

Genetics of Efficient Feed Utilization in Cattle¹

D. H. Crews, Jr.
Department of Animal Sciences, Colorado State University
Fort Collins, Colorado
Denny.Crews@ColoState.edu

Introduction

For several decades, genetic evaluation procedures have been developed for traits of economic relevance to beef production. Statistical procedures to accurately predict additive breeding values in the form of expected progeny differences (EPD) have advanced rapidly. Current genetic evaluation models, based on Henderson's mixed model equations (e.g., Henderson, 1984), provide best linear unbiased predictions (BLUP) of genetic merit, and now represent the standard for genetic prediction. Other advances, such as standardization of recording guidelines for performance data (BIF, 2002), increases in computing capabilities, and the development of specialized genetic analysis software (e.g., Boldman et al., 1995; Gilmour, 1997; Crews et al., 2008) have played significant roles in implementation of models for large scale genetic prediction, commonly referred to as national cattle evaluation (NCE).

Nearly all purebred beef cattle associations conduct NCE. Although all breeds compute EPD for basic weight traits (birth, weaning, and yearling), an increasing number of breeds now conduct research and development programs in genetic improvement that include prototype traits with economic importance. Golden et al. (2000) revived the concept of economic relevance as a framework to guide the process of identifying traits for which EPD should be reported and their indicators in the next generation of NCE programs.

The ERT framework centers on the distinction between economically relevant traits (ERT) and their indicators. Much of the recent scientific literature has focused on development of genetic evaluation systems for traits more complex than weight and growth rate. There has been little concentrated effort of standardize the implementation of prototype traits in beef NCE, although most of the more than 60 traits currently evaluated by the numerous breeds worldwide (Golden, 2001) can be characterized as being related to reproductive efficiency, growth performance, and/or carcass merit (Crews, 2001). Several traits, commonly measured on beef cattle, and used for NCE, do not directly impact revenue or cost and are therefore appropriately termed indicator traits. Because indicator traits are often easier and/or more cost effective to measure than the ERT, and have high genetic correlation with the ERT, they remain an important component of beef NCE worldwide.

Implementation of genetic prediction systems in the beef industry, including data collection, model development, and routine EPD computation, have resulted in significant and permanent changes in the genetic potential of cattle populations around the world. In most populations, however, selection has been primarily aimed at changing the mean of output (revenue) traits such as weight, fertility, and meat yield (Archer et al., 1999; Crews, 2001). Only recently has there been renewed research interest in the other component of profitability: namely the reduction of inputs (cost). Feed costs and supplementation account for approximately 70% of non-fixed beef production costs. Genetic improvement programs aimed at reducing input costs will likely include traits related to feed utilization (Archer et al., 1999; Crews et al., 2003).

Traditional Measures of Efficiency

In the scientific literature, numerous measures of production system efficiency can be found, although efficiency of production in cattle involves a complex of feed inputs and product outputs of animals across several dissimilar industry segments, which likely involve animals evaluated at different ages and stages of production. Most early work described efficiency at the ratio of inputs (e.g., feed) to outputs (e.g., weight gain) within a specific industry segment or stage of animal production, which leads only to limited insight into the efficiency of the entire production system. As such, feed conversion ratio (FCR) is the most common measure of

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efficiency in the literature, although more than two dozen measures of feed efficiency have been discussed (Archer et al., 1999). 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-review of published estimates of genetic parameters for beef production traits (Koots et al., 1994b) found numerous estimates of the genetic correlation of FCR with weights and rates of gain ranging from -0.24 to -0.95, which clearly indicate that increased genetic potential for performance and size is concomitant with improved FCR. Therefore, selection for improved (decreased) FCR would result in increased correlated genetic responses for growth rates, mature size, and presumably, mature maintenance requirement. Koots et al. (1994b) further showed strong evidence that the genetic associations of feed intake with measures of growth rate and weight were positive, with genetic correlation estimates ranging from 0.25 to 0.79. Of particular note among these were estimates of the genetic correlations of mature weight with FCR (-0.14) and feed intake (0.92).

These high estimates of genetic correlation infer that selection for growth rate would be expected to result in correlated responses in both feed intake and FCR. A drawback of this approach is that favorable correlated decreases in FCR due to selection for increased growth rate are not necessarily correlated to improvement in efficiency. This is strongly supported in Mrode et al. (1990) in which a line of Hereford cattle selected for lean growth rate had a higher correlated response in lean feed conversion ratio than the direct response to selection for lean conversion ratio found in a similar line.

Animals with high genetic potential for growth rate are assumed to have improved (i.e., lower) FCR and also have an increased genetic potential for mature size. In addition to being highly heritable ($h^2 = 0.50$; Koots et al., 1994a), mature cow weight has high genetic correlations ($r_g > 0.60$; Koots et al., 1994b) with growth rates measured at younger ages. Therefore, selection to directly increase weight and growth rate in juvenile cattle (e.g., at weaning and/or yearling) would likely result in strongly positive genetic change in mature size, and presumably, maintenance requirements. Archer et al. (1999) pointed out that although FCR may be a relevant measure of efficiency in industry segments devoted to production of growing animals, if an increase in feed requirements of the breeding herd (e.g., through increased mature cow size) offsets the gains in efficiency of market progeny, little to no progress will be made relative to total system efficiency. These results lead to the conclusion that an alternative measure of efficiency would be desirable, to reduce the antagonisms of correlated responses, and which would reflect more the across-segment differences to enable more effective selection for efficiency.

Phenotypic Residual Feed Intake

Residual feed intake (RFI), also referred to as net feed intake and net feed efficiency, was first proposed for cattle by Koch et al. (1963), and is defined as the difference between actual feed intake and that predicted on the basis of individual requirements for body weight maintenance and level of production. The concept was first used after study of several measures of efficiency, and development of the hypothesis that feed intake could be adjusted for level of production and maintenance of body weight. 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 industry segments. For example, whereas hyperplastic and hypertrophic tissue growth may be the major energy requirements for young growing cattle, the requirements for the mature cow herd may be maintenance of body composition for reproductive fitness and lactation. RFI relies simply on partitioning intake into portions required for stage and level of production, and a residual portion that is most likely closely related to true metabolic efficiency which would be more comparable across industry segments. Given that identifiable “energy sinks” will differ and lead to different components of expected feed intake across industry segments, residual feed intake is more appropriately characterized as a methodology rather than a static phenotype. Ultimately, RFI is feed intake (with respect to economic relevance) that has simply been rendered independent of measurable correlates such as weight and growth rate.

More recent research (e.g., Basarab et al., 2003; Crews, 2005; Nkrumah et al., 2007) has focused on characterization of RFI in the feeding segment of the beef industry. Therefore, most of the following discussion will be focused on young, growing cattle although the concept of RFI is not so limited. Calculation of RFI, as reported in several studies (e.g., Archer et al., 1997; Arthur et al., 2001a,b; Basarab et al., 2003; Crews et al., 2003), can be generally summarized as:

$$y = \beta_0 + \beta_1(\text{ADG}) + \beta_2(\text{MWT}) + \text{RFI}$$

where y is daily (dry matter) intake, β_0 is the regression intercept, β_1 is the partial regression of intake on average daily gain (ADG), and β_2 is the partial regression of intake on metabolic body size ($\text{MWT} = \text{LWT}^{0.75}$ where LWT = mid-test live weight).

Using this phenotypic regression approach, the properties of RFI are easily defined using standard statistical procedures. One central feature of these is the distributional property (i.e., $\text{RFI} \sim N(0, \sigma_{\text{RFI}}^2)$) showing that RFI has zero mean (Searle, 1982). Properties of linear regression can also be used to show that RFI is independent of the partial regression terms in the estimation model including both ADG and MWT. This important result has been verified in recent reports, at least in phenotypic terms. The implication is that for any population, approximately equal halves will have RFI above and below zero, respectively. Efficient animals (i.e., with RFI values below zero) have daily intakes less than would be predicted given their own level of production and body weight, whereas the converse is true for (inefficient) animals with RFI greater than zero.

It is important to note that the above multiple linear regression procedure only forces the independence of RFI from production level and weight at the phenotypic level. With the phenotypic regression, important covariances can still exist, resulting in non-zero genetic correlations (Kennedy et al., 1993; Crews, 2005) of RFI with either ADG and/or MWT. Extension of the above method to genetic regression is straightforward (Crews, 2005), which forces genetic independence of RFI with its components. Some studies (e.g., Arthur et al., 2001b) have estimated near zero genetic correlations of phenotypic RFI with weight and production traits; however, this level of independence is not ensured with phenotypic regression.

Phenotypic and Genetic Variation in RFI

To be a candidate for selection, an ERT must exhibit genetic variability, which is to say that variability in phenotypic expression must be to some extent dependent on additive genetic variance (heritable). All studies that have estimated genetic variance for RFI have reported this parameter to be non-zero. Specific heritability estimates include 0.26 to 0.30 (Crews et al., 2003), 0.28 (Koch et al., 1963), 0.39 (Arthur et al., 2001a) and 0.39 to 0.43 (Arthur et al., 2001b). Selection for RFI would be expected therefore to result in genetic change relatively comparable to that obtained with other moderately heritable traits, given enough phenotypic data and selection intensity.

Heritability alone can be misleading for predicting response to selection for RFI. The variability in the phenotype underlying RFI, feed intake, should be examined. In recent studies, considerable variation has been reported for various measures of daily (dry matter) intake. For example, for four biological types of cattle, Archer and Bergh (2000) reported phenotypic standard deviations (SD) ranging from 1.08 to 1.32 kg/d for dry matter intake. Similarly, Angus bulls and heifers (Arthur et al., 2001a) and Charolais bulls (Arthur et al., 2001b) had daily intakes with phenotypic SD of 1.3 kg/d in Australia and France, respectively. Basarab et al. (2003) reported phenotypic SD of 1.02 kg/d for dry matter intake of composite steers in Alberta, Canada. The partitioning of daily intake into production and residual components dictates that RFI will have lower variance than intake. Basarab et al. (2003) for example, reported RFI regression models with R^2 greater than 0.70 for the phenotypic regression of intake on ADG and metabolic body size of steers. In Australia, phenotypic SD of RFI as a proportion of phenotypic SD of feed intake was reported to be approximately 0.46 (Archer and Bergh, 2000), 0.56 (Arthur et al., 2001a) and 0.59 (Arthur et al., 2001b) among young replacement cattle of various breeds. Among Charolais and Charolais cross steers, Crews et al. (2003) showed that metabolic body size and ADG explained approximately 45 to 50% of the phenotypic variance in daily feed intake. These results confirm that after adjustment for growth rate and proxy measures of maintenance requirement, approximately 30 to 50% of the phenotypic variance in feed intake remains as residual (RFI). Considering that large phenotypic differences exist in intake, moderate heritability would be expected to translate to significant additive genetic change for a more true measure of efficiency and perhaps more importantly, for reduced feed costs.

Genetic (Co)variance and RFI

Because beef production extends over a wide range of environmental conditions and includes a wide range of breeds, crossbreds, and biological types, there are many traits that are economically relevant or are important indicators. As a consequence, it is not recommended that any genetic improvement program focus exclusively on

any single trait. An important consideration in comprehensive genetic improvement programs is whether genetic effects among traits and trait-systems are correlated. This consideration is especially important if genetic correlations may be antagonistic.

As noted previously, FCR is a commonly studied measure of feed efficiency and most estimates indicate that a wide array of efficiency measures are at least moderately heritable. Recent studies have reported strongly positive genetic correlations for phenotypic 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 (decreased) RFI would be associated with a corresponding declining genetic change for feed intake. Arthur et al. (2001a) estimated genetic correlations of RFI with some measures of body composition in Angus cattle and reported these to be generally small with the exception of ultrasound rib fat ($r_g = 0.17$), which is a small genetic correlation, but does indicate that genetic effects for feed intake may be related to those for subcutaneous fat deposition. Supporting phenotypic evidence for a positive association between improved RFI and reduced carcass fat has been reported by Basarab et al. (2003). Crews et al. (2003) estimated genetic correlations of different RFI measures with carcass traits. In that study, RFI was calculated separately for postweaning growing and finishing periods (e.g., when diets differed in energy density) for Charolais and Charolais-sired crossbred steers in southern Alberta. Improved RFI was in most cases only weakly associated with carcass merit, although standard errors for the estimated parameters were large. Arthur et al. (2001b) pointed out that among the few feed efficiency studies including body composition, estimates of genetic correlations were generally weak in magnitude, implying that no conclusions were yet warranted. Since that time, further adjustment of intake which results in RFI independent of body composition has become standard, at least in North America (Crews et al., 2006; Nkrumah et al., 2007). Without this adjustment, research consistently shows a small and positive correlation of RFI with various measures of carcass fat content (especially subcutaneous fat) and cattle with more efficient RFI phenotypes produced leaner carcasses (Basarab et al., 2003), but do not necessarily differ from less efficient cattle with regard to carcass lean and retail yield (Crews et al. 2003).

Economic Implications of Selection for RFI

Direct selection for RFI would be expected to result in genetic trend similar to that obtained with other traits with similarly moderate heritability (e.g., growth), assuming a sufficiency of data collection. Recent reports have been more variable with respect to the phenotypic range in calculated RFI. Basarab et al. (2003) reported that RFI (mean = 0.00, SD = 0.66 kg/d) ranged from an efficient -1.95 kg/d to an inefficient +1.82 kg/d among composite steers fed for 120 d (i.e., 3.77 kg daily dry matter intake difference between the most and least efficient steers). Archer et al. (1998) identified efficient breeding bulls which consumed 2.5 kg/d less feed over a 120-d test period while maintaining similar live weights and gains compared to less efficient bulls. Crews et al. (2003) reported that during a postweaning growing period, more efficient Charolais-sired steers (group mean RFI = -1.33 kg/d) consumed 2.73 kg less feed daily than less efficient steers (group mean RFI = +1.40 kg/d); similarly during the finishing period, a difference of 1.69 kg/d was reported between more (group mean RFI = -0.84 kg/d) and less (group mean RFI = +0.85 kg/d) efficient steers. In both comparisons, steers had similar live weight gain, metabolic body size, and carcass composition.

Assuming a feed cost of \$0.101 per kg (Basarab et al., 2003), a daily intake difference of 2.50 kg translates to a feed cost savings of \$0.25 per animal per day, or \$37.37 per animal over a typical 150-d finishing period. More than 28.5 million market steers and heifers are produced annually in the United States. Based on industry standard performance, dry matter conversion, and feedlot gain, Herring and Bertrand (2002) pointed out that a 2% reduction in feed consumption (while holding performance traits constant) would provide an increase of \$111 million in net return to beef producers. Assuming a standard rate of genetic progress in the range of 0.5 to 2.5% of the mean per year, research suggests the potential to maintain performance (e.g., total postweaning live weight gain) while decreasing daily intake (1% per year) by 0.13 kg per animal (assuming average intake of 13 kg and 1% annual improvement, or total finishing period intake by 19.5 kg per animal per year through selection. In regions where more than 2 million head of market cattle are produced annually, this translates to savings in feed costs of over \$5 million. Obviously, these trends and predictions would be considerably impacted by the higher feed costs that have been common in the five years since 2003.

Genetic Evaluation of Efficiency and Future Efficiency Research

ERT related to efficiency of feed utilization have been identified as an example of the next-generation of EPD for the beef industry (E. J. Pollak, personal communication). Important lessons may be learned in terms of selection progress from other species such as poultry and swine, where feed efficiency has been under selection for several generations. Because NCE procedures exist for other relevant traits, the time from the present until actual reported of EPD for efficiency traits can be much shorter than the development required 30 years ago for growth traits. An NCE system requires three essential components: data acquisition, model development, estimation of parameters, and routine genetic evaluation runs.

One factor behind renewed interest in NCE for efficiency is that equipment for measuring individual feed intake is improving. Traditionally, individual feed intake was not measured, and early efficiency research relied on intake at the pen level. Such an approach is inappropriate for an evaluation system with the objective to characterize individual animal differences, because all animals within a pen essentially receive the same phenotypic intake record. When pedigree ties among animals are through sires alone, some of these limitations can be alleviated through removing confounding of sire and pen. Individual feed intake can be recorded when animals are individually housed and fed, but not without serious impacts on feeding behavior and intake. Additionally, technology can be used to house cattle in groups but limit the locations along the feed bunk at which they can feed so that individual intake can be approximated. Technological limitations have always reduced the effectiveness of these approaches. Another concern is that these pseudo-group designs alter feeding behavior such that individual differences are either biased or are not reflective of standard industry practices. Current advances in feed intake measurement equipment have focused on recording individual animal intake in cattle fed in groups while minimally impacting feeding behavior. Such equipment generally couples electronic animal identification or animal-bunk attendance with bunk-based feed disappearance. Results are promising, although the newest technology is also usually the most expensive. Depending on capacity and useful life, the cost of measuring individual feed intake with state-of-the-art equipment has been estimated to range from \$50 to more than \$200 per head.

The major limitation to implementing NCE for efficiency is data acquisition. In addition to the added cost of recording individual animal intake, the suitability of data for NCE programs must be considered. In the case of 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 anonymous with regard to parentage and pedigree. This lack of information is even more of a problem with commercial calves from unregistered parents. A minimum of sire identification on animals with intake phenotypes would be required. 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, but the added cost of parentage testing drives the system cost even higher. A further consideration regarding data suitability is standardization of protocols for individual intake data recording. Regardless of the equipment used, standard testing procedures have not been in place for intake data collection, even among scientific studies. In 2007, the Beef Improvement Federation formed a sub-committee of experts from across North America to develop guidelines and recommendations for the recording and reporting of individual feed intake data.

Some procedures exist to compute EPD for efficiency that do not require recording of individual animal intake. 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 (e.g., 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 for which phenotypic data acquisition is in place, few strongly correlated indicator traits have been identified for efficiency traits such as RFI. This is partially due to the forced independence of RFI with other performance traits.

Mapping of the bovine genome and the development of related genomic tools has prompted an interest in augmentation of traditional genetic evaluation systems with gene marker information. Marker assisted evaluation systems would optimally combine genomic and phenotypic data with pedigree to predict EPD with higher accuracy than would be possible from evaluations based solely on phenotypic data alone. Such marker assisted EPD (MAEPD) would be particularly useful for increasing the accuracy of evaluating young animals which have

yet to make their own phenotypic record or produce progeny with records for the ERT or indicators. Selection index methodology has been applied to this problem of optimally combining genomic and polygenic breeding values. Polygenic and marker-derived breeding values are combined in a linear index with weighting factors that depend solely on accuracy of the polygenic breeding value or EPD, and the proportion of genetic variance attributable to the marker set. Simulation has confirmed that polygenic EPD accuracy and the gain in accuracy of evaluation due to inclusion of marker information are inversely related (Crews, 2008). Therefore, for traits with high heritability, or that accumulate evaluation accuracy quickly on young animals are less viable candidates for genomic selection. However, traits related to feed intake remain likely candidates for gene assisted evaluation because of the cost and time required for traditional polygenic evaluation (e.g., Moore, 2008). Functional genomics studies which report associations of single nucleotide polymorphisms (SNP) markers and SNP haplotypes with economically relevant beef traits are now common, but optimal MAEPD systems will require robust estimates of combined marker effects that have yet to be reported. In fact, marker sets or commercial gene marker tests will likely need to account for at least 10-15% of the genetic variance in feed intake and(or) RFI before marker assisted EPD system development and implementation would be cost effective (Crews, 2008). The time then required to build genomic information databases on a critical mass of animals in large field populations will depend on the effectiveness (information density) of the marker panel and commercial genotyping costs. The potential benefits to genetic evaluation of feed intake and efficiency with the influx of genomics tools and marker assisted evaluation remain very large.

Even though intake and RFI have been well characterized in recent studies (Archer et al., 1999; Basarab et al., 2003; Crews, 2005), there has been little research on the potential for implementation of multiple trait selection programs including RFI. Crews et al. (2006) developed a multiple trait selection index including RFI with the objective to improve net feedlot revenue in market progeny of performance tested Angus sires. The selection objective defined aggregate genetic merit of fed steers as a function of daily dry matter intake, average daily gain on feed, and final (pre-slaughter) live weight. The selection criteria for bulls was then a linear function of RFI, average daily gain on test, and 365-d live weight. Bull RFI included the usual terms of ADG and MWT, but also ultrasound measures of subcutaneous fat depth and ribeye area such that RFI was independent of both production and body composition. Phenotypic index values on Angus bulls (n = 100) were adjusted to a mean of 100 (SD = 7.81), and ranged from 80.1 to 115.7. The phenotypic correlations of index value with other traits measured on the bull test indicated that bulls with higher index values consumed less daily dry matter, had greater ADG, and were more efficient (i.e., lower RFI), but did not differ from low-indexing bulls with respect to yearling weight. There was a trend for the index to be favorably associated ($r = 0.16$) with yearling scrotal circumference, suggesting that selection would not be antagonistic with indicators of bull fertility. Although more research should be conducted, this work illustrates the need to consider intake and efficiency within the context of multiple trait selection.

Implications

Feed and feed supplementation represent the largest non-fixed costs of beef production. Genetic improvement programs for reducing input costs will likely include traits related to feed utilization. In contrast to traditional ratio-type measures of feed efficiency, residual feed intake is uncorrelated with body weight and growth rate (and body composition), which would at least partially alleviate concerns over the long-term implications of selection and correlated responses in mature size and maintenance requirements. Potential unfavorable correlated responses resulting from selection for residual feed intake should be closely investigated before recommendations are made. Expense associated with individual feed intake data collection limits implementation of efficiency NCE, and dictates the use of optimal data acquisition schemes for computation of EPD. Knowledge gained from functional genomics and tools leading to gene assisted EPD have promise in this area but require more development. In the end, implementation of NCE for efficiency has the potential to significantly increase efficiency of cattle production.

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