Lessons Learnt from 25 Years of Feed Efficiency Research in Australia

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ABSTRACT: Since the early 1990s, there has been sustained research in Australia on genetic improvement of feed efficiency in beef and dairy cattle. This paper describes the research findings, highlights lessons learnt and outlines challenges for the future. Residual feed intake (RFI) was chosen as the preferred trait in young growing cattle, and it represents the amount of feed consumed net of the animal's feed requirements for maintenance and production. It is moderately heritable, highly correlated with feed intake, weakly correlated with fatness, and not significantly correlated with other growth, carcass and meat quality traits, thus indicating that progeny of low RFI cattle will consume less feed and produce less methane for the same level of growth performance with slightly lower carcass fat. There is paucity of information on its relationship with reproduction, milk production and cow traits. The challenge is to develop cost-effective programs to efficiently exploit this genetic variation.

Keywords: Cattle; residual feed intake; genetics

Introduction

Providing feed to animals is a major input cost in most livestock production systems but feed intake by individual animals is difficult to measure, hence genetic improvement strategies have concentrated on improving output traits. Advances in computing and electronics have allowed development of reliable automatic feed-intake recorders which make it relatively easier to measure feed intake of individual animals. As a result, there have been sustained research and development activities in Australia for genetic improvement of the efficiency of feed utilization in both beef and dairy cattle since the early 1990s. This paper describes some of the significant scientific findings and outcomes of the R&D in feed efficiency in cattle, and highlights some of the lessons learnt and the challenges for the future.

Measuring the Phenotype

The utilization of the feed consumed by an animal involves complex biological processes and interactions with the environment. In addition, it is complicated by the fact that feed intake is highly correlated with body size and level of production. To overcome these complexities and to relate feed intake to production system efficiency, several measures (or traits) of feed efficiency have been developed over the years. These traits include: feed conversion ratio, residual feed intake (RFI), partial efficiency of growth, maintenance efficiency, and efficiency of lactation. Residual feed intake was chosen as the preferred trait based on critical assessment (later published as Archer et al. (1999); Arthur et al. (2001c)) of available scientific information at the time. It represents the amount of feed consumed net of the animal's requirements for maintenance of body weight and level of production. In young growing beef and dairy cattle it is measured as the difference between actual feed intake of an animal and the expected feed intake based on metabolic body weight and growth. It is typically calculated by fitting the multiple regression model:

 $FI_i = \beta o + \beta_1 ADG_i + \beta_2 MWT_i + e_i$

where: FI_i = daily feed intake of animal i, βo = intercept, β_1 = partial regression coefficient of FI on average daily gain (ADG), β_2 = partial regression coefficient of FI on metabolic weight (MWT; bodyweight raised to the power of 0.73), and e_i = residual error term. Residual feed intake is equal to the residual error value.

Measurement Protocols. The results from a key study (Archer et al. (1997)) on the optimum duration of test underpinned the development of standardized measurement protocols for RFI. The study recommended a minimum of 21 d adjustment period followed by a 70 d test. However, it is more difficult to get accurate weight gain than feed intake data so for FI alone, a 35 d test could be used. In 1999 a Standards Manual for feed efficiency testing was developed and was approved and adopted by the Performance Beef Breeders Association of Australia (Exton (2001)). The manual describes the testing protocol and specifies the mandatory recording requirements. There is a requirement for laboratory analysis of the feed, and the recording of all feed additives and dietary supplements, including straw. The manual also specifies that feed be provided ad libitum, and that the ration be as close to 10 MJ metabolisable energy (ME)/kg dry matter (DM) for postweaning tests, and close to 12 MJ/kg DM for cattle during the finishing phase in a feedlot. This was done in recognition of the fact that growing bulls and heifers intended for breeding are fed and managed differently from steers and heifer intended for slaughter. Results of studies conducted later have shown that the genetic correlation (rg) between postweaning RFI (RFI_p) and finishing RFI (RFIf) is less than 0.80 ($r_g = 0.75$, Arthur et al. (2001b); $r_g = 0.65$, Jeyaruban et al. (2009)) implying that they are genetically different traits.

Genetic Control of Residual Feed Intake

There have been five major projects in Australia related to RFI. Three of these *viz*. the Trangie Project, Beef Cooperative Research Centre (Beef CRC) phase I project and Beef CRC II project, have been described in detail by Arthur et al. (2004). The other two are the Dairy Feed Conversion Efficiency (FCE) Project, which has been described by Williams et al. (2011) and Pryce et al. (2012),

and the Beef CRC III project (<u>www.beefcrc.com</u>), with RFI components on tropical genotypes continued from Beef CRC II (Barwick et al. (2009a)), genomic selection (Bolormaa et al. (2013)) and maternal productivity (Pitchford et al. (2014)).

Genetic Parameters. The review by Arthur and Herd (2012) which included results emanating from Australian and international beef cattle research showed that there is genetic control of RFI, and that genetic variation for RFI exists in Bos taurus and Bos indicus breeds of beef cattle and multiple other species (Pitchford (2004)). The heritability of RFI is moderate and similar to that for growth rate. World-wide, the range of heritability of RFI is from 0.07 to 0.62 (Berry and Crowley (2013)) for beef cattle. In Australia, heritability estimates of 0.41 and 0.34 are used in beef cattle for RFI_P and RFI_f, respectively (Jeyaruban et al. (2009)). Recent heritability estimates for Australian and New Zealand young growing dairy cattle range from 0.22 to 0.38 (Williams et al. (2011); Pryce et al. (2012)). The trait with the most consistent (in all studies) and significant genetic correlation with RFI is FI with a mean of around 0.70. There is also a low genetic correlation (mean around 0.20) between RFI and subcutaneous rib fat depth, with the magnitude of the correlation dependent on breed, age, sex and feeding regime. In general, most growth and carcass traits are not genetically correlated with RFI, indicating that progeny of low RFI cattle will consume less feed for the same level of growth performance with slightly lower level of carcass fat.

Most of the published genetic parameter estimates for RFI are from Bos taurus cattle. The northern (tropical / sub-tropical) Australian component of the Beef CRC II and III programs utilized Brahman and Tropical Composite (Bos indicus - Bos taurus) cattle. Some of the genetic parameters estimates from the RFI related studies are presented in Table 1. Estimates of genetic correlations between RFI and carcass and meat quality traits of feedlot steers were of low to moderate magnitude, and consistent across the two genotypes. However the genetic correlations estimates for steer feedlot RFI with heifer and with female reproduction traits suggest that there could be differences in the trait relationships for Bos indicus compared to Bos taurus cattle. For example, the genetic correlation between RFI and age at first observance of corpus luteum was -0.60 in Brahman and 0.02 in Bos indicus - Bos taurus composite cattle. This highlights the need for more RFI information on tropically adapted cattle in particular, and relationships with meat quality, methane emissions and maternal productivity traits in general.

Divergent Selection lines. At the NSW Department of Primary Industry's Research Centre at Trangie, Australia, Angus cattle have been divergently selected for postweaning RFI since 1994 (Arthur et al. (2001a)). Two generations of selection had been achieved by 1999 and there was evidence of clear divergence between the two lines (Figure 1). Cattle selected for low RFI had similar growth performance as high RFI cattle but consumed less feed. Differences in RFI were accompanied

by differences in body composition, with low RFI steers having slightly less subcutaneous fat (Table 2). Hence the responses to selection predicted from the genetic parameter estimates were all confirmed by the performance of progeny from the selection lines. In addition, the selection lines have provided information on those traits (such as meat quality, methane emissions and reproduction) for which genetic parameters are currently not available. Additional information on the selection lines can be obtained from the report by Herd and Arthur (2012).

Table 1. Heritabilty (SE) of residual feed intake (RFI) in feedlot steers, and the genetic correlations (SE) with steer carcass, and with female scans and reproduction

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Trait [§]	Brahman	TCOMP [¶]	Study [†]					
Heritability	0.24 (0.11)	0.38 (0.12)	1					
Genetic correlations with steer RFI								
Steers - carcass‡								
RIB, mm	0.49 (0	0.19)	2					
EMA, cm^2	-0.42 (0.18)	2					
IMF, %	0.19 (0	0.17)	2					
Shear force, kg	0.23 (0	0.18)	2					
Heifers								
SEMA–WET, cm ²	0.75 (0.27)	-0.02 (0.22)	3					
SEMA–DRY, cm^2	0.66 (0.24)	-0.09 (0.21)	3					
AGECL, d	-0.60 (0.23)	0.02 (0.23)	4					
Reproduction								
DC, d	-0.50 (0.33)	-0.11 (0.30)	5					
M1WR, %	0.76 (0.38)	0.09 (0.36)	5					
LAWR, %	0.29 (0.37)	-0.07 (0.38)	5					

⁸Trait definitions: RIB = rib fat depth, EMA = eye muscle area, IMF = Intramuscular fat (marbling), WET = end of wet season, DRY = end of dry season, SEMA = scanned EMA, AGECL = age at the first observed corpus luteum, DC = Days from start of first mating to subsequent calving, M1WR = weaning rate from first mating, and LAWR = Lifetime (from first mating and up to 6 matings) weaning rate.

⁶Tropical Composite (50% tropically adapted and 50% non-tropically adapted breeds).

^{\dagger}Study code: 1 = Barwick et al. (2009a); 2 = Wolcott et al. (2009); 3 = Barwick et al. (2009b); 4 = Johnston et al. (2009); 5 = Wolcott et al. (2014).

‡Combined across genotype.



Figure 1: Trends in estimated breeding values for postweaning residual feed intake (RFI) for the Low (\Diamond) and High (\bullet) RFI selection lines. [Source: Arthur et al. (2005)]

A recent study which used the selection line steers fed over 205 days in a commercial feedlot was reported by Herd et al. (2014). The results for meat quality (Table 2) indicate that although the low RFI steer carcasses have less rib fat than the high RFI carcasses, the intramuscular fat (IMF) in the meat was similar between the two RFI lines. Shear force of the meat of the low RFI steers was higher (less tender) than that for high RFI after one day of ageing but the meat from the low RFI steers was still considered tender, with mean shear force of 3.48 kg. The selection line differences in shear force were no longer significant after 7 days of ageing.

Table 2. Growth, meat quality and female reproduction of cattle divergently selected for residual feed intake (RFI)

Trait	Low RFI	High RFI	Р	Study [§]
Growth				1
Weaning wt, kg	232.5	228.3	ns	
Yearling wt, kg	384.3	380.7	ns	
ADG, kg/d	1.44	1.40	ns	
Rump fat, mm	6.7	8.8	**	
EMA , cm^2	9.4	10.6	ns	
Feed intake, kg/d	9.4	10.6	**	
FCR	6.6	7.8	**	
RFI, kg/d	-0.54	0.71	**	
Meat Quality				2
Rib fat, mm	15.6	20.7	**	
IMF, % [¶]	14.3	13.5	ns	
Shear force d1, kg^{\dagger}	3.48	3.15	**	
Shear force d7, kg^{\dagger}	3.01	2.87	ns	
Reproduction I				3
Calving (%)	89.2	88.3	ns	
Calving date [‡]	215	210	*	
Milk yield (kg/d)	7.5	7.8	ns	
Weaning (%)	81.5	80.2	ns	
Reproduction II				4
Calving (%)	89.1	92.6	ns	
Calving day ^{‡#}	35.7	27.6	**	
Percent cycling				
By 365 d of age	68.7	74.1	ns	
By 436 d of age	80.6	85.2	ns	

^{*}Trait definitions: wt = weight, ADG = average daily gain, EMA = scanned eye muscle area, FCR = feed conversion ratio, IMF = intramuscular fat. [§]Study codes 1, 2, 3 and 4 are Arthur et al. (2010), Herd et al. (2014), Arthur et al. (2005) and Donoghue et al. (2011), respectively. [†]Shear force measure after 1 day (d1) and 7 days (d7) of ageing. [‡]January 1st is day1.

[#]Number of days from the start of the calving season.

*, **Denotes significance at P < 0.10 and P < 0.05 respectively; *ns*, non-significance at P > 0.05.

In a study using 10 low RFI and 10 high RFI steers from the selection lines, methane was measured by a marker-based method with the marker gas (SF₆) released from an intraruminal permeation device. All steers were fitted with a halter and gas collection apparatus and gas sample collection made over 10 days, after a five day adaptation period. Methane production in the low RFI steers was 25% less than that in the high RFI steers (Hegarty et al. (2007)). In field experiments where methane was measured using open path Fourier Transform infrared spectrophotometer in the selection line cattle, Jones et al. (2011) reported that low RFI cows grazing high quality pastures, emitted less methane than their high RFI contemporaries. However, differences in methane emissions were not significant on low quality low intake pastures. Similar results to those of the Australian selection line steers were reported in a Canadian study where 8 phenotypically extreme low RFI and 11 extreme high RFI steers were used in calorimetry studies. Methane production in the low RFI steers was 28% lower than in the high RFI steers (Nkrumah et al. (2006)).

Pitchford (2004) raised concerns about likely undesirable correlated response to selection for low RFI on reproduction based on results from other species. Three studies have been published on the maternal productivity of the divergent selection line females. Results from the first two studies (Arthur et al. (2005); Donoghue et al. (2011)) showed no significant selection line differences in maternal productivity traits after two generations of selection, except for a significant difference in calving day, which indicates that low RFI cows calved later in the season (Table 2). Similar results were found by Basarab et al. (2007). There was also a trend for low RFI heifers to have onset of puberty at an older age, and this might be reflected in the later calving date. In the third study (Hebart et al. (2014)) high and low RFI cows were maintained for three years on pastures which provided high and low levels of nutrition, to evaluate their reproduction and productivity. The study showed that, relative to high RFI cows, the low-RFI cows ate less, were leaner, had 6.3% lower weaning rate and calved on average 5.4 days later. In spite of that the low RFI cows were more efficient at producing weaner calves primarily due to a 7% reduction in annual feed intake across both nutrition treatments.

In an Australian study by Pryce et al. (2014b), 157 lactation records of dairy cows that were either high RFI or low RFI as growing heifers were used to study 6-week incalf rate. The study reported 10% lower (P = 0.054) in-calf rate for the low RFI cows (Figure 2).



Figure 2: Cumulative in-calf rate of cows that were identified as efficient (low RFI) or inefficient (high RFI) as calves. [Source: Pryce et al. (2014b)]

The findings reviewed here from single trait selection lines have shown the benefits from selection for low RFI but has clearly highlighted the fact that genetic improvement of whole production efficiency should include some measure of reproductive performance in a multi-trait selection index context.

Industry Implementation

After consultation with the industry, Net Feed Intake (NFI) was adopted as the name of the RFI trait for genetic improvement in beef cattle in Australia. The Australian national genetic improvement scheme, BREEDPLAN produced the first NFI Estimated Breeding Values (EBVs) in 2002, as trial single trait EBVs. Adoption rates for testing cattle for NFI had been low, and a review by Arthur et al. (2004) highlighted some of the barriers to adoption, which included:

- i. The high cost of phenotyping animals for NFI.
- ii. The complexity of the operation of automatic feedintake recorders limits their use on-farm, with only a few seedstock cattle breeders prepared to use them.
- iii. The general lack of appreciation in the beef industry of the importance of feed costs to enterprise profitability.
- iv. The practical limitations, animal health concerns and cost associated with centralised NFI testing.
- v. The reluctance of many seedstock breeders to hand over the management of their high value seedstock cattle to central test operators.
- vi. The minimal use of artificial breeding technologies in the beef industry results in the lack of opportunity to recoup costs through high volume dissemination of superior genetics.

Since the review by Arthur et al. (2004) highlighted these barriers to adoption, there has been an increased understanding of NFI and its benefits by seedstock and commercial beef cattle producers, and some of the barriers to adoption are being overcome. For example, feed intake recorders are now more robust, reliable and need minimal maintenance. Remote monitoring of feed-intake recorder and acquisition of data is now possible. This allows the equipment manufacturer to remotely interrogate and check the systems' mechanical functions, software and data integrity. The recent trend in diverting traditional feed grain sources from livestock production to biofuel production, and a series of droughts in several countries, have heightened the awareness of feedlot and cow-calf managers of feed costs, and increased their desire for more efficient cattle to feed. Currently, the difficulty and cost of measurement of the trait are the most important barriers for both beef and dairy cattle. Interest in NFI by beef seed stock breeders has increased of late with recent developments in genomic selection.

Genomic Selection. The major new area of opportunity to reduce the cost of identifying superior breeding cattle has been the advancements through genomic selection. Intensification of research in genomic selection has yielded promising results in both beef and dairy cattle. Analysis of Australian data on 4026 young growing beef cattle with real or imputed genotypes for over 700,000 single nucleotide polymorphism (SNP), generated mean genomic EBV (GEBV) accuracies for RFI greater than 0.3 (Table 3). From Australian and New Zealand data on 1782 young growing dairy heifers with genotypes for over 600,000 SNPs, an analysis generated mean GEBV accuracies greater than 0.4 for RFI (Table 3). Some within breed analyses in the beef data generated GEBV accuracies for RFI of over 0.5 (Bolormaa et al. (2013)). These estimates are encouraging given that the accuracy of the EBV for an animal with only its own RFI record is about 0.64. As the technology advances, further improvements in the accuracies will be achieved. Currently, the cost of genotyping is approximately AUD50 to AUD380 (depending on the size of the SNP chip and the information requested). The SNP information is not only for RFI but for other economically important traits as well. The cost of genotyping is expected to fall over time.

 Table 3. Genomic selection accuracies of feed intake (FI)

 and residual feed intake (RFI) in beef and dairy cattle

Country (Study)§	Trait	Type (No.) [¶]	SNP	ACC^{\dagger}
AUS (1)	FI	Beef (3116)	723619	0.28
CAN (2)	FI	Beef (721)	37959	0.20
AUS, NET, UK(3)	FI	Dairy (1801)	30947	0.35
AUS (1)	RFI	Beef (4026)	721264	0.36
CAN (2)	RFI	Beef (721)	37959	0.43
CAN (4)	RFI	Beef (917)	33321	0.43
AUS, NZ (5)	RFI	Dairy (1782)	624930	0.40

⁸Country codes AUS, CAN, NET, NZ and UK represents Australia, Canada, the Netherlands, New Zealand and the United Kingdom, respectively. The study codes (in parentheses) 1, 2, 3, 4 and 5 are Bolormaa et al. (2013), Mujibi et al. ((2011), de Haas et al. (2012), Chen et al. (2013) and Pryce et al. (2012), respectively.

Values in parentheses are the number of cattle.

[†]Mean accuracy.

Implementation in the Beef Industry. To take advantage of advances in genomic technologies, the Australian beef industry has developed a number of resource herds known as the Beef Information Nucleus (BIN) herds. The BIN is a progeny testing scheme (Banks (2011)) which started in 2011, and current participants include the Angus, Brahman, Charolais, Hereford and Limousin breed societies. Comprehensive records on all economically important traits are collected on steers, heifers and cows, including difficult to measure traits. Net feed intake is measured in steers of each of the breed society's BIN. Data from the BIN herds are entered into BREEDPLAN and is providing valuable information in generating NFI EBVs on current young potential elite sires. In addition, a major pastoral company, the Australian Agricultural Company (AACo), has recently invested in automatic feeders with a capacity to test 500 cattle a year, and has commenced testing their potential breeding stock (Beef Central (2014)).

Implementation in industry involves accounting for NFI in breeding objectives as well as having an EBV available (Barwick et al. (2010)). Barwick et al. (2011) demonstrated the separate importance to selection of having NFI traits in the breeding objective and of having an EBV available. Hence in the 2014 update of BREEDPLAN, the EBV for NFI that was introduced in 2002 as a trial single trait EBV, is now a "fully fledged" EBV computed as part of the BREEDPLAN multiple-trait evaluations. An update of the BreedObject software that is used for deriving breeding objectives and indexes in BREEDPLAN, soon to be released, will include NFI traits in the breeding objective in addition to costing the feed that is independent of production, and it will include an option for costing methane production.

Implementation in the Dairy Industry. Currently feed efficiency is partially accounted for in the national dairy breeding objectives of both Australia and New Zealand. The aim of New Zealand's Breeding Worth index and the Australian Profit Ranking is to identify the most accounting profitable breeding stock after for approximations in feed cost estimated through production and maintenance requirements. However, this approximation is unlikely to cover all the variation in feed efficiency. Furthermore, advances in genomic selection have made it possible to estimate and consequently implement genomic-only breeding values provided a sufficiently large genomic reference population could be established. Hence, in the mid-2000s, New Zealand and Australian researchers (from DEPI, Australia and 2 New Zealand organizations: LIC and Dairy NZ) collaborated on an ambitious project to obtain phenotypes for RFI in 2000 growing heifers (split equally between each partner). Crossvalidation showed that the genomic prediction equations had accuracies of up to 0.4 (Pryce et al. (2012)). This research was applied by one of the research partners, the New Zealand breeding company, LIC who published bull proofs for genomic breeding values for RFI. Reliabilities for RFI are typically around 0.1.

Following the growing heifer study, animals in both countries that were extreme for RFI (i.e. the least and most efficient) were kept for a lactation experiment. Here it was demonstrated, that although the difference between groups was reduced, differences in efficiency were still observed in lactation (Macdonald et al. (2014)). Furthermore, the growing heifer genomic predictions (Pryce et al. (2012)) have been validated in lactating cows in Australia (Pryce et al. (2014a)) with mean accuracy of 0.27 and in New Zealand (Davis et al. (2014)) where differences in RFI measured in lactating cows have been observed between groups extreme for RFI breeding values estimated using growing phase data.

The main limitation to implementation of genomic breeding values for a measure of feed efficiency in Australia is the reliability of genomic breeding values. Consequently, research to increase the size of the reference population has included collaboration, firstly with the Netherlands and UK, both had lactating cows with feed intake phenotypes which saw increases in accuracy from multi-country compared with single country evaluations (de Haas et al. (2012)). More recently, the global dry matter initiative (gDMI) has amassed around 10,000 phenotypes (Berry et al. (2014)) on around 6,000 genotyped animals from 9 partner countries. The aim is to see if a multicountry model can be used to produce dry matter intake breeding values with adequate reliability.

Currently, the preferred trait for implementation in Australia is similar to RFI. A breeding value will be produced and it is also likely to be included as part of the national selection index (Australian Profit Ranking, APR). Research to date suggests that the impact of RFI in the APR may be around 3% of the total economic response to selection (Gonzalez-Recio et al. (2014)) and could be worth around AU\$0.55 million per year in saved feed.

Challenges for the Future

There are a number of gaps in our knowledge, especially estimates of genetic correlations of RFI with meat quality, reproduction and cow traits. The lack of easy and accurate measurement techniques for individual animal pasture intake has limited our understanding of the relationship between growing animal RFI and the efficiency of feed utilization in the breeding herd.

Most research on RFI is based on *ad libitum* feeding on medium to high quality diets. There is some evidence that variation in RFI under restricted feeding is significantly lower than under *ad libitum* feeding to the point that the superiority of low RFI cattle in feed utilization may not be expressed under certain conditions (Herd and Pitchford (2011)). In Australia, cattle are grown on pasture (backgrounding) prior to feedlot finishing and also a proportion of slaughter cattle are finished on pasture. Most breeding herd cattle are maintained on pasture all year round. There is variability in pasture availability and quality across the seasons, but the expression of variation in RFI is not well understood in pasture-based production systems. This highlights the need for accurate individual cattle feed intake measurement technology at pasture.

There is a need for more genetic information on RFI from *Bos indicus* cattle, as most of the currently available information are from *Bos taurus* cattle. As shown in Table 1, some of the genetic correlations between RFI and other economically important traits in *Bos taurus* might be different in *Bos indicus* cattle.

While there is good information on the effect of selection for RFI on productivity, there is currently very little information on its impact on health of cattle.

In the short to medium term, challenges include the development of strategies to improve accuracies of GEBVs for difficult to measure traits such as RFI. Linked to this is the need for the development and long-term maintenance of large, cost-effective resource herds for both cattle industries.

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