of bulls to select for RFI measurement varied depending upon measurement cost, market objective targeted and mating system used, ranging from ~5 to 25%. As the measurement cost increased, the maximum profit decreased and was generated from measuring RFI on fewer bulls. Use of AI reduced the proportion of bulls measured to generate maximum profit, as fewer bulls were required as sires. Although the optimum proportion of bulls to measure for RFI varied for different situations, the profit response surfaces were relatively flat within 5% of the optimum. Where bulls are selected for RFI measurement based on information typically available at weaning, a general rule of measuring RFI on those animals in the top 10–20% of the breed is likely to be close to optimal across a range of breeding schemes, market objectives and RFI measurement costs.

Additional profit from measuring RFI on a proportion of bulls was markedly greater where the Japanese market objective was targeted compared to the Australian domestic market objective. Figure 3 shows the return on breeding objective traits for each objective/mating system combination under the base scenario and with 2-stage selection of a proportion of bulls for RFI measurement. Examination of the returns indicates that the higher additional return from including RFI measurement in the Japanese objective is mainly a function of improvements in residual feed intake of young growing animals (RFIy). This could be expected given the higher economic value assumed for RFIy for the Japanese objective compared to the Australian domestic objective (see Table 3), reflecting the length of time animals are fed high cost diets under this production system. The impact on returns from other traits is also worth examining, particularly the impact on marbling score which has a high economic value for the Japanese market. Under the assumptions of this analysis, both the base scenario and the +RFI scenario generated negative returns for marbling score. However, the +RFI scenario produced a larger negative response in marbling score relative to the

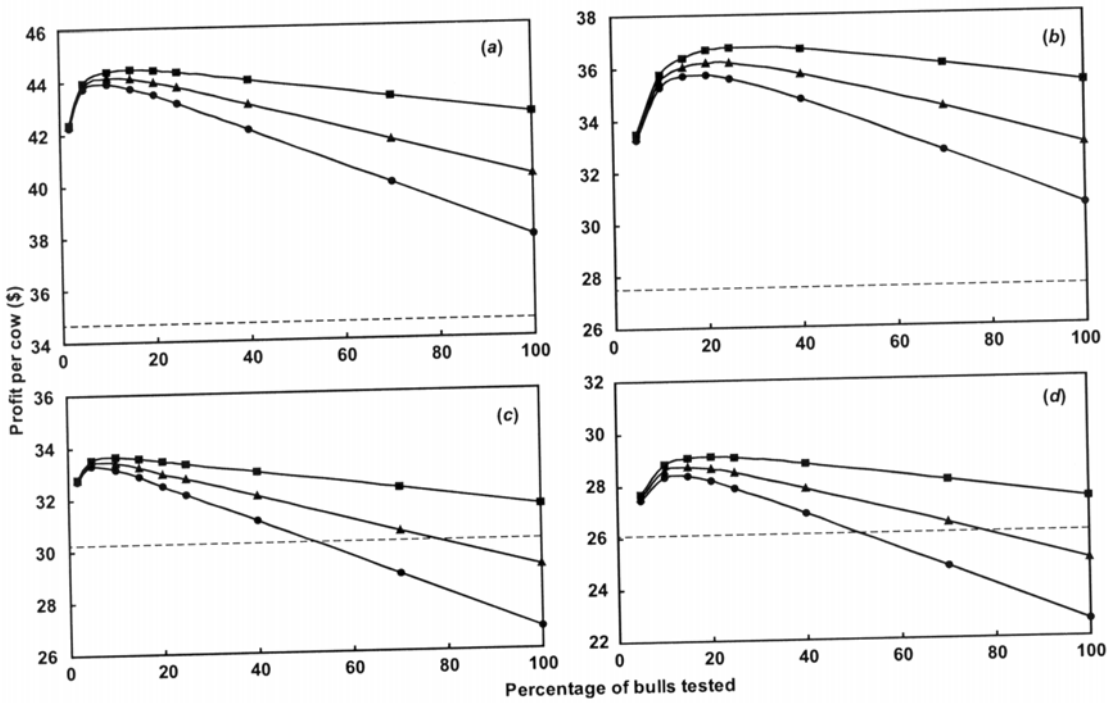

Figure 2. Profit per cow from (*a*) Japanese objective, AI; (*b*) Japanese objective, natural service; (*c*) domestic objective, AI; and (*d*) domestic objective, natural service. Profit from the base (no RFI) scenario in represented as a horizontal broken line, and profit from the +RFI scenarios with different measurement costs are: $150, ■; $300, ▲; $450 ●.

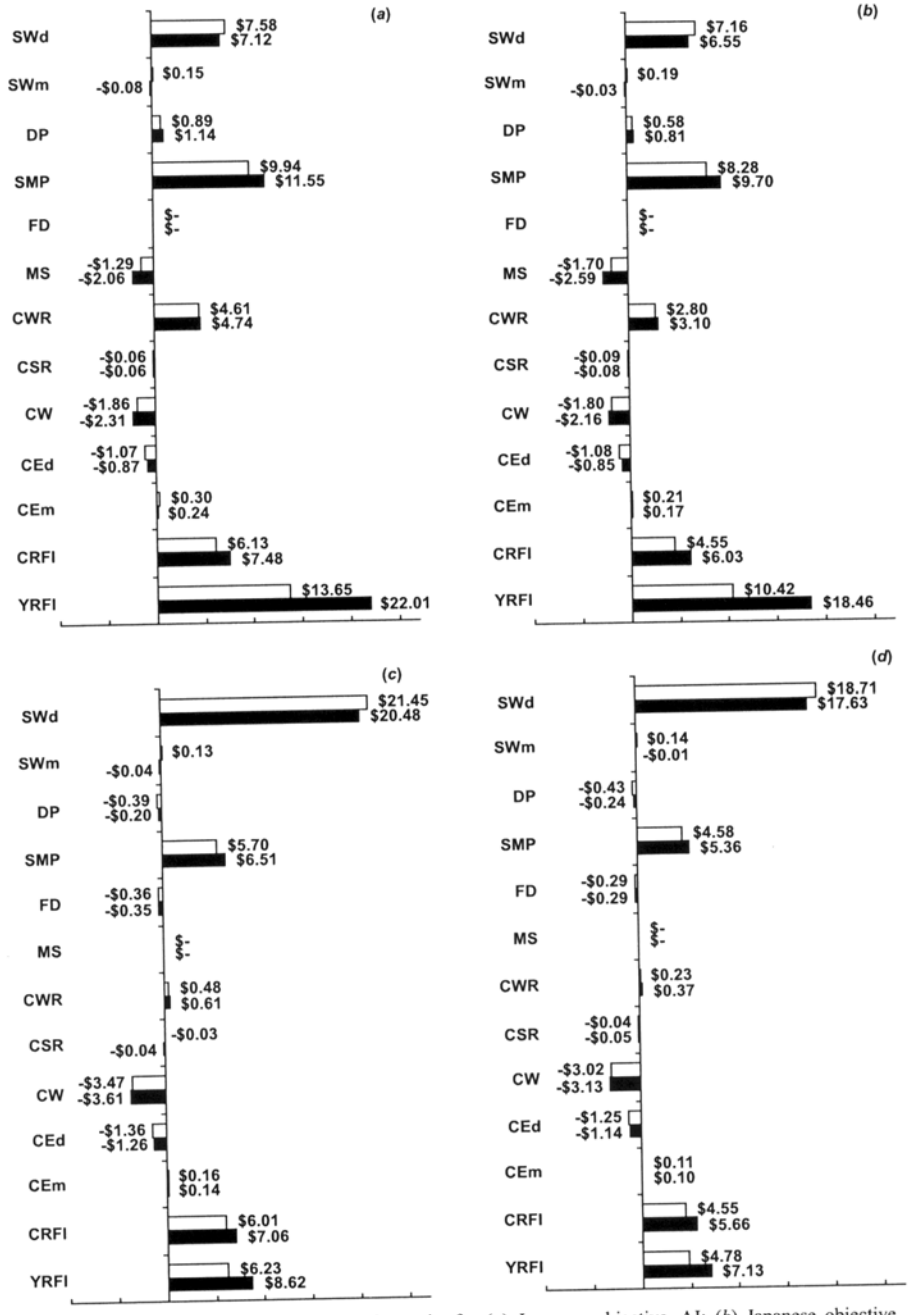

Figure 3. Return ($) on breeding objective traits for (*a*) Japanese objective, AI; (*b*) Japanese objective, natural service; (c) domestic objective, AI; and (*d*) domestic objective, natural service. For each breeding scheme, returns are presented for the base scenario (open bars) and for the +RFI scenario (closed bars) where the proportion of bulls selected after the first stage generated maximum profit per cow (assuming a RFI measurement cost of $300).

base scenario, due to the low but antagonistic relationship assumed between RFI and marbling score. This highlights that, where antagonistic relationships exist between traits of high economic value (such as RFI and marbling score), it is important to collect sufficient information on these traits to manage these antagonisms, as accurate information on both traits enables selection of outlier animals which don't closely follow the general antagonistic relationship. Where insufficient information is collected on 1 trait, the selection index may lead to a negative response in that trait. This can occur despite the selection index optimally weighting traits given the information sources available. In the breeding scheme considered here, further information on marbling score collected through progeny testing would lead to desirable responses in both RFI and marbling score (J. A. Archer and S. A. Barwick unpublished data). It is also worth noting that all breeding schemes considered led to a decline in calving ease (direct), presumably largely influenced by positive selection for increased sale weight.

Sensitivity to cost of feed

Figure 4 presents the impact of increasing the cost of feed on the profit and genetic gain for the Japanese market objective where the breeding scheme uses AI. While increasing feed costs increased the value of genetic gain and profit, the effects on the proportion of bulls to be selected for RFI measurement to produce maximum profit were minor, suggesting that the optimal proportion of bulls tested for feed intake is relatively insensitive to the cost of feed.

Implications for breeding programmes and investment

This analysis has concentrated on incorporating measurement of 1 additional high-cost criterion in breeding programmes to improve profitability. The results demonstrate some general principles of breeding programme design that are likely to apply where other relatively expensive criteria become available for use in breeding programmes. Where criteria are expensive to measure, it is likely that profit will be maximised by measuring only a proportion of selection candidates in the breeding unit, even if positive profit is generated from measuring all candidates. Thompson *et al.* (1996), in examining the application of computer tomography for evaluation of carcass merit in sheep, also found that 2-stage selection generated greater profit than taking measurements on all candidates. Thus, a more targeted approach to measuring high-cost criteria only on candidates likely to have a high impact on the breeding population is required as an alternative to the often adopted strategy of measuring all animals in the breeding unit for relatively inexpensive criteria. In conventional breeding structures for many livestock species, the animals with greatest influence on the entire population are the sires to be used in the highest level breeding unit. Results from the model here indicated that, even for the base scenario, this selection group generated over 60% of the total economic returns. With the addition of other high cost criteria such as RFI targeted at potential seedstock sires, the relative contribution of this group to total economic returns increases. Thus, the efficiency of the seedstock sector in generating genetic gains becomes relatively more important than the selection of commercial sires to pass the genetic gain on to the commercial sector.

Use of AI in the breeding unit influenced the breeding programme outcomes in several ways. First, where AI was used, a higher selection intensity could be applied when selecting breeding unit sires, as fewer sires were required. Second, selection accuracy was increased for all selection groups, as the altered population structure meant that information was available on a greater number of related animals. Both these factors act to increase genetic gain, and profit was significantly increased even after accounting for the cost of AI. Importantly, under the 2-stage selection structure modelled, the use of AI meant that profit was maximised with fewer bulls measured in the second stage,

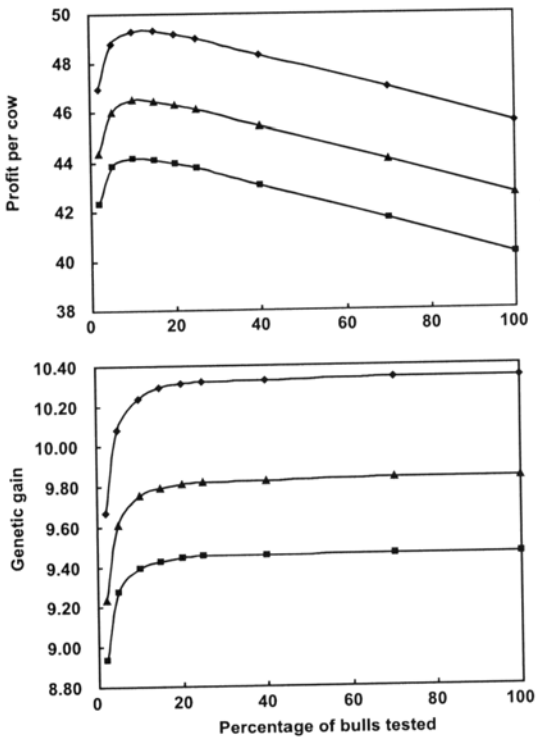

Figure 4. Impact of assumed cost of feed on (*a*) profit per cow; and (*b*) genetic gain in the breeding objective. Feed costs were set at the base level assumed for other analyses (■) and at 115% (▲) and 130% (◆) of the base level. The scenario for this analysis targeted the Japanese market objective with AI used in the breeding unit.

compared to breeding schemes using natural service only. Thus, the impact of using reproductive technologies in association with identified genetic superiority is 2-fold. First, investment in improved processes to identify superior animals is more profitable where breeding schemes are more efficient at distributing the superior genetics through the population. Second, where reproductive technologies are used in combination with a 2-stage selection process, profit can be maximised at a lower level of investment in recording.

The interaction between investment in reproductive technologies and advanced recording programmes means that evaluation of either technology should be performed in the context of the other, over the whole breeding programme. A corollary to this is that changes in either reproductive technologies or recording programmes may significantly alter the economics of applying the other technology. With a number of advances in both reproductive technologies (e.g. sexed semen, adult cloning) and recording programmes (additional phenotypic criteria and genetic markers) becoming closer to commercial application, it will be important to periodically re-evaluate the economic benefit from both new and existing technologies.

This analysis only considered AI as a technology to improve male reproductive potential. Measurement of RFI on heifers in the breeding unit was not considered, as the low selection intensity able to be applied to this group under natural female reproduction means that investment in RFI measurement is unlikely to be profitable. However, extensive use of multiple ovulation embryo transfer (MOET) programmes within the breeding unit might alter this situation, and mean that measurement of RFI on a proportion of females might be profitable.

Where only 10–20% of bulls were measured for RFI, the cost of the measurement per animal had only a moderate impact on profit (within the range of feasible costs). Therefore, where application of relatively expensive measurements is targeted on animals likely to be most influential on the population, the cost of the measurement is of lesser importance when considered across the whole breeding scheme. This does not mean that cost is not important, as it can can present a significant barrier to adoption of the technology in practical breeding programmes.

While the analysis provided information on which bulls might be profitably measured for RFI post-weaning, this rule might change where the first-stage selection of bulls for RFI measurement utilises more available information. This scenario might occur where selection was delayed until bulls were older (e.g. after measurements taken at 400 days of age), or if other criteria correlated to RFI were measured before selection. Examples of such criteria could include a physiological or genetic marker associated with RFI. Existence of such markers might have large impacts on optimal designs for breeding programmes, and further work is required to examine how such markers would best be used together with quantitative criteria measurements in multi-trait selection programmes to optimise investment.

Limitations of the analysis

Many of the limitations of the model used for this analysis were discussed by Nitter *et al.* (1994) and will not be repeated in detail here. However, where the model is used to provide recommendations as to how to best structure breeding programmes, it is important to consider that it is applied across the whole breeding structure and calculates costs and economic returns on this level. The approach does not recognise the fragmented ownership of resources within many breeding structures, and thus caution should be used when extrapolating results to provide guidance to individual businesses within an industry sector. Optimal decisions at an industry level may not be optimal for individual businesses. Issues such as market share and the distribution of costs and returns from genetic improvement programmes between businesses operating in markets which do not perfectly reflect genetic merit in prices are important. Dekkers and Shook (1990) used an alternative approach to evaluate breeding programmes where individual companies are competing within a national (or international) industry.

The deterministic nature of the model means that variance in returns from breeding programmes (i.e. risk) is not considered. In an economic context, analysis of investment returns without consideration of risk is incomplete. Intuitively, it seems that under the +RFI scenarios modelled here, concentrating investment in measuring criteria on a relatively small proportion of the most influential animals in a breeding programme must affect the risk profile of the breeding scheme, and so quantifying risk is particularly important for this type of scenario. Thompson *et al.* (1996) showed that incorporating expensive criteria in breeding programmes markedly increased the risk exposure (assessed as the lowest net present value from investment before positive returns are generated), although they did not calculate the impact on variance of returns. Moreover, the risk carried across an entire breeding programme such as that modelled here is likely to differ from the risk to individual businesses investing in breeding programmes within a wider industry. Despite these limitations, the outcomes from the analyses presented here are considered to provide a reasonable basis for general guidelines on the inclusion of RFI measurement in Australian beef cattle breeding programmes.

Conclusion

Based on the results presented here, it would be profitable for the Australian beef cattle industry to incorporate measurement of (residual) feed intake on a proportion of candidate sires for the seedstock sector. Profit is maximised when the top 10–20% of bulls are measured for RFI, selected

on a multiple-trait index incorporating all information available on the bulls and their relatives at weaning. These results apply to 2 different beef production systems in southern Australia targeting either the domestic market with pasture-based finishing or the Japanese market with animals finished on grain.

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AN ANALYSIS OF INVESTMENT IN ADVANCED BREEDING PROGRAM DESIGNS FOR BEEF CATTLE

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SUMMARY
Investment in breeding programs incorporating two-stage selection and measurement of net feed intake (NFI) was assessed for designs using performance test information only, or including information from progeny tests. Both designs were profitable relative to a performance test scenario without NFI measurement. Profit from optimally designed performance tests (where 5% to 30% of candidate sires for the breeding unit were performance tested for NFI) was higher than profit from optimal progeny test designs (2% to 5% of candidate sires progeny tested). This suggests that progeny testing may not be justified when analysed at an industry-wide level. However, accuracy of selection and genetic gain were greater from progeny testing. Accounting for risk/return relationships and market share might mean that progeny testing is justified at the level of an individual business.
Keywords: Breeding program, selection, beef cattle, performance test, progeny test.

INTRODUCTION
In the past, most beef cattle breeding programs involved comparatively low levels of investment in recording of criteria on which to base selection decisions. Typically, performance information on selection criteria (weight at strategically chosen ages, fertility and more recently ultra-sound scan measurements) were collected only on candidates for selection in seedstock herds. More recently, the level of investment in advanced recording programs being used by industry has increased markedly, with the incorporation of new, more expensive criteria traits in breeding programs (eg. measurement of feed intake), and a move towards recording of criteria on commercial animals in sire progeny tests. With higher levels of investment in breeding programs occurring, greater attention to breeding program design and economic analysis of alternative designs is warranted. This paper uses a model of investment in breeding programs to compare breeding programs utilising performance testing only (with and without measurement of feed intake) or a combination of performance and progeny testing.

METHODS
"ZPLAN", a model of investment in breeding schemes described by Nitter *et al.* (1994), was used for the analysis. The breeding program modelled followed that described by Archer and Barwick (1999), and consisted of a two tier self-replacing population of 200,000 breeding cows, with 10,000 cows in the breeding unit and the remainder in the commercial unit. Genetic improvement was only generated in the breeding unit, and transferred to the commercial unit through the use of bulls selected from the breeding unit. Twenty bulls per year were selected for use in the breeding unit as AI sires, and each sire was used for an average of 2.5 years. Sires for the commercial unit were used by natural mating.

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The breeding objective was based on production of 650 kg liveweight steers fed for the high quality Japanese market where marbling is valued. Further details on the breeding objective are given by Archer and Barwick (1999) and Barwick *et al.* (1999). Phenotypic and genetic parameters used were from BREEDPLAN and from literature values where available. Feed intake traits were expressed as net (or residual) feed intake (NFI) for both the objective traits (intake of cows and growing progeny were treated as correlated traits (assumed r_g=.65) in the objective) and as a selection criterion. Parameters for net feed intake (NFI) were taken from two recent Australian studies of Arthur *et al.* (2001) and the CRC for Cattle and Meat Quality project (Johnston, Robinson and Reverter, unpublished results).

Selection criteria and information sources. The base model (Bull performance test – NFI) was chosen to represent a seedstock sector where most performance criteria currently available in BREEDPLAN V4.1 are routinely recorded on selection candidates. These criteria included weight (at birth, 200, 400 and 600 days of age and on mature cows), fertility traits (days to calving, calving difficulty score and scrotal size) and scan traits (fat depth at $12^{th}/13^{th}$ rib and P8 site, eye muscle area and percent intra-muscular fat, with separate criteria for bulls and heifers), but did not include NFI. Information sources included records on individuals, paternal half sibs, sire, dam, and half-sibs of the sire and dam. The number of animals in half-sib classes were calculated from relevant biological and technical co-efficients describing herd structure. Criteria recording costs were similar to those used by Graser *et al.* (1994).

Modelled breeding program variations. Two advanced breeding program designs were modelled to include additional levels of recording over and above the base model described. Both designs incorporated a two-stage selection process for choosing bulls for use by the breeding unit, and a sub-routine of Wade and James (1996) which calculates response under two-stage selection was adapted and incorporated into the Zplan code. The first design (Bull performance test + NFI) examined selection of sires for the breeding unit using individual performance information on NFI. After weaning, a proportion of bulls (from 2 - 30%) were selected using information available on the individual (weight at birth and 200 days) and on relatives. These bulls then had the criterion of NFI measured (at a cost of $300 per animal) in addition to weights, scan traits and scrotal size already measured in the base model. The top 20 of these bulls (based on an index including all available information on the individual and relatives) were selected as AI sires for the breeding unit, and first used at 2.5 years of age. All bulls were available for selection as sires for the commercial unit irrespective of whether they were chosen for measurement of NFI, but NFI measurements on individuals were not included in the index used to select commercial sires.

The second design (progeny test) examined selection of sires for the breeding unit based on a combination of performance and progeny-test information. Bulls for progeny-testing were selected later (at 400 days of age) and with more available information than bulls selected for performance testing, as fewer bulls are likely to be progeny-tested than performance tested. From 1% to 20% of bulls were selected for progeny-testing using an index with information on the individual (weight at birth, 200 and 400 days, scrotal size and scans) and relatives. These bulls were then performance tested for NFI and progeny-tested. The progeny test generated information on 10, 15 or 25 steer progeny per sire, including weights (at birth, 200, 400 and 600 days), scans, NFI during feedlot finishing (at $300 per steer) and carcass measurements (fat depth, dressing % and marbling score). It

was assumed that heifers generated from the progeny test were retained with measurement of weights (as young heifers and as mature cows), scans and days to calving. The scan criteria measured on steers were assumed to be the same trait as those normally measured on heifers. As the progeny test was conducted under commercial conditions, NFI and carcass characteristics measured on progeny test steers were assumed to be the same trait as in the breeding objective. All other measures on progeny test or seedstock animals were treated as criteria correlated to the objective traits. After the progeny test was completed, sires for the breeding unit were selected from the tested bulls using an index of all available information, and first used at 5 years of age. Bulls for the commercial sector were selected at the same age and using the same individual information (although more information from relatives) as for the performance test only model.

Model outputs. The model calculated total costs (incurred in the breeding unit) and returns (obtained from the commercial unit) from a single round of selection, discounted over a 25 year investment horizon. Costs, returns and profit were expressed as $ per cow in the population. Annual genetic gain in the breeding objective was expressed as $ per year. Further details of the methods for calculating model outputs are given by Nitter *et al.* (1994).

RESULTS AND DISCUSSION

Profit per cow from the breeding programs modelled are shown in Figure 1. The base model (Bull performance test – NFI) is given to represent the current "typical" breeding program where all bulls are performance recorded for standard criteria other than NFI, and are available for selection as breeding unit sires. The profit from performance testing including measurement of NFI and using two stage selection (Bull performance test + NFI) was greater than the base model when 2% to 30% of bulls were selected for NFI measurement, indicating that including a NFI performance test in a two-stage selection process is profitable. Moreover, the response in profit to varying the proportion of bulls tested was almost flat from 5% through to 30%. In contrast, profit from progeny testing was optimised when 2% to 5% of bulls are progeny tested, depending on the number of steer progeny tested per sire. Even at optimal levels, progeny testing was not as profitable as 2-stage performance testing including NFI, although it was still significantly more profitable than the base situation.

The greater profit achieved by the 2-stage performance test design was due to the lower recording costs of this program compared to the progeny test programs. The annual genetic gain (Figure 2) and the economic return (before accounting for costs) generated from progeny testing in the optimal range (3-5% of bulls tested) were greater than the performance test design. This result occurred despite the generation interval being 4.99 years for progeny testing compared with 3.74 years for performance testing. However the increase in return from extra levels of recording in the progeny-test design were not sufficient to offset the increase in costs above the 2-stage performance test design.

Comparison between 2-stage performance testing and progeny testing based on profit alone would suggest that progeny-testing should not be recommended for inclusion in industry breeding programs. However, other issues not covered by the model might influence the comparison when decisions are made by industry participants. One such issue is the potential to increase market share in an industry where ownership is fragmented with-in and across sectors. The annual genetic gain in the breeding objective generated from progeny-testing is higher than the genetic gain generated from performance

testing (Figure 2). Thus individual breeders choosing to progeny-test and generate higher genetic gains may be able to increase market-share, and the investment in progeny testing may be justified after increased market share is accounted for. Thus optimal decisions on an industry-wide basis (as modelled here) are not necessarily optimal for individual businesses within a fragmented industry.

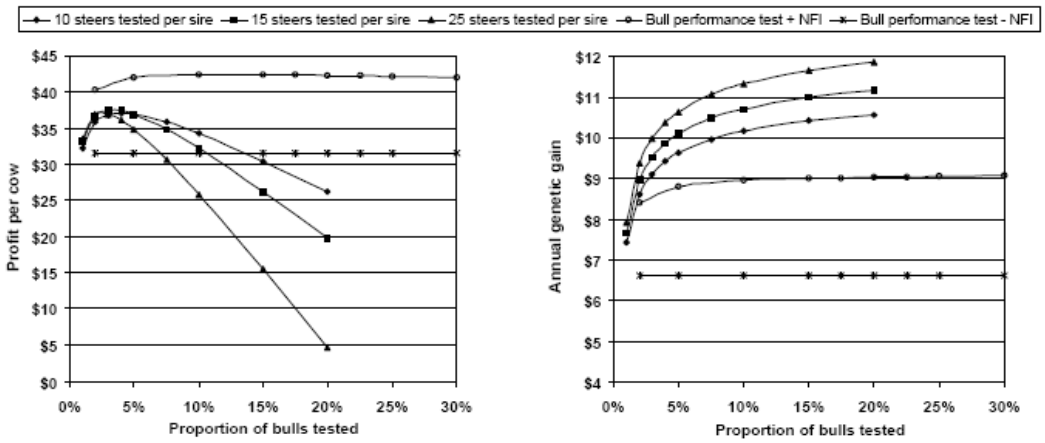

Figure 1. Profit per cow for performance test and progeny test models.

Figure 2. Annual genetic gain in the breeding objective for performance test and progeny test models.

A second issue to consider over profit alone is that of risk. While profit from including progeny testing in breeding programs is lower, the accuracy of selection is considerably higher. The index used to select sires for the breeding unit (after the second stage of selection) had a correlation with the breeding objective of 0.41 for performance testing, compared with 0.69, 0.74 and 0.79 for progeny-testing with 10, 15 and 25 steers per sire respectively. Thus returns (on an industry-wide basis) are likely to be less variable when progeny testing is used. However, deterministic models such as Zplan are generally not suited to incorporating risk in analysing investment decisions. This analysis has shown that increased investment in collecting information on a proportion of potential seedstock sires, whether by performance testing only or including progeny testing, is likely to be profitable at an industry-wide level. However, other models are required to better analyse the impact of investment at the level of individual businesses, and to incorporate assessment of returns relative to risk.

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GENETIC AND ECONOMIC EVALUATION OF IGF-1 AS AN INDIRECT SELECTION CRITERION IN BEEF CATTLE

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INTRODUCTION

With the accumulation of substantial amounts of new information for the previously unmeasured trait insulin-like growth factor (IGF-1), it is timely to make an analysis of the benefits of selection using this information. Alternative breeding schemes for livestock need to be assessed for their efficiency in making genetic progress and for their return and profit for the investment made. Levels of IGF-1 in blood are phenotypically associated with a variety of traits including growth, body size, food conversion efficiency, milk production, and carcase characteristics (Davis *et al*., 1995).

Feed intake is an economically important trait but also expensive to measure. If an indirect trait has sufficient heritability, a high genetic correlation with feed intake and is less costly to measure, indirect selection might become a supplement to direct selection. The benefits of indirect selection using IGF-1 are not only dependent on the achievable response but also on the costs of recording the indirect selection criterion. The aim of the study is to compare the genetic gain, profit and response to varying selection strategies using direct selection and indirect selection on residual feed intake (RFI) and IGF-1 in association with other traits. For the evaluation of selection criteria in an economic context we used the computer program 'ZPLAN' (Karras *et al*., 1997).

MATERIALS AND METHODS

ZPLAN uses a deterministic approach to predict genetic gain considering the impact of one round of selection. The approach models the flow of genes from the breeding sector to the commercial sector and uses selection index theory to calculate genetic gain and the discounted economic benefits accrued over a specified time period, in this study 25 years.

Population structure. The population structure was similar to that previously described for the Australian beef cattle industry (Graser *et al*., 1994). A total population of 200 000 animals was modelled, with 5 % comprising the breeding unit. Selection only occurs in the breeding unit, with no outside replacements. The flow of genes occurs through the movement of bulls selected from the breeding nucleus to the commercial herd, 1 567 bulls are selected for use within the commercial unit each year. Twenty bulls per year are selected for use as AI sires within the breeding unit and used on average 2.5 years. Sires for the commercial unit are utilised by natural service for 3 years.

Breeding Objective. The breeding objective was based on production of 650 kg live weight steers for the high quality Japanese B3 market where a premium is paid for marbling and steers finished within a long-fed (200d+) feedlot production framework. Mature cow weight,

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reproductive traits and other carcass traits also form an important part of the breeding objective. The breeding objective and derivation of economic values for RFI were described by Barwick *et al.* (1999).

Selection criteria and information sources. The base model constitutes the seedstock sector where neither RFI nor IGF-1 is recorded on the selected animals. The selection criteria used include weight (200d, 400d, 600d and mature cow weight), fertility traits (days to calving, calving difficulty and scrotal circumference) and scan traits (fat depth $12^{th}/13^{th}$ rib and P8 site, eye muscle area and intra-muscular fat percentage). The selection system assumes availability of across-herd genetic evaluation and transfer of bulls between herds. Information sources included records on individuals, paternal half sibs, sire, dam and half-sibs of the sire and dam. Initially bulls are selected at weaning with individual information including birth, 200d weight, relatives' information and IGF-1 if measured. Second stage selection has additional individual information with scan traits, scrotal size, and 400d and 600d weight. Depending on the scenario individual RFI information is also available at this second stage selection. No progeny information is used in the selection of bulls. Cows are selected after their first calf. The number of animals providing information to a selection index is determined by biological and technical parameters that set the population dynamics such as survival rates, productive lifetime, age at first calving, AI conception and calving rate.

Input parameters. The fixed and variable costs and time of recording of criteria were similar to those previously described by Graser *et al.* (1994). The additional measurement of IGF-1 and RFI was modelled, alternative costs were investigated for RFI tests ($450, $300, and $150) and for IGF-1 measurement ($30, $20 and $10) to compare various recording strategies and to analyse if less expensive recording would affect their use. The phenotypic and genetic parameters used were similar to those described by Barwick *et al.* (1999). Further genotypic and phenotypic relationships with IGF-1 were obtained from Johnston *et al.* (2001). IGF-1 is moderate to highly heritable (0.32) and demonstrates strong positive correlations with IMF %, P8 and rib fat. Studies in other species have shown strong positive correlations with feed efficiency and initial estimates confirm this with feed intake in cattle (Johnston, 2001 pers. comm). Traits for which correlations with IGF-1 were unavailable were assumed to be zero. A matrix bending routine was used to ensure positive definite genetic and environmental variance-covariance matrices.

Recording scenarios used in the analysis. Trait recording was modelled to reflect different strategies of use of RFI and IGF-1 information recorded within the nucleus. A basic breeding scheme is evaluated first. Scenario 2 and 3 consider the measurement of RFI. Scenarios 4 have IGF-1 recorded as second stage criteria on males while 4 and 5 have IGF-1 measured on all males and all animals respectively. Scenarios 7-10 consider the effect of higher and lower genetic correlations between IGF-1 and RFI and the measurement of all males for IGF-1 with and without RFI tests.

RESULTS AND DISCUSSION

Neither RFI nor IGF-1 measured. Scenario 1 considers the situation where all criteria are measured except IGF-1 or RFI and will be the base from which change in profit will be

considered. For the base scenario a profit of $35.28 is realised. Table 1 summarises economic and genetic returns from the various scenarios.

Measurement of RFI. Numbers of bulls tested at second stage was optimised with respect to profit with percentages shown in table 1. Scenario 2 with two-stage selection for RFI is most profitable when between 10 and 25 % of the breeding bulls are tested. There was little difference in profit between 10 and 25 %. Profitability dramatically decreases with higher testing costs of $300 and $450 when testing more than 25 %, results not shown. The percentage returns from traits in the objective show an increased contribution from RFI with small decreases in all the other traits. Scenario 3 requires knowledge of IGF-1 in all males before second stage selection for RFI. This is the most profitable scheme $48.40 (137.2 %), the increased information before selection for RFI testing gives increased index accuracy and decreases the number of animals required for testing. The three different price structures for RFI test made 5 %, 7 % and 10 % the most optimal percentage tested for the RFI cost of $450, $300 and $150 respectively. Trait returns are notable for the large increase in RFI and corresponding decreased contribution of growth and carcass characteristics.

Table 1. Comparison of various recording scenarios of IGF-1 on males and females, with and without concurrent RFI measurement for returns, cost and profit (relative to base scenario)

Scenario	IGF-1 m./f.	$r_{g\ RFI\text{-}IGF\text{-}1}$ [C]	2nd stage % tested	RFI tested	Returns ($A)	Costs ($A)	Profit ($A)	Profit (%)
1	--/--	0.4	--	no	39.54	4.26	35.28	100
2	--/--	0.4	15[B]	yes	47.52	6.63	40.88	115.9
3	x/--	0.4	5[B]	yes	53.75	5.34	48.40	137.2
4	x/--	0.4	40[A]	no	44.19	4.46	39.73	112.6
5	x/--	0.4	--	no	45.41	4.87	40.64	115.2
6	x/x	0.4	--	no	46.40	5.48	40.95	116.3
7	x/--	0.3	--	no	43.20	4.87	38.33	108.6
8	x/--	0.3	8[B]	yes	51.09	5.44	45.65	129.3
9	x/--	0.5	--	no	47.72	4.87	43.36	122.9
10	x/--	0.5	9[B]	yes	51.92	5.51	46.41	131.5

[A] IGF-1 second stage criteria. [B] RFI second stage criteria. [C] Both RFI traits (mature cow and yearling) assumed to have the same correlation.

Measurement strategies for IGF-1 without RFI. Scenario 4, measured IGF-1 as a second-stage selection criterion with other information available at this time including carcass scan traits, scrotal size, and 400d and 600d weight. The most profitable strategy was measurement of 40 % of the males. This could be the strategy of choice if the direct measurement of feed intake were unavailable. An assumption made was that genetic correlations with IGF-1 do not alter with age. Scenarios 5 and 6 are blanket testing of all males and all animals at time of weaning. While the measurement of males was the most cost effective, measurement of all animals provided the higher gain and profit. Larger emphasis is placed onto increasing returns from growth and decreased on RFI compared to scenarios where RFI is measured.

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Variation in IGF-1 – RFI genetic correlation. Scenarios 7-10 model the effect of varying correlations between IGF-1 and RFI, as parameters can be population specific or may change as more information is gathered. Reducing the genetic correlation from 0.40 to 0.30 (scenario 7 and 8) resulted in a decreased profit relative to the higher correlations due to decreased response in RFI. Increasing the correlation to 0.5 (scenario 9 and 10) saw a corresponding increase in profit when only using IGF-1 information but slightly less when using both information sources, compared with a correlation of 0.4.

CONCLUSION

The implication from this study is that IGF-1 can be best used as a screening test in a two-stage selection policy to identify animals to be placed into RFI trials. The profitability of the selection is increased in three ways : a decrease in the number of animals placed into the feeding trials, returns from lower feeding costs and lastly improvements in marble score. The number of animals measured in RFI tests will depend on the cost of the trial but less costly trials also affect accuracy of the test. Scenarios 4-6 demonstrated that just using IGF-1 without further RFI measurements would also raise profit of the breeding scheme. Cost of IGF-1 had little impact on profit and its implementation as an indirect selection criterion. Generally, the more animals measured for IGF-1 the more profit but some strategies with limited investment gave a better return per dollar spent.

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Response to selection in beef cattle using IGF-1 as a selection criterion for residual feed intake under different Australian breeding objectives

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Abstract

In this study various scenarios of selection in beef cattle using the physiological marker insulin-like growth factor (IGF-1) were investigated. Previous research shows that IGF-1 has favourable correlations with a number of important traits in beef cattle including residual feed intake (RFI), carcass fatness, average daily gain, live weight and carcass weight. The aim of this study was to compare the genetic response and profit to varying selection strategies that used direct selection for RFI and indirect selection with IGF-1 in association with other traits. Two breeding objectives for Australian producers were assessed relating to the high value Japanese export market, of which marbling is paid a premium, and the Australian domestic market. Selection for IGF-1 proved profitable in all scenarios for an export objective with the most optimal use as a first-stage selection tool before a feed intake trial for young bulls. Benefits of selection for IGF-1 with the domestic objective were similar to the export objective but increases in profit were marginal when used without feed intake information.

Keywords: IGF-1; Breeding program design; Two-stage selection; ZPLAN; Feed intake

1. Introduction

IGF-1 is a hormone that has a number of effects on growth and metabolism. It is produced in the liver, muscle and fat tissues and is found circulating in the plasma bound to one of 6 binding proteins, these proteins keep the levels of IGF-1 relatively stable (Hossner et al., 1997). Plasma IGF-1 levels have been demonstrated to be heritable (Herd et al., 1995) and selection experiments have used IGF-1 in other farm animal species (Blair et al., 2002; Bunter et al., 2002) as well as in beef cattle (Davis et al., 1995).

Breeding programs that have increased investment costs due to higher levels of measurement should not

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be appraised solely for the level of genetic gain but also on total profit change due to the increased investment. With the accumulation of substantial new information about IGF-1, it is timely to analyse the benefits of selection using IGF-1. IGF-1 appears to be correlated with a number of economically important traits in cattle, one of those being residual feed intake (RFI) (Johnston et al., 2002). RFI is calculated as the difference between an animal's actual intake and its expected intake based on its size and growth for a specified test period. As RFI is a linear function of feed intake, production and maintenance of body weight it reflects production efficiency and the phenotypic and genetic parameters of RFI can be written as a function of parameters of its constituent traits. Other traits known to be associated with IGF-1 include carcass fatness, live and carcass weight, average daily gain (Johnston et al., 2001) and also body size, food conversion efficiency and milk production (Davis et al., 1995). IGF-1 levels in juveniles has been advocated as a selection criterion in pigs where the breeding objective was lean meat yield and efficient growth (Bunter et al., 2002). Interest has also been shown in the use of IGF-1 as a selection tool in beef cattle, particularly as a possibility of using it as an indirect selection criterion for RFI.

This paper uses RFI in addition to production traits but it has been shown (Kennedy et al., 1993) that RFI does not provide any new information over and above that provided by production and feed intake. It has been claimed that an index with production and feed intake is equivalent to an index of production and residual feed intake (provided the economic values were appropriately derived). Hence, both approaches are sound. The Australian beef cattle industry is familiar with the term RFI and it seemed therefore appropriate that we used an index containing RFI. Archer et al. (2004, 1999) previously examined optimal strategies for use of RFI information in selection of beef cattle. These studies solely considered RFI in the young animal or progeny tests as the selection criteria. The aim of this study was to compare the genetic response and profit to varying selection strategies using either direct selection for RFI or indirect selection for IGF-1 in association with other traits.

2. Materials and methods

The computer program Z-PLAN (Karras et al., 1997) was used for the evaluation of selection criteria and alternate breeding program strategies. Z-PLAN calculates annual genetic gain deterministically using quantitative genetic theory. Selection index theory was applied to predict the response to a single round of selection. The approach models the flow of genes for a given age structure from the breeding to the commercial sector and uses selection indexes to calculate genetic gain and the discounted economic benefits accrued over a 25-year period. Variable costs associated with measurement of traits were included in the model and were used when calculating profit. Archer et al. (2004) outlined the changes made to the source code of Z-PLAN to accommodate the evaluation of a two-stage selection model following the procedure of Wade and James (1996) .

2.1. Population structure

Z-PLAN has been previously used to analyse Australian beef cattle breeding structures (Graser et al., 1994; Nitter et al., 1994; Archer et al., 2004) and similar values were utilised in this analysis. The population structure consists of a pyramid-breeding scheme with a nucleus herd disseminating genes down to the commercial herd and was considered typical of the Australian breeding production system. A self-replacing population of 200,000 animals was modelled, with the breeding unit (nucleus) comprising 5% of the total population. Selection occurred within the breeding unit. The breeding nucleus was closed to entry of animals from either the commercial or other herds. Flow of superior genes was modelled from the breeding nucleus to the commercial herd and required the selection of 1567 bulls for use within the commercial unit each year. It was assumed that bulls were utilised by natural service for 3 years, the bull to cow ratio being 1:40 with a calving rate of 88% and a 50:50 sex ratio in the progeny. Twenty bulls per year were selected for use as AI sires within the breeding unit, 200 cows per AI bull were used for an average 2.5 years. The same calving rate as natural service was assumed. Survival rates for cows in the breeding and commercial herds were 0.9 and 0.8, respectively, while calf survival rates to 200 and 400 days were

Table 1
Animal cohort and index used in the selection of animals

Index	Description
1	Sires from the breeding unit were selected in a first stage and contained base performance information and additionally post-weaning feed intake test information with or without IGF-1 information
2	Sires in the breeding unit produced sires and dams for the breeding unit
3	Dams from the breeding unit to produce sire and dams for the breeding unit
4	Sires from the breeding unit were used to breed sires and dams for the commercial unit
5	Dams from the commercial unit were used to breed sire and dams for the commercial unit
6	Sires from the commercial unit were used to breed dams for the commercial unit

0.97 and 0.96, respectively (Archer and Barwick, 1999). Dams were first used for breeding at 2 years of age in both the breeding and commercial herds. The number of animals providing information to a selection index was determined by these biological parameters.

Table 2
Number of records available for each information source for selection of sire and dam for nucleus and sire for commercial herd (Indexes 1–4)

Selection group	Selection criteria[a]									
Information sources[b]	BW	200d	400d	600d	Scan[c]	SC	DC	CoWt	RFI[d]	IGF-1[d,e]
Bulls for RFI test (Index 1)										
Individual	1	1	–	–	–	–	–	–	–	1,1
PHS-males	59	59	59	59	59	59	–	–	–	59,59
PHS-females	59	59	59	59	59	–	–	–	–	59, –
Sires for breeding unit (Index 2)										
Individual	1	1	1	1	1	1	–	–	1	1,1
PHS-males	59	59	59	59	59	59	–	–	–	59,59
PHS-females	59	59	59	59	59	–	–	–	–	59, –
Dams for Breeding Unit (Index 3)										
Individual	1	1	1	1	1	–	1	–	–	1,1
PHS-males	59	59	59	59	59	–	–	–	–	59,59
PHS-females, not replacement	15	15	15	15	15	–	–	–	–	15, –
PHS-females-replacement	44	44	44	44	44	–	44	–	–	44, –
Sires for Commercial Herd (Index 4)										
Individual	1	1	1	1	1	–	–	–	–	1,1
PHS-males	59	59	59	59	59	–	–	–	–	59,59
PHS-females	59	59	59	59	59	–	–	–	–	59, –
Extra Information All Groups (All Indexes)										
Sire	1	1	1	1	1	1	–	–	1	1,1
Dam	1	1	1	1	1	–	1	1	–	1, –
HS of Sire-all Males	106	106	106	106	106	106	–	–	–	106,106
HS of Sire-females, not replacement	26	26	26	26	26	–	–	–	–	26, –
HS of Sire-females, replacement	80	80	80	80	80	–	80	80	–	80, –
HS of Dam-all males	106	106	106	106	106	106	–	–	–	106,106
HS of dam-females, not replacement	26	26	26	26	26	–	–	–	–	26, –
HS of Dam-female replacement	80	80	80	80	80	–	80	80	–	80, –

[a] Selection criteria abbreviations shown in Table 6.
[b] HS, Half Sibs; PHS, Paternal Half Sibs.
[c] Ultra-sound scan data includes fat depth, rib fat, intra-muscular fat % and eye muscle area, with scans on different sexes considered as different traits.
[d] IGF-1 measurements apply to scenarios 3–6 and RFI measurements apply to scenario 2 shown in Tables 3 and 5.
[e] Male only or both sexes measured.

2.2. Selection criteria, breeding structure and Information sources

The selection system assumed availability of across-herd genetic evaluation and unlimited transfer of bulls or semen between individual herds in the nucleus tier. A two-stage selection procedure was used with first stage selection of bulls at weaning using individual information of birth and 200 day weight and relatives' information on all available traits from sire, dam, paternal half-sibs of individual and paternal half-sibs of the sire and dam. IGF-1, if measured, was available at this first stage. Bulls over 400 days of age were placed in a second selection stage with additional individual information on ultrasound scan traits (fat depth at 12th/13th rib and rump, eye muscle area and intra-muscular fat percentage), fertility traits (days to calving and scrotal circumference) and 400 day and 600 day weight. If measured, individual RFI information was also available on the selected proportion of animals from those initially available. Bulls that were not kept within the nucleus to breed bulls and cows for the breeding unit were moved for use to the commercial herd or were culled. No progeny test information was used in the selection of bulls.

2.3. Selection indexes and selection groups

Six different selection indexes were used on ten different selection cohorts in the population with the cohorts shown in Table 1. All indices contained all available information as described for the base index. Indexes 5 and 6 do not produce gain in the breeding objective but were required to model the gene transmission from nucleus to commercial herds. Details of the various information sources included in selection indices used in the nucleus are shown in Table 2.

2.4. Breeding objectives

Breeding objective traits used in the simulation, economic values and trait abbreviations are shown in Table 3 for the two breeding objectives with economic values being obtained from BreedObject (Barwick et al., 2001). The first breeding objective was aimed at production of 650 kg live weight steers for the high quality Japanese B3 market where a premium is paid for marbling. For this system, steers were finished within a long-fed (200 day plus) feedlot production framework and consequently had higher feed costs compared to pasture-based production. Mature cow weight, reproductive traits and other carcass traits were also included in the objective. The second objective was aimed at a self-replacing commercial herd in temperate Australia targeting grass-finished production for the domestic supermarket trade with no marbling requirement. Sale weight (direct and maternal), fat depth and reproductive traits were important in this breeding objective. This objective had lower associated feed costs and consequently lower relative economic values for RFI compared to the Japanese

Table 3
Economic weights used for both breeding objectives

Breeding objective	Abbreviation	Units	Japanese market[a]	Domestic market[a]
Sale live weight (direct)	SWd	kg	0.655	0.813
Calving ease (direct)	CEd	%	0.671	0.647
Dressing percentage	DP	%	11.07	6.39
Saleable meat percentage	SMP	%	9.04	5.03
Fat depth	FD	mm	0	0.741
Cow weaning rate	CWR	%	3.53	0.934
Marble score	MS	score	56.28	0
Cow survival rate	CSR	%	4.69	3.73
Cow weight	CW	kg	−0.189	−0.152
Residual feed intake (cow)	RFIc	kg/day	−30.50	−27.5
Residual feed intake (yearling)	RFIy	kg/day	−52.61	−20.64
Live sale weight (maternal)	SWm	kg	0.655	0.813
Calving ease (maternal)	CEm	%	0.426	0.426

[a] Economic value per unit change in Australian dollars (Archer et al., 2004).

Table 4
Description of variable costs used in the analysis

Variable costs	Cost ($)	Age (years)
Identification, pedigree recording, computer, etc.	11.00	2.00
Birth weight (BW) per calf	3.00	0.00
200-day weight (200d) per calf	1.00	0.55
400-day weight (400d) per calf	1.75	1.10
600-day weight (600d) per calf	1.75	1.65
Measurement of scan traits per calf	0.50	2.00
Cost of each AI per insemination	30.00	1.30
Mature cow weight	1.00	2.50
Scrotal size per calf	1.10	2.00
Residual feed intake (RFI) per calf[a]	450.00	1.10
IGF-1 per calf[b]	30.00	0.55

[a] Variable cost $450, $300 and $150.
[b] Variable cost $30, $20 and $10.

objective. RFI intake in the mature cow and the growing animal were treated as two separate traits for the calculation of economic values. The breeding objectives and derivation of economic values for RFI have been described by Barwick et al. (1999).

2.5. Input parameters

The Z-PLAN program required fixed and variable costs per cow for each measurement or information source used in the selection indexes. Costs included were those directly related to performance and pedigree recording in the nucleus. Changes in variable costs were related to number of animals that were performance recorded and were a direct multiple of numbers measured. The costs and time of measurement are shown in Table 4. The time at which costs were incurred was important for discounting purposes. Additional measurements of IGF-1 and RFI were modelled, with a range of costs assumed for RFI tests ($450, $300, and $150) and for IGF-1 measurement ($30, $20 and $10).

2.6. Scenarios

Table 5 describes the different recording scenarios used in the analysis modelled to reflect different strategies of use of RFI and IGF-1 information recorded within the nucleus herd. The base model (Scenario 1) simulates the situation where neither RFI nor IGF-1 was recorded on the selected animals. All other selection criterion traits were recorded. Best practice recording of traits was simulated to examine whether additional trait measurement would increase profit for breeders who currently use all current trait measurements available. Scenarios 2 and 3 consider the measurement of RFI with and without additional IGF-1 information on bulls, but including information available in Scenario 1. Scenarios 4 and 5 have IGF-1 measured on either only bulls (4) or bulls and cows (5) without additional RFI measurement. Scenario 6 simulates an alternative use of IGF-1 in a similar manner to RFI as a second stage selection criterion and Scenario 7 has IGF-1 measured on all animals and RFI as a second stage measurement criterion on bulls.

2.7. Phenotypic and genetic parameters

The phenotypic and genetic parameters used were the same as those for Angus cattle in Australia's national beef recording scheme, BREEDPLAN (Johnston et al., 1999) and were based on the parameters described by Archer and Barwick (1999). Further

Table 5
Recording scenarios used in the analysis

Scenario 1	Base scenario—Neither RFI or IGF-1 recorded, all other selection criteria are recorded, scenarios 2–6 have measurements available in scenario 1 as well as any additional measurements
Scenario 2	RFI recorded as second stage selection criteria
Scenario 3	RFI as second stage selection criteria and IGF-1 recorded on all bulls
Scenario 4	IGF-1 recorded on all bulls in nucleus herd, with no RFI information
Scenario 5	IGF-1 recorded on all heifers and bulls in nucleus herd with no RFI information
Scenario 6	IGF-1 recorded as second stage selection criterion, assuming that genetic correlations between traits do not alter with measurement age
Scenario 7	RFI as second stage selection criteria and IGF-1 recorded on all bulls and cows

Table 6
Genetic correlations between selection criteria and breeding objectives

Trait[a,b]	Abbrev.	SWd	Ced	DP	SMP	FD	CWR	MS	CSR	CW	RFIc	RFIy	SWm	CEm
Birth wt	BW	0.49	−0.41	−0.01	0.00	−0.06	−0.02	0.00	−0.02	0.32	−0.06	−0.06	0.00	0.16
200d wt	200d	0.62	−0.19	−0.06	−0.06	0.04	−0.01	−0.06	0.00	0.38	−0.29	−0.26	0.00	0.09
400d wt	400d	0.72	−0.16	−0.06	−0.05	0.06	0.00	−0.14	0.00	0.46	−0.15	−0.14	−0.03	0.00
600d wt	600d	0.88	−0.18	−0.04	−0.05	0.06	−0.01	−0.22	0.00	0.71	−0.16	−0.15	0.00	0.00
Cow wt	CoWt	0.71	−0.25	−0.05	0.00	0.09	0.00	−0.21	0.00	1.00	−0.23	−0.28	0.08	0.00
Days to calving	DC	0.00	−0.07	0.00	0.00	0.00	−0.65	0.00	0.00	0.00	0.36	0.04	0.01	−0.20
Scrotal circumf.	SC	0.14	−0.04	0.00	0.00	0.00	0.21	0.00	−0.01	0.25	0.00	−0.01	0.00	0.00
Fat depth rump (h)	FatD (h)	0.05	0.00	0.15	−0.52	0.86	0.00	0.25	0.00	0.04	0.28	0.24	0.00	0.00
Fat depth rump (b)	FatD (b)	0.05	−0.02	0.15	−0.53	0.64	0.00	0.17	0.00	0.03	0.08	0.06	0.00	0.00
Rib fat depth (h)	Rib (h)	0.09	0.00	0.14	−0.54	0.73	0.00	0.24	0.02	0.04	0.32	0.34	0.00	0.00
Rib fat depth (b)	Rib (b)	0.09	0.00	0.15	−0.52	0.55	0.00	0.16	0.00	0.04	0.21	0.22	0.00	0.00
Eye muscle area (h)	EMA (h)	0.36	−0.09	0.20	0.34	0.27	0.00	−0.15	0.00	0.20	−0.10	−0.11	−0.01	0.00
Eye muscle area (b)	EMA (b)	0.35	−0.09	0.19	0.33	0.29	0.00	−0.15	0.00	0.19	−0.02	−0.04	0.00	0.01
Intramuscular fat (h)	IMF%(h)	−0.22	0.00	0.10	−0.27	0.29	0.00	0.71	−0.02	−0.22	0.19	0.26	0.00	0.00
Intramuscular fat (b)	IMF%(b)	−0.22	0.00	0.10	−0.07	0.11	0.00	0.62	0.00	−0.22	0.16	0.22	−0.01	0.00
RFI post-weaning	RFIpw	−0.19	−0.02	0.03	−0.38	0.14	−0.04	0.17	−0.05	−0.29	0.45	0.71	0.05	−0.05
IGF-1 pre-weaning	IGF-1[c]	0.17	−0.04	0.09	−0.10	0.41	−0.08	0.36	−0.04	0.02	0.35[c]	0.35[c]	0.06	0.02

[a] (h)=heifer, (b)=bull.
[b] Breeding objective trait abbreviations shown in Table 3.
[c] IGF-1 correlation 0.25 in schemes measuring decreased correlations.

genotypic and phenotypic relationships of traits with IGF-1 were obtained from Johnston et al. (2001, 2002). IGF-1 was assumed to be moderately heritable (32%) and positively correlated with intra-muscular, rump and rib fat. Estimates confirm the positive correlations with residual feed intake in cattle (Johnston et al., 2002). Estimates of the correlation between IGF-1 and feed intake were assumed to be around 0.35. Traits for which correlations with IGF-1 were unavailable were assumed to be zero. A matrix bending routine (Henshall and Meyer, 2002) was used to ensure that genetic and environmental variance–covariance matrices were positive definite. Table 5 shows the assumed genetic correlations between

Table 7
Phenotypic standard deviations (σ_p), heritability (h^2) and the genetic (above diagonal) and phenotypic correlation (below diagonal) between selection criteria

	σ_p	h^2	BW	200d	400d	600d	CoWt	Dcal	SSiz	$FatD_h$	$FatD_b$	Rib_h	Rib_b	EMA_h	EMA_b	$IMF\%_h$	$IMF\%_b$	RFI_{pw}	IGF−1
BW	3.81	0.39		0.65	0.54	0.57	0.39	0.00	0.10	−0.05	−0.05	−0.05	−0.05	0.15	0.14	0.00	0.00	−0.32	0.07
200d	22.36	0.10	0.35		0.71	0.69	0.39	0.00	0.10	0.05	0.05	0.05	0.04	0.22	0.21	0.00	0.00	−0.32	0.07
400d	30.89	0.25	0.30	0.54		0.57	0.34	0.00	0.10	−0.05	−0.05	−0.05	−0.05	0.15	0.14	0.00	0.00	−0.05	0.03
600d	34.64	0.31	0.31	0.51	0.68		0.72	0.00	0.14	0.06	0.05	0.10	0.11	0.38	0.38	−0.22	−0.21	−0.16	0.18
CoWt	46.90	0.41	0.20	0.30	0.50	0.63		0.00	0.05	0.10	0.09	0.11	0.07	0.21	0.20	−0.01	0.00	−0.32	0.06
Dcal	23.39	0.07	0.00	−0.04	−0.05	0.00	0.07		−0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.08
Ssiz	2.05	0.39	0.04	0.33	0.21	0.20	0.13	−0.20		0.00	0.00	−0.02	0.00	0.04	0.03	0.00	0.00	0.03	0.00
FatD(h)	1.98	0.41	−0.04	0.13	0.20	0.20	0.10	0.00	0.00		0.74	0.86	0.64	0.29	0.30	0.33	0.10	0.22	0.58
FatD(b)	1.58	0.28	−0.04	0.14	0.22	0.22	0.10	0.00	0.00	0.82		0.66	0.85	0.19	0.11	0.11	0.11	0.13	0.49
Rib(h)	1.38	0.34	−0.04	0.14	0.22	0.23	0.10	0.00	0.00	0.89	0.81		0.77	0.21	0.20	0.34	0.12	0.32	0.66
Rib(b)	1.05	0.23	−0.04	0.15	0.23	0.24	0.10	0.00	0.00	0.80	0.90	0.84		0.19	0.10	0.11	0.11	0.25	0.62
EMA(h)	5.25	0.26	0.07	0.21	0.34	0.36	0.20	0.00	0.08	0.21	0.18	0.19	0.19		0.79	0.00	−0.03	−0.07	0.59
EMA(b)	6.67	0.27	0.07	0.21	0.34	0.36	0.20	0.00	0.08	0.21	0.15	0.18	0.17	0.87		−0.11	0.00	−0.06	0.52
IMF%(h)	1.00	0.25	0.00	−0.01	−0.04	−0.06	0.00	0.00	0.00	0.10	0.03	0.09	0.03	0.00	−0.03		0.78	0.23	0.43
IMF%(b)	0.89	0.12	0.00	−0.01	−0.03	−0.04	0.00	0.00	0.00	0.02	0.02	0.02	0.02	0.00	0.00	0.12		0.20	0.41
RFIpw	0.62	0.39	0.00	0.00	0.00	0.00	−0.07	0.00	0.10	0.11	0.11	0.14	0.14	0.06	0.06	0.00	0.00		0.35
IGF-1	6.87	0.32	0.15	0.15	0.15	0.15	0.00	0.00	0.00	0.20	0.20	0.20	0.20	0.00	0.00	0.08	0.08	0.00	

Table 8
Phenotypic standard deviations (σ_p), heritability (h^2) and the genetic correlations between traits in the breeding objective

Trait[a]	σ_p	h^2	SWd	Ced	DP	SMP	FD	CWR	MS	CSR	CW	RFIc	RFIy	SWm
SWd	34.64	0.31												
Ced	20.03	0.10	0.17											
DP	1.80	0.33	0.06	0.05										
SMP	2.00	0.56	0.03	0.01	0.11									
FD	1.98	0.41	0.06	0.00	0.17	0.63								
CWR	32.50	0.05	0.01	0.07	0.00	0.00	0.00							
MS	0.71	0.38	0.06	0.01	0.11	0.24	0.16	0.00						
CSR	9.95	0.03	0.00	0.05	0.00	0.00	0.00	−0.09	0.00					
CW	46.90	0.41	0.71	0.25	0.05	0.00	0.09	0.00	0.21	0.00				
RFIc	0.62	0.39	0.12	0.02	0.03	0.32	0.28	−0.23	0.20	0.02	0.23			
RFIy	0.62	0.39	0.12	0.03	0.04	0.38	0.26	−0.06	0.28	0.00	0.28	0.55		
SWm	–	0.04	0.01	0.00	0.01	0.01	0.00	−0.01	0.00	0.00	0.08	0.07	0.08	
Cem	–	0.10	0.00	0.50	0.00	0.01	0.00	0.21	0.00	0.26	0.00	0.03	0.00	0.00

[a] Trait abbreviations are shown in Table 3.

selection criteria and traits in the breeding objective. Table 6 shows the assumed phenotypic standard deviations, heritability and phenotypic and genetic correlations between the selection criteria. Tables 7 and 8 shows the assumed phenotypic standard deviation, heritability and genetic correlations between traits in the breeding objective. To test the sensitivity correlations between IGF-1 and both RFIc and RFIy were varied and used under the assumptions of Scenario 3. Alternative correlations were examined within the parameter space, however larger variations in correlations would have meant further bending of the original genetic covariance matrix making comparisons of sensitivity difficult.

3. Results

Table 9 summarises economic responses from the various scenarios for both the breeding objectives.

Table 9
Comparison of return, profit (relative to base scenario) and cost per cow for different scenarios for Japanese and domestic breeding objectives

Scenario	IGF-1[a] m./f.	RFI tested	2nd stage % tested	Costs[b] ($A)	Returns ($)	Profit ($)	Profit (%)
Japanese objective							
1	–/–	No	–	4.26	38.73	34.47	100.0
2	–/–	Yes	10[b]	5.80	47.58	41.78	121.2
3	x/–	Yes	5[b]	5.23	52.53	47.30	137.2
4	x/–	No	–	4.87	42.55	37.68	109.3
5	x/x	No	–	5.48	43.25	37.77	109.6
6	x/–	No	40[c]	4.46	42.06	37.60	109.1
7	x/x	Yes	5[b]	5.48	53.09	47.61	138.1
Domestic objective							
1	–/–	No	–	4.26	34.78	30.52	100.0
2	–/–	Yes	5[b]	5.33	38.16	32.83	107.6
3	x/–	Yes	5[b]	5.23	40.94	35.71	117.0
4	x/–	No	–	4.87	35.17	30.30	99.9
5	x/x	No	–	5.48	37.57	32.09	105.1
6	x/–	No	20[c]	4.37	34.95	30.59	100.2
7	x/x	Yes	5[b]	5.48	41.17	35.69	116.9

[a] IGF-1 tested on males (m) or females (f) shown by (x).
[b] IGF-1 information used in first stage index.
[c] IGF-1 information used in second-stage index.

3.1. Scenario 1: RFI and IGF-1 not measured

The base scenario showed a net profit of $34.47 per cow for the Japanese objective and $30.52 for the domestic objective over a 25-year period. Selection criterion costs were $4.26 per breeding cow. Bull selection criterion measurement costs were incorporated into measurement cost per female to allow comparison across the whole scheme as opposed to individual bull measurement cost. While small changes were made to the genetic variance–covariance matrix of Archer et al. (2004) to ensure positive definiteness, the base returns were similar to those found in that study

3.2. Scenario 2: Measurement of RFI without IGF-1

Selection for RFI was most profitable when 5–25% of the candidate bulls were tested for RFI in a second stage. When targeting the Japanese objective there was little difference in profit when between 10% and 25% of the bulls enter second stage selection, with the optimal percentage for further measurement being 10% as demonstrated in Fig. 1b. Fig. 1d shows the optimum to be around 5% when bulls were tested for the domestic objective. Profitability decreased continually, with higher test numbers. Higher test costs of $300 and $450 resulted in larger decreases in profit when more than optimal numbers were tested for RFI.

3.3. Scenario 3: measurement of RFI with IGF-1

Under this scenario, IGF-1 information was available on all bulls before the first stage selection took place. This was the most profitable scenario for both objectives with increases in profitability of 37% for the Japanese objective and 17% for the domestic objective. Increased information before second-stage selection gave higher accuracy for the Japanese objective and decreased the optimum number of

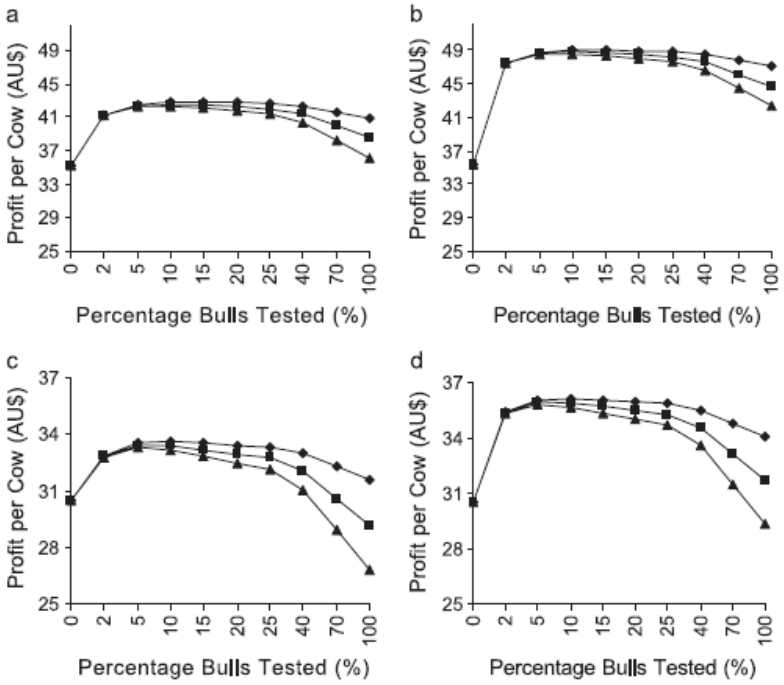

Fig. 1. (a–d) Profit per cow with respect to number of bulls tested for Residual Feed Intake (RFI) with varying price costs of $450 (%), $300 (¦) and $150 (") for RFI test in Scenario 2 (a,c) and 3 (d,d) for both the domestic (c,d) and Japanese B3 (a,b) market objectives, with an IGF-1 cost of $30.

animals required for feed intake tests. With an assumed cost of $450 per bull for testing feed intake, the number of animals tested can be decreased from between 10% and 25% (as noted in Scenario 2) down to testing only 5% of animals in the second stage as shown in Fig. 1b.

Table 10 shows that use of IGF-1 information resulted in a large (15%) increase in contribution to profit of the RFI traits with a relatively small decrease in the contribution of growth, calving ease, cow weight and carcass yield. The extra information from the IGF-1 information resulted in an increase of returns from marble score of 4.3% of total returns from selection, shown in Table 11. Without IGF-1 and only RFI performance (Scenario 2), unfavourable correlations resulted in a negative genetic change for marble score.

As shown in Fig. 1d, the domestic objective did not show a decrease in optimal test numbers under Scenario 3, in contrast to the Japanese objective. The optimal percentage remained the same at 5% of bulls tested but the index accuracy increased, resulting in increased predicted gain for the objective and profit. When a smaller economic emphasis was placed on feed intake, the weight placed on improving the RFI traits decreased. All other scenarios had less than half of total returns from the RFI traits for the domestic objective but with IGF-1 and intake test information returns from RFI traits increased by 13.3–55.5% compared to the base scenario.

Fig. 1 shows that variation in the cost of testing for RFI and IGF-1 resulted in small changes to optimal numbers tested. RFI measurement costs of $300 and $150 resulted in optimal percentages tested of 7.5% and 10%, respectively. Variation in the cost of IGF-1 measurement made little difference to its implementation as a selection criterion. Higher IGF-1 testing cost decreased profit marginally but when costs were confined to a small breeding nucleus as modelled here, no changes in the recommendations for the use of IGF-1 occur.

3.4. Scenarios 4 and 5: measurement strategies for IGF-1 without RFI testing

Blanket testing of all males or all animals at time of weaning for IGF-1 without a further feed intake measurement provides a breeder with a

Table 10
Returns for trait groups as a percentage of overall returns for each breeding objective

Trait group[a]	Growth	Carcass yield	Marbling	Survival rate	Calving ease	Cow weight	RFI
Scenario		FD[b]					
	SWm	DP		CWR	CEm		RFIc
	SWd	SMP	MS[c]	CSR	CEd	CW	RFIy
Japanese Export Objective							
1	17.64	26.56	1.79	10.85	−2.37	−3.97	49.50
2	11.57	22.96	−2.13	14.18	−1.46	−5.62	60.50
3	12.77	18.13	2.19	9.10	−1.41	−5.26	64.48
4	15.52	17.75	3.28	9.45	−1.88	−4.81	60.69
5	16.24	18.28	4.44	6.20	−1.96	−3.52	60.32
6	17.47	20.54	3.00	7.76	−2.21	−3.86	57.30
7	11.43	19.85	−4.21	10.95	−0.99	−5.41	68.38
Domestic Objective							
1	52.69	15.43	–	1.58	−2.70	−9.20	42.21
2	52.07	12.61	–	1.55	−2.93	−8.60	45.30
3	41.95	13.10	–	2.68	−2.08	−11.18	55.52
4	57.88	13.75	–	1.45	−3.27	−9.40	39.59
5	52.09	12.62	–	1.55	−2.93	−8.60	45.28
6	59.26	13.65	–	1.14	−3.35	−1.52	38.83
7	46.38	13.92	–	1.80	−2.335	−8.36	48.60

[a] Trait abbreviations in Table 3.
[b] Fat depth (FD) domestic objective only.
[c] Marble score (MS) Japanese export objective only.

Table 11
Returns ($) in the traits in the breeding objective for the different objectives

Scenario	SWd	SWm	CW	DP	SMP	MS/FD[a]	CWR	CSR	CEd	CEm	RFIc	RFIy
Japanese Export Objective												
1	6.47	0.18	−1.57	0.93	9.58	0.71	4.30	0.00	−0.94	0.33	5.70	13.88
2	6.04	0.09	−2.00	1.15	10.89	−0.87	4.84	0.17	−0.79	0.04	6.72	21.24
3	7.14	−0.08	−2.16	1.15	9.63	1.14	3.85	−0.25	−0.77	0.07	8.35	25.69
4	7.18	0.05	−1.66	1.14	7.65	1.66	3.43	−0.32	−0.94	0.33	7.66	19.32
5	7.17	0.04	−1.63	1.20	7.29	2.06	3.25	−0.37	−0.91	0.32	7.99	20.02
6	7.31	0.07	−1.71	1.10	7.98	1.31	3.69	−0.25	−0.98	0.35	7.09	18.19
7	6.93	−0.01	−2.10	0.54	10.84	2.11	4.26	0.09	−0.65	0.03	9.16	25.21
Domestic Objective												
1	20.58	0.10	−3.34	−0.43	5.71	−0.36	0.36	−0.03	−1.19	0.35	6.39	6.66
2	20.03	0.03	−3.51	−0.33	6.57	−0.36	0.49	0.11	−1.04	0.09	7.21	8.87
3	18.95	0.00	−3.41	−0.27	6.29	−0.39	0.60	0.16	−0.98	0.08	9.10	10.93
4	20.02	0.06	−3.31	−0.26	5.47	−0.37	0.47	0.04	−1.15	0.28	6.85	7.07
5	19.10	0.05	−3.21	−0.24	5.33	−0.39	0.53	0.06	−1.10	0.28	8.38	8.65
6	20.29	0.09	−3.33	−0.43	5.59	−0.38	0.41	−0.01	−1.17	0.34	6.66	6.90
7	19.00	0.03	−3.37	−0.32	6.14	−0.40	0.58	0.11	−0.65	0.17	8.83	10.33

[a] Fat depth (FD) domestic objective only, marble score (MS) Japanese objective only, trait abbreviations found in Table 3.

possible method to select without the feed intake costs. Table 9 shows that both scenarios proved profitable with increases from the base of 15.2% (Scenario 4) and 16.3% (Scenario 5) for the Japanese objective. While IGF-1 information allows earlier selection a decreased generation interval was not modelled.

3.5. Scenario 6: IGF-1 used as second stage selection criterion

Utilizing IGF-1 information for a second stage selection on a selected group of bulls without RFI information reduces the investment in IGF-1 measurement. As expected, reducing the amount of available information also decreases the genetic gain and economic returns. The optimal numbers tested for IGF-1 were 40% and 20% for the Japanese objective and domestic objectives, respectively. Similar to scenario 4, with information on bulls only, returns and profit were considerably reduced when feed intake details were not included.

3.6. Scenario 7: IGF-1 recorded on all animals and RFI on subset of bulls

This scenario was marginally the most profitable for the export objective and marginally less profitable for the domestic objective compared to scenario 3 (only males measured for IGF-1). What should be noted in both though is the increase in returns compared to that of scenario 3 was relatively small, and the increased information on females makes little difference to overall returns. From a nucleus breeding perspective the increase in costs to measure females would be only marginally be compensated for in increased gain in the objective and for a breeder the measurement of females also could be questioned.

3.7. Sensitivity to variation in genetic correlation between IGF-1and RFI

The results of the study may be sensitive to assumed correlations; hence the model was examined with alterations in the genetic correlations. Table 12 shows the sensitivity of profit to variations in these genetic correlations for both objectives. The results show that the model was relatively insensitive to changes in correlation between 0.25 and 0.35. The export objective was relatively more sensitive to variations in the correlation between RFIc and IGF-1. The domestic objective was more sensitive to variation in the correlation between RFIy and IGF-1 and slightly more sensitive overall to variation in correlations. Decreasing the correlation between the traits resulted in lower genetic gain and profit but the

Table 12
Sensitivity of profit to variation in the genetic correlation between RFI and IGF-1

Correlation with IGF-1[a]		Scenario 3		Scenario 5	
RFIc	RFIy	Japanese profit	Domestic profit	Japanese profit	Domestic profit
0.35	0.35	$47.30	$35.71	$37.77	$32.09
0.35	0.30	$46.90	$35.53	$37.42	$31.90
0.35	0.25	$46.86	$35.63	$37.27	$31.77
0.30	0.35	$46.99	$35.74	$37.64	$31.93
0.30	0.30	$46.87	$35.64	$37.35	$31.78
0.30	0.25	$46.86	$35.52	$37.26	$31.67
0.25	0.35	$46.94	$35.67	$37.53	$31.80
0.25	0.30	$46.86	$35.52	$37.27	$31.65
0.25	0.25	$46.80	$34.92	$37.25	$31.57

[a] Trait abbreviations are shown in Table 1.

scenario still remained more profitable than Scenario 1 with no IGF-1 or RFI information. The sensitivity of response to change in correlation between marbling and IGF-1 was also modelled with only a small change in returns.

4. Discussion

This study demonstrated that testing for both IGF-1 and RFI resulted in increased profit levels for both of the breeding objectives assessed. The variance in profit accounted for by IGF-1 levels allowed more accurate selection of candidates for subsequent feed intake measurement. The importance of the feed intake test either alone, or coupled with IGF-1 measurement, indicated the importance of RFI to overall profitability of a beef herd. The value of feed intake to profitability varied according to the economic weight, but added substantially to profit for each objective. While IGF-1 can be considered a useful aid to the selection of more profitable animals, results presented here demonstrate the trait will not be as useful as direct measurement of feed intake, despite the associated costs of the latter.

The cost of IGF-1 measurement had little impact on profit and therefore on its implementation as an indirect selection criterion. Using a small breeding nucleus the costs were relatively small when spread across the entire industry. Generally, the more animals measured for IGF-1 the greater the expected profit. A strategy with limited investment (Scenario 4) gave a better return per dollar invested for the export objective. The benefits of selection with IGF-1 without further feed intake measurement were marginal for the domestic objective. For the domestic objective the use of IGF-1 alone on bulls in the nucleus increased the total returns compared to those of Scenario 1, but the additional gain did not compensate for the increased measurement costs.

For the nucleus herd, the use of IGF-1 alone (Scenarios 4 and 5) yielded lower profit levels when used as an alternative to on-farm or centralised RFI testing stations. However, for an individual herd, the use of IGF-1 without RFI information could be a less risky option due to the smaller investment required. When measuring small numbers of animals, the risk and variance of response to selection are relevant but can not be determined with Z-PLAN. Another limitation of the model was that it does not allow for changes in genetic response in further rounds of selection due to changes in genetic parameters due to selection (Nitter et al., 1994).

ZPLAN does not take into account the effect of selection and the decreases in subsequent generations and this has been discussed by Nitter et al. (1994) previously. While the Bulmer effect will decrease the overall gain in later generations Dekkers (1992) has shown that generally the ranking of breeding schemes remain the same and this could be expected in this study. Pre-selection could have an effect on the family structure in the nucleus but this was not modelled. The superiority of using IGF-1 and RFI information together over the other scenarios analysed was such that deceases in returns and profitability this would be unlikely to change the overall recommendations.

This study assumed optimal management of an advanced breeding scheme, including across-herd

availability of animals and semen, and trait measurement for all selection criterion traits. Breeding operations without full trait measurement were not considered. As a result, implementation of a scheme using IGF-1 could have less benefits in practice than those predicted in this study in a breeding situation where fewer traits are measured than those simulated. This study did not take into account different levels of genetic improvement expected between individual herds within a nucleus population. For example, under Scenario 3, the optimum level of feed intake measurements of 5% was determined at the nucleus level does not necessarily mean 5% of bulls within each herd, but rather the superior 5% across the entire breeding sector. Identifying and targeting those animals for testing across different herds with IGF-1 may be the single largest benefit arising from IGF-1 measurement. In practice, decisions to go ahead with RFI measurements are likely to be at the herd level, implying that the overall efficiency of this measurement will be lower at the level of the nucleus.

Generalisation of results to other situations could apply when the genetic parameters and breeding goals are similar to those of the Angus breed studied here. Selection for efficiency is universal to cattle production objectives as feed costs are generally the highest variable cost. Even with a negatively correlated trait such as marbling in the objective, IGF-1 could still be used to decrease the selection costs for a breeding scheme using feed intake as a criterion. Extrapolating the results to other breeding objectives and breeds must be done with caution but IGF-1 must be regarded favourably as a tool in selection for feed efficiency.

5. Conclusion

Results presented here provide encouragement for further work to be completed on the underlying physiological and genetic relationships of IGF-1 with traits considered important to the breeding objectives of Australian cattle producers. For the breeder, results from this study indicate use of IGF-1 as a selection tool to screen candidates for further RFI assessment. In reality, since the industry has many independent seedstock producers, widespread extensive testing for feed intake is both expensive and difficult to implement. However, IGF-1 provides an opportunity to screen bulls to limit the number of feed intake tests required.

Improvements in profitability resulting from IGF-1 testing came from a decrease in the number of animals needing to be placed into feed tests, increased returns from lower feeding costs and improvements in carcass characteristics in the case of the export market objective. In contrast, its impact on profitability for the domestic breeding objective did not come from decreased first-stage selection percentages, but from increased profitability through higher accuracy of first and second-stage selection. Improvements in RFI traits and the growth and sale weight traits also increased overall profitability. The optimal scenario for both objectives was similar though utilizing IGF-1 as a first stage selection criterion to screen for further feed intake tests.

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Valuing DNA marker tested bulls for commercial beef production

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Abstract. This paper quantifies the benefits of using a sire genotyped for a single recessive gene in a commercial beef herd. A modified gene-flow method was used to account for changing allele frequency over time. The benefits to a commercial breeder of using a genotyped sire were highest when initial allele frequency was moderate and when the sire was used in a self-replacing herd that had increased allele frequency over time. An example of the thyroglobulin gene affecting marbling in beef cattle was used. The value to a self-replacing herd of a sire homozygous for the favourable allele of the thyroglobulin gene was shown to be up to $338 more than of an ungenotyped sire, in a population where the initial gene frequency was 0.3 and the genotype accounted for 0.5 standard deviations of phenotypic variation.

Additional keywords: marbling, beef cattle, genotyping, breeding program design, gene flow, recessive genes.

Introduction

With genotypic information about quantitative trait loci now available, questions arise concerning the value gained by producers using genotyped animals, particularly with respect to recessive traits. Information about the actual genotype of an animal at specific loci gives the commercial producer added accuracy of selection. The value of a breeding animal to a commercial producer is in the expression of its superior genes in its progeny. The flow of genes from parent to progeny and the frequency of expression of genes in future generations should be evaluated when calculating the value of using a particular breeding animal. Return on investment accumulates over time, and hence to make sound decisions there is a need to accurately consider returns and costs accruing over time with respect to selection criteria measurement and genetic improvement.

Hill (1974) developed gene-flow principles for the prediction of selection responses of breeding programs across generations. This method allows evaluation of returns due to genetic improvement in future generations to be assessed. The gene flow method accounts for delays in expression of genes in future generations and a penalty is paid for later expression by discounting. McClintock and Cunningham (1974) considered the selection of dual-purpose cattle and expression of dairy and beef traits when selecting within a closed herd using cumulative discounted expressions. Amer (1999) used discounted genetic expressions to examine the delays in expression of traits among progeny in self-replacing flocks and expressions of a major gene. The current paper is an extension of the work by Amer (1999) by focussing on the value of using genetically superior animals with respect to expression of a recessive single gene.

A commercially available test for the thyroglobulin gene is currently being marketed to breeders as a selection tool to increase marbling (Nicol *et al.* 2001). This gene is recessive in its expression. A gene that expresses itself in a recessive manner requires the strategic use of information to attempt to maximise the number of homozygous progeny produced. The utilisation of genetic markers as selection tools in breeding schemes has been advocated by many authors (Meuwissen and Goddard 1996; Larzul *et al.* 1997) but these authors have mainly focussed on the benefits at the breeding program level in seedstock production scenarios. For breeders to make decisions about genotyping individual animals they need to be able to demonstrate to potential bull buyers the benefit of using a sire of a desired genotype. The value of a recessively expressed genotype to a commercial population not only depends on the genotype of the sires used but also on the gene frequencies of the recessive allele within the herd as well as the change in frequency that is invoked by using such a sire. If a sire is used as a terminal sire then the genotype frequency is only changed in the slaughter progeny but there is no change in the commercial herd. When used as a self-replacing sire the genotype of the commercial herd is changed. This paper quantifies the benefits of using a genotyped sire across a commercial herd in which the genotypes of individual females in the herd are unknown.

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Materials and methods

Discounted genetic expressions of a recessive gene

The discounted gene-flow concept (Hill 1974) was used to calculate the number of discounted gene expressions (DGE) of a sire's alleles expressed in his descendants. The value of the sire is the product of the economic value and the number of DGE. The equations of Amer (1999) were modified to calculate discounted expressions following the introduction of a major recessive gene.

When calculating the flow of genes through a population, various parameters are required. These include survival probabilities (s) resulting in a fixed age distribution, probability of calving (p), age at slaughter of progeny (sa) and the number of dams mated to each sire (e), cull threshold age for cows (c), length of time the sire is used (y), discount rate (r), and planning horizon (h). The values of the parameters used in the calculations are shown in Table 1. To assess the level of sensitivity of the model to changes in base parameters, alternative values were explored for culling threshold age for cows, years of use of a bull, and number of progeny per sire. The base values refer to parameters considered typical of a commercial beef herd in Australia. The values for calving probability and cow survival are shown in Table 2. Given probabilities of survival (s) over the lifetime of the animal, we are able to define a vector (a) of probabilities of a cow surviving to calving age given that it was alive at Year 1:

$$a_i = \begin{cases} \prod_{j=2}^{i} S_j & \text{for } i = 2 \text{ to } c \\ 0 & \text{otherwise} \end{cases} \quad (1)$$

From these initial vectors we are able to calculate the expression of a sire's genes either as a terminal sire or as a sire breeding in a self-replacing herd. To account for the selective expression of a phenotype under a recessive inheritance model a matrix $\boldsymbol{T}$ is defined of dimension $3 \times h$ that describes genotype frequencies in each generation ($T_{i,j}$ = genotype frequency for genotype $i = 0,1,2$ copies of allele, generation = j). Genotype expression is calculated from these frequencies.

The genotype frequency in each generation in the commercial herd depends on genotype frequency in the previous generation of cows and the genotype of the sire used. Starting values at time 0 ($T_{i,0}$) are calculated from the assumed initial gene frequencies and assuming Hardy-Weinberg equilibrium in the cow herd. When using a homozygous sire (i.e. 2 copies of the recessive allele), elements of $\boldsymbol{T}$ can be calculated as follows:

$$\begin{aligned} T_{2,j} &= T_{2,j-1} + 0.5T_{1,j-1} \\ T_{1,j} &= 0.5T_{1,j-1} + T_{0,j-1} \\ T_{0,j} &= 0 \end{aligned} \quad (2)$$

This assumes no selection affecting the genotype of dams in the commercial herd so that on average, culling of cows and choice of replacement heifers do not affect gene frequency. When using a heterozygous sire (i.e. 1 copy of the recessive allele) the genotype frequency in each generation is calculated as follows:

$$\begin{aligned} T_{2,j} &= 0.5T_{2,j-1} + 0.25T_{1,j-1} \\ T_{1,j} &= 0.5 \\ T_{0,j} &= 0.25T_{1,j-1} + 0.5T_{0,j-1} \end{aligned} \quad (3)$$

When using a sire of unknown genotype the $\boldsymbol{T}$ matrix is given by Eqn 4. This equation was used when assessing the benefit of a genotyped sire compared with using a non-genotyped sire (assuming that the unknown sire has the same genotype probabilities as an average animal drawn from the herd has the same genotype).

$$\begin{aligned} T_{2,j} &= T_{2,j-1}p^2 + T_{2,j-1}pq + 0.5T_{1,j-1}p^2 + 0.5T_{1,j-1}pq \\ T_{1,j} &= T_{2,j-1}pq + T_{2,j-1}p^2 + 0.5T_{1,j-1}q^2 + T_{1,j-1}pq + \\ &\quad + 0.5T_{1,j-1}p^2 + T_{0,j-1}q^2 + T_{0,j-1}pq \\ T_{0,j} &= 0.5T_{1,j-1}pq + 0.5T_{1,j-1}q^2 + T_{0,j-1}pq + T_{0,j-1}q^2 \end{aligned} \quad (4)$$

Eqns 2 and 3 are used only for the first generation and thereafter with a random sire drawn from a population with the same initial allele frequency, Eqn 3 is used to calculate the gene frequency within the commercial herd. For self-replacing females a transition matrix ($\boldsymbol{D}$) describes the survival probabilities lagged by one row for each year of birth over the planning horizon h:

$$D_{i,j} = \begin{cases} a_{i-j} & \text{for } j < i-1 \text{ and } i - j = c \\ 0 & \text{otherwise} \end{cases} \quad (5)$$

From the genotype frequency in each generation the expression of a sire's alleles in future generations can be deduced. For sires used in self-replacing herds the vectors describing gene-flow in each of k generations

Table 1. Base values and ranges for variables used in sensitivity analysis

Variable	Symbol	Base value	Range
Cull for age threshold cows (years)	c	10	5–10
Planning horizon (years)	h	20	5–20
Discount rate (%)	r	7.5	0.0–15
Average bull working life (years)	y	3	2–5
Cows calving per sire joined	e	45	30–60
Proportion of calves retained	u	0.85	0.60–1.00
Slaughter age of progeny (years)	sa	2.0	2.0–3.0

Table 2. Probability of cow survival (s) and probability of calving (p) used in gene-flow calculations

Age:	1	2	3	4	5	6	7	8	9	10
s	0	0.95	0.94	0.93	0.88	0.83	0.7	0.6	0.5	0.5
p	0	0.85	0.9	0.9	0.9	0.9	0.85	0.85	0.85	0.8

are calculated using Eqn 6 following Amer (1999). The starting value in generation 1 is equal to $g'_1 = [10 \ldots\ldots 0]$.

$$g_j = \tfrac{1}{2} f \boldsymbol{D} g_{j-1} \quad (6)$$

The value f accounts for the number of replacement heifers required and was calculated from $f = (1/\sum_{i=1}^{c} a_i)$. The sum of the expression of genotype over the horizon (g_{sum}) is given by Eqn 7:

$$g_{sum} = \sum_{j=1}^{m} \boldsymbol{T}_{j,1} g_j \quad (7)$$

A discount rate is used to account for the difference in time of expression of a trait from the time of use of a sire to time of expression in progeny and subsequent descendants. Matrix E shown in Eqn 8 is a transition matrix of cattle produced per cow age group:

$$E_{i,j} = \begin{cases} a_{i-j}(p_{i-j} - f) & \text{for } j < i-1 \text{ and } i-j \le c \\ 0 & \text{otherwise} \end{cases} \quad (8)$$

Eqn 9 is the number of DGE in the progeny of a self-replacing cow:

$$X_S = \tfrac{1}{2} g'_{sum} E \cdot q \quad (9)$$

Expression of slaughter traits is dependent on the slaughter age (sa) of the animal, proportion of calves retained (u), and the discount rate (r). Changes to the original equations of Amer (1999) include the change in discounting matrix (z) and discount vector (q) to account for later expression of traits in progeny. The number of DGE of slaughter traits of a sire breeding self-replacing females is given by Eqn 10 where I is a vector of 1s:

$$\mathrm{DGE}_{(s)} = \tfrac{1}{2} 1' z \cdot e \cdot v \cdot \left(\tfrac{1}{2} u \cdot X_S + \left(1 - \tfrac{1}{2} u\right)(1+r)\right) \quad (10)$$

The expression of phenotypes was examined under 2 alternative sire selection policies. In the first scenario, a homozygous sire was used and thereafter it was assumed that an ungenotyped sire from a population with the initial gene frequency was used. A heterozygous sire and thereafter a non-genotyped sire were used in the second scenario. The genotype of sires used in later generations is important as it determines allele frequencies and therefore the extent of expression of the recessive genotype. In this study it was assumed that ungenotyped sires were used after the first sire and any change in gene frequency was due to the use of the initial sire. For comparison, the value of using an average ungenotyped bull throughout was also calculated.

Additive gene expression model

For comparison with a gene of different inheritance and expression, a major gene with additive inheritance was modelled. Under an additive model of expression the heterozygote has an intermediate level of expression compared with that of the non-carrier and homozygote animal, i.e. dominance effects were assumed absent.

Economic value of marbling

To assess the value of different genotypes, we need to determine the economic value of the trait influenced by the recessive allele. As an example in this paper the thyroglobulin gene affecting marbling (Nicol *et al.* 2001) was considered. The marble score is given in 7 classes (0–6). The underlying trait is assumed to have a normal distribution (AusMeat 1996): $\sim N[\mu, (\mu^* \mathrm{CV})^2]$ where μ is the mean value of the population and variance is dependent on the mean. We used a coefficient of variation of 0.17 (Barwick and Henzell 1999), and this was calculated from an average of literature estimates.

Payment for marbling was by price premiums, with the corresponding score premiums for classes 0–6 being 0, 0, 40, 60, 80, 100, and 120 c/kg, respectively (Barwick and Henzell 1999). Given the mean marble score (μ) and the probability distribution for the trait $f(x|\mu)$, income per carcass $I(\mu)$ can be calculated from the proportion of carcasses in each of the age classes (von Rohr *et al.* 1999):

$$I(\mu) = \sum_{i=1}^{n} P_i \times F_i = \sum_{i=1}^{n} P_i \times \int_{Bi-1}^{Bi} f(x|\mu)\,\mathrm{d}x \quad (11)$$

where $I(\mu)$ is average income per carcass, n is the number of marbling classes, P_i is price per carcass within the ith marbling class, F_i is the fraction of the population within the ith marbling class, B_i is the upper boundary of the ith marbling class, and $f(x|\mu)$ is the probability distribution of x given the mean μ.

The value (V) of a sire with a major gene expressed in his progeny is then given by:

$$V = \mathrm{DGE} \times \{I(\mu + \alpha) - I(\mu)\} \quad (12)$$

where DGE is the discounted genetic expressions and α is the effect of the major gene.

Major gene effect

The thyroglobulin gene has been found to be at an allele frequency of 0.3 in the Australian Angus population (Nicol *et al.* 2001). The effect of the *aa* genotype was equal to 0.5 phenotypic standard deviation units, above that of an animal with either *Aa* or *AA* genotype. The sensitivity of the results to the effect of the major gene was also considered. The population mean and allele frequency were also varied.

Results and discussion

The comparison between sires of unknown and known genotype for the allele of interest is particularly important, as this is how sires are currently being marketed to commercial producers. Table 3 shows the DGE in calf traits, annual cow traits, and slaughter progeny traits with varying initial allele frequency when using a homozygous (*aa*) sire, heterozygous (*Aa*) sire, or average sire of unknown genotype as a terminal or self-replacing sire. The difference between DGE of terminal sires is dependent on the allele frequency among dams, and the number of expressions of the homozygote sire is twice that of the heterozygote. Differences in DGE between use of sires for terminal or self-replacing purposes were due to additional expression of the sire's genes in the female progeny's descendants. In the case of a sire breeding daughters in a self-replacing herd, the number of expressions of the *aa* sire was more than double that of the *Aa* sire. The increase in the number of expressions due to using a genotyped sire was larger for intermediate initial frequencies.

For comparison with the recessive model, an additive model is shown in Table 4 with the same traits and allele frequencies as Table 3. The greatest difference in DGE between the recessive and additive models occurred when the initial genotype frequency was lowest.

Table 5 shows the effect of varying discount rate on the number of DGE of various traits expressed at different stages of an animal's life. Expressions decrease with time due to the discount applied to later expressions and due to dilution of the sire's contribution with each new generation. Higher discount rates led to decreased number of DGE. The

Table 3. Effect of initial allele frequency on number of cumulative discounted genetic expressions in calf, annual cow, and slaughter progeny traits with a recessively expressed gene (with other parameters set at base values shown in Table 1)

Homozygote sire (*aa*)				Heterozygote sire (*Aa*)				Average sire of unknown genotype			
Initial allele freq.	Sires: Terminal sire	Sires: Sire self-replacing cow	Dams: Self-replacing	Initial allele freq.	Sires: Terminal sire	Sires: Sire self-replacing cow	Dams: Self-replacing	Initial allele freq.	Sires: Terminal sire	Sires: Sire self-replacing cow	Dams: Self-replacing
					Trait of calf at birth						
0.1	5.33	10.13	0.23	0.1	2.66	5.13	0.12	0.1	0.53	1.12	0.03
0.3	15.98	31.13	0.74	0.3	7.99	16.11	0.40	0.3	4.79	10.10	0.26
0.5	26.63	53.10	1.29	0.5	13.32	28.07	0.72	0.5	13.32	28.07	0.72
0.7	37.28	76.04	1.89	0.7	18.64	41.00	1.09	0.7	26.10	55.01	1.41
0.9	47.94	99.95	2.54	0.9	23.97	54.90	1.51	0.9	43.14	90.94	2.33
					Trait of cow annual						
0.1	–	9.76	0.48	0.1	–	5.00	0.25	0.1	–	1.20	0.06
0.3	–	30.77	1.51	0.3	–	16.50	0.81	0.3	–	10.79	0.53
0.5	–	53.77	2.64	0.5	–	29.99	1.47	0.5	–	29.99	1.47
0.7	–	78.75	3.87	0.7	–	45.45	2.23	0.7	–	58.77	2.88
0.9	–	105.71	5.19	0.9	–	62.91	3.09	0.9	–	97.15	4.77
					Trait of slaughter progeny						
0.1	4.79	6.07	0.16	0.1	2.40	3.08	0.08	0.1	0.48	0.68	0.02
0.3	14.38	18.72	0.51	0.3	7.19	9.74	0.27	0.3	4.31	6.14	0.18
0.5	23.97	32.04	0.89	0.5	11.98	17.07	0.50	0.5	11.98	17.07	0.50
0.7	33.56	46.03	1.31	0.7	16.78	25.07	0.75	0.7	23.49	33.45	0.98
0.9	43.14	60.69	1.75	0.9	21.57	33.75	1.04	0.9	38.83	55.30	1.61

Table 4. Effect of initial allele frequency on number of cumulative discounted genetic expressions in calf, annual cow and slaughter progeny traits with an additively expressed gene (with other parameters set at base values shown in Table 1)

Homozygote sire (*aa*)				Heterozygote sire (*Aa*)				Average sire of unknown genotype			
Initial allele freq.	Sires: Terminal sire	Sires: Sire self-replacing cow	Dams: Self-replacing	Initial allele freq.	Sires: Terminal sire	Sires: Sire self-replacing cow	Dams: Self-replacing	Initial allele freq.	Sires: Terminal sire	Sires: Sire self-replacing cow	Dams: Self-replacing
					Trait of calf at birth						
0.1	29.29	56.28	1.32	0.1	15.98	31.25	0.75	0.1	5.33	11.23	0.29
0.3	34.62	68.73	1.66	0.3	21.30	43.69	1.09	0.3	15.98	33.68	0.86
0.5	39.95	81.17	2.01	0.5	26.63	56.14	1.44	0.5	26.63	56.14	1.44
0.7	45.27	93.61	2.36	0.7	31.96	68.58	1.79	0.7	37.28	78.59	2.02
0.9	50.60	106.05	2.71	0.9	37.28	81.02	2.14	0.9	47.94	101.05	2.59
					Trait of cow annual						
0.1	–	54.80	2.69	0.1	–	31.02	1.52	0.1	–	11.99	0.59
0.3	–	69.27	3.40	0.3	–	45.49	2.23	0.3	–	35.98	1.77
0.5	–	83.75	4.11	0.5	–	59.97	2.94	0.5	–	59.97	2.94
0.7	–	98.23	4.82	0.7	–	74.45	3.65	0.7	–	83.96	4.12
0.9	–	112.7	5.53	0.9	–	88.92	4.36	0.9	–	107.95	5.30
					Trait of slaughter progeny						
0.1	26.36	33.77	0.91	0.1	14.38	18.80	0.51	0.1	4.79	6.83	0.20
0.3	31.16	41.44	1.15	0.3	19.17	26.47	0.76	0.3	14.38	20.48	0.60
0.5	35.95	49.11	1.39	0.5	23.97	34.14	1.00	0.5	23.97	34.14	1.00
0.7	40.75	56.77	1.63	0.7	28.76	41.80	1.24	0.7	33.56	47.79	1.39
0.9	45.54	64.44	1.87	0.9	33.56	49.47	1.48	0.9	43.14	61.45	1.79

choice of discount rate was based on what current and recent market interest rates are and the value of inflation (Amer 1999). The discount rate can also be used to reflect different risk profiles of the commercial farmer. A higher discount rate is applied if the farmer is risk-adverse and wants returns on capital relatively quickly. Higher discount rates penalise later expressions such as those in a self-replacing herd.

Table 5. Effect of varying discount rate on numbers of cumulative discounted genetic expressions using a homozygous (*aa*) sire with all other parameter variables set to base values

Discount rate (%)	Sires		Breeding females
	Terminal sire	Breed self-replacing cow	Self-replacing
	Trait of calf at birth		
15.0	19.82	46.53	1.06
7.5	15.98	31.13	0.74
0.0	13.11	22.74	0.56
	Trait of cow annual		
15.0	–	54.59	2.16
7.5	–	30.77	1.51
0.0	–	19.06	1.14
	Trait of slaughter progeny		
15.0	17.83	28.7	0.73
7.5	14.38	18.72	0.51
0.0	11.8	13.38	0.39

Table 6. Effect of changing the number of years a sire is used on numbers of discounted genetic expressions using a homozygous (*aa*) sire with all other parameter variables set to base values (initial allele frequency $q = 0.3$)

Years of sire use	Terminal sire	Breed self-replacing cow
	Trait of calf at birth	
2	11.03	21.49
3	15.98	31.13
4	20.58	40.09
5	24.86	48.43
	Trait of cow annual	
2	–	21.25
3	–	30.77
4	–	39.63
5	–	47.87
	Trait of slaughter progeny	
2	9.93	12.92
3	14.38	18.72
4	18.52	24.11
5	22.37	29.12

Table 6 shows the effect of altering the number of years that *aa* sires are used on DGE for slaughter traits assuming an initial gene frequency of 0.3. Increasing the number of years that a sire is used has a large effect on the number of expressions generated by that sire. The trade-off is a decrease in the potential genetic improvement in other polygenic traits due to an increased generation interval and greater lag behind the genetic progress being made in the herd supplying bulls.

Table 7 shows that decreasing the culling age of cows from the base value of 10 years down to culling at 5 years had a minor effect on the number of DGE because it resulted in only a small increase in the proportion of *aa* progeny born in any one year (gene frequency of 0.3). It should be noted that this change has an opposite effect in the terminal sire

Table 7. Effect of changing cow culling age on numbers of discounted genetic expressions with other variables set to base values (initial allele frequency $q = 0.3$)

Cow cull age threshold	Sires		Dams
	Terminal sire	Breed self-replacing cow	Self-replacing
	Trait of calf at birth		
5	16.08	27.97	0.58
7	16.05	30.46	0.70
9	16.00	31.08	0.74
10	15.98	31.13	0.74
	Trait of cow annual		
5	–	24.02	1.17
7	–	29.18	1.43
9	–	30.61	1.50
10	–	30.77	1.51
	Trait of slaughter progeny		
5	14.47	15.46	0.35
7	14.44	17.95	0.47
9	14.40	18.64	0.51
10	14.38	18.72	0.51

and self-replacing sire scenarios. The number of expressions for self-replacing sires increases slightly as cow culling age increases and there are fewer expressions in terminal sires. The decrease for terminal sires is due to an older cow having a smaller chance of producing a calf (see Table 2). The increased expressions of a self-replacing sire are due to the sire's replacement daughters having an increased chance of producing further calves and therefore having increased expressions.

Valuing the thyroglobulin genotype differences

The value of a recessively expressed genotype not only depends on the genotype of sires but also on the gene frequencies within the commercial cow population. The number of DGE of the gene can be used to assess the value of a sire having 1 or 2 copies of the allele. The difference in value between the genotypes can be derived from its effect on the distribution over the different marbling score classes. The profit function is non-linear due to the premium payment system, with no premium for the first two classes and increased payments at higher marble score classes.

The value of a genotyped animal at varying levels of mean marble score of slaughter progeny is shown in Fig. 1*a*. These values represent amounts relative to that of using a sire that has not been genotyped. The value of a genotyped sire was highly dependent on the economic value of marble score and the average marble scores of its descendants. The figure demonstrates that herds with an already high average marble score of approximately 3 units would benefit considerably less than a herd with an average marble score closer to 2. The returns from using a genotyped homozygous (Fig. 1*a*) or heterozygous (Fig. 1*b*) sire once in a self-replacing herd at various initial allele

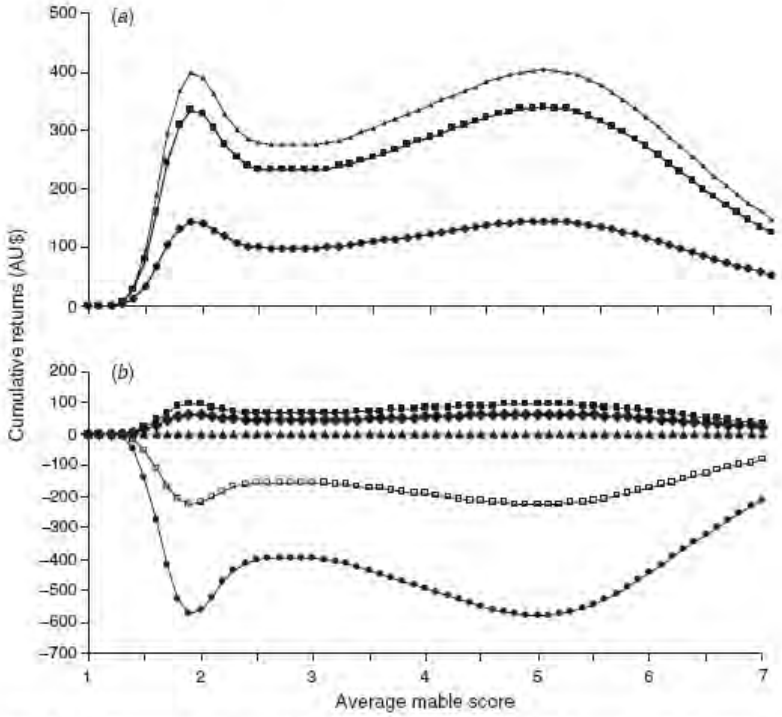

Fig. 1. (*a*) Returns from using a homozygous (*aa*) bull above that of using a bull of unknown genotype and (*b*) returns from using a heterozygous (*Aa*) sire above that of using a sire of unknown genotype in a self-replacing herd at various initial allele frequencies (q). Initial allele frequency (q): 0.1 (◆), 0.3 (■), 0.5 (▲), 0.7 (□), 0.9 (●). Note: Fig. 1(*a*) returns from $q = 0.1$, 0.9 and $q = 0.3$, 0.7 are equal.

frequencies varies markedly. The largest benefits came from populations with initial starting frequencies in the range of 0.3–0.5. With higher frequency there is less to improve, whereas with very low frequencies it takes more time before a reasonable proportion of the population expresses the *aa* phenotype. The large benefits found in other studies (Larzul *et al.* 1997) do not take into account the time lag and subsequent discounting of returns from a selection decision. Use of *Aa* bulls would give a negative revenue compared with using untested bulls for allele frequencies higher than 0.5. As the gene frequency in the commercial herd increased above 0.5 the possible returns from these strategies decreased and so the value of using a genotyped animal in mating rounds thereafter would decrease compared with that of earlier rounds.

Returns under an additive model for both homozygous and heterozygous sires are around AU$200–$400 more than under a recessive model of inheritance. The effect of a lower initial allele frequency is less for a recessive model of inheritance than for the additive model. It has been shown that there would be inherently less risk and increased returns from using a genotyped sire with additive inheritance.

Initial allele frequency can be expected to vary across different populations due to previous selection history. Nicol *et al.* (2001) showed that the Japanese Black Wagyu, a breed known for marbling, had a higher allele frequency (63%) compared with that of Angus. The higher initial allele frequency leads to a higher frequency of the *aa* genotype in the first generation progeny and hence increased expression of the trait. As the genetic expression of the trait increases with higher initial frequencies, the value of knowing the genotype decreases because the chance of selecting a homozygote sire from the population by chance also increases. In practice, a commercial beef producer will not have the benefit of knowledge of the base genotype frequencies within their herd, but this could be estimated from breed averages and would be an appropriate prior assumption about the allele composition of a herd. To marker-type a herd to ascertain the genotype frequencies would be cost-prohibitive when compared with the maximum benefits achievable.

For this simulation, ungenotyped sires were assumed to be used after the initial selection of a genotyped sire. If genotyped sires continued to be used then the expression of the sires' recessive genes would be expected to increase in

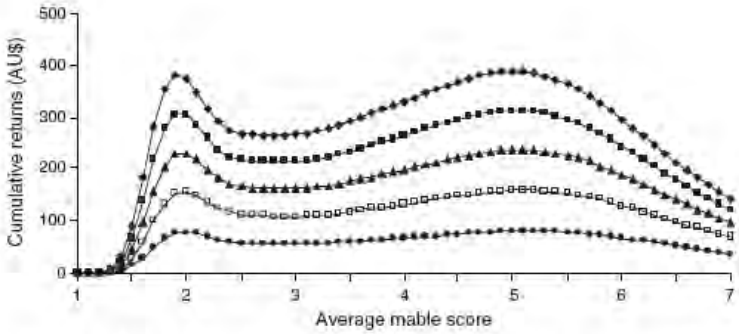

Fig. 2. Sensitivity of cumulative returns for homozygous genotyped sire v. a non-genotyped sire. Difference in major gene of effect measured in phenotypic standard deviations (σ_P). Initial gene frequency $q = 0.3$. Major gene effect (σ_P): 0.1 (●), 0.2 (□), 0.3 (▲), 0.4 (■), 0.5 (◆).

later generations. Using the base values described in Table 1, the proportion of the population having an *aa* genotype is close to 1 by Year 20 when *aa* sires are used at every mating. This holds for both low and high starting frequencies. The rate of increase in the proportion of *aa* genotype is most rapid at low initial gene frequencies. When using a cow culling threshold age of 10 years, 72% of the progeny were homozygous carriers by Year 10. When the cull threshold age was decreased to 5 years, 82% of the progeny born in Year 10 were homozygous for the allele. Although a higher turnover rate of cows does increase the proportion of homozygous progeny, it does not appreciably decrease the time required for fixation. The profits generated by a sire used in a herd where the genotype frequency has been increased would be higher than that of a non-improved herd. Therefore, sires used later would show higher profits that those used earlier.

The gene effect was assumed to be 0.5 phenotypic standard deviations. Figure 2 shows the linear increase in returns where sires are used in a self-replacing herd but with the effect at the locus varied from 0.1 to 0.5 phenotypic standard deviations. If the effect of the gene is higher or lower, then this can have substantial effects on the returns possible as the returns depend in a linear way on the assumed gene affect.

Conclusions

The value of using a bull being either homozygous (*aa*) or heterozygous (*Aa*) for a recessive favourable allele (thyroglobulin) was determined for various allele frequency levels in the commercial population. Homozygous bulls provided substantially higher revenues in both the short and long term, and in uses as both a terminal or self-replacing sire. The value in a self-replacing herd was dependent on the genotype of sires used over the replacement daughters, but assuming that non-genotyped sires are used, the value of an *aa* sire is about $200–$400 higher than using a non-genotyped sire. The differences were largest for intermediate (0.3–0.7) initial allele frequencies within the commercial population. Use of *Aa* bulls would give a negative revenue compared with using untested bulls for allele frequencies >0.5.

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QUANTIFYING THE SELECTION RESPONSE USING A RESIDUAL FEED INTAKE DNA MARKER FOR TWO AUSTRALIAN BREEDING OBJECTIVES

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SUMMARY

A pseudo-BLUP index was used to evaluate the selection response from using a quantitative trait locus (QTL) for residual feed intake (RFI). The index included phenotypic information on the individual, sire, dam, half-sibs and progeny. To compare with marker-assisted selection (MAS), a single locus was assumed to be genotyped that explained a proportion of the variance for RFI and this was included in the selection index. Two breeding objectives were examined with a different relative economic value for RFI, one targeting the Australian domestic market and one targeting a high value Japanese export market. The selection response and optimal age structure altered with the inclusion of genotype information. Response was increased because the pre-selection accuracy, before RFI measurement, was improved. Genotyping increased the earlier selection of sires and decreased the optimum generation interval of sires; consequently, this increased the annual selection response. With a QTL that explained 0.33 phenotypic standard deviations of variance, response was shown to increase by up to 11% when both sexes were genotyped and 7.6% when only males were genotyped. When sire selection was delayed until after 2 years of age, the increase in response from genotyping was 8.1% and 5.1%, respectively. If the QTL explained a relatively large part of the breeding objective, the locus was rapidly fixed resulting in rapid early gains.

Key Words: QTL, selection response, beef cattle, marker-assisted selection

INTRODUCTION

Residual feed intake (RFI) has been adopted by the Australian beef industry for the purpose of genetic improvement in feed efficiency. RFI is a measure of how much more or less an animal eats compared to its expected feed requirement for its size and growth rate. It can be measured post-weaning but it has a significant measurement cost (Archer *et al.* 2004). As a result, the use of a simple to measure marker may make the selection for feed intake in cattle easier. Pitchford *et al.* (2002) has described the a number of areas of putative quantitative trait loci (QTL) for RFI. Consequently, it is prudent to consider the potential gains achievable by using a RFI marker.

A genetic marker can be used as a stand alone test or incorporated into an index with other information sources. Given the economic value of the marked trait a selection index places the appropriate weight on the marker. Markers can increase the selection response above that of using phenotypic measurement alone and are most beneficial when the trait is either difficult or expensive to measure, or when selection occurs before phenotypes can be measured. Marker-assisted selection makes early selection possible. Consequently, the increase in annual response may result from the reduction in generation interval together with the increase in selection accuracy. The aim of this study was to examine the change in response that could be attributed to selection on a significantly sized

Selection Index and Genetic Profiling

QTL for RFI and to assess the change in population structure that may occur if the QTL was used optimally in a beef breeding scheme.

MATERIALS AND METHODS

Genetic model A pseudo-BLUP selection index was used including individual, sire, dam, half-sib and progeny information. A QTL genotype that explains a proportion of the variance of an objective trait is just another information source. Consequently, there is a natural progression to also include this information in the selection index. The gene was assumed to be biallelic and additive in inheritance. The variance (*Vm*) explained by the gene can be calculated as $Vm=2pq(\alpha)$ where p and q are the gene frequencies of alternative alleles and α the allele substitution effect. The QTL was assumed to affect only RFI, but the model could accommodate a QTL having affects on multiple traits. The size of the allele substitution effect was examined for a range of values from 0.11 to 0.33 phenotypic standard deviations of RFI. A genotype was assumed to provide no prior parental genotype information.

The change in gene frequency due to selection was calculated using a method similar to Dekkers and Chakraborty (2001). Selection on genotype is simply truncation across three distributions describing possible genotypes. The genotype frequency was calculated from the contribution of selected parents from each age-sex cohort to the next generation. The favourable allele was assumed to have an initial frequency of 0.1. The reduction in variance due to selection and gametic phase disequilibrium was accounted for with a reduction factor $k=i(i-x)$ where x is the standardised truncation point and i the selection intensity adjusted for finite population size. The response to selection was the weighted sum from each cohort and the genotype frequency was calculated as the weighted contribution of genotypes from each cohort.

Breeding Population Structure A 2000 breeder seedstock herd was modelled that used natural mating with a sire to dam ratio of 1:45. Dams were assumed to be selected in the second year and to have produced progeny by the end of that same year. The majority of males were assumed to be selected after the second year but a proportion (30%) was assumed to be available for selection with a reduced accuracy at the end of the first year. Across age-class truncation selection was used to identify the optimal contribution of class using the bisection method of Ducrocq and Quaas (1988).

Breeding Objectives and Genetic Parameters Two breeding objectives were examined. The first targeted 650kg steers produced for the high quality Japanese export market. This objective had a high relative economic value on RFI as the feed costs are high when finished on a 200-day feedlot ration. Marbling score and final sale weight also form an important part of the objective. The second targeted 400kg steers produced for the domestic market and so had a moderate relative economic value placed on RFI and placed no value on marbling score. The derivation of the economic values was described by Archer *et al.* (2004). Genetic parameters were taken from those used previously by Archer *et al.* (2004) with the addition of the concentration of Insulin-like Growth Factor-I (IGF-I). A bending routine was used to fit the IGF-I parameters such that they satisfy the requirements of being positive-definite (Wood *et al.* 2004).

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Selection Index Information Phenotypic information was available from individual measures of birth, 200d, 400d and 600d weight, IGF-I, ultrasound carcass scans, mature cow weight, and post-weaning RFI on a pre-selected 10% of sire candidates. RFI measurement is profitable when made on a subset of animals, as the magnitude of measurement cost outweighs the selection response when measuring all selection candidates. By including IGF-I, a trait correlated with RFI, the number of candidates presented for RFI measurement can be decreased down to 5-10% (Wood *et al.* 2004) compared to 20-40% as shown by Archer *et al.* (2004). Pre-selection was on an index post-weaning including IGF-I, birth weight, 200d weight and parental information on all other traits and genotype if included. Genotype information was assumed available on all animals or only male candidates.

RESULTS AND DISCUSSION

The maximum response to selection and the year that it occurs is shown in Table 1 with scenarios varying for the genotype information available in the index and minimum age of selection. The Japanese export objective had a greater breeding objective variance and consequently, showed a larger response to selection without marker information (Scenario 1). Marker information increased the selection response in all scenarios. RFI had a greater relative economic value for the export objective and this resulted in the greatest increase in selection response when using MAS for RFI. For this objective, the favourable RFI QTL allele is selected for strongly and as a result, the highest selection response is reached earlier (6yrs) after the initiation of MAS compared to the domestic objective (9yrs). When the both sexes are genotyped the annual selection response is the highest and the favourable allele fixed earlier compared to measuring the genotype of only males. Restricting selection until all phenotypic information has been collected on sires (Scenarios 4-6) decreased the annual selection response. Selection pressure on the favourable allele was also decreased when included in an index with a greater amount of phenotypic information compared to selection in the 1-year-old cohort and as a result fixation takes longer than that when selecting at an earlier age.

Table 1 Selection response and the year of maximum response using a marker for two breeding objectives for a range of scenarios varying the genotype information available in the index and minimum age of selection (QTL effect being 0.33 σ_P units)

Scenario	Minimum Selection Age ♂	Genotype Information ♂	Genotype Information ♀	Domestic			Japanese Export		
				Response	Year	Increase (%)	Response	Year	Increase (%)
1	1	×	×	$4.36	-	-	$5.41	-	-
2	1	✓	×	$4.49	10	3.20	$5.79	7	7.58
3	1	✓	✓	$4.56	9	4.61	$5.98	6	11.06
4	2	×	×	$3.89	-	-	$5.07	-	-
5	2	✓	×	$3.99	20	2.51	$5.33	10	5.10
6	2	✓	✓	$4.03	17	3.75	$5.48	8	8.12

Table 2 shows response for varying size of the QTL and also the year of maximum response to MAS. The year of maximum response corresponds to when the gene frequency equals 0.5 and gives an indication of the pace at which the favourable allele is fixed. With decreasing QTL effect, the

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additional response above non-MAS also decreased. Decreased selection pressure on the QTL, resulted in slower gene fixation.

Table 2 Sensitivity of size and time of maximum selection response to size of QTL effect for Scenarios 2 and 3

QTL Effect (σ_P)		0.11		0.22		0.33	
		% Increase	Year	% Increase	Year	% Increase	Year
Domestic	♂	0.40	41	1.52	17	3.20	10
	♂+♀	0.40	41	2.14	14	4.61	9
Export	♂	0.89	32	3.37	13	7.58	7
	♂+♀	1.28	25	4.90	11	11.06	6

Age Structure The age structure before and after selection with genotypes in the index is shown in Figure 1 for the Japanese export objective. Even without genotyping there was a tendency to select younger animals. The increase in selection index accuracy from progeny information on carcass traits in the 5 year old cohort resulted in only a small increase in the proportion of sires from this cohort being selected. When genotype information was included, the proportion of younger animals increased. If selection was delayed until after the collection of all individual phenotypic information the benefits of selection with a marker for RFI are decreased, this is shown by a smaller change in selection response shown in Table 1 and the small change in age structure shown in Figure 1(b).

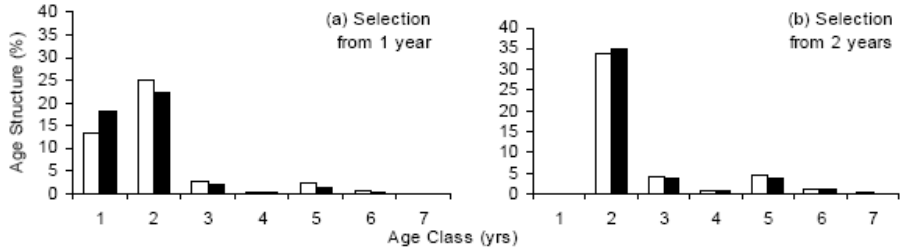

Figure 1 Male age structure when selected with (filled) and without (unfilled) an RFI marker

Practical Implications This study showed the potential to increase selection response by using MAS and selecting more young sires on an index not containing all potential phenotypic measures. Annual response was decreased by between 6.3%-10.8% if delaying sire selection until after two years of age and the benefits of MAS were decreased even more if early sire selection was not practiced.

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