Life-Cycle, Total-Industry Genetic Improvement of Feed Efficiency in Beef Cattle: Blueprint for the Beef Improvement Federation

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Introduction

Beef, as a protein source for humans, has two major positive characteristics relative to pork and chicken: 1) consumers, on average, place greater preference for beef in its eating characteristics and 2) beef animals, on an industry-wide life-cycle basis, consume large amounts of lower-cost forages as compared to higher-cost concentrates. Although these positive characteristics exist, beef production still needs to improve cost per unit of product because it has greater cost per edible pound than chicken and pork. If one compares edible product per unit of feed energy input, beef production is ~1/3 as efficient as pork production and ~1/5 to 1/6 as efficient as broiler production (adapted from Dickerson, 1978). Greatly lower reproduction per breeding female is a major contributor, and adding the consumer-desired intramuscular fat in beef contributes to slaughter beef animals having greater total-carcass waste fat than slaughter pigs and broilers.

Implementing genetic programs and management changes that can improve efficiency of beef production requires answers to several questions. Some of these questions follow, and our goal in this paper is to provide answers to these questions, based on current knowledge. From an industry-wide perspective, what are the opportunities for improving efficiency of feed utilization? What can we learn from the pork and broiler industries in how they have approached genetic improvement of efficiency of feed utilization? Are there potential antagonisms between feed utilization/efficiency measurements and other economically relevant traits in beef cattle? What phenotypic and genomic data collections are warranted, and how will these be incorporated into National Cattle Evaluation programs? Where are the holes in our knowledge base, and what are the needs for future research to generate answers?

Do We Need to Measure Feed?

Efficiency has been conventionally expressed as the ratio of output per unit of input. However, expressing efficiency in a linear form as output minus input has better statistical properties and comes closer to economic measures such as net return (value of output minus cost of input). If we express feed efficiency of the beef life cycle on an average dam basis and in linear form, we have the following (adapted from Dickerson, 1970):

[Dam Weight*Lean Value of Dam + **No. Progeny***Progeny Weight*Lean Value of Progeny]
- [Dam Feed*Value of Feed for Dam + **No. Progeny***Progeny Feed*Value of Feed for Progeny].

Note, there is no requirement that the value terms be expressed in monetary units. They could equally well be expressed in biological units (e.g., kcal) to reflect biological efficiency.

In the positive, income component, we have the output from harvesting the dam (or fraction of the dam accounting for death loss) and from harvesting progeny (again, accounting for death loss); these are multiplied by different per unit prices to obtain the total value output. The negative, feed cost component, accounts for the input of feed energy, where we can account for different feed stuffs in the calculation of energy. The number of progeny per dam is in both components and, thus, increasing number of progeny will increase efficiency. By simply increasing number of progeny per dam through either selection, heterosis from crossing, or better management, we will increase efficiency of production. We do not need to measure feed to get this improvement in feed efficiency.

If we look at feed efficiency of a single animal, we also find that there are possible improvements in efficiency that can be achieved again without measurement of feed. To visualize this, first imagine that we can separate feed intake, at least conceptually, into: 1) feed required to meet maintenance requirements (**M**, basal metabolism, tissue repair, thermal regulation, locomotor activity, etc.) or the energy required for keeping body weight constant; 2) feed required to create new product (**P**, e.g., growth, milk, new offspring); and 3) feed that goes unused (**U**, waste products). For a growing calf, efficiency can be shown simply as:

$$\text{Calf Weight Gain} * \text{Calf weight value} - [\text{Feed}_M + \text{Feed}_P + \text{Feed}_U] * \text{Feed value}$$

For a pair of calves with the **<u>same</u>** start and end weights but with one animal gaining weight more quickly, thus requiring fewer days and less **<u>maintenance</u>** to reach market weight, the faster growing calf would be more efficient. This can occur with <u>no</u> difference in efficiency of feed use for either maintenance or creation of new product; it is "All Mathematical". Similarly, with an improvement in reproduction, there is no need to measure feed to capitalize on methods to improve efficiency. The same would be true for an individual cow; if there is more output per day and no difference in cow size and in partial costs for maintenance and for production, then the cow with a greater rate of output will be the more efficient one.

For a reproducing cowherd, we can express efficiency based on the weight of calf and cull cow as the summed outputs, and total feed intake for the two production components as the feed costs. This gets a bit more complicated compared to the growing calf example above. But, we can express this as:

$$\begin{gathered}[\text{Calf Weight*Calf Weight Value} + \{\text{Culling Rate} * \text{Cull Cow Weight*Cow Weight Value}\}] \\ - \{\text{Feed}_M(\text{cow}) + \text{Feed}_P(\text{cow}) + \text{Feed}_U(\text{cow})\}\text{*Cow Feed Value} \\ - \{\text{Feed}_M(\text{calf}) + \text{Feed}_P(\text{calf}) + \text{Feed}_U(\text{calf})\}\text{*Calf Feed Value} \\ - \{\text{Feed}_M(\text{heifer}) + \text{Feed}_P(\text{heifer}) + \text{Feed}_U(\text{heifer})\}\text{*Heifer Feed Value}\end{gathered}$$

So again, there is 1) feed for maintenance, 2) feed for production, and 3) feed that is wasted. So, one goal for improving efficiency of feed utilization, whether with a growing calf in a feedlot or with a reproducing cow and calf in our cowherds, must be to reduce the feed being used for maintenance, while not reducing output. This also means that we could lose efficiency if we reduce rate of output, and hence reduce feed above maintenance required to produce output. Thus, instead of focusing on single traits, yearling bull buying decisions must consider the multiple-trait associations of feed intake and the implications of making selection decisions in the multiple-trait sense based mainly on data collected from growing bulls, especially with regard to the replacement daughters of selected bulls.

So, if the size of animals, rates of product formation (growth, milk), and reproduction, are known, then why is it necessary to measure feed intake? Feed measurement is costly due to the need for special facilities and equipment and due to labor. To complicate matters, this costly measurement is amenable for high-energy diets but not for low-energy, high-roughage diets, in particular in pasture-based systems. The reproducing cow herd, including calves to weaning, consumes the greater fraction of annual feed energy required in for beef production, as compared to calves grown from weaning to slaughter. The reproducing cow herd consumes mostly roughages, thus any measurement of cow herd intake is not very feasible at this time. We can, however, use research results to formulate appropriate multiple-trait index tools that account for synergisms and antagonisms that may exist among feed intake and other economically relevant traits.

The reason why we might consider measuring feed intake is because we can not explain all the variation in individual-animal intake from simply knowledge of body weight maintained and level of production. Animals differ in their ability to digest feedstuffs and ability to transform feed energy to meet these needs. Within these, the main deficiency in being able to explain feed intake is in predicting the cost of meeting maintenance requirements, adjusted for body size. As noted above, maintenance includes all energy costs to hold body weight and body energy content constant in the particular production situation. During extremely cold ambient conditions, maintenance for a given animal will be greater than for more moderate ambient conditions. Maintenance in an extensive, open grazing situation will be greater than in a confined feeding situation. From a total life-cycle perspective, energy costs for maintenance are estimated to be about 70% of the total energy intake in the beef production system.

Thus, reducing energy for maintenance, while accounting for possible negative effects on other performance characteristics, becomes a clear target for genetic improvement programs. **The focus of these programs is not be to define a single measurement of efficiency which may lead to inappropriate use of single-trait selection**, but to define optimal measures which conform to the marketing practices (e.g., profitability) in the industry.

We can write an expression for feed intake that is unique for each animal in a defined production scenario: Feed Intake = Feed for Maintenance + Feed above Maintenance for Production. This expression can be expanded to:

$$\text{Feed Intake} = b_M \cdot (\text{Body Weight})^{0.75} + b_P \cdot (\text{Amount of Production}) + e.$$

Both b_M and b_P are partial efficiencies, as they represent the amount of feed required per unit of metabolic body size (b_M) or per unit of production (b_P). The error term (e) denotes the feed not used for either maintenance or producing products. If desired, production can be further subdivided into fat and lean gain in the case of a growing calf, or into lactation and fetal growth in the case of a lactating or pregnant cow.

Differences between animals in b_M, including those due to genetics or breeding value that can be changed via selection, have been demonstrated following selection in mice (Nielsen et al., 1997). And, the magnitude of these differences is relatively large enough to lead us to believe that reductions of 15-20% in maintenance costs would be achievable through long-term selection. Less clear is whether there are differences between animals in b_P, and if so, what amount might be due to underlying genetic causes. Work by Eggert and Nielsen (2006), using selected lines of mice, did not reveal genetic differences in b_P.

Selection Practices in Swine and Broiler Production

The general characteristics of broiler and swine selection programs are fairly similar and quite different from beef cattle. Due in part to intensive production, lower value of individual animals, and perhaps most importantly, much shorter generation intervals, broiler and swine selection programs are controlled and directed by a small number of companies. In broiler breeding, only a handful of multi-national companies control the genetic improvement programs Both broiler and swine breeding programs are centered around a limited number of nucleus herds or flocks and multiple sets of contemporary groups occur each year to make for more cost-effective year-round utilization of data collection technology. Costs of implementation in breeding companies are balanced against predicted genetic change and its value recovery to make decisions on implementation of selection programs, including methods, traits, population sizes, phenotypic and genomic data collected, etc.

In beef cattle, the breeding pyramid structure is less fully defined, and thus, evaluation of costs of implementation and value recovery are not easily done. The long generation interval sets a long horizon for recovery of costs in selection programs. With many breeders trying to contribute at a nucleus level, inefficiencies become evident, as compared to the industrial organization that exists in swine and broiler breeding companies.

Broiler breeding programs emphasize feed conversion as the most important trait for improvement. An example of the importance placed on measurement and subsequent selection for decreasing feed needs is that by Aviagen (D. Emmerson, personal communication), an international leader in broiler breeding. This company annually collects feed intake data on more than 150 thousand birds in individual pens for selection decisions, and in addition, collects another 50 thousand feed records, measured on full-sib families, to assess response under commercial conditions. Adjusted feed conversion has been the trait of focus for selection, although feed efficiency selection in egg-laying populations has used RFI as the trait of focus. Because the commercial goal is to reduce feed required to grow birds to a constant, defined market weight, emphasis has long been placed on selecting faster growing birds. Yet for a feed measurement program, a fixed age schedule is employed, and thus, adjustments for body weight are required when using feed conversion as the primary selection trait (Emmerson, 1997).

Data collection of feed intake is for 7 to 14-day periods, starting in the last phase of production (~35 days of age) before market weight is attained. As noted above, in a broiler system, hatches throughout the year keep new birds in queue for use of feed measurement equipment. Aviagen also uses their own proprietary technology for individual bird measurement of feeding behavior (number of visits, length of visits, size of meals, etc.; Howie, et al., 2011). Estimated genetic correlations between feeding behavioral traits and feed intake have not been large, thus behavioral indicators of feed intake have not been uncovered.

The swine industry has increasingly adopted a structure similar to the broiler industry. The largest 25 producers in the United States manage ~3 million sows which represent just less than 50% of the sow inventory. The vast majority of genetics provided to this market originate from a small number of 3-4 suppliers. As in poultry, feed conversion is the dominant trait in the selection objective for terminal lines, and increasingly for maternal lines.

Swine breeding companies leverage unique selection objectives within specialized populations to create commercial sows (maternal lines) and market pigs (terminal lines). Historically, litter size has been the dominant trait in the selection objective of maternal lines. However, as litter size has increased, the incremental value of each additional pig decreases relative to the other traits in the selection objective. Recent changes in the cost of feed, and the performance level achieved for litter size, has increased the relative emphasis on feed conversion in maternal lines. Today, feed efficiency would account for slightly over 50% of the selection objective in a terminal line and between 30 and 40% of the objective in a maternal line.

In general, feed conversion is measured only in the growing pig, specifically during the finishing period. The Danbred breeding program is a typical example that would be representative of most companies. In this program, feed intake is recorded during the period between 11 and 22 weeks of age. Pigs are maintained in pens of 12-15 animals that are equipped with a feeding station designed to record feed intake. Each pig is equipped with an electronic ear tag that identifies the pig as it enters the feeding station. The number of visits to the feeder, the amount of time spent at the feeder and the amount of feed consumed is recorded for each individual pig. These data are recorded on a sample of males that originate from the highest indexing litters resulting in the accuracy for the FCR breeding value being the highest for those animals most likely to be selected to produce the next generation.

Adjusted feed conversion (FCR, adjusted to a fixed end weight) is used as the trait in the selection index. Feed conversion data from the boars is combined with information on growth rate and body composition (percent lean) from the boars and all remaining males and females that undergo the same performance test less feed intake information. A breeding value for FCR is predicted on all animals in the population and weighted by its economic value in the overall index.

The use of feed intake measures in swine has, as in broilers, been used to improve the efficiency of the market pig, which represents the largest cost of producing pork. There is increasing interest in modifying these programs, particularly in maternal lines, to more directly (or perhaps reliably) impact the maintenance energy requirements of sows while maintaining progress in feed utilization by market pigs. It is particularly important that sows are able to maintain high levels of feed intake during the lactation period in order to maintain body condition, support high levels of milk production and prepare for the next reproductive cycle. At the same time, the ideal sow has relatively low maintenance energy requirements during the gestation period. Selection for RFI is one method to address these needs in a more direct manner compared with the current emphasis on FCR during the finishing phase.

<u>Improving Efficiency of Beef Production</u>

As noted earlier in this paper, simply reducing feed intake is not the sole goal for a selection program. Emphasis must be placed in order to not reduce production or output while we attempt to reduce feed intake for maintenance. Thus, selection program with ranking criteria for selection and culling decisions that maximizes efficiency will include multiple traits that include both output(s) and input(s). A selection index that considers both cow/calf performance and postweaning growth and carcass merit characteristics in the definition of net merit breeding value will be optimum.

The efficiency with which an animal utilizes feed can be expressed in different ways. For growing animals, traditional ratio measures are feed efficiency (FE = gain/feed) and feed conversion ratio (FCR = feed/gain). Although FE and FCR are often used in production settings, these traits are problematic because they are the ratio of two traits (Gunsett 1984). Koch et al. (1963) introduced the concept of using residuals for expression of efficiency. Residual feed intake (RFI), defined as the amount of feed that the animal consumed adjusted for expected consumption based on requirements for maintenance and growth. Residual gain (RG), defined as the amount of gain adjusted for feed intake. Thus, animals with negative RFI consume less than expected and are deemed more efficient, and animals with positive RG grow more rapidly than is expected and are thus deemed more efficient. Further elaboration on RG has been given by MacNeil et al. (2011) and Crowley et al. (2010). Arthur et al. (1996), Arthur et al. (2001), and Crews (2005) further elaborate on RFI. For the purpose of improving production efficiency, it is recommended that RFI and(or) RG be computed using genetic regression coefficients based on estimates of genetic (co)variances (Kennedy et al., 1993), preferably from a single multiple-trait mixed model analysis. Both RFI and RG have been found to be moderately heritable.

From a genetic improvement perspective, it is important to recognize that selection for feed efficiency does not require an explicit measure of feed efficiency to be computed. Instead, selection for feed efficiency can be accomplished by selection on a linear index of traits that measure components of output (e.g. gain,) and input (i.e. feed intake), with output traits receiving positive weights and input traits negative weights. Further, Kennedy et al. (1993) showed the equivalence of selection indexes that incorporated intake or RFI, when the economic weights were calculated correctly.

One of the challenges, and a lingering question and need for further research, is to assess and understand the genetic correlation between feed energy requirement for maintenance per unit size (the b_M coefficient described above) in a growing calf in a feedlot, which consumes a high proportion of grain or grain co-products from ethanol production, versus in a reproducing cow, which consumes mostly forages in a range/pasture environment. Basarab et al. (2007) was unable to detect any significant antagonisms among feed intake and reproductive merit or lifetime productivity of dams that were the mothers of calves with different efficiency. Future results from a project nearing completion at the US Meat Animal Research Center with collection of cow feed intake, combined with growing calf data (Rolfe et al., 2011) will provide further insights. In addition, data from the USDA-supported National Program for Genetic Improvement of Feed Efficiency project (http://www.beefefficiency.org) will add clarification to this question.

Past work using breed differences as a method to infer possible genetic correlations, has pointed to strong, positive genetic relationships between growing calf and reproducing cow energy requirements, per unit body size, for maintenance (b_M; Montaño-Bermudez et al., 1990). In addition, Archer et al. (2002) found a strong and positive genetic correlation between RFI of growing calves in a feedlot and RFI of cows in a feedlot. The data on feed intake and utilization on heifers, prior to making replacement selection decisions, is lacking. Therefore, more study is needed to appropriately account for the associations of feed intake and other economically relevant traits in the female.

All of the measures of efficiency discussed above are favorably related to life-cycle production efficiency. Feed conversion ratio is used in many broiler and swine breeding company programs as the measure of "feed efficiency". Measurement is done over a fairly well defined weight and age interval within each company. Because new hatches/farrowings occur frequently, with new birds/animals ready for feed measurement at the starting weight and age, feed conversion is measured in a narrowly defined window and new batches enter and use the feed measurement equipment year-round. Statistical adjustments for weight range are still made to fine-tune the measurement, but the level of adjustment is relatively small. With the annual calving interval of beef cattle, many young cattle are ready for feed measurement at the same time, which results in expensive equipment then sitting idle for much of the year.

Especially for broiler production, but also for swine production, the magnitude of total feed consumption that is used by the reproducing female flock/herd is much smaller than what we observe with cattle. Low reproductive rate (<1 calf/cow/year) and long time between successive reproductive cycles (1 year) result in almost 65% of the feed energy in total-system/life-cycle being used by the reproducing cowherd, as opposed to the growing calf to slaughter. Although we cannot easily measure feed intake for grazing cows, improving the efficiency of feed utilization of cows is still of paramount importance. Thus, either protocols for measuring intake at grazing, or indicator traits indicative of intake at grazing need to be identified in order to maximize improvement in production system efficiency.

Data Recording

Given the desirability of recording feed intake in order to enhance improvement in efficiency relative to that attainable from output traits alone, protocols for data recording take on increased importance. Archer et al. (1997) have demonstrated that a measurement period of 70 d will provide adequate precision in measurement of relevant performance traits in growing calves. The main limitation and need for a minimum of 70 d is precision in measurement of weight gain, rather than feed intake. At this point, protocols for data collection from reproducing females are less well established. However, historical studies of factors affecting life-cycle efficiency considered individually fed cows and calves for an entire production cycle (e.g., Davis et al., 1983; Kirkpatrick et al., 1985).

To make effective use of expensive feed measurement equipment, at least a couple of groups from the same calving season will have data collected in the system. These calves are likely to be more variable in age and weight than what happens in swine and broiler breeding programs. Opportunities to use central testing facilities, where animals from multiple herds can have feed intake data collected can also reduce cost of collection of individual feed intake. However, variation in age and weight at the time of data collection will likely remain.

A National Cattle Evaluation Program

National cattle evaluation seeks to provide producers with information regarding the genetic basis for economically relevant traits (ERT). To the extent that feed costs money, feed intake is an ERT. Alternative measures, derived from feed intake and performance, provide no additional information beyond that contained in the traits used in their calculation (Kennedy et al., 1993). Therefore, it is recommended that NCE analyze feed intake.

Conditions vary between different contemporary groups (Beef Improvement Federation, 2010), potentially affecting not only the mean but also the variance of observations. Across testing facilities, different equipment may be employed, with ramifications for the observed variance in feed intake. Even in the same herd, the variance of feed intake may be altered due to environmental conditions and perhaps diets fed. Finally, differences in sophistication in operating the test may result in feed intake being reported in different units (as fed, DM, ME, etc), which can be assumed to differ only by unobserved multiplicative constants. Further, contemporary groups in which feed intake is recorded tend to be fairly large. Thus, standardization/normalization of data, as proposed by MacNeil et al. (2011), has the desired result that measurement of feed intake within a contemporary group will have mean 0 and standard deviation 1.

Feed intake is known to be genetically and phenotypically correlated with other phenotypes that are more easily obtained, for instance postweaning growth. Including these indicator trait phenotypes in NCE for feed intake has potential for increasing accuracy in the evaluation of feed intake and extending the evaluation of feed intake to many animals beyond those for which feed intake was observed.

Due to reliance on relatively expensive testing facilities, with limited capacity for collection of data on feed intake, only a selected sample of animals may be evaluated. Thus, to overcome selection bias, a NCE for feed intake should also contain correlated trait(s) recorded for all animals in the contemporary groups from which the evaluated animals were selected.

MacNeil et al. (2011) provide concepts and then an example for a NCE program where measures of feed intake plus “more easily measured” indicator traits are incorporated to predict EPD for feed intake requirements. The genetic relationship matrix, in addition, greatly aids in prediction of breeding value for animals that have no measurement of feed intake on them.

Due to the cost of measurement, feed intake (hence, efficiency of feed utilization) will benefit from further development of genomic predictors to enhance prediction of breeding value in a national cattle evaluation system. In a multi-breed population of steers at the US Meat Animal

Research Center, the best 96 SNPs drawn from the BovineSNP50 Chip explained approximately three-fourths of the breeding value variance in genetic RFI (Snelling et al., 2011). Similarly, Rolf et al. (2011) found 55-65 SNPs explained approximately 55% of the additive genetic variance of feed intake in growing Angus steers. A continuing requirement, for the use of genetic markers to enhance the evaluation of feed intake, is an ongoing commitment to collection of phenotypic data for training marker prediction panels. Ideally, these data are collected on animals from different breeds and crossbreds to yield robust predictions across many genetic types.

A number of opportunities exist to derive genetic predictors of merit and efficiency following the NCE analysis of feed intake. These include EPD for RG, RFI, and residual intake and gain (Berry and Crowley, 2012), as well as selection indexes. If the feed intake data were standardized prior to the NCE, then incorporation of the predicted genetic values into indexes or decision support systems may require back adjustment to a given diet formulation and environment, where the mean and standard deviation have estimated or assumed values.
The choice of which measure of feed intake or efficiency should be derived from the NCE of feed intake and provided to breeders in terms of an EPD, should be driven primarily by the goal to provide an EPD that promotes the proper use of the information provided by breeders in a multiple-trait setting. Thus, assuming that not all breeders use selection indexes and that many breeders are concerned about the impact of reducing feed intake capacity, it may be desirable to provide EPD for RG or RFI, rather than EPD for feed intake. While there are compelling reasons for phenotypic measures of efficiency in other contexts, selection decisions in genetic improvement programs should be based on genetic predictions from the multiple trait genetic evaluation of feed intake. The measure should also ensure that it addresses efficiencies both during the growing period and cow-calf phase of production.

Summary

Improvement of production system efficiency is important to the profitability and sustainability of beef production. Substantial improvement results solely from increasing rate of production, by reducing *per diem* costs associated with maintenance, as well as increasing reproduction by minimizing losses from feeding non-productive females. However, because there is variation between animals in utilization of feed energy, especially for maintenance, further improvement is possible through appropriate consideration of feed intake measurement in selection decisions. This consideration should be facilitated by NCE. Absent efficacious indicator traits for intake by reproducing females, difficulty in measuring feed intake of grazing animals compromises improvement of life-cycle efficiency. For the near term, measurement of feed intake will be centered in growing animals. Choosing which measure of feed intake or efficiency should be derived from the NCE of feed intake and provided to breeders as EPD, should be driven primarily by the goal to provide an EPD that promotes proper use of that information in a multiple-trait setting.

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