Development of economic selection indices for beef cattle improvement

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Introduction

Profitability is the primary goal for most beef cattle producers. The main source of long-term profitability for a beef cattle operation lies in its production efficiency relative to other operations (Harris, 1970). There are numerous approaches to achieve greater efficiency including nutrition, reproduction, management, and genetics. The goal in animal breeding and genetics is to improve animal populations and future generations of animals (Dekkers et al., 2004). Expected progeny differences (EPD) are the traditional genetic tools used to select parents. A drawback to EPD is that they represent genetic merit in only one trait while in reality multiple traits influence an animal's value (Hazel, 1943). With EPD as a sole selection tool, producers are left to individually determine their optimal use and ultimately the economic importance of each trait (Bourdon, 1998). Selection indices account for multiple traits simultaneously and consider both biological production levels and economics (Parish, 2011). Falconer and Mackay (1996) recommend the use of selection indices for multi-trait selection in animal populations.

According to Hazel and Lush (1942), selection for an index which gives proper weight to each trait is more efficient than tandem selection or selection for multiple traits with independent culling levels. Tandem selection involves selection for one trait at a time until all traits have been improved to the desired level. This method is inefficient because selection pressure is placed on only one trait at a time, making genetic progress slow. Additionally, progress made in one trait could be eroded as selection pressure is placed on a different trait. When selection is based on independent culling levels, a certain level of merit is established for each trait and all individuals below that level are culled regardless of their performance in other traits. The main concern with this method is that an animal with superior performance in many traits may be culled if it is barely under the thresh hold level for just one trait. In this situation selection indices are an appropriate alternative because they allow for superior performance in one trait to compensate for poor performance in other traits.

Review of Literature

To achieve progress towards any breeding goal, it is important to determine which animals should be chosen as the parents of the next generation. Selection may differ between production systems and goals set forth for a particular operation. It is first important to specify the goal of a particular operation, and then develop a breeding program specific to this goal. Harris et al. (1984) presented an eight-step process for developing a breeding program: (1) describe the production system (2) formulate the objective (3) choose a breeding system and breeds (4) estimate selection parameters and economic values (5) design an animal evaluation system (6) develop selection criteria (7) design mating for selected animals (8) design a system for expansion.

Breeding Objective

The breeding objective is a combination of economic weighting factors and genetic information for traits to be improved (Falconer and Mackay, 1996). Selection on a breeding objective should result in increased profit of the firm that is investing in a breeding program (Goddard, 1998). Defining a breeding objective and developing selection criteria based on that breeding objective should be the primary step in developing a structured breeding program (Ponzoni and Newman, 1989). Defining an objective is critical because highly efficient selection for the wrong objective may be worse than no selection at all (James, 1982). To develop the most appropriate breeding objective several pieces of information are needed: (1) the management and production system of a group, (2) the return and cost of the production system, and (3) the economically relevant traits (ERTs) which influence returns and cost of production.

The breeding objective for a beef cattle breed may vary depending on the production system being used (Phocas et al., 1998). Dickerson et al. (1974) suggested that the breeding objective for efficient beef production should be more efficient growth accompanied by earlier sexual maturity to reduce replacement cost, lengthen productive life and minimize increase in mature body size. Efficiency should be measured as cost per unit of product from females and their progeny over a given period of time. Traits considered for market animals by Dickerson et al. (1974) were carcass composition, meat quality, and optimum weight at slaughter. Traits considered for cows were mature size, milk production and calving difficulty.

Garrick and Golden (2009) suggest that the goal of the beef industry as a whole should be to produce beef that is nutritious, healthful and desirable in a manner that is respectful of the resources used in its production. For a cow-calf system, Garrick and Golden (2009) describe the principal determinants of income as the number of females of breeding age, reproductive performance, calf survival, replacement rate, and the sex, weight and age of sale animals. Downstream factors which may potentially influence income are aspects of meat quality (e.g., marbling and tenderness) and management factors (e.g., adaptability, disease resistance, and docility). Expenses include feed costs,

veterinary costs, and labor. For a feedlot system, income is associated with the weight and carcass attributes of sale animals. Expenses include feed, yardage, labor and animal health.

Literature suggests that breeding objectives should be divided into groups depending on the emphasis of a breed or a specific operation. MacNeil et al. (1994) stated that the breeding system could be divided into three categories: general purpose, maternal and terminal. The U.S. beef production system can generally be divided into two sectors, seedstock and commercial. In seedstock operations, self-replacement is required to keep the breeding system stable so a maternal index can be used for producing reproductively proficient parents. Terminal selection indices can be used for commercial producers looking to purchase animals for use as parents in a system where progeny will be harvested.

It has been argued that biological efficiency should be used in defining breeding objectives instead of economic efficiency to assure sustainability of genetic improvement (Dickerson, 1982). However, difficulties in the expression of costs and revenues in terms of energy or protein consumption and lack of differentiation between values of products when biological efficiency is considered render this criterion unable to describe the overall objective of the producers (Harris and Newman, 1994). In general, even if future economic conditions can be difficult to foresee, the definition of the breeding goal according to an economic criterion allows a more complete description of the production system by also taking into account non-food costs (Dickerson, 1970; Goddard, 1998). Albera et al. (2004) stated that the use of biological rather than economic efficiency would lead to the formation of a different breeding goal. However, Albera et al. (2004) ultimately concluded that improvement in economic efficiency also leads to improved biological efficiency in most traits studied.

Determining traits in the breeding objective

A strong relationship between the breeding objective and changes in profitability is highly desirable, implying that all traits associated with profitability of an animal should be included (Pearson, 1982). Choice of traits to be included in the breeding objective should be based on relative contribution of each trait to the overall efficiency of production, which is usually evaluated from an economic perspective (Goddard, 1998). If efficiency is to be evaluated from an economic perspective, traits to be considered for use should be those which affect the income and cost of the system. Income is related to the number and value of sale animals, while cost is associated with the quantity and price of the resources required for production (Garrick and Golden, 2009).

For selection to be most efficient for individual producers, a comprehensive and systematic way of relating changes in individual performance levels to changes in profitability at the enterprise level must be developed (MacNeil et al., 1997). As such, relative weighting of each contributing trait must be determined. Harris (1970) indicated that the relative emphasis placed on each trait in a selection program depends on the combination of economic importance of the trait, potential for genetic improvement of the trait, genetic interrelationships between the trait and the cost of measurement in labor, facilities and time. Potential for genetic improvement is also highly dependent on genetic variability and accuracy of selection decisions. In most species, using a complete breeding objective would result in including a large number of traits. Gjedrem (1972) considered the definition of the aggregate breeding value and concluded that all traits of economic importance should be included. The disadvantage to this is that it would require estimation of a large number of genetic parameters and economic values. In some cases, these parameters cannot be estimated accurately, and the resulting selection will produce less than maximum change in profitability (Harris, 1964; Vandepitte and Hazel, 1977). A more practical approach may be to include only those traits which account for a significant (perhaps 10%) proportion of the variation in profit (Pearson, 1982).

When determining traits to be included in the selection criteria during development of a selection index, it is important to differentiate between ERT and indicator traits. An ERT is a trait directly associated with profitability, and can be identified by considering whether a change in performance of the trait will result in a change in either income from or cost of production (Golden et al., 2000). If income or expenses change independently of the trait in question, the trait is likely an indicator trait. For example, consider calving ease and birth weight which are two EPD associated with dystocia. Calving ease is the ERT because selection on this trait will result in greater calf survival and heifer rebreeding rates, resulting in greater income. Conversely, birth weight is only an indicator of calving difficulty. Birth weight itself cannot explain all the differences in calving difficulty, and therefore should not be the focus of selection decisions designed to reduce dystocia. When information is available for the ERT, information on the correlated indicator trait need not be considered when calculating a selection index. The concept of ERT can help focus selection pressure on what will directly influence profitability (Enns, 2013).

In practice, some traits in the objective are not readily observed, hence our need to use indicator traits for predicting traits that do hold economic relevance. For some ERT, data collected on the trait may misrepresent the population, and thus prediction on an indicator trait may be more accurate. For example, genetic evaluation for

carcass traits is problematic in seedstock herds because few young animals are harvested. Animals that are harvested are likely individuals deemed unsuitable for breeding, and not representative samples of offspring. It is also most appealing to incorporate traits for which data already exists, which often leads to incorporation of a number of indicator traits rather than ERT. The methodology to develop selection indices from a list of traits including some correlated indicator traits is well-accepted, but requires a priori knowledge of the genetic correlation between the indicator traits and ERT (Garrick and Golden, 2009).

Sivanadian and Smith (1997) showed that response to selection is improved as additional traits are added to the selection criteria, given that the parameters are known without error. They further demonstrated that the change in response increased as the heritability and/or the economic weight of each added trait increased. The magnitude of the change was influenced by the product of the heritability and the economic weight. Hazel (1943) confirmed that information collected on a greater breadth of traits for a greater number of animals will improve the response to selection when using indices based on that information. This was demonstrated through a swine breeding program using individual phenotypic data, productivity of the dam and average weight and score of the litter simultaneously in order to increase genetic progress expected when using an index to make selection decisions. Using an index which combined all three sources of information improved efficiency by 11.3 percent as compared to a selection index based only on an individual's own phenotypic records. Since time and effort expended in keeping records is but a small portion of total labor in a breeding program, it may be worthwhile to collect additional data on a larger number of animals in order to improve response when implementing index selection.

Estimation of relative economic values

Economic values are necessary for each trait in the breeding objective to ensure that selection emphasis is proportional to the economic importance of each trait. Considering that most beef production systems have generation intervals greater than five years and significant genetic improvement requires more than one generation, it is obvious that relative economic values must pertain to the long run (MacNeil et al., 1997). When developing a selection index utilized in pursuit of a breeding objective, prices of concern are those several years into the future when the outcome of selection will be realized in the commercial industry. Selection choices are dependent on the relative prices of inputs and outputs and are therefore essentially unaffected by the general inflation of prices common to all inputs and outputs (Pearson, 1982). When choosing prices, previous price trends must be combined with a prediction of whether or not the trend will continue at a steady rate, intensify, or weaken. Frequent changes in price relationship can have a devastating effect on genetic change. In traits for which prices vary drastically over short periods of time, particularly in a cyclic fashion, considering prices from a larger range of time may be beneficial. Economic values should be changed infrequently, and only after substantial evidence for changing these price relationships has accumulated. Relative economic values should not be influenced by year-to- year fluctuations in prices of inputs or outputs (MacNeil et al., 1997). Further supporting this conclusion, Balaine et al. (1981) found correlations ranging from 0.98 to 1.0 between estimates of profit using widely divergent prices over a 15 year period.

The profit equation is a widely used method to derive the relative economic value. Moav and Moav (1966) presented a profit equation to integrate the cost and returns from production to compare the profitability of animals. In animal breeding, the profit equation is a mathematic form of the production system and the breeding objective. Garrick and Golden (2009) discussed measuring profit of a cow-calf production system in terms of 'profit per unit land', and in a feedlot system in terms of 'profit per pen'. Thus, the specific profit perspective must be chosen in the initial stages of objective development.

Relative economic values recognize that economic return from a one standard deviation increase in one trait will not be equal to the same increase in another trait. Only economically important traits and indicator traits that will respond to selection are ultimately used by the seedstock producer. It is not efficient to measure or base selection on traits without economic value. Ponzoni and Newman (1989) outlined and implemented a method for determining relative economic values for beef production. In their example, they calculated relative economic values for the biological traits as partial derivatives of profit with respect to each trait holding the other traits constant at their mean levels.

The relative economic value for any one trait may differ depending on the goal of the breeding objective and the subsequent markets that the particular breeding objective targets. Melton (1995) discovered that a breeding objective generated specifically for a non-integrated cow-calf producer resulted in greater relative economic value for maternal and reproductive traits and lower relative economic value for retail product than an objective encompassing the entire beef industry. MacNeil et al. (1994) found that for Canadian beef production, cow weight, female fertility and maternal weaning weight had economic importance in maternal lines but not in terminal lines. Additionally, it was discovered that growth had higher relative economic value for the finishing phase than for the backgrounding phase. In the U.S. beef system, MacNeil (2005) found a high correlation among breeding objectives for four terminal sire lines.

This study demonstrated the importance of increasing calf survival, weight gain, dressing percentage and marbling score while decreasing feed intake and back fat. Quantifying the importance of each trait in the breeding objective is essential not only to effectively select animals with higher rank, but also to determine the priority of traits in relation to future research and to develop systems for data collection and evaluation of these traits (Garrick and Golden, 2009).

While studying effects of production conditions on economic values, Koots and Gibson (1998) found that changes in some specific conditions resulted in large shifts in economic values. Reducing fertility and survival rate caused the largest changes to economic values. The economic value for mature weight was affected by practically all alternatives considered in the study. These results suggest that economic values will differ between production and marketing circumstances. MacNeil et al. (1997) pointed out that resources available for production and level of production vary among production units resulting in different economic structures. Thus, a customized approach to estimation of economic values, as described by Upton et al. (1988), may be warranted. Still, in practice the effects of changes of economic values on selection response depend on which traits appear in the index. Additionally, it has been shown that small changes in economic values do not significantly affect selection response (Vandepitte and Hazel, 1977; Smith, 1983). As such, a relatively small number of selection indices should cover a wide range of production and economic circumstances.

Selection Index Construction

In his seminal paper, Hazel (1943) outlined the following statistics which are necessary for selection index construction:

- A. Phenotypic constants
 - 1. Standard deviation for each trait
 - 2. Phenotypic correlation between each pair of traits
 - 3. Phenotypic correlations between the traits of relatives
- B. Genetic constants
 - 1. Heritable fraction of the variance in each trait
 - 2. Genetic correlation between each pair of traits

Hazel (1943) introduced the analytical method for calculating a selection index. The aggregate value (H) of an animal is defined as the sum of its genotypes for each economic trait (Gi), with each genotype being weighted according to the relative economic value of that trait (ai). An animal's genotype for a specific trait is the sum of the average additive effects of genes which influence the trait. Therefore, aggregate genotype is defined as:

(1) H = a1G1 + a2G2 + ... + anGn

Recognizing that environmental factors, dominance and epistasis may influence phenotypic performance, selection for improved breeding value must be practiced indirectly by selecting for a correlated variable (I) based on the phenotypic performance of each individual for several traits. Hazel (1943) defines I as:

(2) I = b1X1 + b2X2 + ... + bnXn

where Xi represents the phenotypic performance for the several traits which influence the goal trait and bi represents the multiple regression coefficients designed to make the correlation between H and I as large as possible.

MacNeil et al. (1997) demonstrated how to calculate the vector (b) of weighting coefficients for each source of information in the index using the equation:

(3) b= P-1Gv

where P is a n x n matrix of the phenotypic (co)variances among the n traits measured and available as selection criteria, G is a n x m matrix of the genetic (co)variances among all m objective traits, and v is a m x 1 vector of relative economic values for objective traits.

Indices using EPD

Bourdon (1998) pointed out two serious drawbacks in applying index weighting factors to phenotypic values for an individual. First, this method lacks accuracy because it does not incorporate information on relatives. Second, it is biased because genetic differences among contemporary groups are not accounted for. These issues can be overcome by using genetic predications derived from best linear unbiased prediction (BLUP) instead of individual phenotypic performance. Henderson (1963) demonstrated that if genetic predictions derived from multitrait BLUP are available for all traits in the breeding objective, genetic predications can simply be substituted for true breeding values in the breeding objective. Schneeberger et al. (1992) reconfirmed the equivalence of weightings derived using BLUP and conventional selection index. Further, they presented the models needed to compute index weights for the more likely case in which traits in the breeding objective differ from those for which genetic predictions are available. The equation to estimate index weights to be applied to EPD is:

b= G11-1G12v

where G11 is a n x n matrix of genetic (co)variances among the n selection criteria, G12 is a n x m matrix of the genetic (co)variances among the n selection criteria and m objective traits, and v is a m x 1 vector of relative economic values for all objective traits. Index weights calculated in this way account for potentially large amounts of information on relatives. The index will also be unbiased because predictions derived from BLUP procedures are themselves unbiased (Bourdon, 1998).

Improving accuracy of selection indices

Information gleaned from large scale genetic evaluation has led to an ever increasing number of EPD being made available to producers. The amount of information available is often overwhelming to producers when trying to make the best selection and purchase decisions. The increase in the number of EPD was based on the presumption that EPD for more traits helped better characterize the genetic capability of animals (Bourdon, 1998). In many cases, little consideration was given to the value of EPD and instead they were produced simply because data were cheaply and easily collected. Improvements in current selection indices still need to be made by increasing the number of ERT that have EPD reported. Spangler (2015) expressed his concern that many ERT are not currently evaluated nor collected routinely in the seedstock sector, even though they drive value downstream. Some ERT that fall into this category are reproductive performance, disease, tenderness, primal yield and dark cutters. In the future it is recommended that enterprise-level profitability moves closer to industry-level profitability.

Generally, some and perhaps most traits in the breeding objective are not observed so predictions for them must be calculated through covariances with measured traits. Since the relationships between observed traits and traits in the breeding objective are defined by covariances, they are assumed linear. While the use of covariance matrices is mathematically straightforward, it is not without problems (Bourdon, 1998). The linearity between some of these traits is questionable. Evans (1996) reported a nonlinear genetic relationship between scrotal circumference and heifer pregnancy. Scrotal circumference is an easily measured trait likely to be used as selection criteria while heifer pregnancy is an ERT likely to appear in a breeding objective. The accuracy of selection based on an index including scrotal circumference as selection criteria could be greatly improved if instead EPD for heifer pregnancy were reported and could be included in the selection criteria.

Conclusions and Implications to Genetic Improvement of Beef Cattle

Enns and Nicoll (2008) determined the long-term genetic change in a commercial beef breeding program resulting from selection for indices developed for an economic breeding objective. Changes in each of the breeding objective component traits were applied to the breeding objective equation to estimate average change in the aggregate breeding value (H). Selection based on an economic breeding objective in a New Zealand Angus nucleus herd described by Nicoll et al. (1979) was initiated in 1976, and significant improvement in H was realized from 1976 through 1993. During this time, the increase in net income at an annual rate was equated to US\$24.68 per cow lifetime. This study was among the first to report genetic improvement in commercial beef cattle breeding programs resulting from selection for an economic breeding objective and using indices that did not contain all traits of economic importance. Traits included in the index were weaning weight, yearling weight, mature cow weight and cow fertility. Results support the use of multi-trait selection indices to predict an economic breeding objective in beef cattle genetic improvement programs.

Livestock industries have relied increasingly on selection indices as a tool for maximizing profitability in individual livestock operations. Many breed associations have produced and published selection indices for use by producers. Literature provides ample evidence that selection indices are an efficient tool to utilize when making selection decisions. The power of selection indices can be improved by the willingness of producers to adopt selection index technology through guidelines for deriving relative economic values and implementing selection index technology in national cattle evaluation (MacNeil et al., 1997). The key to successful use of a selection index lies in identifying the index that best suits a particular operation while keeping in mind the goal to improve multiple traits simultaneously (Enns, 2013). Recognizing that the beef industry is dynamic and ever-changing, the selection index is a versatile tool to increase profitability of an operation by selecting for multiple traits of economic importance.

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