Producing and using genetic evaluations in the United States beef industry of today¹

D. J. Garrick*†2 and B. L. Golden‡

*Iowa State University, Ames 50011; †Institute of Veterinary, Animal and Biomedical Sciences, Massey University, Palmerston North, New Zealand; and ‡California Polytechnic State University, San Luis Obispo 93407

ABSTRACT: The overall motivation for the development of an information system for beef cattle improvement is the belief that knowledge of breeding values and heterosis effects allows one to determine the consequences of alternative selection and mating options. With this information, livestock managers can easily shift populations in a desirable direction. The foundation principles for establishing a sound breeding program, including the prediction of animal performance for economically relevant traits and their incorporation into a single index of aggregate economic merit, have been well established over the last half century. Rather than this goal-based approach, the industry adopted a data-driven approach to the production of genetic evaluations that has been characterized by an overemphasis on the evaluation of productive traits, notably BW at various ages, with inadequate regard for other economically important traits, such as reproduction, animal health, and feed requirements. Production of evalua-

tions is breed association centered, and this has delayed the introduction of national across-breed evaluations for all breeds and crosses of cattle. The computational aspects of producing evaluations are now migrating from land-grant universities to breed associations, but not yet to a single entity. The introduction of genomic information in the form of high-density SNP panels will introduce threats, challenges, and new opportunities for the production of evaluations, and represents the largest force to alter the structure of the beef improvement industry since the advent of AI. The use of evaluations has, until recently, stopped short of the provision of index merit as a basis for selection. Accordingly, the value propositions associated with annual improvement or the selection of alternative sires has not been well communicated. Technology, along with economic and other issues related to stakeholder acceptance, will collectively determine the future nature of the industry in terms of the production and use of evaluations.

Key words: beef cattle, genetic evaluation, improvement

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INTRODUCTION

Genetic improvement results when collective benefits of selection and crossbreeding exceed measurement and infrastructure costs to empower the change. The last half century has seen the visual selection process expanded to include quantitative evaluations of merit, known in the US beef industry as EPD. A portfolio of EPD may be combined into indexes that are aggregate measures of genetic or economic worth. Pedigree and performance records of identified animals in a cohort or contemporary group are prerequisite for accurate

²Corresponding author: dorian@iastate.edu

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genetic evaluation. The production and use of evaluations has led to significant change in performance attributes.

The beef industry involves stakeholders representing cow-calf, backgrounding, feedlot, processing, and ancillary sectors. The cow-calf sector comprises a component responsible for producing sires for breeding (i.e., bull breeders) and another that focuses on calf production using sires bred by others (i.e., bull buyers). The bull-breeding sector is represented by many breeds and by corresponding breed associations. These are principally funded by bull breeders (Middleton and Gibb, 1991) and actively promote their breed, maintain its purity, and facilitate its improvement. Development of techniques and strategies for breed improvement has, for almost a century, been the focus of scientists at USDA-ARS research stations and at land-grant universities. The collective activities and interactions of all these stakeholders have developed without central

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direction or management. Accordingly, the nature and scope of data recording and information systems for genetic evaluation have changed over time and differ from what would have been developed from either technical or efficiency perspectives.

This paper reviews some historical and current aspects of infrastructure related to the production and use of genetic evaluations in the US beef industry. It also highlights some opportunities and challenges for the immediate and near future.

BEEF IMPROVEMENT

Improving Performance in the National Beef Herd

The cow-calf enterprises that represent the national population of beef-breeding cows can be classified into the bull-breeding and bull-buying sectors. The bull-breeding sector represents less than 5% cows, mostly registered with a breed association, and supplies breeding bulls to the bull-buying sector. Most of the national beef supply is produced by offspring of cows in the bull-buying herds. Improvements over successive generations in the efficiency of beef production, and in product quality, can be achieved by changing the nature of cows in these bull-buying herds, through selection within breed or within composite strains, and by exploitation of systematic crossbreeding.

The ability of individual bulls to sire numerous offspring and the longevity of breeding cows ensures that many more candidates are available for selection as parents than the number required to maintain a population of constant size. Selection can be a powerful tool for livestock improvement, provided it can be achieved on an informed basis. That is, through robust prediction of the likely performance of the offspring that would result from the choice of particular candidates as parents. Fully informed prediction would require prediction of breed effects, heterosis, and additive effects for all relevant traits in all production environments across the nation and would allow the maximum response to selection (Smith and Banos, 1991). It is not necessary for such predictions to be available on every animal in the national herd, because changes in the bull-breeding sector are passed on to the bull-buying sector through the sale of breeding bulls. In any particular environment, the rate of genetic change in the bull-breeding herds will be identical to the rate of change in those herds that buy bulls from that particular source (Bichard, 1971). Accordingly, the data and analytical systems to provide informed decision making with respect to selection have focused on the bull-breeding sector.

Most current information systems for beef cattle evaluation are held and administered by breed associations. This is not because breed associations are the most appropriate organizations for such endeavors, but for historical reasons whereby they have recorded pedigree information in breed registries for many decades, before

the advent of performance recording and the realization that prediction of merit could be enhanced by knowledge of pedigree information. Current information systems provide predictions of performance for individual traits, presented as EPD or some form of economic index. The following sections will consider the production of EPD and their use in an index context, after briefly reviewing a logical framework to predict and report relevant performance.

Logical Framework for Identifying Traits to Evaluate

In practice, livestock industries and their infrastructure for genetic change develop from historical foundations as systems for animal identification, pedigree recording, performance recording, and genetic evaluation are progressively implemented and enhanced. The potential for new developments is often limited by existing infrastructure. For example, fertility evaluations cannot easily be researched and implemented in the absence of inventory-based recording schemes, known as total herd reporting, because females without offspring in a particular year may represent either neglect of the owner to record the offspring or reproductive failure. Genetic evaluation for carcass traits is problematic in bull-breeding herds because few young animals are slaughtered, and these are likely to be only individuals deemed unsuitable for breeding, and not representative samples of offspring. Accordingly, genetic evaluation from carcass traits relies on measuring offspring in bull-breeding herds. This has been problematic because parentage is often not identified in those herds, different animal identification systems may be used, the owners of the animals may not be members of the breed association, and animals may change ownership and identification between weaning and slaughter ages. In attempting to enhance an improvement program, it is easy to be distracted by such infrastructure problems, which leads to research being focused on problems that are easy to solve, rather than addressing problems in relation to their potential to benefit national improvement. It is therefore useful to consider the steps that would be involved in the logical development of a breeding program (Harris et al., 1984; Harris and Newman, 1994) to benchmark our current status with this academic ideal and to identify opportunities for enhancement.

The first step involves specification of the goal of the breeding program. Given the goal, the next few steps are to 1) identify the list of traits that influence the goal (these are the traits for which EPD are required); 2) determine the relative emphasis that should be attributed to each trait in the list; and 3) quantify the value and cost of using pedigree, phenotypic, and molecular information to predict each of the traits in the list. Beyond the scope of this paper, the logical framework (Figure 1) would involve 1) determination of the breeding scheme (i.e., defining which animals should be

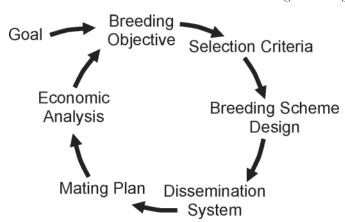


Figure 1. Steps involved in a logical approach to improvement (adapted from Harris et al., 1984).

measured for which traits and at what stage of life); 2) the dissemination system, or what to do with the elite animals; 3) the mating plan, or how chosen animals should be paired; and 4) an economic analysis of the total breeding program costs and benefits, among other factors.

There is no well-defined goal for national beef cattle improvement. This is unfortunate because goal setting promotes long-term vision, focuses acquisition of knowledge, and helps to organize resources. A Web search identifies logos and mottos, such "Beef, it's what's for dinner." Does this suggest the goal of the industry is that every person should eat beef every dinnertime? Other commentators suggest the goal should be based on profit. However, is this cow-calf profit, or feedlot profit? Is it profit per cow, or profit per unit of land or feedlot pen?

Our opinion is that our goal should be to produce beef that is nutritious, healthful, and desirable. It should be produced in a manner that is respectful of the resources used in its production, including the environment (e.g., visual, land, air, water, wildlife), labor (e.g., ranch, feedlot, and processor), and welfare of the animals. Further, it should be priced to provide fair returns to all involved in the supply chain. This definition does not imply that satisfaction or utility will necessarily be changed simply by increasing or decreasing the beef supply. In the context of the cow-calf production system, this goal could be interpreted in terms of "profit per unit land" and in the feedlot system as "profit per pen." It is future rather than current profit that is of interest, and therefore future costs and payments that must be considered along with the circumstances of today.

It could be argued that it is risky to have only a single goal, because the goal relates to future production, economic, and management circumstances, and there is uncertainty concerning what future conditions might be realized. However, the nature and scope of genetic change depend on much more than the goal; different stakeholders will identify different lists of traits that influence the goal and have their own unique relative

emphasis on each trait. Further, the breeding strategies adopted to increase selection accuracy can vary widely. For example, the use of progeny testing, the recording of novel traits such as feed intake, and the use of genetic markers can provide individuality to many bull breeders even when they share the same goal. Historical selection that led to the increase in the snorter dwarf gene was not simply the result of breeders sharing a goal, but was due to the overemphasis on a selection strategy that focused on early maturity, shorter legs, and extreme masculinity in bulls (Marlowe, 1964).

The reader might question the inclusion of being respectful to the environment, labor, and welfare of the animals in the goal. These factors represent features of the beef cattle production system that have historically been externalities (Pigou, 1920), but that are now affecting or that will in the future affect revenues and costs. Externalities occur when an economic activity causes external costs or benefits to participants that cannot directly affect an economic transaction. That is, the producer does not bear all the costs or reap all of the benefits of the economic activity. Greenhouse gas emissions and nitrogen excretion associated with cattle production are subject to tax in some countries and influence the goal. Consumers have indicated in other industries (e.g., manufacturing) that they will pay more for products manufactured in circumstances that pay their workers a fair wage. The development of labeling that allows consumers to track the supply chain can also lead to market signals based on perceived welfare of the animals in the production system.

Given the goal, the next step is to define the list of traits that influence the goal. This is typically an easier task than defining the goal. A profit-based goal might best be considered by identifying the traits that influence income and the traits that influence costs.

In the cow-calf system, the principal determinants of income are the number of sale animals and the value per sale animal. The number of sale animals will be dictated by the number of females of breeding age, the reproductive performance, calf survival, and the replacement rate. The value per sale animal will principally be determined by the sex, BW, and age of the sale animal, along with attributes that influence costs and prices downstream in the supply chain. These might include aspects of meat quality (e.g., marbling and tenderness) along with management factors (e.g., adaptability, disease resistance, docility). Expense items include feed costs, veterinary and animal health costs, and labor.

In the feedlot system, revenues are determined by the number of sale animals, their BW, and other attributes. A critical determinant of the number of sale animals in relation to purchases is the survival rate to sale. Expenses include feed, yardage, labor, and animal health. In the processing sector, income is determined by total saleable meat and by-products. Along with purchase BW, the dressing percentage, meat yield, and distribution of high-priced cuts are important. Diseased and bruised tissues reduce revenue and may increase slaugh-

ter costs. The consumer sector is principally concerned with demand attributes, including appearance, taste, nutrition, healthfulness, wastage, and perceptions, in relation to price and competition from other protein sources.

The common problem in creating a list of traits that influence the goal is that the list may contain indicator traits along with economically relevant traits (ERT; Golden et al., 2000). Indicator traits are not of direct economic importance, but are correlated with one or more traits of economic importance. The construction of an economic index and its adoption as a basis for selection is considerably simplified if the list of traits is limited to those that are economically relevant and excludes any indicator traits. The specific list of traits that influence the goal from these considerations may not be unique because some traits can be alternatively partitioned into components. For example, one stakeholder might identify heifer pregnancy as a trait, whereas another might propose the components of heifer pregnancy, age at puberty and conception rates, as 2 alternatives. Accordingly, there is little benefit in prescribing a particular list beyond recognizing that it might contain groups of traits that influence the goal in the categories of production, carcass, beef or meat, reproduction and longevity, feed requirements, animal health, and survival.

Given a list of traits that influence the goal, the next logical step in the development of an improvement program is to determine the relative emphasis of the traits in the list. This information is valuable for selection because it provides a formal means of determining the compromise between animals that are superior for some traits of interest but inferior for others. It is also valuable for determining the priority in relation to research and development efforts to develop systems for collecting information and evaluating these traits.

Producing Genetic Evaluations

The process of predicting genetic merit is known as genetic evaluation, and it involves partitioning observed performance into several effects, according to a model equation that describes the factors that influence performance for a particular trait. Solutions to the effects of interest, used in EPD, are currently obtained by setting up and solving mixed model equations (Henderson, 1973). Those equations involve a coefficient matrix or left-hand side that, when multiplied by the solution vector, will equal the right-hand side vector. The leftand right-hand sides must be quantified to obtain the estimates that constitute the solution vector. The formation of these equations requires 3 kinds of data. For each animal with a record, knowledge of its herd, contemporary group, sex, birth date, and the age of its dam is required because these nongenetic effects influence the construction of the equations. Pedigree information dictates the nature of genetic relationships between animals represented in the equations (Quaas and Pollak, 1980). Collectively, the nongenetic effects and animal relationships determine the coefficient matrix. The performance records themselves are the major determinant of the right-hand side. Accordingly, genetic evaluation requires access to a database of pedigree information, contemporary group information, and records of performance on cohorts of animals. Historical developments in computing strategies, the scope of traits evaluated, and the nature of the models used for each trait have been reviewed elsewhere (Golden et al., 2009).

The database and evaluation activities have traditionally been undertaken by different entities. The breed associations had long been recording ancestry, or pedigree information, and were the natural organizations to collect contemporary group and performance information. However, the kinds of computer platforms suitable for database activities were not exactly the same as those that were optimal for the numerical analysis required to set up and solve equations. Furthermore, although there were many established techniques and software systems for database activities, the numerical techniques were still being developed, principally at land-grant universities, and no commercial software existed for routine application.

Four land-grant universities dominated activities associated with the production of genetic evaluations. These were Colorado State University, Cornell University, University of Georgia, and Iowa State University. Various breed associations aligned themselves with these universities. The American Angus Association (AAA) in St. Joseph, MO, became aligned with Iowa State University in nearby Ames. Cornell University undertook analyses for the American Simmental Association (ASA), which, by nature of the recent introduction of the breed to the United States and its upgrading programs, included Simmental and Simmental-cross animals. The ASA served as a conduit for Maine Anjou and Chianina databases to the evaluation system, so those breeds and their crosses were included in the Cornell University activities. Colorado State University was actively involved in the development of the Red Angus breed, and undertook their analyses as well as those of several other breed associations. The University of Georgia likewise undertook analyses for a wide portfolio of breed associations. This was an ideal structure for the 1980s. Access to field data provided real-life motivation for animal breeders in all these institutions, as well as providing outreach opportunities. Resources for these land-grant endeavors were principally through the federally and state-funded agricultural experiment stations, with the breed associations providing some direct funding of technical activities. The healthy competition between these 4 institutions encouraged development of new algorithms that allowed more rapid computations, providing for larger data sets with more animals, more correlated traits, or more appropriate underlying models to describe phenotypic performance.

During this period, the Beef Improvement Federation provided an active role in coordinating guidelines for uniform activities associated with performance recording and genetic evaluation across the portfolio of players involved in these endeavors (Willham, 1982). Evaluations had been within breed or, more precisely, within breed association, reflecting the fact that performance records were principally collected on purebred animals. However, the grading-up strategies adopted by ASA, the Red Angus Association of America, and some other breed associations allowed for the limited inclusion of crossbred animals, either by characterizing crossbreds in their own contemporary groups, or by including relevant breed and heterosis effects. Gradual expansion occurred in the scope of traits evaluated, from weaning and yearling BW, to include BW at birth, mature BW, calving ease, carcass traits, and ultrasound measures. The list of traits varied by breed association, but its expansion was largely data driven.

Early genetic evaluations were typically within breed (Willham, 1979), because they relied on data collected by breed associations that, for obvious reasons, tended to be narrowly focused on the interests of their own breed. Although various strategies were known for deriving across-breed EPD, these required the motivation of across-breed data to be developed for field circumstances. Researchers at Cornell University were particularly interested in the academic aspect of such developments (Pollak and Quaas, 1998), and the ASA had a relevant data set because the scarcity of Simmental animals encouraged the recording and grading up of Simmental animals from a variety of breeds by successive back-crossing to produce 50% Simmental, 75% Simmental, and so forth. In some parts of the country, cow performance was considerably enhanced by inclusion of Bos indicus breeds in a crossbred animal, as was apparent in the development of the Simbrah breed. This led to the calculation of across-breed EPD by using mixed-breed data from ASA. Similar approaches were applied to separate data extracts from other associations that collected records from composite cattle.

Some industry stakeholders identified the merit of wider across-breed EPD. To estimate breed and heterosis effects, these require access to data that include pure and crossbred animals in the same contemporary groups. The US Meat Animal Research Center had such data in various cycles from the Germplasm Evaluation Program and has undertaken across-breed evaluation by using those records based on the approach given by Notter and Cundiff (1991) with some refinements, as outlined by the Beef Improvement Federation (1996). These results have been published annually by the Beef Improvement Federation, since the report by Cundiff (1993) to the most recent results extended to carcass traits in Kuehn et al. (2008). The bulls used in that program included high-accuracy sires from various breed associations that have allowed the calculation of breed adjustment factors that account for different genetic bases being used in different breeds. Estimates of heterosis factors, along with the breed adjustment factors, enable the calculation of national across-breed EPD. However, to compute these EPD, one must understand how to calculate direct and maternal coefficients for heterosis and recognize that such coefficients will be different according to the breed of dam, thereby necessitating national EPD that are unique, according to circumstances of the dam breed. The extent to which these annually published breed adjustment factors have been used by industry is uncertain.

The National Beef Cattle Evaluation Consortium (NBCEC) was established in 2001 with congressional line-item funding administered by the USDA Cooperative State Research, Education, and Extension Service, and with the task of developing the vision for a sustainable system for research and servicing of genetic evaluations. It included the 4 key universities involved in genetic evaluation activities. Training graduate students in various aspects of livestock improvement was also recognized as an important aspect of the NBCEC activities, as was the provision of extension and outreach related to developments in animal breeding (Bullock et al., 2006). The collective activities of the 4 university partners immediately before establishing the NBCEC resulted in a change from data-driven to goal-driven approaches to the production of EPD. Colorado State University led efforts to obtain EPD for the goal trait groups of reproduction, including stayability (Snelling et al., 1995; Brigham et al., 2007) and heifer pregnancy (Martin et al., 1992; Evans et al., 1999; Doyle et al., 2000), and feed requirements, namely, cow maintenance energy (Speidel et al., 2004). The concept of ERT (Golden et al., 2000) has gradually been adopted by industry, and industry has seen the use of ultrasound composition data to predict EPD for carcass traits (MacNeil and Northcutt, 2008), rather than having EPD for both carcass and ultrasound traits. However, scrotal circumference EPD continue to be published and have yet to be used to predict female reproductive traits directly, despite its predictive value (Toelle and Robison, 1985), albeit in limited circumstances (Evans et al., 1999).

The NBCEC prototyped systems for across-breed EPD and demonstrated that there were relatively few technical problems associated with expanding the analysis of across-breed data from individual breed associations to a national scale. A few breed associations chose not to participate in the prototype, so it did not represent all US records. The prototyping identified technical difficulties associated with data management of records from multiple registration systems when no consistent scheme is adopted for identifying parents registered in other breed associations. These issues lead to duplication of parents in multiple registries and prevent all available information from being used in the evaluation of sires across breeds.

The NBCEC promoted a vision of a single acrossbreed database and a single entity to undertake genetic evaluation activities on behalf of industry. However, without long-term funding, the establishment of such systems relies on industry leadership and funding. The NBCEC identified a timeline to migrate the servicing of evaluations from land-grant universities. The industry has responded well to the concept of taking greater responsibility for the servicing of genetic evaluations, but no progress has been achieved in developing an industry-wide single across-breed database for pedigree and performance recording. The ASA undertakes its own evaluations; the AAA has created a subsidiary, Angus Genetics Inc., to provide EPD servicing, and that organization runs analyses for AAA, the North American Limousin Foundation, and the American Gelbvieh Association, with more breeds likely to follow. A company has been created to undertake analyses for Brangus and Red Angus breeds. Other associations are still considering their options. Ultimately, there is unlikely to be the finance or critical mass of expertise for duplication of servicing entities. These activities will be challenged further in the new era of genomic initiatives.

Incorporating Genotypes in the Production of Genetic Evaluations

The last decade of QTL experiments and expensive approaches for characterizing genetic markers has produced relatively few tools of real benefit for beef cattle selection (Garrick and Johnson, 2003; Dekkers, 2004; Van Eenenaam et al., 2007). The sequencing of the bovine genome and the 2008 release of the 50K chip (Van Tassell et al., 2007) promises to offer new opportunities for genomic selection (Meuwissen et al., 2001). Exploiting these opportunities will require access to relevant populations of sufficient size for estimating genomic effects. The NBCEC has provided leadership and established partnerships to collect these resources together, with direct focus on goal trait groups that are the most poorly resourced for improvement by using conventional phenotypic-based approaches. This has included reproduction, healthfulness, and feedlot health.

The success of chip-based genomic efforts will influence the future for conventional evaluation of merit. The proportion of variation that can be accounted for by using markers will be a critical variable, as will the number of markers required for each trait and the genotyping costs in relation to the size of a customized panel. A high proportion of variance accounted for by markers, in conjunction with low genotyping costs, will likely erode the demand for conventional pedigree and performance recording. A moderate to low proportion of variation accounted for by markers will result in benefits being obtained by pooling genomic and existing evaluation technologies.

Evaluations that utilize information on genotypes, along with conventional pedigree and performance information, may take several forms. Genomic predictions may be used as data in conventional evaluation systems, influencing national evaluations. In that case, EPD might continue in a conventional form, but benefiting from molecular information. Alternatively, national evaluations may be incorporated into genomic

predictions, and genomic predictions themselves may not be available for use in national evaluations. Unlike the development of pedigree and performance-based initiatives, the genomic era introduces issues relating to intellectual property and return on investment in genotyping. These activities will challenge the existing structure that forms the basis for beef cattle selection, more so than any other technology since AI.

Robust genomic predictions allow the separation of the "information nucleus" and the "seedstock nucleus." Conventionally, information for prediction was obtained from bull-breeding herds and measured directly on candidates for selection or on their close relatives. Genomic predictions can result from training analyses in bull-buying herds, with results applied in bull-breeding herds. This has particular benefits when purebreds are being selected for crossbred performance (Dekkers, 2007) or in different management and environmental circumstances.

Using Genetic Evaluations

The most well-known papers establishing the selection index were written by Hazel and Lush (Hazel and Lush, 1942; Hazel, 1943) from Iowa State University. The selection index assumed that the breeding goal was influenced by several different, possibly correlated, traits. It argued that each of these ERT could be characterized by an economic weight obtained as the partial derivative of the profit function. Given these economic weights, knowledge of the genetic relationships represented in the data set (i.e., the relationship matrix), and genetic and phenotypic relationships between the traits, the selection index methodology allowed a single measure of aggregate economic merit to be calculated for each individual in a one-step procedure that did not involve predicting the merit for each individual trait. This approach was shown in theory and by practice to be a very effective technology for multiple-trait selection. However, there were several limitations to immediate adoption in the form presented by Hazel and Lush (1942).

Genetic and residual covariances among indicator traits could be estimated from field data, but genetic covariances between ERT that had not been observed and the indicator traits that are widely available for performance recording could not. This precluded the development of selection indexes that included traits such as reproduction and stayability. Further, there was little interest by academics in or emphasis on the practical derivation of economic values. Henderson (1963) showed that the aggregate economic merit of Hazel and Lush (1942) could be derived equivalently in a 2-step procedure. The first step involved predicting the genetic merit of all the ERT for all the candidate individuals. The second step was adding together the EPD for each trait in the objective weighted by its economic value. This rationalized technical focus on the analysis, rather than on the interpretation or delivery of the information. The most appealing traits to study were those for which data already existed. This led to efforts concentrating on weaning BW, and later on BW at birth and yearling BW or postweaning gain. This was the beginning of the data-driven approach to selection. That is not to say that the traits investigated were not goalinspired, but the research and publication priorities often lost sight of the goal. For the next few decades, new traits were added to evaluation systems by identifying characteristics that could be measured, by collecting exploratory information, and by generating the analytical tools. This led to EPD being generated for several indicator traits, rather than the corresponding ERT. The methodology to predict an EPD from a correlated indicator trait was a well-accepted application of prediction methodology, but required a priori knowledge of the genetic correlation between the indicator and ERT. Henderson (1963) had established procedures for calculating such a correlation; however, these required access to data sets that included observations on both traits. The one exception was ultrasound measurement of carcass traits when carcass measurements were already available, allowing derivation of the genetic correlations, and most breeds used the ultrasound data as a correlated trait and rightly published only the EPD on the carcass scale.

Furthermore, the scientists involved in producing evaluations tended to have little motivation, expertise, or access to information to calculate the relative economic values required for index construction. Accoordingly, evaluations were delivered in terms of EPD rather than in terms of some measure of aggregate economic merit (Harris and Newman, 1994; Harris, 1998). These EPD included indicator traits along with ERT. In marked contrast to the swine, poultry, sheep, and dairy cattle industries, in which economic indexes are a critical component of selection strategies, the US beef industry has done little to promote the value proposition associated with improvement. Inspection of any breed association Web site or sire catalog will demonstrate annual progress in some individual traits, but some goal trait groups are totally absent. There is no guidance to the overall impact of the known changes in relation to overall system profitability.

Some breed associations have produced and published indexes, but corresponding details concerning the specific goal of each index, the list of traits that are assumed to influence the goal, and the nature of the assumed cost and price information has been inadequately detailed. In many cases, the resultant economic weights are not presented. Such indexes will work as planned if used as the basis of selection, but they provide little information to convince a producer to use the information as the principal basis for selection. The basis for these indexes is some kind of economic model, which is then used to estimate the partial derivative of profit for each ERT. In cases in which the published

traits include indicator traits, or when some ERT are missing, the index construction may use selection index principles to determine weights for each trait that account for genetic covariances between the traits in the objective and the characters with EPD. This can further complicate the explanation of index weights in a rational manner.

The NBCEC has promoted an alternative approach (Garrick, 2005, 2006a,b) to the construction and presentation of measures of aggregate economic merit. Rather than using an economic model and perhaps selection index principles to derive weighting factors in a first step, which are then applied to EPD to construct an index value in a second step, the NBCEC approach uses the concept of selection by simulation (Bourdon, 1988, 1998). In the first step, EPD of a small portfolio of user-selected bulls are used to predict the phenotypic performance of offspring in user-defined production, management, and economic circumstances. Phenotypes can be predicted in relation to current phenotypic performance. These phenotypes are then used to predict revenues and costs, including feed requirements, and present the user with an estimate of the difference in bottom profit between each candidate bull and the current circumstances in a total system context. This system facilitates the incorporation of heterosis values and across-breed EPD when available. The system also supports decision making (Newman et al., 2000) by providing users with the revenue and cost information used to obtain the bottom-line results. They can therefore see the implications of using alternative sires in terms of the number and value of sale animals that are predicted to result from using alternative bulls as maternal or terminal sires. The system can be used to compare the merit of average animals across time and thereby quantify the value proposition from industry rates of genetic change. The prototype system is limited to the cow-calf component of the supply chain. Ultimately, it is expected that such a system will be commercialized and delivered by the entity responsible for servicing genetic evaluations.

Summary and Conclusions

The technical approaches and organizational structures for producing and using genetic evaluations are evolving from a data-driven to a goal-driven approach. They are progressively accounting for a wider portfolio of goal trait groups. Further, they are developing to incorporate genomic information, as appropriate. Many obstacles continue to delay extension of current systems to an all-trait-encompassing, across-breed evaluation suitable for the range of US production, management, and environmental circumstances. Technological, economic, and other issues relating to stakeholder demand for new and existing practices will collectively determine the future structure of the industry from the perspective of producing and using genetic evaluations.

LITERATURE CITED

- Beef Improvement Federation. 1996. Guidelines for Uniform Beef Improvement Programs. 7th ed. Beef Improv. Fed., Athens, GA.
- Bichard, M. 1971. Dissemination of genetic improvement through a livestock industry. Anim. Prod. 13:401–411.
- Bourdon, R. M. 1988. Bovine nirvana—From the perspective of a modeler and purebred breeder. J. Anim. Sci. 66:1892–1898.
- Bourdon, R. M. 1998. Shortcomings of current genetic evaluation systems. J. Anim. Sci. 76:2308–2323.
- Brigham, B. W., S. E. Speidel, R. M. Enns, and D. J. Garrick. 2007. Stayability to alternate ages. Proc. West. Sect. Am. Soc. Anim. Sci. 58:27–30.
- Bullock, K. D., D. R. Strohbehn, R. L. Weaber, E. J. Pollak, D. J. Garrick, J. K. Bertrand, D. W. Moser, and J. M. Reecy. 2006. From research to application: A model for educating beef producers in animal breeding technologies. Proc. 8th World Congr. Genet. Appl. Livest. Prod. 34:601–850.
- Cundiff, L. V. 1993. Breed comparisons adjusted to a 1991 basis using current EPDs. Pages 114–123 in Proc. Beef Improv. Fed. Res. Symp., Asheville, NC. Beef Improv. Fed., NC.
- Dekkers, J. C. M. 2004. Commercial application of marker- and gene-assisted selection in livestock: Strategies and lessons. J. Anim. Sci. 82(E Suppl.):E313–E328.
- Dekkers, J. C. M. 2007. Marker-assisted selection for commercial crossbred performance. J. Anim. Sci. 85:2104–2114.
- Doyle, S. P., B. L. Golden, R. D. Green, and J. S. Brinks. 2000. Additive genetic parameter estimates for heifer pregnancy and subsequent reproduction in Angus females. J. Anim. Sci. 78:2091–2098.
- Evans, J. L., B. L. Golden, R. M. Bourdon, and K. L. Long. 1999. Additive genetic relationships between heifer pregnancy and scrotal circumference in Hereford cattle. J. Anim. Sci. 77:2621–2628.
- Garrick, D. J. 2005. Making the web equal profit—Surfing for genetics. Proc. Beef Improv. Fed. 37th Ann. Res. Symp. Annu. Meet. 37:105–111.
- Garrick, D. J. 2006a. Development of genetic evaluations and decision support to improve feed efficiency. Proc. Beef Impr. Fed. 38th Ann. Res. Symp. Annu. Meet. 38:32–40.
- Garrick, D. J. 2006b. Genetic improvement—Assessing the ramifications of genetic change. Proc. 8th World Congr. Genet. Appl. Livest. Prod., Belo Horizonte, Brazil. CD-ROM Communication No. 03-17. 8th WCGALP Secretariat, Belo Horizonte, Minas Gerais, Brazil.
- Garrick, D. J., and P. L. Johnson. 2003. Examples of marker-assisted selection in sheep and cattle improvement in New Zealand. Proc. Beef Improv. Fed. 8th Genet. Prediction Workshop 8:5–23.
- Golden, B. L., D. J. Garrick, and L. L. Benyshek. 2009. Milestones in beef cattle genetic evaluation. J. Anim. Sci. 87(E. Suppl.):E3– E10.
- Golden, B. L., D. J. Garrick, S. Newman, and R. M. Enns. 2000. A framework for the next generation of EPD. Proc. Beef Improv. Fed. 32nd Ann. Res. Symp. Annu. Meet. 32:2–13.
- Harris, D. L. 1998. Livestock improvement: Art, science, or industry? J. Anim. Sci. 76:2294–2302.
- Harris, D. L., and S. Newman. 1994. Breeding for profit: Synergism between genetic improvement and livestock production (a review). J. Anim. Sci. 72:2178–2200.
- Harris, D. L., T. S. Stewart, and C. R. Arboleda. 1984. Animal Breeding Programs: A Systematic Approach to their Design. Advances in Agricultural Technology. USDA-ARS Bull. AAT-NC-8. USDA-ARS, Peoria, IL.
- Hazel, L. N. 1943. The genetic basis for constructing selection indexes. Genetics 28:476–490.
- Hazel, L. N., and J. L. Lush. 1942. The efficiency of three methods of selection. J. Hered. 33:393–399.

- Henderson, C. R. 1963. Selection index and expected genetic advance. Pages 141–163 in Statistical Genetics and Plant Breeding. W. D. Hanson, and H. F. Robinson, ed. Publ. No. 982. NAS, NRC, Washington, DC.
- Henderson, C. R. 1973. Sire evaluation and genetic trends. Pages 10–41 in Proc. Am. Breed. Genet. Symp. in Honor of Jay L. Lush. Am. Soc. Anim. Sci., Champaign, IL.
- Kuehn, L. A., L. D. Van Vleck, R. M. Thallman, and L. V. Cundiff. 2008. Across-breed EPD tables for the year 2008 adjusted to breed differences for birth year of 2006. Proc. Beef Imp. Fed. 40th Annu. Res. Symp. Annu. Meet. 40:53–74.
- MacNeil, M. D., and S. L. Northcutt. 2008. National cattle evaluation system for combined analysis of carcass characteristics and indicator traits recorded using ultrasound in Angus cattle. J. Anim. Sci. 86:2518–2524.
- Marlowe, T. J. 1964. Evidence of selection for the snorter dwarf gene in cattle. J. Anim. Sci. 23:454–460.
- Martin, L. C., J. S. Brinks, R. M. Bourdon, and L. V. Cundiff. 1992. Genetic effects on beef heifer puberty and subsequent reproduction. J. Anim. Sci. 70:4006–4017.
- Meuwissen, T. H. E., B. J. Hayes, and M. E. Goddard. 2001. Prediction of total genetic value using genome-wide dense marker maps. Genetics 157:1819–1829.
- Middleton, B. K., and J. B. Gibb. 1991. An overview of beef cattle improvement programs in the United States. J. Anim. Sci. 69:3861–3871.
- Newman, S., T. Lynch, and A. A. Plummer. 2000. Success and failure of decision support systems: Learning as we go. J. Anim. Sci. 77:1–12.
- Notter, D. R., and L. V. Cundiff. 1991. Across-breed expected progeny differences: Use of within-breed expected progeny differences to adjust breed evaluations for sire sampling and genetic trend. J. Anim. Sci. 69:4763–4776.
- Pigou, A. C. 1920. Economics of Welfare. Macmillan and Co., London, UK.
- Pollak, E. J., and R. L. Quaas. 1998. Multi-breed genetic evaluations in beef cattle. Proc. 6th World Congr. Genet. Appl. Livest. 23:81–88.
- Quaas, R. L., and E. J. Pollak. 1980. Mixed model methodology for farm and ranch beef cattle testing programs. J. Anim. Sci. 51:1277-1287.
- Smith, C., and G. Banos. 1991. Selection within and across populations in livestock improvement. J. Anim. Sci. 69:2387–2394.
- Snelling, W. M., B. L. Golden, and R. M. Bourdon. 1995. Withinherd genetic analyses of stayability of beef females. J. Anim. Sci. 73:993–1001.
- Speidel, S. E., D. J. Garrick, and R. M. Enns. 2004. Genetic prediction for estimating mature cow maintenance energy requirements. J. Anim. Sci. 82(Suppl. 1):450. (Abstr.)
- Toelle, V. D., and O. W. Robison. 1985. Estimates of genetic correlations between testicular measurements and female reproductive traits in cattle. J. Anim. Sci. 60:89–100.
- Van Eenennaam, A. L., J. Li, R. M. Thallman, R. L. Quaas, M. E. Dikeman, C. A. Gill, D. E. Franke, and M. G. Thomas. 2007.
 Validation of commercial DNA tests for quantitative beef quality traits. J. Anim. Sci. 85:891–900.
- Van Tassell, C. P., L. K. Matukumalli, C. Taylor, T. P. L. Smith, T. S. Sonstegard, R. D. Schnabel, M. V. B. De Silva, G. R. Wiggans, G. Liu, S. Moore, and J. F. Taylor. 2007. Construction and application of a bovine high-density SNP assay. J. Dairy Sci. 90(Suppl. 1):421. (Abstr.)
- Willham, R. L. 1979. Evaluation and direction of beef sire evaluation programs. J. Anim. Sci. 49:592–599.
- Willham, R. L. 1982. Genetic improvement of beef cattle in the United States: Cattle, people, and their interaction. J. Anim. Sci. 54:659–666.