The Genetics of Feed Efficiency in Beef Cattle

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Introduction

Whereas it is well established that feed supplementation accounts for a large majority of the non-fixed costs of beef production, there has recently been renewed interest in the design and implementation of genetic evaluation and improvement programs for efficient feed utilization. The National Beef Cattle Evaluation Consortium (NBCEC) working group on efficiency and feedlot traits has been formed among scientists across North America to make recommendations for improved methods for genetic evaluation of feed efficiency. The development of such procedures requires knowledge of phenotypic and genetic properties among the numerous measures of feed efficiency that have been proposed in the scientific literature. As such, this paper will address issues related to the genetics of efficient feed utilization in beef cattle. The discussion will draw heavily on recent scientific reports and reviews (Archer et al., 1999; Crews, 2005).

Why Efficiency?

Selection for the wide range of traits for which most beef breed associations calculate expected progeny differences (EPD) focus on increasing the outputs of the production system, thereby increasing the genetic potential of cattle for reproductive rates, weights, growth rates, and end-product yield. Feed costs, however, represent the largest portion of the variable cost of beef production and genetic improvement programs for reducing input costs should include traits related to feed utilization. Beyond the usual prediction of response to selection which involves genetic variation and parameters, selection intensity and generation interval, considerations for optimal selection

programs also include several issues, including biological significance, the potential for antagonism with other traits under selection, and costs of data collection. Within the context of economic relevance, feed intake is the input or cost stream, whereas growth or other outputs are the revenue streams. To relate production efficiency to profitability, both streams must be considered.

Traditional Measures of Efficiency

In their review, Archer et al. (1999) summarized that more than two dozen measures of "efficiency" have been proposed in the scientific literature in the last 40 or more years, and to varying extent, characterized phenotypically and genetically in the literature. Most of these have been reported to have at least moderate heritability (i.e., $h^2 = 0.20$ to 0.40), and as with most phenotypes or traits, have various genetic correlations with other traits. Historically, the most common measure of efficiency has been gross efficiency, or its inverse, feed conversion ratio (FCR), which is defined as the ratio of some measure of feed intake to some measure of output. Several papers have reviewed the definitions of numerous other so-called efficiency measurements (e.g., Arthur et al., 2001b). Much of the difference among these measures relates to whether or not individual feed intake must be recorded which has been a major time and cost limitation to large-scale efficiency research in cattle.

In addition to the fact that most early work described efficiency as the ratio of inputs to outputs (i.e., similar to FCR), studies were generally limited within a specific industry

segment or stage of animal production. This led to only limited insight into efficiency of the total production system. A more desirable measure of efficiency would not only describe differences in individual animals, but also be highly repeatable across industry segments and animal classes. Differences in the energy status of animals (e.g., growing, lactating, mature, etc.) across segments and through time make it difficult to compare their efficiencies unless the traits measured have similar biological and genetic properties.

Feed intake and FCR are well known to be phenotypically and genetically correlated with measures of growth and therefore mature size. For example, in their meta-analytic review of published parameter estimates for beef production traits, Koots et al. (1994b) summarized numerous estimates of the genetic correlation of FCR with weights and gains ranging from -0.24 to -0.95, which clearly indicate that increased genetic potential for performance and size is negatively correlated with FCR. Therefore, selection for improved (i.e., decreased) FCR would result in increased correlated genetic responses for growth rates, mature size, and presumably, mature maintenance requirements. Koots et al. (1994b) also showed strong evidence that the genetic associations of feed intake with measures of growth rate and weight were positive, with estimated genetic correlations ranging from 0.25 to 0.79. Of particular note are estimates of the genetic correlation of mature weight with FCR (-0.14) and feed intake (0.92). These results underscore two intuitive principles: 1) cattle with larger mature size have higher intake requirements, and 2) decreasing selection for FCR is expected to result in larger mature size.

An antagonistic implication of these generally moderate to high genetic correlations among intake, growth, size, and FCR is that favorable decreases in FCR due to selection do not necessarily translate specifically to improvements in efficiency of feed utilization. Because FCR is defined as inputs divided by

outputs, changes in FCR could be due to decreases in feed intake or increases in growth rate (e.g., average daily gain). In fact, the mean genetic potential of cattle for FCR has probably been changing along with the general trend for increasing selection on growth for as long as large-scale growth trait genetic evaluations have been available. Therefore, growth rates and age-specific weights have been increasing for the past 25 years in beef cattle, feed conversion ratios have probably also been decreasing, but true efficiency remains relatively unchanged.

To summarize, ratios and other measures of efficiency generally suffer from similar limitations: they are "too related" to other economically important traits. Using well-established selection index theory, it is possible to design selection programs that moderate or even eliminate antagonistic response. However, a more desirable measure of efficiency would be preferred, at least to the extent that unfavorable genetic correlations could be moderated or eliminated.

Residual Feed Intake

Residual feed intake (RFI), sometimes referred to as net feed intake or net feed efficiency, was first proposed for beef cattle by Koch et al. (1963), and is traditionally defined as the difference between actual feed intake and that predicted on the basis of mean requirements for body weight maintenance and level of production. Koch et al. (1963) realized that a robust measure of efficiency would allow for adjustment of feed intake for any of the various requirements, or "energy sinks" that differentiate cattle in different industry segments and stages of production. For example, whereas growth may be the major energy sink for growing cattle, the requirements for the mature cow herd may be maintenance of body weight and condition for reproductive fitness and lactation. RFI relies simply on partitioning feed intake into portions required for stage and level of production, and a residual or left-over portion that would be comparable

across animals of varying age, industry segment, and stage of production.

Recent research (e.g., Archer et al., 1999; Crews, 2005) has focused on characterization of RFI in the feeding segment of the beef industry. Therefore, most of the remaining discussion will be focused on young, growing cattle although the concept of RFI is not so limited. Computation of RFI phenotypes for individual animals is simply an application of a statistical procedure referred to as multiple linear regression. What I refer to as the "base" RFI model can be represented as

$$INTAKE = \mu + ADG + WT + RFI$$

where feed intake is simply the sum of some common overall or group average (μ), requirements for average daily gain (ADG), requirements related to body weight (WT) and RFI. This leads to a more functional definition of RFI as *that portion of feed intake that is not accounted for by measurable factors*.

The properties of this regression procedure can be used to show several phenotypic attributes of residual feed intake. First, the mean RFI value within a group is zero. Secondly, by definition, RFI is *uncorrelated* to those measurable factors included in the base model. This has important and desirable implications with respect to the design of selection programs. This important result has been verified in several recent reports (Arthur et al., 2001a,b; Basarab et al., 2003), at least in phenotypic terms. The implication here is that approximately equal numbers of animals within a group will have RFI values above and below zero. Efficient animals (i.e., with RFI < 0) have daily feed intake values that are less than what would be expected on the basis of their growth rate and body weight, whereas the converse is true of the less efficient animals (i.e., RFI > 0). Given that RFI may be thought of as that part of feed intake that is not explained by growth and(or) body weight, RFI is independent of growth rate and body weight, and may offer the potential to selection for improved efficiency regardless of animal size. If it were possible to perfectly estimate feed intake for individual animals using indicator traits, the variance of RFI would be zero.

Variation in RFI

Traits that are candidates for selection must have several properties, the most important of which is that for any specific trait or phenotype, observed differences among animals must be due in part to additive genetic effects. All studies that have estimated genetic variance for RFI have reported this parameter to be significant and heritability estimates for RFI have ranged from 0.26 to 0.58 (Koch et al., 1963; Arthur et al., 2001a,b; Crews et al., 2003; Schenkel et al., 2004). These estimates generally fall within the moderate heritability range and are similar to estimates for traditional growth traits. Table 1 summarizes published heritability estimates for residual feed intake. We can therefore expect that given a sufficiency of data, selection would be effective for RFI.

Heritability alone may be misleading for predicting response to selection for RFI. The variability in the phenotype underlying RFI (daily feed intake) should also be considered. In recent studies, considerable variation has been reported for various measures of daily feed and(or) dry matter intake (Arthur et al., 2001a,b; Basarab et al., 2003; Crews et al., 2006). The partitioning of feed intake into "measurable energy sinks" plus RFI dictates that residual feed intake will have lower variance than feed intake. In these same recent studies, the base model accounts for 55 to 70% of the variance in feed intake, which implies that after adjustment for growth rate and proxy measurements of maintenance requirements, approximately 30 to 45 % of the variance in feed intake remains as RFI.

Table 1. Summary of heritability estimates for residual feed intake

Breed	N	$h^2 \pm SE$	Source
British	1,324	0.28 ± 0.11	Koch et al. (1963)
British	966	0.44 ± 0.07	Arthur et al. (1997)
Angus	1,177	0.39 ± 0.03	Arthur et al. (2001a)
Charolais	792	0.39 ± 0.03	Arthur et al. (2001b)
Multiple	2,284	0.38 ± 0.07	Schenkel et al. (2004)
Charolais-sired	641	0.58 ± 0.20	Crews et al. (2003)
Weighted avg. h^2		**0.39 ± 0.09**	**Koots et al. (1994a) method**

Genetic Correlations Involving RFI

Selection for single, component traits is never recommended in beef cattle due to the potential for correlated response which may affect more than one economically important trait, particularly if genetic correlations are antagonistic or unfavorable. Recent studies have reported strongly positive genetic correlations for RFI with FCR (0.70, Herd and Bishop, 2000; 0.85, Arthur et al., 2001a; 0.66, Arthur et al., 2001b). Similarly, positive genetic correlations of 0.64 (herd and Bishop, 2000), 0.69 (Arthur et al., 2001a), and 0.79 (Arthur et al., 2001b) have been reported for RFI with feed intake. These results suggest that selection for improved (i.e., decreased) RFI will be associated with a corresponding declining genetic trend in feed intake. A sample of reported genetic correlations of RFI with other traits is listed in Table 2.

Table 2. Genetic correlations involving residual feed intake

Correlated trait	Genetic correlation	Source
FCR	0.70	Herd and Bishop, 2000
	0.85	Arthur et al., 2001a
	0.66	Arthur et al., 2001b
	0.69	Schenkel et al., 2004
Feed intake	0.64	Herd and Bishop, 2000
	0.69	Arthur et al., 2001a
	0.79	Arthur et al., 2001b
	0.81	Schenkel et al., 2004
Subcutaneous fat	0.17	Arthur et al., 2001a
	0.16	Schenkel et al., 2004
Longissimus muscle area	-0.17	Schenkel et al., 2004

Some reports have estimated genetic correlations of RFI with measures of body composition and reported these to be generally small with the exception of ultrasound rib fat (r_g = 0.17, Arthur et al., 2001a; r_g = 0.16, Schenkel et al., 2004), which are small in magnitude, but do indicate that genetic effects for feed intake are related to those for subcutaneous fat deposition. Supporting phenotypic evidence for a positive association between RFI and carcass fatness has been reported by Basarab et al. (2003), wherein crossbred steers with lower RFI tended to also be leaner to the extent that carcass fat depth was slightly lower. It is important to note, however, that any covariance or association between intake and body composition can be accommodated in the RFI computation model, thereby increasing the numbers of traits to which RFI is uncorrelated. Computation of a body composition-adjusted has been discussed, for example, in Schenkel et

al. (2004), Crews (2005), and Crews et al. (2006).

Refining Residual Feed Intake by Adjustment for Body Composition

Variation in RFI reflects variance in feed intake after adjustment in the base model for average daily gain (growth rate) and body weight (maintenance requirements). However, differences in efficiency of growth may also be due to differences in composition of gain. In other words, easily-measured body composition traits may be another "energy sink" which explains daily feed intake. Ferrell and Jenkins (1998), for example, showed that differences in rate of water, protein and fat deposition influence efficiency and rate of body weight gain primarily because fat has higher energy density than either protein or water. Although more energy expenditure is required for fat versus protein deposition, maintenance of protein requires more energy than maintenance of fat. Several researchers have noted a weak, positive phenotypic correlation between RFI and measures of body fat content, and similarly weak but negative correlations between RFI and carcass lean content (Herd and Bishop, 2000; Arthur et al., 2001a; Basarab et al., 2003). Basarab et al. (2003) reported that approximately 4% of the variation in daily feed intake was attributable to differences in empty body fat, compared to 67.9 and 8.6% attributable to body weight and daily gain, respectively. Generally, additional adjustment of RFI for body composition accounts for approximately 5% or less of the variance in feed intake. Additional evidence was offered by Richardson et al. (2001), who reported that a single generation of selection for RFI resulted in reduced carcass fat content. RFI computed with adjustment for body fat and(or) lean content would have similar variance to that from a base model due to the relatively small increase in model R^2 of the "body composition" versus the "base" models. However, it is important to note that the increase in total model fit due to the additional adjustment for body composition only reflects the variance in feed intake due to fat and(or) lean *after* adjustment for terms in the base model, which to some extent share a part-whole relationship. Therefore, the advantages of an RFI phenotype that is completely independent of body composition should be considered. The relative importance of adjusting RFI for measures of fat versus lean body composition may be dependent on the application. For example, Basarab et al. (2003) showed that after adjustment for live weight and daily gain, on-test gains in ultrasound fat were relatively more important in steers than adjustment for on-test gains in muscle area. Conversely, Crews et al. (2006) reported that in yearling Angus bulls, on-test changes in ultrasound muscle area were more highly correlated to base-model RFI than changes in on-test ultrasound fat thickness.

Potential Diet × Genotype Interactions for Residual Feed Intake

Considering the costs associated with collection of individual feed intake data that is required to compute RFI, the amount of data likely to be available in the short- and medium-term will be relatively small. The relative lack of commercial test facilities capable of individual feed intake recording may in fact restrict such data collection to centralized bull tests, and perhaps to a lesser extent, on-farm programs where investment in equipment can be justified. Crews et al. (2003) studied differences in RFI between two common diet regimes. Weaned calves are often placed on roughage-based growing (i.e., backgrounding) diets prior to the finishing period wherein diets are grain-based with higher energy density. In this study, we calculated RFI separately for 84-d growing and 112-d finishing periods. Estimates of phenotypic and additive genetic variance for RFI in the growing period were greater than corresponding estimates for the finishing period. The estimate of the genetic correlation between growing- and finishing-period RFI was high and positive ($r_g = 0.55 \pm 0.30$). These results led us to suggest that cattle would be ranked similarly for RFI measured on

roughage versus grain diets, but further study is needed to confirm the genetic equivalence of RFI across different diets. This preliminary study involved only a very limited number of animals. These results have implications for genetic evaluation of efficiency where the most likely source of data will be postweaning bull tests but where the selection objective will be improvement in efficiency of market progeny and(or) replacement heifers. In other words, more study is needed to confirm that bulls selected on the basis of RFI computed from intake, growth and body composition data when on a relatively low-energy test diet will be the same bulls that will sire more efficient replacement daughters and market progeny in the feedlot.

Implications of Selection on Replacement Females

Optimal genetic improvement schemes place appropriate relative economic weights on several to many component traits that directly impact either costs or revenues of production. It is always important to consider what impact sire selection will have across the various industry segments and animal types. Relatively little information is available regarding the genetic association between intake and efficiency measures in the mature cow herd and similar measures from the postweaning periods at or near yearling age, when selection decisions are commonly made. Archer et al. (1999) hypothesized that because RFI was uncorrelated with growth rate and body size, the genetic correlation between RFI during postweaning test and a corresponding measure on mature cows would be an indication of the biological similarity between the measurements at distinct ages. They found that both feed intake and RFI during the postweaning period and at maturity had genetic correlations greater than 0.90. This result suggests selection decisions made on the basis of RFI EPD during the postweaning (i.e., pre-breeding) period would translate nearly perfectly to genetic improvement in efficiency of the cow herd. Archer et al. (2002) concluded

that these strong genetic correlations present an opportunity to improve efficiency in growing animals and mature cows simultaneously, based on measurements taken during the postweaning period prior to when selection decisions are made.

Economics of Phenotypic and Genetic Differences in Residual Feed Intake

Direct selection for RFI would be expected to result in genetic trend similar to that obtained with other with similarly moderate heritability. Recent reports have been variable with respect to the phenotypic range in computed RFI. Basarab et al. (2003) reported that RFI (mean = 0.00, SD = 1.46 lb/d) ranged from an efficient -4.30 lb/d to an inefficient +4.01 lb/d among composite steers fed 120 days (i.e., 8.31 lb/d dry matter intake difference between the most and least efficient steers). Archer et al. (1998) identified efficient bulls which consumed 5.51 lb/d less feed over a 120-d test period while maintaining similar live weights and rates of gain compared to less efficient bulls. Crews et al. (2003) calculated mean differences in daily feed intake in Charolais-sired steers and concluded that the more efficient steers consumed 3.73 lb less feed per day during a 112-d finishing period than the less efficient steers. In these comparisons, steers in the high-efficiency (RFI < 0) and low-efficiency (RFI > 0) groups produced similar live weight gains, carcass yield, and marbling scores. Assuming a finishing ration cost of $0.05/lb, a daily intake difference of 3.50 lbs translates to feed cost savings of $0.18 per animal per day, or $26.25 per animal over a typical 150-d feeding period. The economic implications of these differences in the large-scale cattle feeding regions of North America should be readily apparent, especially given that these potential feed savings would not be associated with reduced performance or carcass merit with RFI.

Herring and Bertrand (2002) pointed out that a 2% reduction in consumption (while holding other performance traits constant) would

provide an increase of $111 million in net return to beef producers. This result and other studies imply that the potential to maintain performance (e.g., postweaning gain) while decreasing intake (through selection) by 0.30 lb per day (assuming average daily intake of 30 lb and 1% annual genetic improvement), or total 150-d finishing period intake by 45 lb per animal per year. The genetic gains from this simulation translate to very large feed cost savings in the feedlot sector alone. It is important to note that such genetic improvement could be predicted for longer periods of selection in an additive manner. Further, based on results reported by Archer et al. (2002), improvement in cow herd efficiency would be similar to that obtained the feedlot sector, based on genetic correlation estimates suggesting the biological equivalence of RFI following weaning with RFI measured closer to maturity. Given the limitations associated with measuring forage intake in cows, the value of these savings remains difficult to predict accurately.

Multiple Trait Selection with Residual Feed Intake

There has been little research on the potential implementation of multiple trait selection programs which include RFI. There is a relative lack of published estimates of genetic (co)variances of RFI with other economically relevant traits (Archer et al., 1999). Also, the cost associated with large-scale collection of individual feed intake data makes well-designed studies rare. Recent technological developments have reduced the cost of measuring intake in cattle, thus providing opportunities to measure feed efficiency in growing bulls in postweaning test centers.

Crews et al. (2006) proposed a three trait selection index with the objective to increase profitability during the feedlot phase of the market progeny of centrally-tested Angus bulls. We reported that a large majority of net revenue differences in steers on feed could be explained by feed intake, average daily gain on feed, and final live weight, which were defined as traits in the breeding objective. Then, traits commonly measured on centrally-tested bulls were added to the index and included RFI (adjusted for body composition), daily gain on test, and adjusted 365-d weight. The steer traits to be improved in the objective were linked to the information on bulls in the index by approximating genetic correlations among all six traits. Using routine selection index procedures, bull index value was defined as

$$INDEX = -10.12(RFI) + 24.79\ (ADG) + -0.09\ (YWT)$$

which incorporated RFI, daily gain (ADG), and yearling weight (YWT) of bulls on test with their appropriate weighting factors. These factors show that index value placed a negative weight on RFI (i.e., decreasing) and a positive weight on gain (i.e., increasing). The small weight placed on yearling weight reflects that RFI is relatively unrelated to live weight. Phenotypic correlation estimates for index values with bull daily intake, ADG, and RFI were -0.22, 0.53, and -0.74, respectively. In addition to providing a single index value on which bulls may be selected to increase profitability of their market progeny in the feedlot, bulls with higher index values consumed less feed, had higher ADG, and were more efficient on central test. Index value was not related to YWT, which suggests that selection could be practiced independent of yearling weight. Further, index value had a low, but favorable, phenotypic association ($r_p = 0.16$) with yearling scrotal circumference. This may suggest that such an index would not be antagonistic to indicators of bull fertility. We recognize the limited profit objective of this index (i.e., feedlot sector), however, this approach illustrates one application of RFI in a multiple trait selection program. Other indexes could be developed with different profit or improvement objectives (e.g., heifer development), and other, equivalent index calculations could be applied using EPD.

Challenges to (Inter)national Evaluation of Efficiency with Residual Feed Intake

Traits related to efficient feed utilization, primarily reducing input costs while optimizing output traits such as growth, have been identified in the NBCEC as next-generation EPD for the beef industry. Advances in large-scale genetic prediction combined with decision support will enable reporting of EPD for efficiency-related traits. However, (inter)national cattle evaluation systems (NCE) require three essential components: 1) data acquisition, 2) model development, 3) estimation of relevant genetic parameters, and 4) routine genetic evaluation runs.

In this paper, all but the first of these essential requirements have been addressed. Therefore, the current limitation of an efficiency evaluation is data acquisition. In addition to the added cost of recording individual animal intake, the suitability of data for NCE systems must be considered. In the case of commercial feedlot animals, parentage identity is usually unknown. With the exception of central test station programs and a limited number of progeny testing programs currently in place for evaluation of carcass merit, most calves destined for slaughter are somewhat anonymous with regard to parentage and pedigree. Pollak and Kirschten (2002) mentioned studies underway to combine DNA-based parentage testing with individual intake recording to maximize the information gained per dollar invested in data acquisition.

Some procedures exist to predict EPD for efficiency that do not require recording of individual animal intake. It is important to note that these procedures are not equivalent to RFI. The accuracy of these predictions depends on the genetic correlation between traits for which phenotypes are available (e.g., indicator traits) and the trait of interest (i.e., feed intake). Ultimately, there is always a less than 1.0 upper limit on the accuracy of EPD for an unmeasured trait. While animals can be very accurately evaluated for traits where phenotypic data acquisition is straightforward, few strongly correlated indicator traits are likely to be identified for RFI. This is partially due to the forced independence of RFI with other performance traits that have an association with feed intake.

The implementation of NCE for efficiency will require facilities with intake recording equipment. Given the current lack of widespread availability of such facilities, it may be reasonable to question whether commercial testing of progeny will be on a scale sufficient to support NCE. Existing central bull test stations may be retrofit to collect individual intake and efficiency phenotypes on bulls. Cost analyses need to be conducted to establish the cost effectiveness of these options.

Future Research Requirements

Significant gaps exist in the understanding of the genetics of efficient feed utilization. RFI is an alternative to older, ratio-type efficiency traits. Animals appear to be ranked equivalently on the basis of RFI whether measured early in life or near maturity. Directional (decreasing) selection for RFI is associated with reduction in feed required to produce market-ready animals. The EPD for RFI during finishing have been similar. Therefore, improvement of feedlot RFI should also result in improvement in efficiency of the cow herd.

Opportunities also exist for identification of major genes which account for significant portions of variation in RFI and therefore efficiency. Studies in North America and Australia are underway using molecular and(or) single gene approaches with candidate genes to identify potential markers for various measures of efficiency. Once identified, such markers can be incorporated into genetic evaluation models, resulting in marker- or gene-assisted evaluations. The EPD resulting from marker-assisted evaluation will contain a genomic value corresponding to the effect linked to the marker

and a polygenic portion due to remaining polygenic effects. For example, the Alberta (Canada) bovine genomics research group has completed several studies wherein candidate genes have been identified and association studies conducted to determine the usefulness of various single nucleotide polymorphisms (SNP) and multiple SNP haplotypes for prediction of RFI and related measures. Other, similar studies are also ongoing across North America.

Summary

Feed costs represent a significant fraction of the total cost of beef production, therefore genetic improvement programs for reducing input costs will likely include traits related to feed utilization. In contrast to traditional ratio-type measure of efficiency, residual feed intake is uncorrelated with body weight, growth rate, and other "energy sinks" which at least partially alleviates concerns over the long-term implications of selection and antagonistic correlated responses for mature size and maintenance requirements. The expense associated with collection of individual feed intake dictates the use of optimal data acquisition schemes and models for prediction of EPD. The incorporation of candidate gene or marker information into genetic evaluation models has promise, but more in-depth marker-association studies will be required.

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