DEVELOPMENT OF TERMINAL AND MATERNAL ECONOMIC SELECTION INDICES IN BEEFMASTER CATTLE

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DEVELOPMENT OF TERMINAL AND MATERNAL ECONOMIC SELECTION INDICES IN BEEFMASTER CATTLE

by

Kathleen Pearl Ochsner

A THESIS

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In the design of economic selection indices, the relative importance of traits in the breeding objective is reflected by their relative economic weighting. The objective of this study was to develop two economic selection indices for Beefmaster cattle: one for a terminal production system and one for a maternal production system. The terminal index was developed assuming bulls are mated to mature cows with all resulting progeny harvested. The maternal index was developed assuming bulls are mated to a combination of heifers and mature cows, with resulting progeny retained as replacements or sold at weaning.

National average prices from 2010 to 2014 were used to establish income and expenses for each system. Economic values were determined by simulating 100,000 animals using SAS 9.3 and approximating the partial derivatives of the profit function by perturbing one trait at a time, by one unit, holding the other traits constant at their respective means. Relative economic values for the terminal objective traits hot carcass weight (HCW), marbling score (MS), ribeye area (REA), 12\textsuperscript{th}-rib fat (FAT) and feed intake (FI) were 91.29, 17.01, 8.38, -7.07 and -29.66, respectively. Relative economic values for the maternal objective traits calving difficulty direct (CDd), calving difficulty maternal (CDm), weaning weight direct (WWd), weaning weight maternal (WWm), mature weight (MW) and heifer pregnancy (HP) were -2.11, -1.53, 18.49, 11.28, -33.46 and 1.19, respectively.
Selection criteria were chosen from expected progeny differences (EPD) currently reported by Beefmaster Breeders United (BBU). Index coefficients for the terminal selection criteria yearling weight (YW), ultrasound ribeye area (UREA), ultrasound 12\textsuperscript{th}-rib fat (UFAT) and ultrasound intramuscular fat (UIMF) were 1.715, 0.806, -36.600 and 12.375, respectively. Index coefficients for the maternal selection criteria birth weight (BWT), WWd, WWm, YW and scrotal circumference (SC) were -1.371, 1.426, 0.945, -0.660 and 2.725, respectively. The application of these indices in operations with specific production goals would facilitate genetic improvement by aiding Beefmaster breeders in their sire selection decisions.
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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). Maximizing beef production efficiency is of critical importance to all segments of the beef industry. 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). Genetic improvements provide a way for beef producers to achieve greater efficiency. Expected progeny differences (EPD) are the traditional genetic tools used to select breeding livestock. While EPD are a sound selection tool, a drawback 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 et al., 2011). Falconer and Mackay (1996) recommended the use of selection indices for multitrait 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 threshold level for just one trait. In this situation selection indices are an appropriate alternative because they allow for superior performance in some traits to compensate for poor performance in other traits.

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 that goal. Harris et al. (1984) presented a nine-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 weights, (5) design an animal evaluation system, (6) develop selection criteria, (7) design matings for selected animals, (8) design a system for expansion (dissemination of genetic superiority) and (9) compare alternative combined programs.

After defining the breeding objective, information on genetic parameters, phenotypic parameters and economic values are needed. These may be calculated from available phenotypic data or obtained from previous literature estimates. Estimates of genetic parameters vary little across breeds. However, economic values may differ significantly between different production systems and different production goals. Smith (1983) indicated that large differences in economic values may affect the efficiency of
the selection index. The economic value is typically obtained by constructing a profit equation and applying partial differentiation. The profit equation is constructed according to the breeding objective. Selection criteria will be unique to each production system. Considering that the selection index is influenced by many factors, the efficiency of the index should be calculated to determine whether the index will be sufficient in helping producers achieve their goals.

Literature suggests that breeding objectives should be divided into specific aims or categories depending on the desired 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. commercial beef production system can generally be divided into two sectors, those that retain replacement heifers and those that do not. For those commercial herds that are self-replacing, a general purpose index would be the most appropriate given that selected females will be kept for breeding purposes and all cull animals will be sold either at weaning or at a later endpoint. Terminal selection indices would most frequently be used by commercial beef producers looking to purchase animals for use as parents in a system where all progeny will be harvested. Although not pervasive in the U.S. beef industry, commercial producers whose primary revenue is generated through the sale of replacement females to other commercial producers should select sires based on a maternal index.

The objective of this study was to develop economic selection indices for terminal and maternal purpose Beefmaster cattle. Implementation of these indices will increase profitability of individual beef cattle operations and facilitate genetic improvement.
Literature Review

History of the Beefmaster breed

In 1931, Tom Lasater began developing the Beefmaster breed (ISA Beefmasters, 2015). America’s first composite breed, the Beefmaster was developed from a systematic crossing of one-half Brahman, one-fourth Hereford and one-fourth milking Shorthorn. These three very different breeds were combined to complement each other. Today, it is estimated that the breed is composed of slightly less than one-half Brahman and slightly more than one-fourth each of Hereford and Shorthorn (Ritchie, 2009).

The United States Department of Agriculture first recognized the Beefmaster as a pure breed in 1954. In 1961, a breed association was established in San Antonio, TX, under the name of Beefmaster Breeders Universal (Ritchie, 2009). Since then, the name has changed to Beefmaster Breeders United (BBU). From 1974 to 1998, membership in BBU grew from 300 to nearly 7,000 (BBU, 2012). Beefmaster Breeders United is one of the top five largest beef breed registries in the United States in terms of membership, and ranks top ten in registrations (BBU, 2012). While brownish red is the most common color of Beefmaster cattle, BBU enforces no color standards (BBU, 2012). Colors vary greatly and include red, reddish brown, brown, dun and black. Some Beefmasters are solid colored, but many have some white markings. With the current commercial demand for black-hided cattle, more breeders are producing black Beefmasters (Ritchie, 2009).

Beefmaster cattle are appropriately named for their ability to thrive in the harsh brush terrain of the southern United States (BBU, 2012). The Beefmaster breed is unique in that it is the sole beef breed to implement a guiding production philosophy.
Beefmaster Breeders United is dedicated to producers who breed for the ‘Six Essentials’ of disposition, fertility, weight, conformation, hardiness and milk production. The concept behind the original development of these ‘Six Essentials’ was to select cattle only based on traits of economic relevance. This unique approach is why Beefmasters are known by the slogan “The Profit Breed” (ISA Beefmasters, 2015).

**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 (ERT) 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.
Objective traits considered for market animals by Dickerson et al. (1974) were carcass composition, meat quality and optimum weight at slaughter. Objective 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.

It may be the case that a single livestock operation wishes to implement multiple breeding objectives. Howarth et al. (1997) investigated three strategies in the literature for the concurrent improvement of several breeding objectives: (1) specialist - select all animals on a single index derived to maximize one of the objectives (2) split herd - select within specialist sub herds for each of the different objectives (3) average - select all animals on an index derived to maximize the average of the objectives. Del Bosque Gonzalez and Kinghorn (1990) considered the implications when contributors to an open nucleus breeding scheme were selected for an objective that differed from that of the nucleus. They concluded that for moderately correlated objectives, the ‘split herd’
strategy was the best option. However, when the nucleus was retained, selection on an ‘average’ index resulted in the greatest benefits. Selection on one ‘specialist’ index to maximize its corresponding objective resulted in the least improvement. Phocas et al. (1995) examined the need for specific selection indices to improve breeding objectives for two types of production, concluding that the ‘average’ strategy, produced selection response comparable to ‘split herd’ selection. Howarth et al. (1997) summarized that when different breeding objectives are moderately or highly correlated, the best method for concurrent selection is the ‘average’ strategy. However, when the correlation between objectives is low or when recording costs for objectives differ markedly, the ‘split herd’ strategy is better suited for multiple objective selection.

Amer et al. (1996) considered a breeding objective for beef suckler herds in order to estimate economic values for reproductive traits. It was concluded that economic values of reproductive traits are important when determining the advantages of direct selection on reproductive variables to improve the economic merit of suckler herds. In a later study, Amer et al. (2001) considered five breeding objective trait groups which were: growth, weaned calf, calving, carcass and reproduction. These were used to define selection sub-indices, with the intention to simplify selection decisions by commercial bull and semen buyers for situations where all resulting progeny are slaughtered, or when some female progeny are retained as replacements. Breeding objectives in the form of six sub-indices and two total indices were proposed to simplify selection decisions of commercial dairy and beef cattle owners purchasing beef bulls. The total indices may be used in situations where average portions of female progeny are kept as replacements.
Sub-indices are used in more specific systems, such as when bulls are purchased either as terminal sires or for mating primarily to heifers.

It has been argued that biological efficiency should be used in defining breeding objectives instead of economic efficiency to ensure 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 in the objective (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 considered 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). Dekkers et al. (2004) pointed out that traits included in the objective should directly contribute to profit and have enough genetic variation that selection for improvement of the trait will change overall profitability of the operation. In the beef industry, important objective traits include growth, reproduction and carcass traits.

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 economic importance of the trait, potential for genetic improvement of the trait, genetic interrelationships 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 would 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).
Estimation of relative economic values

Relative 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 to be 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.

Multiple approaches have been previously used to determine economic values. Originally, Hazel (1943) obtained economic values by determining the economic input of
a one unit change in a trait by summing the cost of all changes in inputs and outputs. This method is intuitively appealing for its advantages of being simple, based on established biological relationships, and reasonably free of the (co)variance structure of the traits in the breeding objective and profit. However, this method will not work if there are no established biological relationships between the traits and corresponding outputs (Pearson, 1982), for example the relationship between the sale price of breeding stock and the breeding values for production traits of those animals.

An alternative approach is to calculate the regression of profitability of each animal on the traits in the breeding objective (Pearson and Miller, 1981). Computationally, this method provides a simple approach to determining economic values, but it too presents challenges. The traits necessary to calculate profitability are accurately recorded in only a limited number of herds, which do not necessarily represent the breadth of the population to which it is meant to be applied. Given this, the (co)variance structure may be quite different from the population as a whole. Multiple regression estimates are dependent on the traits included. Therefore, an incomplete breeding objective might yield economic values unique to the management conditions represented and consequently can be misleading when applied in different conditions. Using multiple regression to estimate economic values works best when the data used is representative of the population to which it is being applied, the (co)variance structure is similar to that of the population as a whole and a complete breeding objective is in use (Pearson, 1982).

The most widely used method to derive the relative economic value of breeding objective traits is the profit equation. Moav and Moav (1966) presented a profit equation
that integrated the costs and returns of production to compare the profitability of animals. In animal breeding, the profit equation is a mathematic representation of the production system and the breeding objective. Previous literature demonstrates that the profit equation varies greatly across operations as a reflection of the traits involved in the equation (Hirooka et al., 1998; Amer et al., 2001; Conington et al., 2004; Fernandez-Perea and Alenda Jiménez, 2004). Furthermore, profit equations vary between profit units, e.g., per female, per individual or per unit of product. 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’. It is important that the specific profit perspective be chosen in the initial stages of breeding objective development.

Traditionally, the profit equation and selection index are both the linear expressions of traits. Nonetheless, in some situations the profit equation can be a nonlinear expression of those traits (Moav and Hill, 1966). Nonlinear profit equations create challenges because the economic value of a trait is not constant, but changes as the population mean changes. Nonlinear selection indices have been considered but these resulted in a lower selection response than the best linear index (Goddard, 1983). Ponzoni et al. (1998) suggested that non-linearity can be accommodated by periodically revising the economic value assigned to the trait in question. Goddard (1983) found that for any profit equation (even nonlinear) the linear index derived by the graphical method of Moav and Hill (1966) either achieved the maximum increase in profit possible for a given selection intensity, or reached the maximum of the profit surface with the minimum selection intensity. Kluyts et al. (2004) reconfirmed this, indicating that profit maximization can be achieved though implementation of a simple linear profit equation.
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 biological traits as partial derivatives of the profit equation with respect to each trait, holding the other traits constant at their respective mean levels.

The relative economic value for any one trait may differ depending on 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).

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 effect of changes to economic values on selection response depends 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.

It is vital to consider whose economic benefit will be maximized during the selection process (Harris, 1970). If the livestock producer’s primary objective is to maximize efficiency of their operation relative to other operations, the producer’s primary reason for purchasing certain breeding stock will be based on their assessment of how the resulting generations will contribute to the profit of their operation. This in mind, the seedstock producer should base breeding decisions on the objective of their potential customers, provided that market signals are transmitted up the marketing chain. Yet, as pointed out by Pearson (1982), decisions which maximize net income at the producer level may not always be ideal from other viewpoints within the industry (i.e., packers, retailers, consumers, etc.). When developing a breeding objective from the individual producer’s point of view, the prices received could be adjusted to consider the impact they will have on other segments of the industry. For instance, consider a dairy
industry supplying a market with a relatively inelastic demand for dairy products. A genetic improvement in milk yield per cow will decrease the cost of producing each kg of milk, leading to a downward shift in the supply curve and a decreased equilibrium price. Therefore, relative economic weights are unaffected by accounting for the change in price caused by genetic improvement. For the industry as a whole, establishing economic weights based on an integrated firm is the correct method. Even if market signals are not transmitted up the marketing chain, the benefits of genetic improvement are captured by some participants, and competition will eventually cause them to be passed on to other parts of the industry (Goddard, 1998).

Determining traits in the selection criteria

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 change of either income 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 for 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 ease. Birth weight itself cannot explain all the differences in calving ease, 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).

Ideally, the selection criteria would include all ERT in the breeding objective. However, in practice some traits in the objective are not readily observed, hence our need to use indicator traits for predicting traits that 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 \textit{a priori} knowledge of the genetic correlation between the indicator traits and ERT (Garrick and Golden, 2009).

Adding additional traits to the selection criteria improves response to selection, given that the parameters are known without error. Sivanadian and Smith (1997) demonstrated that response to selection increased as the heritability and/or 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 larger 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 to increase genetic progress expected when using a selection index. 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.

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 genotype ($H$) of an animal is defined as the sum of its genotypes for each economic trait ($G_i$), with each genotype being weighted according to the relative economic value of that trait ($a_i$). An animal’s genotype for a specific trait is the sum of the average additive effects of genes which influence the trait. Thus, $H$ is defined as:
\[ H = a_1G_1 + a_2G_2 + \ldots + a_nG_n \]

Environmental factors, dominance and epistasis may make phenotypic performance different than the genotype for that trait. Therefore, animals having the highest values for \( H \) can’t be recognized directly with perfect accuracy. Hence, selection for improved breeding value must be practiced indirectly by selecting directly for a correlated variable (\( I \)) based on the phenotypic performance of each individual for several traits. Hazel (1943) defines \( I \) as:

\[ I = b_1X_1 + b_2X_2 + \ldots + b_nX_n \]

where \( X_i \) represents the phenotypic performance for the several traits which influence the objective trait and \( b_i \) 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:

\[ b = P^{-1}Gv \]

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

*Phenotypic and genetic parameters*

MacNeil et al. (1997) provided an example to demonstrate the use of phenotypic and genetic parameters in development of a selection index. In the example, selection
emphasis was placed on five traits including: birth weight (BW), yearling weight (YW), scrotal circumference (SC), net reproduction (NR) and carcass merit (CM). Three measures for the traits were available including BW, YW and SC. Phenotypic constants (indicated by subscript P) were used to construct the P matrix, while genetic constants (indicated by subscript A) were used to construct the G matrix. The v matrix is composed of the economic weights (EW) of the objective traits. The P, G, and v matrices are as follows:

\[
P = \begin{bmatrix}
\text{var}_{P_{BW}} & \text{cov}_{P_{BW,YW}} & \text{cov}_{P_{BW,SC}} \\
\text{cov}_{P_{BW,YW}} & \text{var}_{P_{YW}} & \text{cov}_{P_{YW,SC}} \\
\text{cov}_{P_{BW,SC}} & \text{cov}_{P_{YW,SC}} & \text{var}_{P_{SC}}
\end{bmatrix}
\]

\[
G = \begin{bmatrix}
\text{var}_{A_{BW}} & \text{cov}_{A_{BW,YW}} & \text{cov}_{A_{BW,SC}} & \text{cov}_{A_{BW,NR}} & \text{cov}_{A_{BW,CM}} \\
\text{cov}_{A_{BW,YW}} & \text{var}_{A_{YW}} & \text{cov}_{A_{YW,SC}} & \text{cov}_{A_{YW,NR}} & \text{cov}_{A_{YW,CM}} \\
\text{cov}_{A_{BW,SC}} & \text{cov}_{A_{YW,SC}} & \text{var}_{A_{SC}} & \text{cov}_{A_{SC,NR}} & \text{cov}_{A_{SC,CM}}
\end{bmatrix}
\]

\[
v = \begin{bmatrix}
\text{EW}_{BW} \\
\text{EW}_{YW} \\
\text{EW}_{SC} \\
\text{EW}_{NR} \\
\text{EW}_{CM}
\end{bmatrix}
\]

Precision of genetic and phenotypic parameters is essential for estimation of selection index weights because they directly determine the accuracy of the index. The method stated above calculates an economic selection index based on phenotypic records. However, when phenotypic records are not available, as is often the case, the method presented in the following section may be used.

*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 predictions 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 predictions can simply be substituted for true breeding values
when calculating the aggregate genotype. Schneeberger et al. (1992) 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 coefficients to be applied to EPD is:

$$b = G_{11}^{-1}G_{12}v$$

where $G_{11}$ is a $n \times n$ matrix of genetic (co)variances among the $n$ selection criteria, $G_{12}$ is
a $n \times m$ matrix of the genetic (co)variances among the $n$ selection criteria and $m$ objective
traits, and $v$ is an $m \times 1$ vector of economic values for objective traits. Index coefficients
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).

Accuracy of an index

The accuracy of the selection index ($r_{HI}$) is defined as the correlation between $H$ and
$I$, which is calculated as:

$$r_{HI} = \frac{\sigma_{HI}}{\sigma_t \sigma_H}$$
where $\sigma_{HI}$ is the covariance between $H$ and $I$, $\sigma_I$ is the standard deviation of the index, and $\sigma_H$ is the standard deviation of aggregate genotype. In matrix notation, the equation becomes:

$$r_{HI} = \frac{b'Gv}{\sqrt{(b'Pb)(v'Cv)}}$$

where $C$ is an $m \times m$ matrix of genetic (co)variances among the objective traits, and $b$, $P$, $G$ and $v$ are as previously defined.

Information gleaned from large scale genetic evaluation has led to an ever increasing number of EPD being made available. Producers often experience information overload when trying to make the best selection and purchase decisions. The increase in the number of EPD has been based on the presumption that EPD for more traits helps better characterize the genetic capability of animals (Bourdon, 1998). In many cases, little consideration has been 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 selection criteria. Since the relationships between observed selection criteria 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.

Sensitivity of selection indices to estimates of (co)variances

Selection index theory largely assumes that the genetic and phenotypic parameters are known without error. In practice however, these parameters have to be estimated from samples of data and use of the estimates rather than the true parameters will lead to errors in predicting the response to selection and to a loss of efficiency relative to using the optimum index (Sales and Hill, 1976). The reliability of genetic and phenotypic parameters is dependent on numerous variables including the estimation procedure, the data structure and the sample size. Harris (1963) points out the importance of using a considerable amount of data for index construction. The effect of errors in the phenotypic and genetic correlations is different from trait to trait, depending upon the magnitude of the correlations and the relationships with other traits. Pease et al. (1967) determined that errors in heritability estimates do not seem to affect the index as much as errors in some individual (co)variances. Furthermore, they showed that the efficiency of an index is more sensitive to errors in the phenotypic correlations than to errors in the
genetic correlations. In the most sensitive case studied, an error of 0.3 in the correlation between feed efficiency and lean cuts resulted in approximately a 6 percent loss in efficiency.

Being as (co)variance parameters used in selection index development are merely estimates, an index which is insensitive to changes in (co)variance parameters would be superior. The sensitivity of an index to these estimates is calculated as the proportion of maximum selection response we expect in the aggregate genotype if one set of variances was used \((u)\) to derive our index coefficients when another set of variances was true \((t)\). This sensitivity measure is denoted as \(E_{ut}\), and is expressed in the following equation:

\[
E_{ut} = \frac{b'uG_t v}{\sqrt{b'uP_u b_u}} \ast \frac{1}{\sqrt{b'tG_t v}}
\]

where \(b_u = P_u^{-1}G_u v\) and \(b_t = P_t^{-1}G_t v\). Selection indices are often criticized for involving assumptions about genetic parameters. To be used confidently in animal improvement programs, selection indices must be fairly robust to changes in (co)variances. Thus, sensitivity calculations are important to determine the practical application of an index to real industry conditions. Simm et al. (1986) evaluated the sensitivity of two selection indices to changes in parameters. Individual genetic correlations between traits were increased or decreased by 0.2, which never reduced efficiency below 0.99. When individual correlation changes of 0.4 were applied, predicted efficiency of selection was only reduced to 0.97. The insensitivity of indices to moderate changes in genetic correlations reported by this study is in accordance with other literature (Fowler et al., 1976; Vandepitte and Hazel, 1977; Smith, 1983).
Sensitivity of selection indices to estimates of economic values

Vandepitte and Hazel (1977) emphasized the insensitivity of index selection to changes in economic values. Smith (1983) opted to further investigate the question, using larger changes in economic weights than had previously been evaluated. His discovery was that large changes in economic weights may or may not result in considerable losses in efficiency, depending on the distribution of traits in the index. In the instance where one trait dominates an index, the efficiency will be sensitive mainly to changes in that particular trait. In this case, efficiency may remain high when the economic weight of the dominate trait is accurate, regardless of changes in economic weights of the minor traits. When there is a balance among traits, moderate losses in efficiency may be incurred through changes in economic weights. The most significant losses in efficiency will occur when important traits are omitted, unimportant traits are given importance, or the direction of selection is reversed for an important trait.

Rønningen (1971) studied the effect of false economic ratios between two traits on the change in aggregate genotype for a two-trait index. It was concluded that the loss in efficiency was not exceedingly serious when moderate deviations from the true economic ratios were used. The loss increased as the deviation from the true economic ratio increased. When the most economically important trait was given a negative weight, the loss was substantial, especially when the heritability was high.

Koots and Gibson (1998) worked to quantify the sensitivity of economic values to changes in production and marketing circumstances by re-estimating economic values for a number of different conditions. They 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. Still, their overall conclusion was that the majority of economic values were insensitive to economic inputs. It was also discovered that economic values were largely insensitive to differences in management.

Simm et al. (1986) reported the efficiency of two selection indices to a proportional increase or decrease of 0.5 in the relative economic value of each trait in the aggregate breeding value. Efficiency never fell below 0.967 when relative economic values were changed one at a time, indicating that the indices examined were insensitive to wide changes in economic weights. The variation in economic values considered by Simm et al. (1986) is likely to exceed variation between production systems and between different methods of calculation.

*Implementation of selection indices in the beef industry*

Enns and Nicoll (2008) determined the long-term genetic change in a commercial beef breeding program resulting from selection based on 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. 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 the aggregate breeding value 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 multitrait selection indices to predict an economic breeding objective in beef cattle genetic improvement programs.

Many breed associations have produced and published selection indices for use by producers. The various indices described below are intended for use within specific production goals (Spangler, 2015):

<table>
<thead>
<tr>
<th>Breed</th>
<th>Selection Index</th>
<th>Abbreviation</th>
<th>Progeny Endpoint</th>
<th>System</th>
</tr>
</thead>
<tbody>
<tr>
<td>Angus</td>
<td>Cow Energy Value</td>
<td>$EN</td>
<td>replacement heifers</td>
<td>M</td>
</tr>
<tr>
<td></td>
<td>Weaned Calf Value</td>
<td>$W</td>
<td>weaned feeder calves</td>
<td>A</td>
</tr>
<tr>
<td></td>
<td>Feedlot Value</td>
<td>$F</td>
<td>live fed cattle</td>
<td>T</td>
</tr>
<tr>
<td></td>
<td>Grid Value</td>
<td>$G</td>
<td>carcass sold on CAB grid</td>
<td>T</td>
</tr>
<tr>
<td></td>
<td>Beef Value</td>
<td>$B</td>
<td>retained ownership carcass sold on CAB grid</td>
<td>T</td>
</tr>
<tr>
<td>Charolais</td>
<td>Terminal Sire Profitability Index</td>
<td>TSPI</td>
<td>carcass sold on grid</td>
<td>T</td>
</tr>
<tr>
<td>Gelbvieh</td>
<td>$Cow</td>
<td>$Cow</td>
<td>replacement heifers</td>
<td>M</td>
</tr>
<tr>
<td></td>
<td>Efficiency Profit Index</td>
<td>EPI</td>
<td>feedlot efficiency</td>
<td>T</td>
</tr>
<tr>
<td></td>
<td>Feeder Profit Index</td>
<td>FPI</td>
<td>carcass sold on grid</td>
<td>T</td>
</tr>
<tr>
<td>Hereford</td>
<td>Baldy Maternal Index</td>
<td>BMI$</td>
<td>carcass sold on grid; replacement heifers</td>
<td>A</td>
</tr>
<tr>
<td></td>
<td>Brahman Influence Index</td>
<td>BII$</td>
<td>carcass sold on grid; replacement heifers</td>
<td>A</td>
</tr>
<tr>
<td></td>
<td>Calving Ease Index</td>
<td>CEZ$</td>
<td>matings to replacements</td>
<td>M</td>
</tr>
<tr>
<td></td>
<td>Certified Hereford Beef Index</td>
<td>CHB$</td>
<td>carcass sold on CHB grid</td>
<td>T</td>
</tr>
<tr>
<td>Breed</td>
<td>Selection Index</td>
<td>Abbreviation</td>
<td>Progeny Endpoint</td>
<td>System</td>
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<td>------------</td>
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<td>--------</td>
</tr>
<tr>
<td>Limousin</td>
<td>Mainstream</td>
<td>MTI</td>
<td>carcass sold on grid</td>
<td>T</td>
</tr>
<tr>
<td></td>
<td>Terminal Index</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Simmental</td>
<td>All-Purpose Index</td>
<td>API</td>
<td>carcass sold on grid; replacement heifers</td>
<td>A</td>
</tr>
<tr>
<td></td>
<td>Terminal Index</td>
<td>TI</td>
<td>carcass sold on grid</td>
<td>T</td>
</tr>
<tr>
<td>Red Angus</td>
<td>HerdBuilder</td>
<td>HerdBuilder</td>
<td>carcass sold on grid; replacement heifers</td>
<td>A</td>
</tr>
<tr>
<td></td>
<td>GridMaster</td>
<td>GridMaster</td>
<td>carcass sold on grid</td>
<td>T</td>
</tr>
</tbody>
</table>

M=maternal, A=all-purpose, T=terminal

Livestock industries have relied increasingly on selection indices as a tool for maximizing profitability in individual livestock operations. 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.
Literature Cited


Development of terminal and maternal economic selection indices in Beefmaster cattle

Abstract

Two economic selection indices were developed for Beefmaster cattle, one for a terminal objective and one for a maternal objective. For the terminal index it was assumed that bulls will be mated to mature cows with all resulting progeny harvested. For the maternal index it was assumed that bulls will be mated to a combination of heifers and mature cows, with resulting progeny being retained as replacements or sold at weaning. National average prices from 2010 to 2014 were used to establish income and expenses for each system. Economic values were determined by simulating 100,000 animals and approximating the partial derivatives of the profit function by perturbing traits one at a time, by one unit, while holding the other traits constant at their respective means. Relative economic values for the terminal objective traits hot carcass weight (HCW), marbling score (MS), ribeye area (REA), 12th-rib fat (FAT) and feed intake (FI) were 91.29, 17.01, 8.38, -7.07 and -29.66, respectively. Relative economic values for the maternal objective traits calving difficulty direct (CDd), calving difficulty maternal (CDm), weaning weight direct (WWd), weaning weight maternal (WWm), mature weight (MW) and heifer pregnancy (HP) were -2.11, -1.53, 18.49, 11.28, -33.46 and 1.19, respectively. Selection criteria were chosen from expected progeny differences (EPD) currently reported by Beefmaster Breeders United (BBU). Phenotypic and genetic parameter values among the selection criteria and objective traits were obtained from literature. Index coefficients for EPD of the terminal selection criteria yearling weight
(YW), ultrasound ribeye area (UREA), ultrasound 12th-rib fat (UFAT) and ultrasound intramuscular fat (UIMF) were 1.715, 0.806, -36.600 and 12.375, respectively. The accuracy of the terminal index was 0.503. Index coefficients for EPD of the maternal selection criteria birth weight (BWT), WWd, WWm, YW and scrotal circumference (SC) were -1.371, 1.426, 0.945, -0.660 and 2.725, respectively. The accuracy of the maternal index was 0.428. The application of these indices in operations with specific production goals would facilitate genetic improvement of Beefmaster cattle by aiding producers in their sire selection decisions.

Introduction

Since they were first proposed by Hazel (1943), multitrait selection indices have become the method of choice for maximizing genetic gain in a specific breeding objective. Economic selection indices simplify comparisons of animals by combining expected progeny differences (EPD) and the economic value of economically relevant traits (ERT) into a single value that represents an animal’s total genetic worth. Economic values are required for each ERT in the breeding objective to ensure that selection emphasis is proportional to the economic importance of each of these traits.

Most currently available indices are designed to be used by multiple breeders for specific marketing endpoints. These typically use industry economic averages to determine economic weights, and there is considerable evidence that index selection by this method is successful (MacNeil, 2003; Enns and Nicoll, 2008). Currently, Beefmasters Breeders United (BBU) reports ten EPD, but provides no tool for multitrait selection. Thus, economic selection indices are needed to assist producers with selection
decisions. The objective of the current study was to develop two economic selection indices for Beefmaster cattle in terminal and maternal production systems.

**Materials and Methods**

*Choice of objective traits*

The breeding objective assumed for development of the terminal index was to increase profitability of an operation where all calves were born from mature cows, retained through the feedlot phase and sold on a grid based system. The five objective traits considered for the terminal index included hot carcass weight (HCW), marbling score (MS), ribeye area (REA), 12\textsuperscript{th}-rib fat (FAT) and feed intake (FI), with the latter representing the only expense related phenotype among the objective traits. Yardage, labor and animal health were considered as fixed costs in the terminal simulation and did not vary based on the phenotype of an individual animal.

The breeding objective assumed for development of the maternal index was to increase profitability in a system where calves were born from a combination of heifers and mature cows. Male calves from the system were assumed to be sold at weaning, and heifer calves were either retained or sold at weaning alongside their male counterparts. Six objective traits were considered including calving difficulty direct (CDd), calving difficulty maternal (CDm), 205-day weaning weight direct (WWd), 205-day weaning weight maternal (WWm), mature weight (MW) and heifer pregnancy (HP). Calving difficulty (direct and maternal) were both considered as objective traits because of the potential of this trait to result in additional expenses at calving time. Weaning weight direct was included because of its direct effect on income through value of the calf when
sold at weaning. Increased WWm will result in additional income through weight of the
calf at weaning, but also additional expenses due to increased cow feed intake. Mature
weight influences the expense side of the profit equation because increased MW results
in increased feed intake. Mature weight also influences income given cull cows will be
sold and their value determined on a live-weight basis. Increased HP will result in
increased profitability of an operation through additional calves to be marketed at
weaning and decreased feed expenses for feeding replacements. Veterinary expenses,
bedding, marketing, custom operations, fuel, repairs, and processing were considered as
fixed costs and did not vary based on the biological merit of an individual animal.

Choice of selection criteria

Selection criteria for both indices were selected from the ten EPD currently
reported by BBU. The suite of BBU EPD includes: birth weight (BWT), WWd, WWm,
365-day yearling weight (YW), scrotal circumference (SC), ultrasound ribeye area
(UREA), ultrasound 12th-rib fat (UFAT), ultrasound rump fat (URUMP), ultrasound
intramuscular fat percentage (UIMF) and total maternal (TM). Selection criteria
considered for the terminal index were YW, UREA, UFAT and UIMF.

Selection criteria for the maternal index using EPD were BWT, WWd, WWm,
YW and SC. Birth weight is an indicator trait for the objective traits CDd and CDm, and
was included among the selection criteria since an EPD for calving difficulty was not
available. For a maternal objective, YW is an indicator of MW. Scrotal circumference
was included among the selection criteria because it was the only trait which has a non-
zero genetic correlation with HP.
Simulation for a terminal objective

A method to derive economic values is partial differentiation of a profit equation (Hill, 1974; Ponzoni and Newman, 1989; Forabosco et al., 2004). The identification of sources of income and expense in the beef cattle herd enable the development of a profit equation where profit is a function of income and expense (Ponzoni and Newman, 1989). Sources of income and expense for the terminal production system were indentified and the profit was simulated for 100,000 animals using SAS 9.3.

In the production and marketing system assumed for the terminal index, half of the calves were fed through a calf-fed system where they were in the feedlot for 211 days and slaughtered at 416 days of age. The other half were assumed to be fed through a yearling system where they were on pasture for 315 days, fed in the feedlot for 90 days and slaughtered at 610 days of age. It was assumed that all replacement females were obtained from outside the herd. The sex ratio for offspring was assumed to be 1:1. Income was derived solely from the marketing of animals for slaughter on a grid based system. Market price was determined based upon the carcass weight, quality grade and yield grade (YG) of the animal. Income was estimated for steers and heifers sent to slaughter from both yearling and calf-fed systems. Phenotypes for HCW, MS, FAT and REA were simulated from a random normal distribution with the means and standard deviations (SD) for each respective trait obtained from literature (Table 1). The genetic relationships between traits were accounted for by a Cholesky decomposition applied to the genetic covariance matrix between all objective traits considered for the terminal index.
The 5-year (2010-2014) average price for steers and heifers at slaughter was obtained from the Livestock Marketing Information Center (LMIC, 2015) and used as the base price for all slaughter animals. The base price was US$3.858/kg with a SD of US$0.642/kg. Premium and discount values based on YG, quality grade, and HCW were obtained from United States Department of Agriculture - Agricultural Marketing Service (USDA-AMS, 2015) and are presented in Table 2. Quality grade of each carcass was assigned based on simulated marbling score, and each animal received a premium or discount accordingly. Since it was assumed that animals sent to slaughter will be younger than 30 months of age, age was not considered as a contributing factor to quality grade. Yield grade was assigned using the following equation: $YG = 3.0 + 0.984 \times \text{FAT} - 0.0496 \times \text{REA} + 0.00838 \times \text{HCW}$. Weight discounts were applied to animals for which the simulated carcass weight was under 272 kg or over 409 kg. Carcass price was calculated as the sum of base carcass price, YG premium/discount, quality grade premium/discount and weight discount (if applicable). Income for each animal was calculated by multiplying the carcass price (US$/kg) by the weight of the animal in kg. Total income per animal was estimated by averaging the income for calf-fed animals and yearling-fed animals.

Expenses for the production system assumed in development of the terminal index included: feed, veterinary, medicine, bedding, marketing, custom operations, fuel, repairs, processing and yardage. A 5-year (2010-2014) average and standard error (SE) of prices for feedstuffs used in the production system were calculated using information obtained from the USDA–National Agricultural Statistics Service (USDA-NASS, 2015). The correlation between corn prices and other feedstuffs (Table 3) was included in the
simulation to ensure that the relationship between prices did not deviate from their true relationship in the industry. Prices for each feed ingredient were simulated on a random normal distribution as a function of the average price, SE and correlation with the price of corn. Feed intake was simulated on a random normal distribution with mean and SD presented in Table 1. Feed costs for animals fed through the calf-fed system were simulated assuming animals were consuming the feedlot diet outlined in Table 3 for 211 days. Cattle in the yearling system were fed the winter yearling system diet for 198 days, the summer yearling system diet for 117 days and the feedlot diet for 90 days (Table 3).

Other costs for the terminal system included veterinary, medicine, bedding, marketing, custom operations, fuel, repairs, processing and yardage. These costs were considered fixed while building the profit equation since they did not vary based on the biological merit of an individual animal. Veterinary and medicine costs were estimated by calculating a 5-year average from data provided by D. W. Gillings (Christiansen Land and Cattle Ltd., Kimball, SD, personal communication). Means and SE of other costs including bedding, marketing, custom operations, fuel, repairs, processing and yardage were obtained from Barron Lopez (2013). Costs were simulated using the defined means and SE (Table 4) for the various expenses and a random seed on a normal distribution.

Total cost was calculated as a sum of feed costs and other costs through all phases of production, and was expressed as dollars per animal.

*Simulation for a maternal objective*

In the present study, there were three traits considered in the breeding objective that would be recorded on a categorical scale: CDd, CDm and HP. In order to estimate
the economic value of these categorical traits, it was assumed that there was an underlying normal distribution of the categorically expressed phenotypes (Falconer and Mackay, 1996). The latent variable was simulated and binary phenotypes (e.g., 0 or 1) were assigned by imposing a threshold to the normal distribution of latent variables according to the desired probability of success. To estimate the economic value for the threshold traits, the truncation point was perturbed by one percentile such that the probability of success increased by one unit. The phenotypes for growth traits WWd, WWm and MW were simulated from a normal distribution. The mean and SD assumed in the simulation for all maternal objective traits are summarized in Table 5. The relationships between traits were accounted for by a Cholesky decomposition applied to the genetic covariance matrix between all objective traits.

Income was derived from marketing calves at weaning and non-pregnant cows. Average prices and SE of animals ranging in weight from 159 to 318 kg were calculated from 5 years of filtered data (2010-2014) from the USDA-AMS (2015) (Table 6). Data was filtered to include only states in the region where Beefmaster cattle are the most prevalent. States included were Alabama, Arkansas, Georgia, North Carolina, South Carolina, Florida, Mississippi and Texas. Average prices and SE of cull females represent a 5-year average (2010-2014) obtained from the LMIC (2015) (Table 6). Sex was randomly assigned using a uniform distribution. To account for the effect of sex on weaning weight, the weaning weight obtained from the random simulation was multiplied by 0.95 for females and 1.05 for males. If the pregnancy status was simulated as being pregnant, income was calculated as the product of the weight of the calf and the price per
kg assigned based on sex and weight. If the pregnancy status was simulated as being open, income was derived from marketing the cull female.

A 5-year (2010-2014) average and SE of prices for feedstuffs used in the production system was calculated using information obtained from the USDA-NASS (2015). The correlation between corn prices and other feedstuffs was accounted for in the simulation. Prices for each feed ingredient were simulated on a random normal distribution as a function of the average price, SE and correlation with the price of corn. Feedstuff composition was extracted from the Nutrient Requirements of Beef Cattle (NRC, 1996). Dry matter content, metabolic energy content and prices of feedstuffs can be found in Table 7. Energy cost per energy metabolized (US$/Kcal) was estimated based on the price, dry matter content and energy value of each component of the diet. Feed costs were calculated as the sum of costs for maintenance, growth, lactation and gestation. These costs were estimated as a function of the metabolizable energy requirement (Kcal) and the cost per energy metabolizable (US$/Kcal). The metabolizable energy requirement for maintenance, growth, lactation and gestation were calculated using methods described by Barron Lopez (2013). Feed cost was estimated on the basis of the total metabolic energy requirement per animal (Kcal/animal/period) and the cost of metabolizable energy (US$/Kcal).

Feed cost was estimated for calves from birth to weaning (205 d), replacement heifers from weaning to breeding (450 d), replacement heifers from breeding to calving (730 d) and cows from calving to weaning (935 d). Amount of feed consumed during each time period from 205 d to 935 d is outlined in Table 8. To estimate the feed cost for calves from birth to weaning the energy content of milk consumed by the calves was
subtracted from the total energy requirement of calves. Total energy that calves obtained from milk was calculated assuming 12.3 kg DM in milk, 5.45 Mcal of energy per kg DM of milk (Chenette and Frahm, 1981), 0.88 ME per energy gross in milk (Webster, 1985), and 1.06 Mcal ME/kg of milk (NRC, 1996). Calving difficulty cost was calculated as a function of the frequency of calving difficulty incidences and the price of calving difficulty treatment. Calving difficulty cost was assumed to be $169 for each incidence. Total expense was calculated as the sum of the simulated feed cost for calves, heifers and cows, and costs associated with calving difficulty. When a heifer was simulated as open, the expense of feeding her replacement was also accounted for.

Determining economic values

Profit of each system (terminal and maternal) was calculated on a per animal basis by subtracting simulated cost from simulated income. Using methods described by MacNeil et al. (1994), economic values of the objective traits were determined by approximating partial derivatives of profit at the point of mean performance with respect to each driving variable. The model was parameterized and a base profit calculated. Each driving variable was then perturbed upward one unit in separate iterations of the simulation. Differences between profits observed in these latter iterations and the profit from the baseline iteration were the economic values for each respective driving variable. Economic values are expressed as dollars in profit/loss per unit change for each trait. The relative economic value of each objective trait was estimated as a product of the respective economic value and the genetic SD for that trait. 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.
**Selection index coefficients**

Hazel (1943) first introduced the selection index equations to calculate index coefficients (b) for each of the selection criteria:

\[ b = P^{\dagger}Gv \]

where \( P \) is a \( n \times n \) matrix of the phenotypic (co)variances among the \( n \) traits measured and available as selection criteria, \( G \) is a \( n \times m \) matrix of the genetic (co)variances among the \( n \) selection criteria and \( m \) objective traits, and \( v \) is an \( m \times 1 \) vector of economic values for all objective traits. This method was used to calculate economic index coefficients to be applied to phenotypic measures for both the terminal and maternal index. Genetic covariances were calculated from the genetic SD and genetic correlations using the method described by Cameron (1997). Phenotypic covariances were also calculated by the method described by Cameron (1997), using the phenotypic SD and phenotypic correlations between traits. The heritability, genetic variances and phenotypic variances of the objective traits and selection criteria used to calculate the \( P \) and \( G \) matrices were extracted from literature and are presented in Tables 9 and 10 for the terminal and maternal indices, respectively. Phenotypic correlations among the selection criteria and genetic correlations between the selection criteria and objective traits needed for calculation of the (co)variance matrices were extracted from scientific literature and are presented in Tables 11 and 12 for the terminal and maternal indices, respectively. The resulting \( P \) and \( G \) matrices for the terminal index are presented in Tables 13 and 14, respectively. The \( P \) and \( G \) matrices for the maternal index are presented in Tables 15 and 16, respectively.
Schneeberger et al. (1992) presented a method to calculate a vector of index coefficients to be applied to EPD for the selection criteria in the index. The equation to estimate index coefficients to be applied to EPD is:

$$b = G_{11}^{-1}G_{12}v$$

where $G_{11}$ is a $n \times n$ matrix of genetic (co)variances among the $n$ selection criteria, $G_{12}$ is a $n \times m$ matrix of the genetic (co)variances among the $n$ selection criteria and $m$ objective traits and $v$ is an $m \times 1$ vector of economic values for all objective traits. Index coefficients to be applied to EPD for selection criteria were calculated using this method. Note that the $G_{12}$ matrix is synonymous to the previous $G$ matrix for the terminal index. For the maternal index, the $G_{12}$ matrix (Table 17) is different due to the different selection criteria, where the direct and maternal effects on weaning are combined. The genetic (co)variance matrices among selection criteria ($G_{11}$) are presented in Tables 18 and 19 for the terminal and maternal indices, respectively. For each selection index, it was ensured that a positive definite (co)variance matrix existed.

**Selection index parameters**

Following the notation of Van Vleck (1993), the accuracies ($r_{HI}$) of the indices that utilize phenotypic measures were calculated as:

$$r_{HI} = \frac{b'Gv}{\sqrt{(b'Pb)(v'Cv)}}$$

where $b'Gv$ represents the covariance between the index and aggregate genotype, $b'Pb$ represents the index variance, and $v'Cv$ represents the aggregate genotype variance. $C$ is
an \( m \times m \) genetic (co)variance matrix among the objective traits. The \( \mathbf{C} \) matrix is presented in Tables 20 and 21 for the terminal and maternal indices, respectively.

For indices that utilize EPD as the selection criteria, the following equation was used to calculate the accuracy of the index:

\[
    r_{\text{HI}} = \frac{\mathbf{b}'G_{12}\mathbf{v}}{\sqrt{(\mathbf{b}'G_{11}\mathbf{b})(\mathbf{v}'\mathbf{C}\mathbf{v})}}
\]

where \( \mathbf{b}'G_{12}\mathbf{v} \) represents the covariance between the index and aggregate genotype, \( \mathbf{b}'G_{11}\mathbf{b} \) represents the index variance, and \( \mathbf{v}'\mathbf{C}\mathbf{v} \) represents the aggregate genotype variance. The substitution of \( \mathbf{G}_{11} \) for \( \mathbf{P} \) in calculating the index variance is accompanied by several assumptions. In presenting the index coefficient equations using EPD as the selection criteria, Schneeberger et al. (1992) explained that \( \mathbf{G}_{11} \) is the genetic (co)variance matrix of the selection criteria which is assumed to be known without error. However, EPD would never be known with complete certainty given the heterogeneity of the residual variance. Thus, the index accuracy estimated herein would be the ‘best case scenario,’ presuming that the accuracy of each EPD included in the index for each animal was unity. We would expect the true accuracy of the index to lie somewhere between the two accuracies presented herein that were produced by assuming the index was comprised of either phenotypic measures or by EPD that are known without error.

Predicted response in aggregate genotype (\( R_H \)) when phenotypic measures were considered as selection criteria was calculated as:

\[
    R_H = i \frac{\mathbf{b}'G\mathbf{v}}{\sqrt{\mathbf{b}'P\mathbf{b}}}
\]
where $i$ is selection intensity and the other terms are as previously defined. When EPD were the selection criteria, $R_H$ was calculated using the following equation:

$$R_H = i \frac{b'G_{12}v}{\sqrt{b'G_{11}b}}$$

Response in a given objective trait ($R_{at}$) when phenotypic measures were the selection criteria was calculated for each of $t$ traits as:

$$R_{at} = i \frac{b'G_t}{\sqrt{(b'Pb)}}$$

When EPD were the selection criteria, the equation was:

$$R_{at} = i \frac{b'G_{12t}}{\sqrt{(b'G_{11}b)}}$$

*Selection index sensitivity*

Economic selection index coefficients are seldom known without error because of uncertainties in (co)variances and in economic values. One way to determine the sensitivity of indices to changes in the (co)variances and economic values assumed is to calculate the efficiency of the index. The efficiency ($E_u$) is given as:

$$E_u = R_{Ht} = \frac{b'_{u}G_{12t}v}{\sqrt{b'_{u}G_{11t}b_{u}}} \ast \frac{1}{\sqrt{b'_{t}G_{12t}v}}$$

where $b_u$ are coefficients derived from ‘used’ values and $b_t$ are true index coefficients, given by $P^{-1}_uG_u\nu$ and $P^{-1}G_t\nu$, respectively. The ‘used’ index coefficients are arbitrary, while the ‘true’ index coefficients are assumed to be optimum. In reality, index
coefficients assumed to be optimum may not always be accurate, which is why it important to calculate the efficiency and determine the impact of inadvertently using incorrect index coefficients.

Sensitivity to absolute changes in genetic correlations between objective traits and selection criteria of ±0.2 and ±0.4 were calculated for both the terminal and maternal index. These changes in genetic correlations are equivalent to those investigated by Simm et al. (1986). It is important to note that in some cases adding or subtracting these values resulted in a change of sign. In instances where these changes would have resulted in a correlation greater than unity, the genetic correlation was assumed to be 1.

Sensitivity to a 50% increase or decrease in the magnitude of the economic value of each trait in the breeding objective was calculated for both the terminal and maternal index. This follows the methods of Simm et al. (1986), who also calculated the efficiency of two selection indices following an increase or decrease of 50% in the economic value of each trait in the aggregate breeding value.

**Rank correlation**

In order to objectify the difference in ranking based on selection using either the terminal or maternal index, a rank correlation was calculated. One hundred high accuracy sires, based on weaning weight EPD accuracy, were selected from the BBU database and their index values calculated for both the terminal and maternal index. Sires were ranked based on both indices, and the Spearman’s rank correlation was calculated.
Results and Discussion

Economic values

Economic values, relative economic values, and the proportion of emphasis placed on each objective trait in both systems are presented in Table 22. In the terminal objective, HCW is the driving variable receiving 59.5% of the emphasis, implying that selection based on the index will result in the most gain in HCW. Feed intake receives the next highest emphasis at 19.3%. In the maternal objective, MW is the primary driver receiving 49.2% of the emphasis, implying that decreasing MW will do the most to improve profitability of operations with a maternal objective. Weaning weight direct is the second highest priority receiving 27.2% of the emphasis.

To enable comparisons to results from the current study, the economic values reported in the literature were converted to US dollars using the June 2016 exchange rate. As expected, in the present study the economic values estimated for HCW, MS and REA in the terminal objective were positive. Amer et al. (2001) reported a similar economic value of carcass weight in a sub-index targeting carcass traits for beef cattle in Ireland. The economic value of HCW reported by Amer et al. (2001) was 2.13 US$/kg. The economic value for MS reported herein is consistent in sign with the value reported by Melton (1995) of US$18.30/score for formula sales of slaughter beef in the U.S. For the Japanese beef industry, Hirooka et al. (1998) estimated economic values of marbling for a series of alternative management and economic systems. The economic value for marbling ranged from 0.34 to 0.52 US$/Japanese beef marbling standard. Hirooka et al. (1998) showed that economic values for marbling remained positive across a variety of
production systems and economic assumptions. The economic value of REA in the present study was positive, which was anticipated because increased REA will result in a lower numerical YG and thus a higher carcass value. MacNeil and Newman (1994) reported an economic value of US$3.93 per cutability percentage for a Canadian terminal sire line.

Twelfth rib fat was characterized by a negative economic value. This was expected because increasing FAT will also increase numerical YG, and consequently raise the carcass discount when the YG exceeds 4. This result aligns with the negative economic values for carcass fat reported by Amer et al. (2001) and Barron Lopez (2013). Amer et al. (2001) estimated an economic value of -US$5.64 per point of carcass fat in a breeding objective emphasizing growth and carcass traits, where carcass fat was represented by a 15-point scale. Barron Lopez (2013) reported an economic value of -US$39.29/cm for a general purpose beef herd, which closely aligns in direction and magnitude with the economic value for FAT estimated in the current study.

Considering that FI is an expense trait, it was no surprise that the economic value for this trait was strongly negative at -US$57.05/kg of feed. Other studies also estimated negative economic values for this trait. Amer et al. (2001) estimated economic values of -US$0.0035/effective energy (EE) units for summer feed intake and -US$0.011/EE units for winter feed intake of beef cattle in Ireland. Hietala et al. (2013) reported an economic value of -US$32.74/kg of DM of residual feed intake for Finnish dairy cattle in fattening.

For the maternal objective, CDd and CDm had negative economic values which is logical considering the veterinary costs, labor and possible mortality associated with this
trait. Hietala et al. (2013) reported an economic value for calving difficulty of US$24.53/score, where score for calving difficulty was divided into four score groups. This was for a Finnish dairy production system where surplus calves were sold at a young age, and no subsidies were applied. The larger magnitude of the economic value reported by Hietala et al. (2013) compared to the values presented herein can be attributed to the different scale used to represent calving difficulty.

Economic values for WWd and WWm were both found to be positive, though WWm to a lesser magnitude. This can be attributed to the fact that there is an expense associated with the added milk production of the dam. Similarly, MacNeil et al. (1994) reported positive economic values for WWd and WWm in maternal strains of Canadian Beefbooster cattle, with the economic value of WWm being lower in magnitude compared to WWd. MacNeil et al. (1994) estimated economic values of percent direct effect on weaning weight ranging from US$0.17 to US$0.21 in three strains of maternal Canadian cattle. Economic values of percent maternal effect on weaning weight ranged from US$0.08 to US$0.12.

The economic value estimated in the present study for MW was US$0.96/kg, which is rational considering that an increase in MW will result in increased feed expenses for the cow herd. This is consistent with what is reported in literature. MacNeil et al. (1994) found an economic value of US$0.25 per kg of MW in a Canadian Beefbooster population treated as general purpose. Amer et al. (2001) reported an economic value of US$0.14 per kg of MW for a reproduction selection index for Irish beef cattle. Hietala et al. (2013) estimated an economic value of US$1.11 per kg of MW for Finnish dairy cows in a system where surplus calves are sold at a young age.
The economic value for HP was US$2.68 per percent, which is logical because HP affects the number of calves available to be marketed at weaning time. This is consistent with what is reported by MacNeil et al. (1994), who found an economic value of US$1.01 for female fertility on a percentage basis in maternal strains of Canadian Beefbooster cattle. Amer et al. (1996) estimated the economic value of conception rate at first post partum oestrus in four herds at either average, high or low rates of conception. Economic values estimated for average conception rates ranged from US$0.15 to US$0.65 per 1% change. Populations with a high mean conception rate had the lowest economic values for heifer pregnancy, while populations with low mean conception rates had the highest economic values for heifer pregnancy. The results of Amer et al. (1996) indicate that the economic values for improvements in cow fertility will depend on the assumed population mean.

Index coefficients for phenotypic measures

Index coefficients for terminal phenotypic measures of YW, UREA, UFAT and UIMF were 0.74, 0.08, -31.04 and 13.32, respectively. The variance of the terminal index for phenotypic measures was 752.05. The variance of the aggregate genotype was 6,574.61. The accuracy of the terminal index for phenotypic measures was 0.338. The accuracy of the index describes how reliable the index is, and is the correlation between the index and the aggregate genotype. The response in aggregate genotype was 27.42i, which describes the genetic response from selection based on the index. This is expressed in units of selection intensity since response in aggregate genotype will also be dependent on the selection intensity applied. The response of each individual goal trait is reported in Table 22.
Index coefficients for maternal phenotypic measures of BWT, weaning weight, YW and SC were -1.83, 0.37, -0.03 and 1.45, respectively. The selection criteria differ from those used as selection criteria for EPD in that weaning weight is treated as a single phenotypic measure and not decomposed into direct and maternal effects. The variance of the index was 46.68. The variance of the aggregate genotype was 978.98. The accuracy of the index was 0.218 and the response in aggregate genotype was 6.83. The response of individual objective traits is reported in Table 22.

While it is good practice to calculate the index coefficients for phenotypic measures, for an index designed for a beef breed association index coefficients should be applied to EPD. Not only is this more practical, but literature supports the argument that index coefficients applied to EPD are more accurate. From a practicality standpoint, phenotypic measures will rarely be available for all animals on all traits included in the selection criteria. Sex-limited traits and traits such as carcass merit cannot be measured directly on all breeding animals. Initial selection decisions are often made before an animal expresses all the traits which determine its overall genetic merit. Additionally, 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 EPD instead of individual phenotypic performance. Another benefit of using index coefficients to be applied to EPD is that EPD are adjusted for heterosis effects, which is especially important in a composite breed like Beefmaster.
Index coefficients for EPD

Terminal index coefficients to be applied to EPD for YW, UREA, UFAT and UIMF were 1.715, 0.806, -36.600 and 12.375, respectively. Positive index coefficients for YW were also reported by Enns and Nicoll (2008) and by Barron Lopez (2013). For New Zealand beef cattle, Enns and Nicoll (2008) reported index coefficients for YW ranging from 0.6095 to 0.6292 for an economic breeding objective aimed at increasing net income per cow lifetime. Barron Lopez (2013) estimated index coefficients for a variety of indices including different combinations of selection criteria, all aimed at improving the efficiency of general purpose beef production. Estimates of index coefficients reported by Barron Lopez (2013) for YW ranged from 0.03 to 0.64. An index coefficient for REA of 1.92 was estimated by Barron Lopez (2013), which is similar to that reported for UREA in the present study. The negative index coefficient reported herein for UFAT is in agreement with the estimate by Swiger et al. (1965), who reported an index coefficient of -45.3 for a terminal breeding objective where net merit was determined from the retail value of the carcass less feed costs. An index coefficient for marbling of 25.3 was estimated by Barron Lopez (2013) for a breeding objective including eleven traits designed to improve the efficiency of beef cattle, which is similar in direction to the index coefficient reported in the current study for UIMF.

The variance of the terminal index, which describes the variance of the selection criteria, was 1,663.83. The variance of the aggregate genotype, which describes the variance of the objective traits, was 6,574.61. The accuracy of the terminal index was 0.503. The response in aggregate genotype was 40.79, which describes the genetic response from selection based on the index. This is expressed in units of selection
intensity since response in aggregate genotype will also be dependent on the selection intensity applied. The response of individual objective traits describes the response that is expected in each objective trait following selection decisions based on the index. These are reported in Table 22.

To test the implication of assuming part of the animals being fed through a calf-fed system and part being fed through a yearling system, two alternative sets of index coefficients were calculated. One set of index coefficients were calculated assuming all calves were fed through a calf-fed system. The other set of index coefficients were calculated assuming all calves were fed through a yearling system. The correlation between these two indices was found to be 0.99. Based on this result, it can be concluded that the index coefficients are relatively insensitive to which system is used to feed animals. Therefore, the index coefficients presented can be applied to a broad range of terminal objectives regardless of the system used to feed them out.

Index coefficients to be applied to EPD for the maternal index for BWT, WWd, WWm, YW and SC were calculated as -1.371, 1.426, 0.945, -0.660 and 2.725, respectively. Similar negative index coefficients for BWT have been reported in literature (Simm et al., 1986; MacNeil and Newman, 1994; Barron Lopez, 2013). Simm et al. (1986) reported an index coefficient for BWT of -3.675 for a breeding objective designed to increase efficiency of lean meat production for beef cattle in the United Kingdom. MacNeil and Newman (1994) found an index coefficient for BWT of -0.333 for a maternal dam line of Canadian beef cattle. Barron Lopez (2013) reported an index coefficient for BWT of -3.52 for general purpose beef cattle. Positive index coefficients for WWd were also reported by Dickerson et al. (1974) and Zeng (2013). Dickerson et
al. (1974) estimated standard partial regression coefficients for weaning weight ranging from 4 to 9 over several indices containing various combinations of component traits for selection to maximize efficiency. Zeng (2013) found an index coefficient for weaning weight of 5.461 for selection of females in a maternal breeding objective. An index coefficient for WWm of -0.72 was found by Barron Lopez (2013). The difference in sign compared to the coefficient presented herein is likely due to the difference in assumed genetic correlations. The difference may also be caused by different assumptions regarding the maternal effect on weaning. In the present study the index coefficient for YW is negative due to the fact that YW is a strong indicator of MW. This is in agreement with other estimates of index coefficients for MW in maternal objectives reported by MacNeil and Newman (1994) and Barron Lopez (2013) of -0.013 and -0.11, respectively. MacNeil and Newman (1994) also found a positive index coefficient for SC of 0.938 for a specialized maternal dam line.

The variance of the maternal index was 179.29 and the variance of the aggregate genotype was 978.98. The accuracy of the index was 0.428 and the response in aggregate genotype was 13.39. Response in individual objective traits is reported in Table 22. As expected, the accuracy of the maternal index was slightly lower than that of the terminal index because a higher number of indicator traits were included among the selection criteria. Some indicator traits (i.e., SC) were used because they were the only traits with a non-zero correlation to important breeding objective traits (i.e., HP). However, SC and HP are lowly correlated, meaning that SC is not a strong indicator of HP. The accuracy of selection based on an index including SC as selection criteria could be greatly improved if EPD for HP were instead reported and could be included in the selection
criteria. Having EPD available for other ERT such as stayability (STAY) would also greatly improve the accuracy and response to selection. However, in this case STAY was not even included among the objective traits because there were no correlated selection criteria available.

Sensitivity to changes in genetic correlations

The sensitivity to changes in genetic correlations is reported as the efficiency of the index after adding 0.2, subtracting 0.2, adding 0.4 or subtracting 0.4 from the genetic correlations between the objective traits and selection criteria, one at a time. Efficiencies for the terminal and maternal indices are reported in Tables 23 and 24, respectively.

For the terminal index, a change of ±0.2 in the genetic correlations resulted in efficiencies ranging from 0.97 to 1.00, with the exception of correlations involving HCW. Selection efficiencies resulting from the adjustment of correlations between HCW and other traits ranged from 0.85 to 0.97. The increased sensitivity of HCW to changes in its correlation with other traits may be due to the fact that it had the largest relative economic value of all traits considered. A change of ±0.4 resulted in selection efficiencies ranging from 0.94 to 1.00, with the same exception as before. Efficiencies resulting from the adjustment ±0.4 in genetic correlations between HCW and other traits ranged from 0.23 to 0.93. The efficiency 0.23 resulted from subtracting 0.4 from the ‘true’ genetic correlation between YW and HCW, and indicates that this index is sensitive to uncertainties in genetic correlations between these two traits. To further test the sensitivity to changes in the genetic correlation between YW and HCW, 0.3 was subtracted from the ‘true’ genetic correlation and the efficiency was calculated as 0.57.
The genetic relationship between HCW and YW is known to be moderate to strong and positive. Decreasing this genetic correlation by more than 0.2 assumes a genetic relationship that is not biologically reasonable. Consequently, it can be concluded that the index is insensitive to realistic changes in the assumed genetic correlation between these two traits.

For the maternal index, a change of ±0.2 in the genetic correlations between selection criteria and objective traits resulted in efficiencies ranging from 0.90 to 1.00, with the exception of correlations involving MW. Selection efficiencies after changing genetic correlations between MW and other traits ranged from 0.60 to 0.95. The increased sensitivity of the index to changes in genetic correlations between MW and other traits can likely be attributed to the fact that MW had the highest relative economic value of all traits considered. A change of ±0.4 in the genetic correlations resulted in efficiencies ranging from 0.73 to 1.00, again with the exception of correlations between MW and other traits. Efficiencies resulting from the adjustment ±0.4 in genetic correlations between MW and other traits ranged from -0.21 to 0.92. Two negative efficiency estimates were calculated. In these instances $R_{H_d}$ became negative, indicating that selection based on an index calculated with the ‘used’ parameters would result in a negative response in the aggregate genotype. The efficiency of -0.21 resulted from adding 0.4 to the ‘true’ genetic correlation between WWd and MW, which indicates very high sensitivity of the index to the genetic correlation between these two traits. This makes sense because these two moderately correlated traits are being selected for in opposite directions and are antagonistic to each other relative to the breeding objective.
In many cases, deviating the assumed genetic correlation by 0.4 from the ‘true’ genetic correlation is outside the biologically reasonable value and creates assumed genetics correlations that are not supported by the literature. To further investigate the sensitivity of the index, an intermediate value of 0.3 was added to the ‘true’ correlation between WWd and MW. The efficiency was calculated as 0.13. While this still is a low efficiency value, bringing the genetic correlation closer to what we assume to be true at least results in a positive value of $R_{Hu}$. Within the range of reasonable correlation values that could be assumed in calculation of the index coefficients, the index was insensitive.

_Sensitivity to changes in economic values_

The sensitivity to changes in economic values is reported as the efficiency of the index after a 50% increase or decrease in the economic value of each objective trait, one at a time. Efficiencies after changes in economic values of the terminal and maternal objective traits are reported in Table 25. Efficiency values for the terminal index ranged from 0.84 to 1.00. The index was the most sensitive to a 50% decrease in the economic value of HCW. The same rationale applies here as for the sensitivity of HCW to changes of genetic correlation. Aside from the sensitivity of HCW to the decrease in economic value, all other efficiencies calculated for the terminal index were above 0.97. This result indicates that the terminal index examined is relatively insensitive to wide changes in economic values. For the maternal index, efficiency values ranged from 0.79 to 1.00. The index is most sensitive to changes in the economic values of MW and WWd. This can likely be attributed to the fact that these two traits have relative economic values of higher magnitude than other objective traits. Both indices prove to be reasonably insensitive to changes in genetic correlations and economic values, indicating that they
can be used confidently regardless of uncertainties in genetic parameters and economic circumstances.

*Rank correlation*

The rank correlation between the terminal and maternal index was 0.446. Although the correlation is positive, considerable re-rank of sires would be expected when comparing the two indices and thus clearly delineating breeding objectives will be important to avoid undesired selection responses.
Implications

Multiple trait selection is critical given that more than one trait impacts overall profitability of a beef cattle operation. The most efficient way to conduct multiple trait selection is by using an economic selection index. Since an economic selection index is developed based on a specific production and marketing system, it should only be used to rank animals if the animals are to be used in a similar production and marketing system as that assumed in the creation of the index. A different production system would have a different profit equation, and thus different economic values for the same traits. For either a terminal or maternal breeding objective in Beefmaster herds, selection based on the traits considered for each respective objective would improve the profitability of an individual beef producers operation.

In the terminal objective considered for this study, decreasing FAT and FI while increasing HCW, REA and MS would increase profitability. Hot carcass weight and FI are the top two drivers of profit, implying that improving efficiency is crucial to increasing the profitability of an operation with a terminal objective. In the maternal objective, decreasing CDd, CDm and MW while increasing WWd, WWm and HP would increase profitability of the operation. Mature weight received the most emphasis in the maternal objective, implying that for the assumed parameters placing downward selection pressure on mature weight will do the most to increase profitability for a maternal breeding objective. Weaning weight direct was also a major driver of profit in the maternal index. Although MW and WWd are antagonistic to each other relative to the breeding objective, since the assumed correlation between them is not unity progress can be made in both traits simultaneously.
Defining the breeding objective and the marketing system of an individual operation should occur prior to implementation of selection based on any index. This is an important step to determine which index, if any available, most closely aligns with the objectives of the operation. Furthermore, the accuracy of both the terminal and maternal index may well be improved if additional ERT could be included in the selection criteria. For the terminal index, increased accuracy could be achieved if EPD for carcass traits reported by BBU were based on actual measures rather than ultrasound measures. Inclusion of important ERT for production traits such as HP, CD and STAY in the maternal index could greatly improve the accuracy and response in aggregate genotype. Creating additional EPD for ERT will be an important next step for BBU to improve genetic evaluation of animals, and in particular improve the accuracy and response to selection based on selection indices.
Literature Cited


Table 1. Means and standard deviations for terminal objective traits.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Mean</th>
<th>SD</th>
<th>Literature Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>HCW, kg</td>
<td>318.6</td>
<td>38.8</td>
<td>Moser et al. (1998)</td>
</tr>
<tr>
<td>MS, units</td>
<td>5.4</td>
<td>0.9</td>
<td>Wheeler et al. (2006)</td>
</tr>
<tr>
<td>REA, sq. cm</td>
<td>76.5</td>
<td>9.3</td>
<td>Moser et al. (1998)</td>
</tr>
<tr>
<td>FAT, cm</td>
<td>1.2</td>
<td>0.3</td>
<td>Moser et al. (1998)</td>
</tr>
<tr>
<td>FI, kg</td>
<td>6.6</td>
<td>1.1</td>
<td>Rolfe et al. (2011)</td>
</tr>
</tbody>
</table>

1HCW = hot carcass weight, MS = marbling score, REA = ribeye area, FAT = 12th-rib fat, FI = feed intake
2Marbling score units where 4.0 = Sl0 and 5.0 = Sm0
Table 2. Premiums and discounts for carcass sales based on 5-year average (2010-2014).

<table>
<thead>
<tr>
<th>Category</th>
<th>USDA Quality Grade</th>
<th>USDA Yield Grade</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 Adjustment (US$/kg)</td>
<td></td>
</tr>
<tr>
<td>Prime</td>
<td>0.402</td>
<td>0.092</td>
</tr>
<tr>
<td>Choice</td>
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<td>0.048</td>
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<tr>
<td>Select</td>
<td>-0.195</td>
<td>0.045</td>
</tr>
<tr>
<td>Standard</td>
<td>-0.480</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4.0-5.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>&gt;5.0</td>
</tr>
<tr>
<td>Carcass weight (kg)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;227</td>
<td>-0.702</td>
<td></td>
</tr>
<tr>
<td>227-250</td>
<td>-0.483</td>
<td></td>
</tr>
<tr>
<td>250-272</td>
<td>-0.061</td>
<td></td>
</tr>
<tr>
<td>272-409</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>409-431</td>
<td>-0.005</td>
<td></td>
</tr>
<tr>
<td>431-454</td>
<td>-0.006</td>
<td></td>
</tr>
<tr>
<td>&gt;454</td>
<td>-0.511</td>
<td></td>
</tr>
</tbody>
</table>

1 USDA Agricultural Marketing Service. Values reflect adjustments to the base carcass price.
Table 3. Diet composition for animals in calf-fed and yearling systems and prices of feedstuffs based on a 5-year average (2010-2014).

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>Inclusion (% DM)</th>
<th>Price (US$/kg)</th>
<th>SD (US$/kg)</th>
<th>Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Feedlot Diet Composition</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry-rolled corn</td>
<td>43.8</td>
<td>0.211</td>
<td>0.051</td>
<td>1.00</td>
</tr>
<tr>
<td>Wet distillers grains + solubles</td>
<td>43.8</td>
<td>0.200</td>
<td>0.048</td>
<td>1.00</td>
</tr>
<tr>
<td>Alfalfa hay</td>
<td>7.5</td>
<td>0.200</td>
<td>0.042</td>
<td>0.84</td>
</tr>
<tr>
<td>Urea</td>
<td>1.1</td>
<td>0.663</td>
<td>0.050</td>
<td>0.72</td>
</tr>
<tr>
<td>Limestone</td>
<td>1.9</td>
<td>0.028</td>
<td>0.002</td>
<td>0.92</td>
</tr>
<tr>
<td>Potassium</td>
<td>0.8</td>
<td>0.648</td>
<td>0.071</td>
<td>0.65</td>
</tr>
<tr>
<td>Salt</td>
<td>0.6</td>
<td>0.289</td>
<td>0.011</td>
<td>0.84</td>
</tr>
<tr>
<td>Trace minerals</td>
<td>0.43</td>
<td>0.877</td>
<td>0.037</td>
<td>0.18</td>
</tr>
<tr>
<td>Rumensin</td>
<td>0.03</td>
<td>19.575</td>
<td>3.915</td>
<td>0.40</td>
</tr>
<tr>
<td>Tylan</td>
<td>0.02</td>
<td>17.775</td>
<td>3.555</td>
<td>0.40</td>
</tr>
<tr>
<td>Vitamins</td>
<td>0.02</td>
<td>2.950</td>
<td>0.360</td>
<td>0.40</td>
</tr>
<tr>
<td><strong>Winter Yearling System Diet Composition</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prairie hay</td>
<td>74</td>
<td>0.140</td>
<td>0.022</td>
<td>0.66</td>
</tr>
<tr>
<td>Corn</td>
<td>20</td>
<td>0.211</td>
<td>0.051</td>
<td>1.00</td>
</tr>
<tr>
<td>44% protein supplement</td>
<td>6</td>
<td>0.436</td>
<td>0.060</td>
<td>0.87</td>
</tr>
<tr>
<td><strong>Summer Yearling System Diet Composition</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer Grazing</td>
<td>75</td>
<td>0.105</td>
<td>0.022</td>
<td>0.90</td>
</tr>
<tr>
<td>Prairie Hay</td>
<td>19</td>
<td>0.140</td>
<td>0.022</td>
<td>0.66</td>
</tr>
<tr>
<td>Corn</td>
<td>5</td>
<td>0.211</td>
<td>0.051</td>
<td>1.00</td>
</tr>
<tr>
<td>44% protein supplement</td>
<td>1</td>
<td>0.436</td>
<td>0.060</td>
<td>0.87</td>
</tr>
</tbody>
</table>

1 Based on Barron Lopez (2013)
2 USDA National Agricultural Statistics Service
3 Correlation with the price of corn. Based on Barron Lopez (2013).
Table 4. Price of other costs in terminal system based on average prices from 2010-2014.

<table>
<thead>
<tr>
<th>Expense Object</th>
<th>Average Cost (US$/head)</th>
<th>SE of cost</th>
</tr>
</thead>
<tbody>
<tr>
<td>¹Veterinary and Medicine</td>
<td>19.220</td>
<td>4.464</td>
</tr>
<tr>
<td>²Bedding</td>
<td>0.49</td>
<td>0.12</td>
</tr>
<tr>
<td>²Marketing</td>
<td>10.407</td>
<td>3.534</td>
</tr>
<tr>
<td>²Custom Operations</td>
<td>30.877</td>
<td>11.915</td>
</tr>
<tr>
<td>²Fuel</td>
<td>53.463</td>
<td>10.636</td>
</tr>
<tr>
<td>²Repairs</td>
<td>42.190</td>
<td>9.208</td>
</tr>
</tbody>
</table>

¹D. Gillings, Christiansen Land and Cattle Ltd., Kimball, SD, personal communication
²Barron Lopez (2013)
Table 5. Means and standard deviations for maternal objective traits.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Mean</th>
<th>SD</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>CDd, %</td>
<td>26</td>
<td>2.6</td>
<td>Ahlberg et al. (2016)</td>
</tr>
<tr>
<td>CDm, %</td>
<td>26</td>
<td>2.6</td>
<td>Ahlberg et al. (2016)</td>
</tr>
<tr>
<td>WWd, kg</td>
<td>82</td>
<td>11.02</td>
<td>2 BBU database</td>
</tr>
<tr>
<td>WWm, kg</td>
<td>23</td>
<td>5.52</td>
<td>2 BBU database</td>
</tr>
<tr>
<td>MW, kg</td>
<td>571</td>
<td>47.55</td>
<td>Costa et al. (2011)</td>
</tr>
<tr>
<td>HP, %</td>
<td>78</td>
<td>1.08</td>
<td>McAllister et al. (2011)</td>
</tr>
</tbody>
</table>

1CDd = calving difficulty direct, CDm = calving difficulty maternal, WWd = weaning weight direct, WWm = weaning weight maternal, MW = mature weight, HP = heifer pregnancy

2Beefmaster Breeders United unpublished data
Table 6. Market prices for weaned calves and cull cows based on a 5-year average (2010-2014).

<table>
<thead>
<tr>
<th>Animal Type</th>
<th>Animal Weight (kg)</th>
<th>Price (US$/kg)</th>
<th>SE (US$/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1Weaned Steer</td>
<td>159 – 181</td>
<td>3.838</td>
<td>0.980</td>
</tr>
<tr>
<td>1Weaned Steer</td>
<td>181 – 204</td>
<td>3.711</td>
<td>0.942</td>
</tr>
<tr>
<td>1Weaned Steer</td>
<td>204 – 227</td>
<td>3.690</td>
<td>0.920</td>
</tr>
<tr>
<td>1Weaned Steer</td>
<td>227 – 250</td>
<td>3.532</td>
<td>0.873</td>
</tr>
<tr>
<td>1Weaned Steer</td>
<td>250 – 273</td>
<td>3.466</td>
<td>0.898</td>
</tr>
<tr>
<td>1Weaned Steer</td>
<td>273 – 295</td>
<td>3.309</td>
<td>0.794</td>
</tr>
<tr>
<td>1Weaned Steer</td>
<td>295 – 318</td>
<td>3.312</td>
<td>0.871</td>
</tr>
<tr>
<td>1Weaned Heifer</td>
<td>159 – 181</td>
<td>3.405</td>
<td>0.939</td>
</tr>
<tr>
<td>1Weaned Heifer</td>
<td>181 – 204</td>
<td>3.295</td>
<td>0.882</td>
</tr>
<tr>
<td>1Weaned Heifer</td>
<td>204 – 227</td>
<td>3.228</td>
<td>0.854</td>
</tr>
<tr>
<td>1Weaned Heifer</td>
<td>227 – 250</td>
<td>3.150</td>
<td>0.838</td>
</tr>
<tr>
<td>1Weaned Heifer</td>
<td>250 – 273</td>
<td>3.078</td>
<td>0.773</td>
</tr>
<tr>
<td>1Weaned Heifer</td>
<td>273 – 295</td>
<td>3.043</td>
<td>0.718</td>
</tr>
<tr>
<td>1Weaned Heifer</td>
<td>295 – 318</td>
<td>3.048</td>
<td>0.676</td>
</tr>
<tr>
<td>2Cull Cow</td>
<td>408 – 499</td>
<td>1.698</td>
<td>0.510</td>
</tr>
</tbody>
</table>

1USDA Agricultural Marketing Service  
2Livestock Marketing Information Center
Table 7. Dry matter content, metabolic energy content and prices based on a 5-year average (2010-2014) of feedstuffs consumed by animals in the maternal system.

<table>
<thead>
<tr>
<th>Feedstuff</th>
<th>% DM of feedstuff</th>
<th>(^1)Metabolic energy content (Mcal/kg)</th>
<th>(^2)Average price (US$/kg)</th>
<th>SE of price (US$/kg)</th>
<th>(^3)Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer grazing</td>
<td>100</td>
<td>2.42</td>
<td>0.105</td>
<td>0.022</td>
<td>0.90</td>
</tr>
<tr>
<td>Winter grazing</td>
<td>100</td>
<td>1.92</td>
<td>0.053</td>
<td>0.011</td>
<td>0.90</td>
</tr>
<tr>
<td>Prairie hay</td>
<td>91</td>
<td>1.74</td>
<td>0.140</td>
<td>0.022</td>
<td>0.66</td>
</tr>
<tr>
<td>Corn</td>
<td>90</td>
<td>3.25</td>
<td>0.211</td>
<td>0.051</td>
<td>1.00</td>
</tr>
<tr>
<td>44% protein supplement</td>
<td>89</td>
<td>3.04</td>
<td>0.436</td>
<td>0.060</td>
<td>0.87</td>
</tr>
</tbody>
</table>

\(^1\)NRC (1996)  
\(^2\)USDA National Agricultural Statistics Service  
\(^3\)Correlation with the price of corn. Based on Barron Lopez (2013).
Table 8. Feeding program assumed for maternal system\textsuperscript{1}.

<table>
<thead>
<tr>
<th>Period</th>
<th>2\textsuperscript{Summer grazing}</th>
<th>3\textsuperscript{Winter grazing}</th>
<th>Prairie Hay</th>
<th>Corn</th>
<th>44% protein supplement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Begin</td>
<td>End</td>
<td>Days</td>
<td>kg/d</td>
<td>kg/d</td>
<td>kg/d</td>
</tr>
<tr>
<td>Weaning to breeding</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oct. 15</td>
<td>Apr. 30</td>
<td>198</td>
<td>0</td>
<td>0</td>
<td>4.42</td>
</tr>
<tr>
<td>May 1</td>
<td>May 31</td>
<td>31</td>
<td>0</td>
<td>0</td>
<td>5.13</td>
</tr>
<tr>
<td>Jun 1</td>
<td>Jun 15</td>
<td>15</td>
<td>7.21</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Breeding to calving</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jun. 16</td>
<td>Aug. 31</td>
<td>77</td>
<td>7.21</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sept. 1</td>
<td>Oct. 31</td>
<td>61</td>
<td>8.24</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nov. 1</td>
<td>Dec. 31</td>
<td>61</td>
<td>0</td>
<td>8.24</td>
<td>0</td>
</tr>
<tr>
<td>Jan. 1</td>
<td>Mar. 23</td>
<td>82</td>
<td>0</td>
<td>0</td>
<td>7.15</td>
</tr>
<tr>
<td>Lactation period</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mar. 24</td>
<td>May 31</td>
<td>69</td>
<td>0</td>
<td>0</td>
<td>6.59</td>
</tr>
<tr>
<td>Jun. 1</td>
<td>Oct. 15</td>
<td>137</td>
<td>13.29</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

\textsuperscript{1}Based on feeding program assumed by Barron Lopez (2013)
\textsuperscript{2}From June 1 to October 31
\textsuperscript{3}From November 1 to December 31
Table 9. Genetic and phenotypic parameters for selection criteria and objective traits in the terminal index.

<table>
<thead>
<tr>
<th>Traits</th>
<th>$h^2$</th>
<th>$\sigma^2_d$</th>
<th>$\sigma^2_p$</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>YW, kg</td>
<td>0.40</td>
<td>480.982</td>
<td>1,202.455</td>
<td>Moser et al. (1998)</td>
</tr>
<tr>
<td>UREA, sq. cm</td>
<td>0.29</td>
<td>16.501</td>
<td>56.900</td>
<td>Moser et al. (1998)</td>
</tr>
<tr>
<td>UIMF, %</td>
<td>0.375</td>
<td>0.176</td>
<td>0.470</td>
<td>MacNeil and Northcutt (2008)</td>
</tr>
<tr>
<td>UFAT, cm</td>
<td>0.392</td>
<td>0.012</td>
<td>0.031</td>
<td>MacNeil and Northcutt (2008)</td>
</tr>
<tr>
<td>FI, kg</td>
<td>0.39</td>
<td>0.275</td>
<td>0.705</td>
<td>Arthur et al. (2001)</td>
</tr>
<tr>
<td>HCW, kg</td>
<td>0.59</td>
<td>520.010</td>
<td>881.373</td>
<td>Moser et al. (1998)</td>
</tr>
<tr>
<td>REA, sq. cm</td>
<td>0.39</td>
<td>19.008</td>
<td>48.738</td>
<td>Moser et al. (1998)</td>
</tr>
<tr>
<td>FAT, cm</td>
<td>0.27</td>
<td>0.019</td>
<td>0.070</td>
<td>Moser et al. (1998)</td>
</tr>
<tr>
<td>MS, score</td>
<td>0.55</td>
<td>0.203</td>
<td>0.360</td>
<td>Gregory et al. (1995)</td>
</tr>
</tbody>
</table>

1 Selection criteria: YW = yearling weight, UREA = ultrasound ribeye area, UIMF = ultrasound intramuscular fat percentage, UFAT = ultrasound rib fat.

Objective traits: FI = feed intake, HCW = hot carcass weight, REA = ribeye area, FAT = 12\textsuperscript{th}-rib fat, MS = marbling score.

$h^2$ = heritability, $\sigma^2_d$ = genetic variance, $\sigma^2_p$ = phenotypic variance.

2 Marbling score units where 4.0 = Sl\textsuperscript{0} and 5.0 = Sm\textsuperscript{0}
Table 10. Genetic and phenotypic parameters for selection criteria and objective traits in the maternal index.

<table>
<thead>
<tr>
<th>Traits</th>
<th>$h^2$</th>
<th>$\sigma_a^2$</th>
<th>$\sigma_p^2$</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWT, kg</td>
<td>0.35</td>
<td>10.68</td>
<td>30.51429</td>
<td>Ahlberg et al. (2016)</td>
</tr>
<tr>
<td>WWd, kg</td>
<td>0.22</td>
<td>128.72</td>
<td>585.0909</td>
<td>Schiermiester et al. (2015)</td>
</tr>
<tr>
<td>WWm, kg</td>
<td>0.17</td>
<td>97.75</td>
<td>575</td>
<td>Schiermiester et al. (2015)</td>
</tr>
<tr>
<td>YW, kg</td>
<td>0.40</td>
<td>480.982</td>
<td>1202.455</td>
<td>Moser et al. (1998)</td>
</tr>
<tr>
<td>SC, cm</td>
<td>0.36</td>
<td>1.5876</td>
<td>4.41</td>
<td>Knights et al. (1984)</td>
</tr>
<tr>
<td>CDd, %</td>
<td>0.4</td>
<td>2.704</td>
<td>6.76</td>
<td>Ahlberg et al. (2016)</td>
</tr>
<tr>
<td>CDm, %</td>
<td>0.18</td>
<td>1.2168</td>
<td>6.76</td>
<td>Ahlberg et al. (2016)</td>
</tr>
<tr>
<td>MW, kg</td>
<td>0.54</td>
<td>1221</td>
<td>2261.111</td>
<td>Costa et al. (2011)</td>
</tr>
<tr>
<td>HP, %</td>
<td>0.17</td>
<td>0.1989</td>
<td>1.17</td>
<td>McAllister et al. (2011)</td>
</tr>
</tbody>
</table>

1Selection criteria: BWT = birth weight, WWd = weaning weight direct, WWm = weaning weight maternal, YW = yearling weight, SC = scrotal circumference. Objective traits: CDd = calving difficulty direct, CDm = calving difficulty maternal, WWd, WWm, MW = mature weight, HP = heifer pregnancy. $h^2$ = heritability, $\sigma_a^2$ = genetic variance, $\sigma_p^2$ = phenotypic variance.
Table 11. Genetic correlations (above diagonal) between selection criteria and objective traits, and phenotypic correlations (below diagonal) between selection criteria for the terminal index.

<table>
<thead>
<tr>
<th>Traits</th>
<th>YW</th>
<th>UREA</th>
<th>UIMF</th>
<th>UFAT</th>
<th>FI</th>
<th>HCW</th>
<th>REA</th>
<th>FAT</th>
<th>MS</th>
</tr>
</thead>
<tbody>
<tr>
<td>YW</td>
<td>0.44(^7)</td>
<td>0.31(^7)</td>
<td>0.03(^3)</td>
<td>0.5(^{10})</td>
<td>0.61(^3)</td>
<td>0.6(^3)</td>
<td>0.32(^2)</td>
<td>-0.2(^{11})</td>
<td></td>
</tr>
<tr>
<td>UREA</td>
<td>0.41(^3)</td>
<td>-0.25(^7)</td>
<td>0.04(^3)</td>
<td>0.44(^9)</td>
<td>0.41(^3)</td>
<td>0.66(^3)</td>
<td>-0.11(^8)</td>
<td>-0.3(^8)</td>
<td></td>
</tr>
<tr>
<td>UIMF</td>
<td>0.03(^7)</td>
<td>-0.08(^7)</td>
<td>0.36(^7)</td>
<td>0.53(^9)</td>
<td>0.25(^2)</td>
<td>0.23(^4)</td>
<td>0.33(^6)</td>
<td>0.47(^4)</td>
<td></td>
</tr>
<tr>
<td>UFAT</td>
<td>0.13(^3)</td>
<td>0.11(^3)</td>
<td>0.17(^7)</td>
<td>0.29(^9)</td>
<td>0.27(^4)</td>
<td>-0.24(^6)</td>
<td>0.69(^3)</td>
<td>0.45(^6)</td>
<td></td>
</tr>
<tr>
<td>FI</td>
<td>0.66(^9)</td>
<td>0.21(^9)</td>
<td>0.49(^9)</td>
<td>0.5(^9)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HCW</td>
<td>0.12(^3)</td>
<td>-0.1(^3)</td>
<td>0.25(^2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>REA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.05(^5)</td>
<td>-0.21(^2)</td>
<td></td>
</tr>
<tr>
<td>FAT</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.35(^2)</td>
<td></td>
</tr>
</tbody>
</table>

1 Selection criteria: YW = yearling weight, UREA = ultrasound ribeye area, UIMF = ultrasound intramuscular fat percentage, UFAT = ultrasound rib fat.

Objective traits: FI = feed intake, HCW = hot carcass weight, REA = ribeye area, FAT = 12\(^{th}\)-rib fat, MS = marbling score.

2 Koots et al. (1994)
3 Moser et al. (1998)
4 Reverter et al. (2000)
5 Devitt and Wilton (2001)
6 Kemp et al. (2002)
7 Stelzleni et al. (2002)
8 Bergen et al. (2005)
9 Nkrumah et al. (2007)
10 Arthur et al. (2001)
11 Within the range of estimates reported by Koots et al. (1994)
Table 12. Genetic correlations (above diagonal) between selection criteria and objective traits, and phenotypic correlations (below diagonal) between selection criteria for the maternal index.

<table>
<thead>
<tr>
<th>Traits</th>
<th>BWT</th>
<th>WWd</th>
<th>WWm</th>
<th>YW</th>
<th>SC</th>
<th>CDd</th>
<th>Cdm</th>
<th>MW</th>
<th>HP</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWT</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WWd</td>
<td>0.79²</td>
<td>-0.28⁶</td>
<td></td>
<td>0.7³</td>
<td>0.19⁵</td>
<td>0.2¹¹</td>
<td>-0.2⁷</td>
<td>0.4¹²</td>
<td>0⁹</td>
</tr>
<tr>
<td>WWm</td>
<td></td>
<td></td>
<td></td>
<td>0¹¹</td>
<td>0.19⁵</td>
<td></td>
<td></td>
<td>0⁹</td>
<td>0¹¹</td>
</tr>
<tr>
<td>YW</td>
<td>0.57²</td>
<td>0.35²</td>
<td>0.3⁹⁵</td>
<td>0.3⁶⁷</td>
<td>-0.2³⁷</td>
<td>0.5¹²</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SC</td>
<td>0.2²</td>
<td>0.1²</td>
<td>0.3⁸⁴</td>
<td>0.1⁶⁸</td>
<td>-0.2⁷⁸</td>
<td>0.1⁰¹²</td>
<td>0.0⁶⁹</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CDd</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-0.2⁶⁷</td>
<td>0⁹</td>
<td>0⁹</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cdm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0⁹</td>
<td>0⁹</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MW</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0⁹</td>
<td></td>
</tr>
</tbody>
</table>

¹Selection criteria: BWT = birth weight, WWd = weaning weight direct, WWm = weaning weight maternal, YW = yearling weight, SC = scrotal circumference.
Objective traits: CDd = calving difficulty direct, CDm = calving difficulty maternal, WWd, WWm, MW = mature weight, HP = heifer pregnancy.

²Knights et al. (1984)
³Bourdon and Brinks (1986)
⁴Northcutt and Wilson (1993)
⁵Koots et al. (1994)
⁶MacNeil and Newman (1994)
⁷Bennett and Gregory (2001a)
⁸Bennett and Gregory (2001b)
⁹Barron Lopez (2013)
¹⁰Ahlberg et al. (2016)
¹¹Within the range of estimates reported by Koots et al. (1994)
¹²American Hereford Association genetic evaluation
Table 13. Phenotypic (co)variance matrix among selection criteria for the terminal index\(^1\).

<table>
<thead>
<tr>
<th>Traits</th>
<th>YW</th>
<th>UREA</th>
<th>UIMF</th>
<th>UFAT</th>
</tr>
</thead>
<tbody>
<tr>
<td>YW</td>
<td>1202.455</td>
<td>107.244</td>
<td>0.713</td>
<td>0.789</td>
</tr>
<tr>
<td>UREA</td>
<td>56.900</td>
<td>-0.414</td>
<td>0.145</td>
<td></td>
</tr>
<tr>
<td>UIMF</td>
<td>0.470</td>
<td>0.020</td>
<td></td>
<td></td>
</tr>
<tr>
<td>UFAT</td>
<td></td>
<td></td>
<td>0.031</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)Also referred to as the P matrix
\(^2\)YW = yearling weight, UREA = ultrasound ribeye area, UIMF = ultrasound intramuscular fat percentage, UFAT = ultrasound rib fat
Table 14. Genetic (co)variance matrix between selection criteria and objective traits in the terminal index\(^1\).

<table>
<thead>
<tr>
<th>Traits</th>
<th>FI</th>
<th>HCW</th>
<th>REA</th>
<th>FAT</th>
<th>MS</th>
</tr>
</thead>
<tbody>
<tr>
<td>YW</td>
<td>5.750</td>
<td>307.227</td>
<td>57.370</td>
<td>0.967</td>
<td>-1.974</td>
</tr>
<tr>
<td>UREA</td>
<td>0.937</td>
<td>38.413</td>
<td>11.689</td>
<td>-0.062</td>
<td>-1.358</td>
</tr>
<tr>
<td>UIMF</td>
<td>0.117</td>
<td>2.394</td>
<td>0.421</td>
<td>0.019</td>
<td>0.089</td>
</tr>
<tr>
<td>UFAT</td>
<td>0.017</td>
<td>0.195</td>
<td>-0.115</td>
<td>0.010</td>
<td>0.022</td>
</tr>
</tbody>
</table>

\(^1\)Also referred to as the G or \(G_{12}\) matrix

\(^2\)Selection criteria: YW = yearling weight, UREA = ultrasound ribeye area, UIMF = ultrasound intramuscular fat percentage, UFAT = ultrasound rib fat.

Objective traits: FI = feed intake, HCW = hot carcass weight, REA = ribeye area, FAT = 12\(^{th}\)-rib fat, MS = marbling score.
Table 15. Phenotypic (co)variance matrix among selection criteria for the maternal index

<table>
<thead>
<tr>
<th>Traits</th>
<th>BWT</th>
<th>WW</th>
<th>YW</th>
<th>SC</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWT</td>
<td>30.514</td>
<td>78.834</td>
<td>109.184</td>
<td>1.740</td>
</tr>
<tr>
<td>WW</td>
<td>585.091</td>
<td>662.633</td>
<td>9.651</td>
<td></td>
</tr>
<tr>
<td>YW</td>
<td>1202.455</td>
<td>27.672</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SC</td>
<td>4.410</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Also referred to as the P matrix
2 BWT = birth weight, WW = weaning weight, YW = yearling weight, SC = scrotal circumference
Table 16. Genetic (co)variance matrix between selection criteria and objective traits for calculation of maternal index coefficients for phenotypic measures\(^1\).

<table>
<thead>
<tr>
<th>Traits</th>
<th>CDd</th>
<th>CDm</th>
<th>WWd</th>
<th>WWm</th>
<th>MW</th>
<th>HP</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWT</td>
<td>3.439</td>
<td>-0.360</td>
<td>18.539</td>
<td>-4.523</td>
<td>39.968</td>
<td>0.000</td>
</tr>
<tr>
<td>WW</td>
<td>3.731</td>
<td>-2.503</td>
<td>128.720</td>
<td>-31.408</td>
<td>158.577</td>
<td>0.000</td>
</tr>
<tr>
<td>YW</td>
<td>12.983</td>
<td>-5.564</td>
<td>174.175</td>
<td>0.000</td>
<td>383.171</td>
<td>0.000</td>
</tr>
<tr>
<td>SC</td>
<td>0.332</td>
<td>-0.375</td>
<td>2.716</td>
<td>2.367</td>
<td>4.403</td>
<td>0.034</td>
</tr>
</tbody>
</table>

\(^1\)Also referred to as the G matrix

\(^2\)Selection criteria: BWT = birth weight, WW = weaning weight, YW = yearling weight, SC = scrotal circumference.

Objective traits: CDd = calving difficulty direct, CDm = calving difficulty maternal, WWd = weaning weight direct, WWm = weaning weight maternal, MW = mature weight, HP = heifer pregnancy.
Table 17. Genetic (co)variance matrix between selection criteria and objective traits for calculation of maternal index coefficients for expected progeny differences\(^1\).

<table>
<thead>
<tr>
<th>Traits</th>
<th>CDd</th>
<th>CDm</th>
<th>WWd</th>
<th>WWm</th>
<th>MW</th>
<th>HP</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWT</td>
<td>3.439</td>
<td>-0.360</td>
<td>18.539</td>
<td>-4.523</td>
<td>39.968</td>
<td>0.000</td>
</tr>
<tr>
<td>WWd</td>
<td>3.731</td>
<td>-2.503</td>
<td>128.720</td>
<td>-31.408</td>
<td>158.577</td>
<td>0.000</td>
</tr>
<tr>
<td>WWm</td>
<td>0.000</td>
<td>0.000</td>
<td>-31.408</td>
<td>97.750</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>YW</td>
<td>12.983</td>
<td>-5.564</td>
<td>174.175</td>
<td>0.000</td>
<td>383.171</td>
<td>0.000</td>
</tr>
<tr>
<td>SC</td>
<td>0.332</td>
<td>-0.375</td>
<td>2.716</td>
<td>2.367</td>
<td>4.403</td>
<td>0.034</td>
</tr>
</tbody>
</table>

\(^1\)Also referred to as the G\(_{12}\) matrix

\(^2\)Selection criteria: BWT = birth weight, WWd = weaning weight direct, WWm = weaning weight maternal, YW = yearling weight, SC = scrotal circumference. Objective traits: CDd = calving difficulty direct, CDm = calving difficulty maternal, WWd, WWm, MW = mature weight, HP = heifer pregnancy.
Table 18. Genetic (co)variance matrix among selection criteria in the terminal index\(^1\).

<table>
<thead>
<tr>
<th>Traits</th>
<th>YW</th>
<th>UREA</th>
<th>UIMF</th>
<th>UFAT</th>
</tr>
</thead>
<tbody>
<tr>
<td>YW</td>
<td>480.982</td>
<td>39.199</td>
<td>2.855</td>
<td>0.082</td>
</tr>
<tr>
<td>UREA</td>
<td>16.501</td>
<td>-0.427</td>
<td>0.017</td>
<td></td>
</tr>
<tr>
<td>UIMF</td>
<td>0.176</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>UFAT</td>
<td>0.012</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)Also referred to as the G\(_{11}\) matrix

\(^2\)YW = yearling weight, UREA = ultrasound ribeye area, UIMF = ultrasound intramuscular fat percentage, UFAT = ultrasound rib fat
Table 19. Genetic (co)variance matrix among selection criteria in the maternal index\(^1\).

<table>
<thead>
<tr>
<th>Traits</th>
<th>BWT</th>
<th>WWd</th>
<th>WWm</th>
<th>YW</th>
<th>SC</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWT</td>
<td>10.680</td>
<td>18.539</td>
<td>-4.523</td>
<td>37.986</td>
<td>0.165</td>
</tr>
<tr>
<td>WWd</td>
<td>128.720</td>
<td></td>
<td>-31.408</td>
<td>174.175</td>
<td>2.716</td>
</tr>
<tr>
<td>WWm</td>
<td></td>
<td>97.750</td>
<td></td>
<td>0</td>
<td>2.367</td>
</tr>
<tr>
<td>YW</td>
<td></td>
<td></td>
<td></td>
<td>480.982</td>
<td>10.777</td>
</tr>
<tr>
<td>SC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.588</td>
</tr>
</tbody>
</table>

\(^1\)Also referred to as the $G_{11}$ matrix

\(^2\)BWT = birth weight, WWd = weaning weight direct, WWm = weaning weight maternal, YW = yearling weight, SC = scrotal circumference
Table 20. Genetic (co)variance matrix among objective traits for terminal index\textsuperscript{1}.

<table>
<thead>
<tr>
<th>Traits</th>
<th>FI</th>
<th>HCW</th>
<th>REA</th>
<th>FAT</th>
<th>MS</th>
</tr>
</thead>
<tbody>
<tr>
<td>FI</td>
<td>0.275</td>
<td>7.893</td>
<td>0.480</td>
<td>0.035</td>
<td>0.118</td>
</tr>
<tr>
<td>HCW</td>
<td>520.010</td>
<td>11.930</td>
<td>-0.314</td>
<td>2.565</td>
<td></td>
</tr>
<tr>
<td>REA</td>
<td>19.008</td>
<td>-0.030</td>
<td>-0.412</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FAT</td>
<td>0.019</td>
<td>0.022</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MS</td>
<td></td>
<td>0.203</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\textsuperscript{1}Also referred to as the C matrix
\textsuperscript{2}FI = feed intake, HCW = hot carcass weight, REA = ribeye area, FAT = 12\textsuperscript{th}-rib fat, MS = marbling score
Table 21. Genetic (co)variance matrix among objective traits for maternal index\textsuperscript{1}.

<table>
<thead>
<tr>
<th>Traits</th>
<th>CDd</th>
<th>CDm</th>
<th>WWd</th>
<th>WWm</th>
<th>MW</th>
<th>HP</th>
</tr>
</thead>
<tbody>
<tr>
<td>CDd</td>
<td>2.704</td>
<td>-0.472</td>
<td>3.731</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>CDm</td>
<td>1.217</td>
<td>-2.503</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>WWd</td>
<td>128.720</td>
<td>-31.408</td>
<td>158.577</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>WWm</td>
<td>97.75</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MW</td>
<td>1221</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HP</td>
<td>0.199</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\textsuperscript{1}Also referred to as the C matrix
\textsuperscript{2}CDd = calving difficulty direct, CDm = calving difficulty maternal, WWd = weaning weight direct, WWm = weaning weight maternal, MW = mature weight, HP = heifer pregnancy
Table 22. Economic values, relative economic values, and response of individual objective traits in the terminal and maternal selection indices.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Economic value (US$/trait unit)</th>
<th>Genetic SD ($\sigma_a$)</th>
<th>Relative emphasis (%)</th>
<th>Relative economic value (per $\sigma_a$)</th>
<th>Response of individual objective traits from selection index for EPD</th>
<th>Response of individual objective traits from selection index for phenotypic measures</th>
</tr>
</thead>
<tbody>
<tr>
<td>Terminal Objective</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FI, kg</td>
<td>-57.05</td>
<td>0.52</td>
<td>19.3</td>
<td>-29.66</td>
<td>0.14i</td>
<td>0.07i</td>
</tr>
<tr>
<td>HCW, kg</td>
<td>4.00</td>
<td>22.80</td>
<td>59.5</td>
<td>91.29</td>
<td>14.23i</td>
<td>9.40i</td>
</tr>
<tr>
<td>REA, sq. cm</td>
<td>1.92</td>
<td>4.36</td>
<td>5.5</td>
<td>8.38</td>
<td>2.87i</td>
<td>1.93i</td>
</tr>
<tr>
<td>FAT, cm</td>
<td>-50.51</td>
<td>0.14</td>
<td>4.6</td>
<td>-7.07</td>
<td>0.04i</td>
<td>0.02i</td>
</tr>
<tr>
<td>MS, units</td>
<td>37.80</td>
<td>0.45</td>
<td>11.1</td>
<td>17.01</td>
<td>-0.10i</td>
<td>-0.04i</td>
</tr>
<tr>
<td>Maternal Objective</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CDd, %</td>
<td>-1.28</td>
<td>1.64</td>
<td>3.1</td>
<td>-2.11</td>
<td>-0.53i</td>
<td>-0.72i</td>
</tr>
<tr>
<td>CDm, %</td>
<td>-1.39</td>
<td>1.10</td>
<td>2.2</td>
<td>-1.53</td>
<td>-0.03i</td>
<td>-0.09i</td>
</tr>
<tr>
<td>WWd, kg</td>
<td>1.63</td>
<td>11.35</td>
<td>27.2</td>
<td>18.49</td>
<td>1.55i</td>
<td>1.72i</td>
</tr>
<tr>
<td>WWm, kg</td>
<td>1.14</td>
<td>9.89</td>
<td>16.6</td>
<td>11.28</td>
<td>4.50i</td>
<td>0.01i</td>
</tr>
<tr>
<td>MW, kg</td>
<td>-0.96</td>
<td>34.94</td>
<td>49.2</td>
<td>-33.46</td>
<td>-5.21i</td>
<td>-3.09i</td>
</tr>
<tr>
<td>HP, %</td>
<td>2.68</td>
<td>0.45</td>
<td>1.7</td>
<td>1.19</td>
<td>0.01i</td>
<td>0.01i</td>
</tr>
</tbody>
</table>

*FI = feed intake, HCW = hot carcass weight, REA = ribeye area, FAT = 12th-rib fat, MS = marbling score, CDd = calving difficulty direct, CDm = calving difficulty maternal, WWd = weaning weight direct, WWm = weaning weight maternal, MW = mature weight, HP = heifer pregnancy*

*From additive genetic variances in Tables 9 and 10*

*Marbling score units where 4.0 = SI$^0$ and 5.0 = Sm$^0$*
Table 23. Sensitivity of terminal index to changes in genetic correlations between selection criteria and objective traits.

<table>
<thead>
<tr>
<th>Traits</th>
<th>FI</th>
<th>HCW</th>
<th>REA</th>
<th>FAT</th>
<th>MS</th>
</tr>
</thead>
<tbody>
<tr>
<td>YW</td>
<td>0.99</td>
<td>0.97</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>UREA</td>
<td>0.98</td>
<td>0.87</td>
<td>1.00</td>
<td>1.00</td>
<td>0.97</td>
</tr>
<tr>
<td>UIMF</td>
<td>0.98</td>
<td>0.87</td>
<td>1.00</td>
<td>1.00</td>
<td>0.99</td>
</tr>
<tr>
<td>UFAT</td>
<td>0.99</td>
<td>0.94</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Relative efficiency after subtracting 0.2 from assumed genetic correlation

<table>
<thead>
<tr>
<th>Traits</th>
<th>FI</th>
<th>HCW</th>
<th>REA</th>
<th>FAT</th>
<th>MS</th>
</tr>
</thead>
<tbody>
<tr>
<td>YW</td>
<td>0.99</td>
<td>0.85</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>UREA</td>
<td>0.98</td>
<td>0.88</td>
<td>1.00</td>
<td>1.00</td>
<td>0.97</td>
</tr>
<tr>
<td>UIMF</td>
<td>0.98</td>
<td>0.89</td>
<td>1.00</td>
<td>1.00</td>
<td>0.99</td>
</tr>
<tr>
<td>UFAT</td>
<td>0.99</td>
<td>0.89</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Relative efficiency after adding 0.4 to assumed genetic correlation

<table>
<thead>
<tr>
<th>Traits</th>
<th>FI</th>
<th>HCW</th>
<th>REA</th>
<th>FAT</th>
<th>MS</th>
</tr>
</thead>
<tbody>
<tr>
<td>YW</td>
<td>0.95</td>
<td>0.93</td>
<td>1.00</td>
<td>1.00</td>
<td>0.99</td>
</tr>
<tr>
<td>UREA</td>
<td>0.94</td>
<td>0.66</td>
<td>1.00</td>
<td>1.00</td>
<td>0.89</td>
</tr>
<tr>
<td>UIMF</td>
<td>0.94</td>
<td>0.63</td>
<td>0.99</td>
<td>1.00</td>
<td>0.98</td>
</tr>
<tr>
<td>UFAT</td>
<td>0.95</td>
<td>0.84</td>
<td>1.00</td>
<td>1.00</td>
<td>0.99</td>
</tr>
</tbody>
</table>

Relative efficiency after subtracting 0.4 from assumed genetic correlation

<table>
<thead>
<tr>
<th>Traits</th>
<th>FI</th>
<th>HCW</th>
<th>REA</th>
<th>FAT</th>
<th>MS</th>
</tr>
</thead>
<tbody>
<tr>
<td>YW</td>
<td>0.98</td>
<td>0.23</td>
<td>1.00</td>
<td>1.00</td>
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<tr>
<td>UREA</td>
<td>0.94</td>
<td>0.70</td>
<td>1.00</td>
<td>1.00</td>
<td>0.90</td>
</tr>
<tr>
<td>UIMF</td>
<td>0.94</td>
<td>0.71</td>
<td>1.00</td>
<td>1.00</td>
<td>0.98</td>
</tr>
<tr>
<td>UFAT</td>
<td>0.97</td>
<td>0.60</td>
<td>1.00</td>
<td>1.00</td>
<td>0.99</td>
</tr>
</tbody>
</table>

1Selection criteria: YW = yearling weight, UREA = ultrasound ribeye area, UIMF = ultrasound intramuscular fat percentage, UFAT = ultrasound rib fat. Objective traits: FI = feed intake, HCW = hot carcass weight, REA = ribeye area, FAT = 12th-rib fat, MS = marbling score.
Table 24. Sensitivity of maternal index to changes in genetic correlations between selection criteria and objective traits.

<table>
<thead>
<tr>
<th>Traits</th>
<th>CDd</th>
<th>CDm</th>
<th>WWd</th>
<th>WWm</th>
<th>MW</th>
<th>HP</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWT</td>
<td>1.00</td>
<td>1.00</td>
<td>0.94</td>
<td>0.98</td>
<td>0.89</td>
<td>1.00</td>
</tr>
<tr>
<td>WWd</td>
<td>1.00</td>
<td>1.00</td>
<td>0.99</td>
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<tr>
<td>WWm</td>
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<td>1.00</td>
<td>0.98</td>
<td>0.84</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>YW</td>
<td>1.00</td>
<td>1.00</td>
<td>0.90</td>
<td>0.97</td>
<td>0.93</td>
<td>1.00</td>
</tr>
<tr>
<td>SC</td>
<td>1.00</td>
<td>1.00</td>
<td>0.96</td>
<td>0.98</td>
<td>0.85</td>
<td>1.00</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Traits</th>
<th>CDd</th>
<th>CDm</th>
<th>WWd</th>
<th>WWm</th>
<th>MW</th>
<th>HP</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWT</td>
<td>1.00</td>
<td>1.00</td>
<td>0.96</td>
<td>0.98</td>
<td>0.81</td>
<td>1.00</td>
</tr>
<tr>
<td>WWd</td>
<td>1.00</td>
<td>1.00</td>
<td>0.98</td>
<td>0.96</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>WWm</td>
<td>1.00</td>
<td>1.00</td>
<td>0.96</td>
<td>0.95</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>YW</td>
<td>1.00</td>
<td>1.00</td>
<td>0.97</td>
<td>0.98</td>
<td>0.60</td>
<td>1.00</td>
</tr>
<tr>
<td>SC</td>
<td>1.00</td>
<td>1.00</td>
<td>0.95</td>
<td>0.98</td>
<td>0.90</td>
<td>1.00</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Traits</th>
<th>CDd</th>
<th>CDm</th>
<th>WWd</th>
<th>WWm</th>
<th>MW</th>
<th>HP</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWT</td>
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<td>1.00</td>
<td>0.78</td>
<td>0.91</td>
<td>0.75</td>
<td>1.00</td>
</tr>
<tr>
<td>WWd</td>
<td>1.00</td>
<td>1.00</td>
<td>0.97</td>
<td>-0.21</td>
<td>0.33</td>
<td>1.00</td>
</tr>
<tr>
<td>WWm</td>
<td>1.00</td>
<td>1.00</td>
<td>0.95</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>YW</td>
<td>1.00</td>
<td>1.00</td>
<td>0.73</td>
<td>0.84</td>
<td>0.86</td>
<td>1.00</td>
</tr>
<tr>
<td>SC</td>
<td>1.00</td>
<td>1.00</td>
<td>0.88</td>
<td>0.95</td>
<td>0.56</td>
<td>1.00</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Traits</th>
<th>CDd</th>
<th>CDm</th>
<th>WWd</th>
<th>WWm</th>
<th>MW</th>
<th>HP</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWT</td>
<td>1.00</td>
<td>1.00</td>
<td>0.88</td>
<td>0.94</td>
<td>0.49</td>
<td>1.00</td>
</tr>
<tr>
<td>WWd</td>
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<td>1.00</td>
<td>0.88</td>
<td>0.92</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>WWm</td>
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<td>1.00</td>
<td>0.79</td>
<td></td>
<td>0.89</td>
<td>1.00</td>
</tr>
<tr>
<td>YW</td>
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<td>1.00</td>
<td>0.92</td>
<td>0.96</td>
<td>-0.07</td>
<td>1.00</td>
</tr>
<tr>
<td>SC</td>
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<td>1.00</td>
<td>0.82</td>
<td>0.93</td>
<td>0.75</td>
<td>1.00</td>
</tr>
</tbody>
</table>

1Selection criteria: BWT = birth weight, WWd = weaning weight direct, WWm = weaning weight maternal, YW = yearling weight, SC = scrotal circumference. Objective traits: CDd = calving difficulty direct, CDm = calving difficulty maternal, WWd, WWm, MW = mature weight, HP = heifer pregnancy.
Table 25. Sensitivity of terminal and maternal indices to changes in economic values.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Efficiency after a 50% increase in magnitude of economic value</th>
<th>Efficiency after a 50% decrease in magnitude of economic value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Terminal Objective</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FI</td>
<td>0.97</td>
<td>0.98</td>
</tr>
<tr>
<td>HCW</td>
<td>0.99</td>
<td>0.84</td>
</tr>
<tr>
<td>REA</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>FAT</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>MS</td>
<td>0.98</td>
<td>0.99</td>
</tr>
<tr>
<td>Maternal Objective</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CDd</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>CDm</td>
<td>1.00</td>
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<td>0.80</td>
</tr>
<tr>
<td>WWm</td>
<td>0.95</td>
<td>0.91</td>
</tr>
<tr>
<td>MW</td>
<td>0.88</td>
<td>0.79</td>
</tr>
<tr>
<td>HP</td>
<td>1.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>

1FI = feed intake, HCW = hot carcass weight, REA = ribeye area, FAT = 12th-rib fat, MS = marbling score, CDd = calving difficulty direct, CDm = calving difficulty maternal, WWd = weaning weight direct, WWm = weaning weight maternal, MW = mature weight, HP = heifer pregnancy