



Review

Genetics of efficient feed utilization and national cattle evaluation: a review

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ABSTRACT. Selection for the wide range of traits for which most beef breed associations calculate expected progeny differences 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 a large proportion of the variable cost of beef production and genetic improvement programs for reducing input costs should include traits related to feed utilization. Feed conversion ratio, defined as feed inputs per unit output, is a traditional measure of efficiency that has significant phenotypic and genetic correlations with feed intake, growth rate, and mature size. One limitation is that favorable decreases in feed to gain either directly or due to correlated response to increasing growth rate do not necessarily relate to improvement in efficiency of feed utilization. Residual feed intake is defined as the difference between actual feed intake and that predicted on the basis of requirements for maintenance of body weight and production. Phenotypic independence of residual feed intake with growth rate, body weight, and other energy depots can be forced. However, genetic associations may remain when a phenotypic prediction approach is used. Heritability estimates for phenotypic residual feed intake have been moderate, ranging from 0.26 to 0.43. Genetic correlations of phenotypic residual feed intake with feed intake

have been large and positive, suggesting that improvement would produce a correlated response of decreased feed intake. Residual feed intake estimated by genetic regression results in a zero genetic correlation with its predictors, which reduces concerns over long-term antagonistic responses such as increased mature size and maintenance requirements. The genetic regression approach requires knowledge of genetic covariances of feed intake with weight and production traits. Cost of individual feed intake measurements on potential replacements must be considered in implementation of national cattle evaluations for efficiency of feed utilization. These costs need to be compared to expected, and, if possible, realized rates of genetic change and the associated reduction in feed input requirements.

Key words: Beef cattle, Feed efficiency, Genetic evaluation

INTRODUCTION

For several decades, genetic evaluation procedures have been developed for traits of economic relevance to beef production. Statistical procedures required to accurately predict 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 capability and the development of specialized genetic analysis software (e.g., Boldman et al., 1995; Gilmour, 1997; Golden et al., 2000a) have played a significant role in implementation of models for large scale genetic evaluation.

Nearly all purebred beef cattle organizations conduct national cattle evaluations (NCE). Although all breeds calculate EPD for basic weight and growth traits (e.g., birth, weaning and yearling weights), an increasing number of breeds now conduct research and development programs in breed improvement that include prototype traits with economic importance. Golden et al. (2000b) revived the concept of economically relevant traits (ERT) as a framework to guide the process of identifying traits for which EPD should be calculated in the next generation of NCE programs.

The ERT concept of Golden et al. (2000b) centers on the distinction between ERT and indicator traits. 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 to standardize the implementation of prototype traits in beef NCE, although most of the more than 60 traits currently evaluated in 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 risk and are therefore appropriately termed indicator traits. Because indicator traits are often easier and(or) more cost effective to measure, and have high

genetic correlations with ERT which may be cost or time prohibitive to measure, indicator traits remain an important component of beef NCE worldwide. The ERT concept provides a framework to distinguish ERT which directly predict revenue or risk from indicators which are relatively easy and(or) cost effective to measure and have high genetic correlations with ERT but do not have inherent economic value.

Implementation of genetic evaluation systems in the beef industry, including data collection, model development, and routine calculation of EPD, have resulted in additive and permanent changes in the genetic potential of beef cattle populations around the world. The fact is that producers use EPD which are available, as evidenced by the results of selection in experimental populations (e.g., Smith, 1984), and in field populations where genetic trend has been significant for birth, weaning and yearling weights (Crews, 2001). In most populations, however, selection has been primarily aimed at changing means for output 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. Feed costs represent a significant fraction of the total cost of beef production and genetic improvement programs for reducing input costs will likely include traits related to feed utilization (Archer et al., 1999; Crews et al., 2003a).

TRADITIONAL MEASURES OF FEED EFFICIENCY

In the scientific literature, numerous measures of production system efficiency can be found, although efficiency of production in beef cattle involves a complex of feed inputs and product outputs of animals across several dissimilar industry segments, which may involve animals evaluated at different ages and stages of production. Most early work described efficiency as 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 to only limited insight into efficiency of the entire production system. As such, feed to gain or feed conversion ratio (FCR) is the most common measure of efficiency in the scientific 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, Koots et al. (1994b) found numerous estimates of the genetic correlations 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 genetic correlation estimates ranging from 0.25 to 0.79. Of particular note are estimates of 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 for both 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 specifically to improvement in efficiency of feed utilization. This idea is strongly supported by the study of 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 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.

In addition to the concern with antagonistic correlated response to selection for decreased feed to gain ratio, Gunsett (1984) discussed the problems of selection for traits defined as ratios. A disproportionate amount of selection pressure is placed on the component of ratio traits with higher genetic variance resulting in unpredictable responses to selection. The statistical argument made by Gunsett (1984) is that genetic changes in FCR do not translate to equivalent improvement in efficiency because genetic trend can result from changes in either the denominator or numerator of a ratio somewhat independent of the other. Some researchers have hypothesized that although growth rates and mature size of most breeds have experienced positive genetic change in the past 20 years, the correlated response for FCR has not been comparably large. Gunsett (1984) compared the efficiency of direct selection for a two-component ratio with a linear index derived from the same two components and concluded that the index approach was associated with increased selection response compared to selection based on the ratio.

PHENOTYPIC RESIDUAL FEED INTAKE

Residual feed intake (RFI), sometimes referred to as 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 mean 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 mature cow herd may be maintenance of body condition 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 related to true metabolic efficiency which would be comparable across industry segments.

Recent research (e.g., Archer et al., 1999) 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 recent studies (e.g., Archer et al., 1997; Arthur et al., 2001a,b; Crews et al., 2003a), can be generally summarized as:

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

where y is daily feed intake (e.g., dry matter), β_0 is the regression intercept, β_1 is the partial regression of daily intake on average daily gain (ADG), and β_2 is the partial regression of daily intake on body weight (WT). In most cases the weight of the animal is expressed as average or midweight on test, and may further be transformed to a so-called metabolic equivalent by raising midweight to the power of 0.75 or 0.73. Some evidence suggests that such power transformations are unnecessary, as similar animal rankings with respect to RFI are obtained using either actual or metabolic weights (Jenkins, T.G., personal communication).

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 be used to show that RFI is independent of the partial regression terms in the estimation model including both ADG and (metabolic) body weight. 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 is that for any population, approximately equal halves will have RFI values 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 animals with positive RFI values. The independence of RFI from production is forced by its method of estimation; as a result, RFI probably reflects more variation in basic metabolic processes than variation due to differences in level of production.

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. 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., 2003a), 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 may be misleading for predicting response to selection for RFI. The variability in the phenotype underlying RFI, daily feed intake, should be examined. In recent studies, considerable variation has been reported for various measures of daily feed and (or) 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 1.31 kg/day for dry matter intake. Similarly, Angus bulls and heifers (Arthur et al., 2001a) and Charolais bulls (Arthur et al., 2001b) had daily feed intakes with phenotypic SD of 1.3 kg/day in Australia. Basarab et al.

(2003) reported phenotypic SD of 1.02 kg/day for dry matter intake of composite steers in Alberta, Canada. The partitioning of variance in feed or dry matter intake into weight gain and weight maintenance components dictates that variation in RFI will be numerically smaller than for feed intake. Basarab et al. (2003) reported models with R^2 greater than 70% for the phenotypic regression of daily dry matter intake on ADG and metabolic midweight of steers. In Australia, phenotypic SD of RFI as a proportion of phenotypic SD of feed intake have been 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. (2003a) showed that metabolic midweight 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 requirements, approximately 30 to 50% of the phenotypic variance in feed intake remains as RFI. Considering that large phenotypic differences exist in daily 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 RESIDUAL FEED INTAKE

Although RFI can be shown to be phenotypically independent of production, maintenance, and other energy depots, RFI estimated by phenotypic regression as described above may not necessarily be genetically independent of regressors in the model, thereby raising concerns over the long-term implications of responses to selection. Kennedy et al. (1993) stated that RFI based on phenotypic regression of daily feed intake on production usually contains a genetic component due to production.

The phenotypic prediction of feed intake from information on metabolic mid-test body weight and ADG (e.g., Archer et al., 1999) can be represented in matrix notation as

$$y^* = Xb$$

where y^* , the vector of phenotypic feed intake predictions, is equal to a function of maintenance requirements (e.g., body weight) and production (e.g., daily gain) with design matrix, X . The vector b contains partial regression coefficients, defined as

$$b = (X'X)^{-1}X'y$$

where X is the design matrix as defined before and y is a vector of observed feed intake phenotypes. The difference between observed feed intakes (y) and the predictions (y^*) from the regression are equivalent to RFI (i.e., $y - y^* = y - Xb$) which follows from the standard matrix representation of the linear regression equations (e.g., Searle, 1982), $y = Xb + e$, with $e = \text{RFI}$. Phenotypic predictions of feed intake can also be represented as

$$y^* = Xb = XP^{-1}c$$

where P^{-1} is the t ($t = 2 =$ regressors in the model) $\times t$ inverse of the matrix containing phenotypic (co)variances between body weight and daily gain, and c is a $t \times 1$ vector containing the

phenotypic covariances of feed intake with body weight and daily gain.

The extension of the phenotypic regression approach presented above to what may be called genetic regression can be represented in matrix notation as

$$u^* = UG^{-1}k$$

where u^* is an n ($n = \text{animals}$) $\times 1$ vector containing feed intake estimated breeding values (EBV) predicted by genetic regression, U is an $n \times t$ matrix of body weight and daily gain EBV, G^{-1} is a $t \times t$ inverse of a matrix containing genetic (co)variances between body weight and daily gain (i.e., the regressors), and k is a $t \times 1$ vector of genetic covariances of feed intake with body weight and daily gain. Genetic residual feed intake, therefore, is the difference between feed intake EBV (u) from the solution to Henderson's mixed model equations (e.g., Henderson, 1984) and feed intake EBV from genetic regression (u^*) (i.e., $u - u^* = u - UG^{-1}k$). The independence of the genetic RFI values ($u - u^*$) from the regressors in G^{-1} can be shown in a manner analogous to that for $(y - y^*)$ and P^{-1} (e.g., Searle, 1982). This approach potentially alleviates concerns over responses to selection for RFI leading to antagonistic correlated response for growth rate and mature maintenance requirements.

Arthur et al. (2001a,b), for example, argued that estimates of near-zero genetic correlations of phenotypic RFI with daily gain and body weight were evidence that the potential antagonistic correlated responses to selection for RFI were negligible. However, the approach above for derivation of a genetic RFI provides for estimation of breeding values having zero genetic covariance with any identifiable source of variance in daily feed intake. Kennedy et al. (1993) predicted that little variance in genetic RFI remained after adjustment for maintenance and production with simulated dairy records, and that genetic parameters of genetic RFI were simply a function of genetic parameters in the underlying traits. They also showed equivalence of genetic RFI to a multiple trait selection index to decrease feed intake while holding production constant. As a consequence of its equivalence to restricted selection index, selection on genetic RFI may be considered sub-optimal. One inherent limitation to implementation of NCE for genetic RFI is the comparative lack of published information on the genetic covariance of intake with production and maintenance traits (Archer et al., 1999), although this body of literature is growing.

GENETIC (CO)VARIANCE AND PHENOTYPIC 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 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). Simi-

larly, 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 efficiency (i.e., decreased RFI) will 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 (i.e., reduced) RFI and carcass fatness has been reported by Basarab et al. (2003). Crews et al. (2003a) estimated genetic correlations of different RFI measures with carcass traits. In that study, RFI was calculated separately for postweaning growing and finishing periods (i.e., 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 measures of body composition, estimates of genetic correlations were generally weak in magnitude, implying that no conclusions are yet warranted. There has been little or no definitive evidence of genetic antagonisms of RFI with other ERT, although more research is needed.

GENOTYPE × DIET AND AGE INTERACTIONS AND RESIDUAL FEED INTAKE

Archer et al. (1999) reviewed the potential for selection to improve efficiency of feed use in beef cattle. Because feed is a major cost component, accounting for more than half of variable costs, increases in beef production per unit of feed input would be of significant economic value to the industry. Although various measures of feed efficiency may be suitable within specific industry segments, total system efficiency depends on feed inputs and product outputs over several classes of cattle. Therefore, a robust measure of efficiency that accurately describes underlying genetic variability in efficiency of feed utilization would be useful. Archer et al. (1999) suggested indices of efficiency must be identified which are correlated with efficiency of the entire production system, and for which genetic improvement would provide correlated improvement in profitability.

Relatively little information is available regarding genetic association between intake and efficiency measures in the mature cow herd and similar measures from the postweaning periods at or near yearling ages, when selection decisions are commonly made. Archer et al. (2002) 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 that selection decisions made with regard to RFI during the postweaning period would translate nearly perfectly to genetic improvement in efficiency of the cow herd. Archer et al. (2002) concluded that these strong genetic associations present opportunity to improve feed efficiency of growing animals and mature cows simultaneously, based on measurements taken during the postweaning period prior to when selection decisions are made.

Crews et al. (2003a) studied differences in phenotypic RFI between two common diet regimes. Weaned calves are often placed on roughage-based growing (i.e., backgrounding) diet prior to the finishing period wherein diets are grain-based with higher energy density. The RFI of Charolais-sired steers was calculated separately for 84-day growing and 112-day finishing periods. Estimates of phenotypic and additive genetic variance for RFI in the growing period were greater than corresponding estimates for the finishing period. Heritability estimates for the growing and finishing periods were $0.30 (\pm 0.06)$ and $0.26 (\pm 0.07)$, respectively. The estimate of the genetic correlation between them (0.55 ± 0.30) was high. These results led Crews et al. (2003a) to suggest that a high and positive genetic association exists between RFI measured for cattle consuming roughage- or grain-based diets, although the traits may not be biologically equivalent. This result has implications for NCE for efficiency where the most likely source of data will be postweaning bull tests but where the selection objective is improvement in efficiency of their market progeny, which will probably largely remain unmeasured. Crews et al. (2004) discussed an analogous scenario where data collection and the selection objective were for different classes of animals, and offered a procedure for expressing EPD on the economically relevant scale.

REFINING RESIDUAL FEED INTAKE WITH ADJUSTMENTS FOR BODY COMPOSITION

Variation in RFI probably reflects underlying biological efficiency after adjustment for body weight and growth rate. However, differences in efficiency of growth may also be due to differences in composition of live weight gain. Ferrell and Jenkins (1998) showed that differences in rates 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 than for 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 carcass fat content and similarly weak but negative correlations between RFI and carcass lean content (e.g., Herd and Bishop, 2000; Arthur et al., 2001a; Basarab et al., 2003). Basarab et al. (2003) reported that approximately 4.0% 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. Basarab et al. (2003) further showed that rate of deposition of fat, measured as ultrasound subcutaneous fat gain and ultrasound intramuscular fat gain, increased the proportion of variance in daily feed intake explained by regression on weight and gain alone by 2.9% from 78.0 to 80.9%. Richardson et al. (2001) found that a single generation of selection for reduced RFI also resulted in reduced carcass fat content. Crews et al. (2003a) estimated a genetic correlation of -0.44 between finishing period RFI and carcass marbling score, indicating that selection for improved RFI would be associated with a favorable correlated response in carcass quality grade. Adjustments of daily feed intake using the phenotypic approach to RFI estimation for longissimus muscle area, or other measures of carcass muscling, have not been reported.

ECONOMIC IMPLICATIONS OF SELECTION FOR PHENOTYPIC RFI

Direct selection for RFI would be expected to result in genetic trend similar to that

obtained with other traits with similarly moderate heritability. Recent reports have been variable with respect to the phenotypic range in calculated RFI. Basarab et al. (2003) reported that RFI (mean = 0.00, SD = 0.66 kg/day) ranged from an efficient -1.95 kg/day to an inefficient +1.82 kg/day among composite steers fed for 120 days (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/day less feed over a 120-day test period while maintaining similar live weights and gains compared to less efficient bulls. Crews et al. (2003a) reported that during a postweaning growing period, more efficient Charolais-sired steers (group mean RFI = -1.33 kg/day) consumed 2.73 kg less feed daily than less efficient steers (group mean RFI = +1.40 kg/day); similarly during the finishing period, a difference of 1.69 kg/day was reported between more (group mean RFI = -0.84 kg/day) and less (group mean RFI = +0.85 kg/day) efficient steers. In both comparisons, steers had similar live weight gain, metabolic body weight, and carcass merit (e.g., carcass yield and meat quality).

Assuming a feed cost of \$0.101 per kg (Basarab et al., 2003), a daily intake difference of 2.50 kg translates to feed cost savings of \$0.25 per animal per day, or \$37.87 per animal over a typical 150-day finishing period. In the southern Alberta cattle feeding region, for example, where approximately 2.4 million head of market cattle are fed, small genetic improvements in RFI could easily translate into annual savings of more than \$100 million in finishing feed costs alone with no loss in animal performance. More than 28.5 million market steers and heifers were produced in the U.S. in 2001. 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 other traits constant) would provide an increase of \$111 million in net return to beef producers. Smith (1984) showed that rates of genetic progress for key economic traits have been in the range of 0.5 to 2.5% of the mean per year. This result implies 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 daily intake of 13 kg and 1% annual genetic improvement), or total finishing period intake by 19.5 kg per animal per year through selection. Again, in southern Alberta, which produces 2.4 million head of market cattle annually, this translates to savings in feed costs of over \$4.7 million. It is important to note that such genetic improvement could be predicted for longer periods of time in an additive manner.

Based on results reported by Archer et al. (2002), improvement in cow herd efficiency would be similar to that obtained in the feeding sector, based on genetic correlation estimates suggesting the biological equivalence of RFI measured following weaning versus closer to maturity. The total system efficiency would therefore be improved in terms of total feed costs, although the economic value of these savings would be more difficult to estimate in the cow herd. These results emphasize the economic potential for genetic improvement in efficiency of feed utilization in beef cattle.

LIMITATIONS TO NATIONAL CATTLE EVALUATION FOR RESIDUAL FEED INTAKE

ERT related to efficiency of feed utilization have been identified as an example of the next-generation of EPD for the beef industry (Pollak, E.J., 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

programs exist for other relevant traits, the time from now to actual reporting of EPD for efficiency traits can be shorter than for traits such as growth. 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 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 of characterizing individual differences among animals, because all animals within a pen essentially receive the same phenotypic measure. 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. Additionally, technology can be used to house cattle in groups but limit the locations in the feed bunk at which individual animals can feed so that individual intake can be measured. Technological limitations have always reduced the effectiveness of these approaches. Another concern is that these 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 for cattle fed in groups while minimally impacting feeding behavior. Such equipment generally incorporates electronic identification of cattle with bunk-based feed disappearance. Results have been promising, although the newer technology is also usually the most expensive. Depending on capacity and useful life, the cost of measuring individual feed intake has been estimated to range from \$50 to more than \$200 per head.

The current limitation to implementation of an 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 (i.e., non-purebred) 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.

Some procedures exist for EPD for efficiency that do not require recording of individual animal feed 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 (Cameron, 1997). 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 feed intake or RFI. This is partially due to the forced independence of RFI with other performance traits.

The implementation of an 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 could possibly be retrofit to collect individual

intake and efficiency phenotypes on bulls and where progeny testing programs are in place, some individual intake data on bull progeny could be collected. 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 with RFI whether measured early in life or near maturity. Directional selection for RFI is associated with reduction in feed required to produce market-ready animals. However, meaningful EPD for efficiency should be for feeder cattle because a significant portion of realized gains from selection would be during the postweaning feeding period. The EPD for RFI during finishing and at maturity have been similar. Therefore, improvement of feedlot RFI should also result in improvement in the efficiency of the cow herd. This conclusion, however, requires further verification through replicated study.

The association between RFI of bulls and efficiency phenotypes of their slaughter progeny requires further study. Whether the biological properties of RFI are equivalent across gender and management schemes is unknown. Validation studies also need to be conducted to verify that selection based on EPD for RFI will result in realized phenotypic improvement. Studies have shown that differences in sire EPD for growth and carcass traits were related to phenotypic differences among progeny at or near theoretical expectation (Basarab et al., 1994; Crews, 2002). Such validation has not been conducted for RFI.

In an analogous scenario with live animal measurements taken on yearling replacements to predict carcass merit EPD, Crews and Kemp (2001) and Crews et al. (2003b) estimated genetic correlations using a model that treated live animal measurements on yearlings and carcass traits of slaughter progeny as separate but correlated traits. In the case of RFI, measurements on bulls from central test and on slaughter progeny during finishing would be fit with a similar genetic model. A genetic correlation between live animal and carcass measurements of progeny (i.e., traits measured on different animals) above 0.90 would indicate sufficient biological equivalence between the trait pairs, and that selection on one would be effective in improving the other trait (Crews et al., 2004).

With RFI, genetic correlations significantly less than 1.0 (e.g., less than 0.90) would be evidence that biological differences exist between bull and progeny phenotypes to the extent they should be considered separate traits. Through the use of an appropriate multiple trait genetic model, however, EPD would be estimated for all animals for all traits, and EPD for the trait measured on progeny may be more optimal for selection.

Opportunities also exist for identification of major genes which account for significant portions of variation in RFI. 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 residual portion due to remaining polygenic effects. Interest in application of marker-assisted evaluation to RFI is widespread, because feed intake is costly to measure and has relatively few effective indicators.

IMPLICATIONS

Feed costs represent a significant fraction of the total cost 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 potentially other energy depots), which would at least partially alleviate concerns over the long-term implications of selection and correlated responses for mature size and maintenance requirements. Potential unfavorable correlated responses resulting from selection for residual feed intake should be closely investigated before recommendations for selection are made. Expense associated with collection of individual feed intake dictates the use of optimal data acquisition schemes and models for calculation of EPD. Implementation of national cattle evaluations for efficiency has the potential to significantly increase efficiency of beef production systems.

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