Reducing the cost of beef production through genetic improvement in residual feed intake: Opportunity and challenges to application[1]

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ABSTRACT: There is considerable individual animal variation in feed intake above and below that expected or predicted on the basis of size and growth rate. This difference in intake is calculated as residual (or net) feed intake (RFI). Genetic variation in RFI of beef cattle exists both during growth (slaughter generation and replacement females; heritability estimates since 1996 range from 0.16 to 0.43) and in adult cattle (the breeding herd; the one published heritability estimate is 0.23). Evidence shows that selection for lower RFI measured postweaning will lead to a decrease in feed intake by young cattle and by cows, with no compromise in growth performance or increase in cow size. Results from a single generation of divergent selection on postweaning RFI between 8 to 12 mo of age demonstrated favorable correlated changes in average daily feed intake (9.2 ± 0.2 vs. 9.8 ± 0.2 kg/d), RFI (–0.20 ± 0.11 vs. 0.17 ± 0.10 kg/d), and feed:gain ratio (F:G; 7.0 ± 0.2 vs. 7.6 ± 0.2 kg/kg) in Angus feedlot steers. In Angus cattle, the genetic correlation between postweaning RFI with average daily feed intake by the cow is high (0.64), and the correlation between postweaning RFI and cow RFI is very high (0.98); however, the correlation between postweaning RFI and cow F:G is low (–0.06). These genetic correlations indicate that selection against postweaning RFI has the potential to lead to a decrease in feed intake and improvement in feed efficiency of growing animals and mature animals. Measurement of feed intake might occur in central test stations, or on-farm, and uniform guidelines are required to ensure that standardized and accurate data are generated. Ways of utilizing information generated in genetic evaluations are discussed. An EBV for feed intake after a phenotypic adjustment for growth performance (growth rate and BW) seems most practical. Such EBV would best be used in an economic selection index to account for genetic correlations with other traits in the breeding objective, including feed intake of the breeding herd, and the economic value of feed in relation to other traits. Further research is needed to examine these genetic relationships and to find ways for cost-effective identification of superior cattle.

Key Words: Beef Cattle, Feed Intake, Genetic Correlation, Heritability, Selection

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Introduction

Providing feed to animals is a major cost input in almost any animal production system. This has long been recognized by the pig and poultry industries, in which cost of feed is easily quantified. These industries have made significant improvements in feed efficiency through both genetic and nongenetic means (Luiting, 1991). Although the cost of providing feed to grazing animals is more difficult to quantify in extensive grazing industries, the provision of feed is a major cost in beef production, and improvement of the output of beef per unit of feed used over the whole production system would be of significant economic benefit.

The majority of national genetic improvement programs for beef cattle have emphasized selection to improve outputs, such as BW, and more recently, fertility and carcass traits. There is a need to also consider avenues for reducing inputs in order to improve efficiency of production and to increase profit. Avenues for genetic improvement of production system feed efficiency include choice of breed, crossbreeding and selection within breeds. Research has shown that there is considerable individual animal variation in feed intake

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above and below that expected or predicted on the basis of size and growth rate (e.g., mice: Archer et al., 1998; poultry: Luiting and Urff, 1991; pigs: Foster et al., 1983; cattle: reviewed by Archer et al., 1999b). This difference in intake is generally calculated as residual feed intake **(RFI).** In some reports RFI is also called net feed intake, referring to its derivation as actual feed intake net (or less) of expected feed intake for BW maintained and ADG by an animal over a test period. The term "net feed efficiency" is also used and refers to feed efficiency net of size and level of production. This paper reviews new evidence for the potential of within-breed selection on RFI to improve production system feed efficiency and the application challenges to industry adoption.

Genetic Variation in Feed Efficiency of Beef Cattle

Feed intake is generally correlated with output traits, and therefore examination of feed intake or production outputs in isolation from each other usually provides little or no indication of the efficiency of production. To make comparisons between animals, many researchers have considered feed intake and production outputs over a limited part of the production cycle and expressed "feed efficiency" using an index, which combines feed intake (the input) with production (the output). Evidence for genetic variation in indices of feed efficiency, including RFI, published for beef cattle up to 1996 was reviewed by Archer et al. (1999b). Since 1996, genetic variation in RFI has been reported in a range of beef cattle breeds in studies from Australia (Arthur et al., 2001b), Britain (Herd and Bishop, 2000), Canada (Liu et al., 2000), and France (Renand et al., 1998).

The efficiency of a beef production system depends on the summation of many traits that include feed intake of both the breeding herd and slaughter generation, growth traits, and other cow traits, such as mature size and reproductive rate (Archer et al., 1999b). Selection for lower RFI (a measure of net feed efficiency, which accounts for feed required to maintain BW and for growth) measured postweaning has the potential to lead to a reduction in the intake of young cattle and of cows, with no compromise in growth performance or increase in cow size. This is not the case for selection to reduce feed:gain ratio (F:G) in which the genetic correlation with growth rate can lead to an increase in cow size and feed intake, which is not always desirable (Archer et al., 1999b).

Residual Feed Intake: Opportunity

That individuals of the same BW require rather widely different amounts of feed for the same level of production was acknowledged by Byerly (1941) in his preparation for experiments to determine whether or not individual differences in net efficiency of laying hens are inherited. In growing beef cattle, Koch et al. (1963) recognised that differences in both weight maintained and weight gain affect feed requirements. They suggested that feed intake could be adjusted for BW and weight gain, effectively partitioning feed intake into two components: 1) the feed intake expected for the given level of production and 2) a residual portion. The residual portion of feed intake could be used to identify animals, which deviate from their expected level of feed intake, and was heritable (0.28 ± 0.11), with efficient animals having lower (negative) RFI. While the utility of RFI for within-breed genetic improvement in feed efficiency is the subject of this review, it is worth noting that the concept of RFI can also be used in nutrition studies to detect differences in the efficiency of feed utilization not revealed by measurement of ADFI, ADG or F:G, presumably because of the correlation between these traits. The report by Okine et al. (2001) provides an illustration of the use of RFI to detect differences in efficiency of utilization of energy in feeds.

Literature estimates of genetic variation in RFI of growing cattle published to 1996 were summarized by Archer et al. (1999b). Some more recent estimates are presented in Table 1. Low values for the heritability of RFI reported in some studies appear to reflect higher measurement error (e.g., Herd and Bishop, 2000; CRC, 2001). Nevertheless, these new reports continue to show that there are both phenotypic and genetic variation in feed efficiency of growing cattle beyond that explained by differences in BW and level of production.

The opportunity to improve whole-herd production efficiency through exploitation of genetic variation in RFI is dependent not only on the existence of genetic variation in young cattle but also on the magnitude of the genetic correlations with other key production traits. These traits include growth and feed intake during finishing, carcass and meat quality traits at slaughter, and cow traits, such as mature size, feed intake, milk production, and lifetime reproductive performance. In young beef cattle, results from postweaning tests show that RFI has strong, favorable genetic correlations with F:G of the growing animal (Table 1). Estimates for the genetic correlation for postweaning RFI with measures of fatness at the end of the RFI test are positive but variable (Table 1). They are evidence for a genetic association of low RFI (high efficiency) with lower fatness (increased lean). The variation in estimates for this correlation presumably reflects differences between the actual measurements recorded and the age of the cattle being tested. For example, the genetic correlations reported for RFI of weanling bulls and heifers tested from 8 to 12 mo of age with subcutaneous rib fat and rump fat depths were 0.17 ± 0.05 and 0.06 ± 0.06 (Arthur et al., 2001b) and weaker than reported for steers and heifers tested in a feedlot (RFI with subcutaneous rump fat depth 0.42; CRC, 2001), possibly the result of greater genetic expression of fatness in the feedlot cattle due to older age and a higher-energy diet (CRC, 2001). If this genetic correlation with fatness is expressed in progeny destined for slaughter or in daughters entering the cow herd, then selection

Table 1. Literature estimates published since 1996 for the heritability of residual feed intake in growing beef cattle and genetic correlations with selected postweaning test and mature cow traits

				Genetic correlation				
				Postweaning test		Mature cow		
Breed	Sex[a]	Number	Heritability	F:G[b]	Fatness	RFI[c]	BW	Source
Hereford	M	540	0.16 ± 0.08	0.70 ± 0.22	–0.43 ± 0.23[d]	—	–0.09 ± 0.26	Herd and Bishop (2000)
Limousine and Charolais	M	1,629	0.21 to 0.39[e]	—	0.70[f]	—	—	Renand et al. (1998)
Beef and dairy	M	282	0.29	—	—	—	—	Liu et al. (2000)
British	M & F	1,180	0.39± 0.03	0.66 ± 0.05	0.17 ± 0.05 to 0.06 ± 0.06[g]	—	—	Arthur et al. (2001b)
British	F	751	0.23[h]	—	—	0.98	–0.22	Archer et al. (2002)
Charolais	M	792	0.39 ± 0.04 to 0.43 ± 0.06[e]	0.85 ± 0.05	—	—	—	Arthur et al. (2001c)
British and tropically adapted	S & F	2,155	0.18	—	0.42[i]	—	—	CRC (2001)

[a]M = males; S = steers; F = females.
[b]Feed:gain ratio.
[c]Residual feed intake.
[d]Estimated lean content.
[e]Two ages/feeding regimen and two methods for estimating residual feed intake were used.
[f]Whole body fat.
[g]Scanned subcutaneous fat depth at rib and rump.
[h]Mature cow RFI.
[i]Scanned subcutaneous rump fat thickness.

for low RFI might affect market suitability and reproductive performance of the progeny. Results from divergent selection on postweaning RFI found no change in subcutaneous fat depths in progeny in weanling tests (Herd et al., 1997), no compromise in meeting market specifications by feedlot steers (Richardson et al., 1998), and no change in subcutaneous fat depths in cows (Arthur et al., 1999).

It would be desirable that the genetic correlations for RFI measured on seedstock animals in a postweaning test, with RFI and F:G of their progeny in the feedlot were high, but these correlations are not reported yet. However, there is evidence that this genetic correlation is likely to be high. Arthur et al. (2001d) reported results for Charolais bulls tested as weanlings from 9 to 14 mo of age and then again as yearlings from 14 to 19 mo of age. The genetic correlations were high: 0.75 ± 0.12 between RFI in weanling tests and RFI in yearling tests and 0.54 ± 0.17 for RFI in the weanling tests with F:G in the yearling tests. Furthermore, results from a single generation of divergent selection on postweaning RFI demonstrate favorable correlated changes in RFI and F:G in feedlot steers (Richardson et al., 1998).

Knowledge of the genetic relationships between feed efficiency traits measured in weanling tests with mature cow performance traits is required for breeding programs that are designed to improve whole herd production efficiency. Genetic correlations between postweaning RFI and mature cow size are low or zero (Table 1), indicating that breeding to improve feed efficiency in growing animals though selection against postweaning RFI need not be accompanied by an increase in cow size. This is not the case if selection to reduce postweaning F:G is employed because of the stronger genetic correlation of postweaning F:G with cow size (–0.29 ± 0.24, Herd and Bishop, 2000; and –0.54, Archer et al., 2002). The genetic correlation between postweaning RFI with feed intake by the cow is high and with RFI of the cow very high (0.64 and 0.98, respectively; Archer et al., 2002). There are few reports of the genetic correlations of feed intake and RFI from young growing animals to mature adults for comparison. Niewhof et al. (1992) found a genetic correlation between RFI of dairy heifers measured postweaning with ME-intake during first lactation of 0.52 and with RFI of 0.58. Archer et al. (1998) found a genetic correlation between RFI of mice measured postweaning with ADFI at maturity of 0.50 and with RFI of 0.60. The genetic correlations for postweaning F:G with cow feed intake and cow F:G appear to be low (0.15 and 0.20; Archer et al., 2002) suggesting that selection to reduce postweaning F:G to likely to be accompanied by only small reduction in cow feed intake and F:G. These genetic correlations indicate that selection against postweaning RFI has the potential to lead to a reduction in feed intake by cows with little change in cow size, thus improving the efficiency of the cow herd. This is an important advantage over selection for increased postweaning growth or decreased F:G that can be accompanied by an increase in cow size, which is not always desirable. It is not known whether genetic reduction in cow feed intake would be accompanied by a reduction in foraging activity of cows at pasture, which might not be desirable. Reduction in physical activity, at least within the confines of the test environment, has been shown for low-RFI animals (e.g., laying hens: Luiting et al., 1991; pigs: De Haer et al., 1993; young beef bulls: Richardson et al., 1999).

Because RFI is by definition phenotypically independent of the production traits used to calculate expected feed intake, it allows comparison between individuals differing in level of production during the measurement period. This independence of RFI from production has led some authors to suggest that RFI may represent inherent variation in basic metabolic processes. For example, genetic variation in maintenance energy requirement per kilogram of metabolic BW is closely associated with genetic variation in RFI in young Hereford bulls (genetic correlation 0.93 ± 0.06; Herd and Bishop, 2000). In laying hens, variation in RFI is mainly caused by variation in maintenance energy expenditure between hens with similar egg mass production and BW (Luiting et al., 1991). In a typical beef cattle herd, the feed energy for maintenance represents 60 to 75% of the total energy requirements of individual breeding cows, and the cost of maintaining cows is clearly an important factor in determining the efficiency and profitability of beef production systems (Archer et al., 1999b). It seems likely that there will be a genetic association between RFI and maintenance efficiency of the cow, but this remains to be demonstrated.

Predictive Value of RFI

There is evidence for genetic variation in RFI measured in young cattle, and the estimates for heritability and genetic correlations with other traits raise expectations for favorable direct and correlated responses in the next generation that include a reduction in RFI and feed intake with little change in size or growth rate for both young cattle and for cows and thus an improvement in feed efficiency in both groups. The validation of the predictive value of RFI in bringing about these favorable changes comes from demonstration of the direct and correlated responses to selection.

The most comprehensive study of the responses to selection on postweaning RFI in beef cattle is that conducted by NSW Agriculture at the Agricultural Research Centre, Trangie, NSW Australia, between 1993 and 2001. The design of the breeding program and postweaning test procedures are described by Arthur et al. (2001b) and the establishment of divergent selection lines for postweaning RFI by Arthur et al. (2001a; 2001b). The following sections present results for the direct and correlated responses to this divergent selection.

Response to Selection— Postweaning Traits

Parents were divergently selected on the basis of their own RFI measured over a postweaning test from 8 to 12 mo of age and their bull and heifer progeny were subsequently evaluated for postweaning RFI under the same test regimen used to test their parents. After 5 yr of divergent selection (1999-born animals; approximately two generations) the direct response was –0.54 ± 0.18 kg/d in the low RFI-line and 0.70 ± 0.17 kg/d in the high RFI-line (Arthur et al., 2001a). Selection for low RFI (more efficient cattle) was accompanied by corresponding reduction in daily feed intake (9.4 ± 0.3 vs. 10.6 ± 0.3 kg/d) and reduced (improved) F:G (6.6 ± 0.2 vs. 7.8 ± 0.2 kg/kg). Yearling weight (384 ± 7 vs. 381 ± 7 kg) and postweaning ADG (1.44 ± 0.03 vs. 1.40 ± 0.03 kg/d) were not affected by divergent selection on postweaning RFI.

Response to Selection—Cow Traits

Preliminary results for the correlated response in cow traits following divergent selection for postweaning RFI were reported by Herd et al. (1998) and Arthur et al. (1999). The cows had been separated into high- and low-efficiency herds based on their own postweaning RFI to form the parent generation for divergent selection. Herd et al. (1998) measured pasture intake by 41 lactating cows that had previously been ranked as either low postweaning RFI (high efficiency) or high RFI (low efficiency), when tested as young heifers on a pelleted ration. The low-RFI cows were 7% heavier (618 ± 16 vs. 577 ± 11 kg), had similar rib fat depths (12.0 ± 0.7 vs. 11.7 ± 0.8 mm) and rump fat depths (15.8 ± 0.8 vs. 15.6 ± 0.8 mm), and reared calves of similar BW to the high-RFI cows (111 ± 4 vs. 104 ± 4 kg) but consumed no more feed than the high RFI cows. The advantage in efficiency of the low RFI cows, when expressed as a ratio of calf BW to cow feed intake, was 15% (9.3 ± 0.5 vs. 8.1 ± 0.4 kg/kg.d, P = 0.07). The study suggests a phenotypic association between postweaning RFI of the young female and her later efficiency as a cow/calf unit at pasture.

Arthur et al. (1999) reported results for 284 4-yr-old cows retested for RFI on a pelleted ration after weaning their second calf. Only cow RFI and feed intake over the 70-d test differed between the RFI selection lines, with high efficiency cows having a lower RFI (–29 ± 11 vs. 18 ± 11 kg) and consuming less feed (1093 ± vs. 1144 ± 16 kg) than low-efficiency cows. There were no significant differences in BW (551 ± 7 vs. 550 ± 7 kg) and rib fat depth (4.9 ± 0.3 vs. 5.2 ± 0.3 mm) at the start of the test, nor in ADG over the test (1.20 ± 0.04 vs. 1.21 ± 0.04 kg/d),) between the high-efficiency and low-efficiency lines. Milk yield, measured once during lactation by the calf weigh-suckle-weigh method on 104 cows, did not differ between high- and low-efficiency lines (4.4 ± 0.2 vs. 4.1 ± 0.2 kg/d). The results indicate that females, which were more efficient as weanlings, required less feed as mature cows, with no compromise in performance.

Response to Selection—Steers on Pasture

One cohort of steers born following a single generation of divergent selection for postweaning RFI, as described by Arthur et al. (2001a), were evaluated for their growth and feed efficiency on improved pastures (Herd et al., 2002c). The cohort of 53 steers (22 from the low-RFI line, progeny of six sires; 31 from the high-RFI line, progeny of five sires) had pasture intake measured using alkanes as markers. This experiment demonstrated a favorable response in growth and feed efficiency on pasture by steers whose parents had been selected for low postweaning RFI. Significant regression coefficients for traits measured on the steers with their mid-parent EBV for postweaning RFI were used as evidence for genetic association. Steers from the low-RFI selection line tended to grow faster than steers from the high-RFI selection line (0.50 ± 0.02 vs. 0.42 ± 0.02 kg/d; $P < 0.1$), consistent with the negative regression coefficient for ADG with mid-parent EBV for RFI (−0.11 ± 0.05; $P < 0.05$). The difference in daily pasture intake between the selection lines was not significant (3.04 ± 0.11 vs. 3.23 ± 0.14 kg DM/d; $P > 0.1$), nor was the regression coefficient with mid-parent EBV for RFI (0.28 ± 0.29; $P > 0.1$). Feed conversion ratio was 6.4 ± 0.4 kg/kg for low-RFI selection line steers and 8.5 ± 0.8 kg/kg ($P = 0.1$). The positive regression coefficient for F:G with mid-parent EBV for RFI (2.9 ± 1.5; $P < 0.1$) provided evidence for low RFI in the parents being genetically associated with superior efficiency of feed conversion on pasture by their steer progeny, with an approximate three-unit improvement in F:G accompanying a 1-kg reduction in mid-parent EBV for postweaning RFI.

Response to Selection—Steers in the Feedlot

A cohort of Angus and of Angus-crossbred steers born following a single generation of divergent selection for postweaning RFI, as described by Arthur et al. (2001a), were evaluated for their growth, feed intake, feed efficiency, and some carcass attributes in the feedlot. Results were reported by Richardson et al. (1998). For the Angus steers, there was no difference between the progeny of parents selected for low RFI or for high RFI in BW at the start of the RFI tests (283 ± 6 vs. 293 ± 6 kg, respectively), ADG over the test (1.35 ± 0.05 vs. 1.30 ± 0.04 kg/d), and BW at the end of the test (369 ± 7 vs. 375 ± 6 kg). Steers in the low-RFI selection line had lower DMI over the tests (9.2 ± 0.2 vs. 9.8 ± 0.2 kg/d), lower F:G (7.0 ± 0.2 vs. 7.6 ± 0.2 kg/kg) and lower RFI (−0.20 ± 0.11 vs. 0.17 ± 0.10 kg DM/d) than did steers in the high-RFI line. Individual feed intake was not recorded for the crossbred steers. There were significant differences between the selection lines in carcass traits measured ultrasonically before slaughter. The low-RFI line steers had less subcutaneous fat depth at the 12/13th rib and rump (Angus: rib 7.1 ± 0.5 vs. 8.3 ± 0.4 mm; rump 8.3 ± 0.6 vs. 10.2 ± 0.6 mm; crossbred: rib 10.1 ± 0.2 vs. 12.2 ± 0.2 mm; rump 13.3 ± 0.2 vs. 14.3 ± 0.2 mm), and a smaller cross-sectional area of the longissimus dorsii muscle (Angus: 48.5 ± 1.1 vs. 51.4 ± 0.9 cm^2; crossbred: 48.2 ± 1.1 vs. 50.4 ± 1.1 cm^2). Richardson et al. (1998) concluded that the steer progeny of low-RFI (high efficiency) parents grew as fast, or faster, than steers of high RFI (low efficiency) parents but ate less feed per unit gain and produced carcasses of acceptable fat finish with no compromise in retail meat yield, and as a consequence, should be more profitable to feed in a feedlot.

Postweaning RFI and Nutrition Interactions (Genotype × Environment)

Genes conferring advantage in net feed efficiency in a particular test environment may not necessarily confer advantage in other environments. Tests for postweaning RFI usually employ medium-to-high energy density rations both for practical reasons, such as ease of feed handling and measurement of feed intake, and to contain sufficient energy so as not to inhibit potential animal performance. For example, test rations with metabolizable energy contents of 10 and 12 MJ/kg DM for weanling seedstock and feedlot RFI tests are recommended in the Australian Net Feed Efficiency Standards Manual (Exton, 2001). Such metabolizable energy contents are well above those of pastures typically grazed by cows or by steers before feedlot entry. It is then legitimate to ask if the progeny of bulls and cows found to be genetically superior for net feed efficiency, as identified by low RFI of a medium-to-high energy test ration, will grow as well and be more efficient on pasture compared to progeny whose parents displayed a greater appetite and higher RFI when similarly tested. From the studies reported above on the Trangie RFI divergent selection lines, there is no evidence that selection for low RFI (high efficiency) measured postweaning on a high-quality, pelleted ration available ad-libitum was accompanied by inferior growth performance by cows and their calves on pasture (Herd et al., 1998; Arthur et al., 1999), or by steers on pasture (Herd et al., 2002c). Moreover, evidence was presented indicating improvement in feed efficiency on pasture accompanied selection for low RFI (Herd et al., 1998; Herd et al., 2002c).

Measurement of RFI

Measurement of feed intake with current technology is expensive, and so the cost of measurement compared to the benefits obtained is an important issue if performance testing of animals for feed efficiency is to be used to select animals. In Australia, a standards manual—*Testing Beef Cattle for Net Feed Efficiency* (Exton, 2001)—has been produced by the Australian Performance Beef Breeders Association, representing breed societies, and forms the basis of a national accreditation scheme to ensure that standardized and accurate data are generated for genetic analyses. This provides uniform guidelines that enable a cattle breeder to measure feed intake of animals, either in centralized testing facilities or on-farm, and to use this information in a genetic evaluation.

Given that measuring feed intake is expensive, the length of a RFI test and the amount of data collected needs to be optimized to reduce the cost of testing animals. The current recommendation to the Australian industry for a 70-d RFI test is based on the results reported by Archer et al. (1997). They showed that for British breed cattle tested for RFI, with feed intake recorded daily and animal BW measured weekly, that while 35 d was adequate to measure feed intake, 70 d was required to accurately measure growth and RFI. Archer and Bergh (2000) analyzed data from centralized tests in South Africa for young bulls from five breeds and four biological types to conclude that while a test of between 42 and 56 d was sufficient for measurement of growth rate, feed intake required 56 to 70 d to measure accurately, and RFI required around 70 to 84 d. Differences between the two studies for minimum periods for measurement of growth rate and feed intake were attributed to differences in the procedures used to measure BW and feed intake.

For RFI tests conducted following Australian standards, if the accuracy in measuring growth could be improved, then it might be possible to reduce the length of the RFI test, with a consequent reduction in the cost of testing and an increase in the number of animals that can be tested per year at the same testing facility (Archer et al., 1999a). Advances in livestock weighing technology that incorporate animal electronic identification allow automatic frequent capture of animal BW. Preliminary evaluations have shown that more frequent weighing of cattle can improve the accuracy of measurement of growth (Archer et al., 1999a; Graham et al., 1999; Tatham et al., 2000) and thereby offer the potential to reduce the length of the standard 70-d RFI test. However, to confirm these results and to determine the optimal length of test with frequent weighing, more animals with good genetic links need to be tested, and a comprehensive genetic analysis conducted, as done by Archer et al. (1997).

Cattle may be tested for RFI either at centralized test facilities or on-farm. Archer et al. (1999b) reviewed the merits of both test regimens, and Australian experience is that both will be used by cattle breeders. An issue common to both approaches is the influence of pretest environmental affects on subsequent test performance. Archer et al. (1999b) recognized two approaches might be used to remove differences due to the previous history, one biological and the other statistical. A common pretest adjustment phase might be used to biologically remove differences between animals measured in a test group. An alternative approach is to restrict comparisons between animals to those raised in the same environment from conception to measurement (i.e., in the same contemporary group), as currently occurs with other traits recorded in BREEDPLAN, the national program for genetic evaluation of beef cattle in Australia (Skinner and Sundstrom, 1997). The Australian standards manual requires a minimum pretest adaptation period of 21 d and testing of animals in contemporary groups. Comparisons of RFI may be less influenced by pretest environmental affects than are growth-related traits. For example, Herd and Bishop (2000) showed that RFI over a performance test was not affected by differences in pretest rearing treatments, in contrast to growth related traits, such as start-of-test BW and end-of-test BW, and, in some years, ADG and F:G. Age of dam is another nongenetic factor known to influence liveweight and growth of young cattle. Arthur et al. (2001d) showed that where age of dam affected ADG, feed intake, F:G, and final BW, it did not affect RFI in weanling tests on Charolais bulls.

Using Feed Efficiency in Selection Decisions

The method used to incorporate feed intake and growth information in selection decisions is an important issue for consideration and is discussed in detail by Archer et al. (1999b). Combining feed intake and growth information into an index for feed efficiency does not add any new information to that which is obtained directly from the component traits (Kennedy et al., 1993). Where use of postweaning feed intake and growth as separate criteria traits in an economic selection index is theoretically optimal, currently the level of usage of economic selection indices in the beef industry is low. For the medium term, it is likely that a large proportion of bull breeders and bull purchasers will continue to base decisions on EBV for individual traits. Presentation of separate EBV for feed intake and growth, which are antagonistic and highly correlated, is likely to cause difficulty in interpretation as it is difficult to compare an animal with high intake and high growth rate with another with lower intake but lower growth also. Conceptually, an EBV for feed intake after adjustment for differences in growth performance (i.e., RFI) would be easier to interpret than an EBV for feed intake unadjusted for growth, as the correlation between growth EBV and the adjusted feed intake EBV would be lower and comparisons between feed intake of animals with different growth performance would be simplified. Therefore an EBV for RFI, calculated using a phenotypic or genetic adjustment for growth performance, may be the best way to present the information. However, EBV for RFI should be presented as feed intake EBV with an adjustment for growth, rather than as EBV for "efficiency" per se. Moreover, the EBV, or its component traits, should be used in an economic selection index to optimize selection decisions based on all available information not just feed efficiency.

Industry Adoption

In Australia, BREEDPLAN EBV are accepted as the most appropriate method of estimating genetic merit of an animal for a given trait (Sundstrom, 1997). Recent research and extension has focused on developing EBV for RFI for those cattle breeds already enrolled in

GROUP BREEDPLAN and that have begun testing cattle for RFI (Exton et al., 1999). The breed societies control the databases and determine which traits will be included in the BREEDPLAN analysis, accuracy levels for publication, and cost structures for their members. The Australian Performance Beef Breeders Association referred to above is responsible for implementing policy regarding testing for RFI and subsequent submission of data for development of EBV. This association has developed a standards manual (Exton, 2001) for the measure of net feed efficiency and forms the basis of a national accreditation scheme to ensure that standardized and accurate data are generated for to use in a genetic evaluation.

Trial EBV for net feed intake (i.e., RFI) were published in the 1999 Autumn Australian Angus GROUP BREEDPLAN genetic evaluation report (sire summary). Trial BREEDPLAN single-trait EBV for net feed intake were published for Australian Angus, Hereford, and Poll Hereford bulls in 2002. The Angus RFI EBV were computed using 2,128 animals with individual feed intake records. The EBV generated ranged from –1.41 to +1.14 kg/d, compared to an average feed intake by the cattle of about 12 to 13 kg/d (Angus Society of Australia, 2002; D. J. Johnston, personal communication). This implies that there exists genetic variation in feed intakes ranging from at least 10% below to 10% above that expected on the basis of an animals size and growth rate. This provides an opportunity to select low-RFI bulls for use in breeding programs to reduce the feed cost of beef production. Fewer records existed for the Hereford and Poll Hereford breeds, EBV being computed using 579 animals with individual feed intake records. The EBV generated ranged from –0.63 to +0.90 kg/d (Australian Hereford Society, 2002).

Challenges to Application

Measurement of feed intake with current technology is expensive, and this is the major barrier to industry adoption. Lack of comprehensive demonstration of the whole farm economic benefit for the beef cattle breeder and his clients under the specific conditions of their farm enterprise is also a barrier to adoption to cost-sensitive farmers. Modeling studies can be illustrative (e.g., Arthur et al., 1996; Exton et al., 2000; Tatham et al., 2000; Archer and Barwick, 2001), but more research is required to demonstrate improvement in individual animal utilization of pasture and supplements, benefits to pasture sustainability, and improvement in whole-farm enterprise efficiency in good seasons and drought seasons. Reduction in manure and methane emissions are other tangible benefits that can be expected from genetic improvement in RFI (Basarab et al., 2001; Herd et al., 2002b) but remain to be demonstrated.

In the past, most beef cattle breeding programs involved comparatively low levels of investment in recording traits on which to base selection decisions. The cost of measuring RFI requires an increased level of investment. Breeding program design incorporating two-stage selection can reduce the number of potential sires that need to be evaluated for RFI and thereby reduce the cost of investment in performance test information number and optimize the return (Archer and Barwick, 2001). Designs using performance test information on bulls only, or including information from progeny tests, were profitable relative to designs without RFI measurement. Including information from progeny testing can improve the accuracy of selection and genetic gain, but accounting for risk and market share is required to justify progeny testing for this expensive-to-measure trait at the level of an individual business (Archer and Barwick, 2001).

An alternative to costly direct RFI testing would be to identify one or more traits that are genetically correlated with RFI and could be used to indirectly select for efficiency. These traits could include phenotypic markers measured from a blood sample or genetic markers. Measurements of marker traits made on an individual or on related animals can then be used to make inferences about the genetic merit of the selection candidate. The direct and indirect approaches are not mutually exclusive, and using both methods in tandem may provide the most cost-effective strategy to identify animals of superior genetic merit for RFI. For example, a phenotypic marker might be used as a pretest screen to identify animals on which further measurement is warranted. The use of selection against the concentration of the hormone IGF-1 in blood to improve growth, feed efficiency, and carcass lean content has been patented for livestock species by an international patent variously registered as WO9635127, AU694025, NZ306348, and EP0830607 by Owens and others in 1996: "Selection of Livestock Using IGF levels." This invention has been shown to be reliable for identification of genetically superior pigs and is the basis of commercial mass screening of pigs and selection to improve growth and feed efficiency and to reduce carcass fatness of pigs (Luxford et al., 1998ab; Hermesch et al., 2001). Recent results in beef cattle show circulating levels of IGF-1 are genetically associated with growout and finishing performance of beef cattle and may prove useful as a genetic predictor of carcass and feed efficiency traits (Johnston et al., 2001; 2002; Herd et al., 2002a). A genetic and economic evaluation of the use of IGF-1 as an indirect selection criterion in beef cattle showed it can increase the profitability of selection decisions and would best used as a screening test to identify animals to be placed into RFI tests in a two-stage selection program (Wood et al., 2002).

Recent interest in gene mapping of cattle to identify genetic markers associated with production traits suggests the possibility of using genetic markers in a breeding program to aid selection for feed efficiency. However, it is unlikely that use of phenotypic or genetic markers will obviate the necessity for direct measurement of feed intake and efficiency of some individuals in the medium term, although markers may still play a role in improving the cost effectiveness of measuring feed intake and efficiency.

Other barriers to industry adoption exist, for example, capacity of RFI test stations and availability of measurement equipment, disease quarantine barriers to cattle movement to and from test facilities, the scheduling of testing between weaning, and sale of bulls. Our knowledge of the genetic relations for RFI with other traits is incomplete, especially for the relationships of postweaning RFI with cow efficiency at pasture, reproduction, and maternal traits. Indications from dairy cattle show a favorable genetic correlation between RFI of growing heifers and lactating heifers (Nieuwhof et al., 1992). In beef cattle, a very high genetic correlation between postweaning RFI and mature cow RFI was reported by Archer et al. (2002), and there is a favorable phenotypic association with efficiency on pasture (Herd et al., 1998). The genetic correlations for RFI measured on seedstock animals in a postweaning test, with RFI and F:G of their progeny in the feedlot are not yet known, but evidence presented above indicates that they are likely to be high. Lack of an inexpensive, accurate method to measure pasture intake by individual animals (Archer et al., 1999b) prevents testing for RFI on pasture and restricts the opportunity to demonstrate correlated responses in feed efficiency at pasture. Finally, only a handful of cattle breeds has been investigated thus far.

Implications

Genetic variation in feed efficiency of cattle exists both during growth (slaughter generation and replacement females) and in adult cattle (the breeding herd). Strong genetic relationships exist between feed intake and efficiency measured postweaning and these traits in the breeding herd. Selection for lower residual feed intake (a measure of net feed efficiency that accounts for feed required to maintain body weight and for growth) measured postweaning will lead to a decrease in feed intake by cows, with no increase in cow size. Significant barriers to industry application remain. Measurement of residual feed intake is very expensive compared with other traits currently measured and used in genetic improvement programs. Further research is needed to examine the genetic relationships between residual feed intake and other traits in the breeding objective and to find ways for cost-effective identification of superior cattle.

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