Beef Sire Selection Manual

National Beef Cattle Evaluation Consortium

2nd EDITION 2010

National Beef Cattle Evaluation Consortium

Colorado State University • Cornell University • Iowa State University • University of Georgia

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SECOND EDITION — 2010

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A special "thank you" goes out to the following individuals who reviewed the material included in this publication.

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Dedication

The authors and editor of the NBCEC Sire Selection Manual dedicate this publication to Dr. John Pollak. John was the founding director of the NBCEC and has worked tirelessly for the advancement of beef cattle genetic evaluations for many years. John's tenure as Director of the NBCEC ended in January of this year and his leadership will be missed. John continues to serve the beef industry as Director of the Roman L. Hruska U.S. Meat Animal Research Center in Clay Center, Nebraska.

Foreword

This manual was sponsored by the National Beef Cattle Evaluation Consortium (NBCEC). The NBCEC is an organization of universities that have been involved in beef cattle genetic evaluations over the last several decades, plus affiliate universities doing research critical to beef cattle selection and evaluation. The consortium, which started operations in 2000, is funded by a Special Research Grant from the Cooperative State Research, Education, and Extension Service of the USDA. The focus of the NBCEC is research, but we strongly believe in the need for an active extension program in beef cattle genetics. As such, we have held workshops and symposia on a variety of topics and have conducted several series of distance-education programs. This manual represents another effort by the NBCEC Extension team to provide current and meaningful information to the industry. As director of the NBCEC, I would like to take this opportunity to pay special thanks to the editors, authors, and reviewers who made this manual come to life.

We live in an age of accelerated scientific discovery, which leads to new technologies that must be understood by members of the production sector of the industry to assure that technology is applied appropriately. Today, producers face the challenges of learning about DNA testing and its application to their selection programs. However, one very appropriate use of any new technology is to synchronize it with tried and tested programs. The beef industry still must use tools like EPD and programs such as crossbreeding and/or composite breeding. The Beef Sire Selection Manual incorporates information on both tried and tested programs as well as on new genetic technology. It is meant to be a reference to help producers understand the important genetic concepts that are the tools for profitable cattle breeding.

Knowledge is a powerful asset for any undertaking, and profitable beef production is an endeavor the members of the NBCEC are committed to support. As such, we the faculty members of the NBCEC hope that you find this to be a useful educational tool and a unique resource.

John Pollak
Director
U.S. Meat Animal Research Center, ARS
Director Emeritus
National Beef Cattle Evaluation Consortium

In principle, genetic improvement is a straight-forward exercise that results from using above-average selection candidates as the parents of the next generation. In practice, the devil is in the details. Both bull breeders and bull buyers need to consider their breeding objectives, defining the list of traits that need to be modified to advance the towards their goal. The bull breeder further needs to determine the characteristics that can be cost-effectively measured on the live animals in order to predict the merit of the candidates for the traits in their objective. The bull buyer needs to know how to interpret the sale information, and to have a working knowledge of the jargon to sensibly converse

with bull breeders and other stakeholders in genetic improvement. Knowledge and understanding of these and other issues has never been more relevant than today, with some calling for belt-tightening due to economic pressures on the beef industry, while others are offering new investment opportunities such as DNA-based technologies that may assist in the selection process.

This second revised edition of the sire selection manual builds on the successful first edition and provides many details as to the important aspects of beef cattle improvement. It has been written, edited, refereed and revised by experts in the nation, driven by their interest in education, informed decision making, and the genetic improvement of the beef industry. They deserve special thanks. The manual will be of interest to stakeholders in all sectors of the beef industry, those bull breeders and bull buyers involved directly in animal management and selection, those that assist them in this task, including breed associations, sales representatives, extension agents, and aspiring students looking for career opportunities in any of those areas. The Scientific and Industry Councils of the National Beef Cattle Evaluation Consortium are proud of their role in facilitating this publication and trust you will find it can add value to your business, wherever that may be in the beef industry.

Dorian Garrick
Lush Chair in Animal Breeding and Genetics
Iowa State University
Executive Director
National Beef Cattle Evaluation Consortium

The first edition of the Beef Sire Selection Manual, sponsored by the National Beef Cattle Evaluation Consortium, was printed in 2005. The Consortium is pleased to present this second edition in 2010. A talented set of beef genetics experts from across the USA have authored the chapters. We are indebted to their abilities to present sometimes challenging materials in clear form that is easily understood by readers with a wide array of backgrounds. Many others have reviewed and critiqued the authors' efforts. A new chapter appears near the end, adding new developments in the utilization of molecular information in beef cattle selection decisions. Some chapters have remained quite similar to the initial version, while others have been updated and improved. There has been some reordering of chapters too.

Whether a seedstock breeder, a commercial breeder, a provider of selection decision tools, an educator or simply a casual reader, we believe everyone will gain from the manual. Sire selections are the premier selection decisions that all cattle breeders make, whether in a seedstock situation or in a commercial, crossbreeding one. Understanding the concepts and the tools is the first step in increasing our chances of success.

Merlyn K. Nielsen
Wagner Professor
University of Nebraska-Lincoln
Editor, Second Edition

The Importance of Sire Selection

Dan W. Moser, Kansas State University

Bull selection presents an important opportunity to enhance the profitability of the beef production enterprise. For several reasons, bull selection is one of the most important producer decisions, and as such, requires advance preparation and effort to be successful. To effectively select sires, producers must not only be well versed in the use of expected progeny differences (EPD) and understand breed differences, they must accurately and objectively assess their current genetics, resources and management. Furthermore, recent advances in DNA technology and decision-support tools add complexity to selection, but will ultimately enhance selection accuracy. Producers who stay up to date on advances in beef cattle genetics should profit from enhanced revenue and reduced production costs, as they best match genetics to their production situation.

Opportunity for Genetic Change

Sire selection represents the greatest opportunity for genetic change. Genetic change in cow-calf operations can occur both through sire selection and through replacement female selection in conjunction with cow culling. Most producers raise their own replacement heifers rather than purchasing from other sources. This greatly limits contribution of female selection to genetic change because a large fraction of the heifer crop is needed for replacements. Depending on culling rate in the cowherd, usually one-half or more of the replacement heifer candidates are retained at weaning to allow for further selection at breeding time. So even if the best half of the heifers are retained, some average heifers will be in that group. Finally, the information used to select replacement heifers in commercial herds is limited. Producers may use in-herd ratios along with data on the heifers' dams, but these types of data on females do not reflect genetic differences as well as do the EPD used to select bulls.

In contrast, whether selecting natural service sires for purchase or sires to be used via artificial insemination (AI), the amount of variation available can be almost overwhelming. Producers can find bulls that will increase or decrease nearly any trait of economic importance. Furthermore, since a relatively few bulls will service a large number of cows, producers can select bulls that are fairly elite even when natural mating. Use of AI allows commercial producers to use some of the most outstanding bulls in the world at a reasonable cost, allowing for enormous amounts of genetic change, if desired. Finally, selection of bulls is more accurate than female selection. Seedstock breeders provide genetic information in the form of EPD, which allow for direct comparison of potential sires across herds and environments. Unlike actual measurements, EPD consider the heritability of the trait to accurately predict genetic differences between animals. If AI is used, even greater accuracy is possible. Bulls used in AI may have highly proven EPD, calculated from thousands of progeny measured in many herds and environments.

Permanent and Long-Term Change

Genetic change is permanent change. Among management decisions, genetic selection differs from others in that the effects are permanent, not temporary. Feeding a supplement to meet nutritional requirements is beneficial as long as the feeding continues and health protocols, while important, must be maintained year after year. However, once a genetic change occurs, that change will remain until additional new genetics enter the herd. Whether selecting for growth, carcass traits or maternal performance, those traits, once established in the herd, are automatically passed on to the next generation.

Sire selection has a long-term impact. Regardless of whether a selected sire has a favorable or unfavorable effect on the herd, if his daughters enter the cowherd, his effects will remain for a considerable period of time. Assuming a sire is used for four years and his daughters are retained, his impact will easily extend into the next decade. And, while each generation dilutes his contribution, his granddaughters and great-granddaughters may remain in the herd a quarter-century after last sired calves. For this reason, purchases of bulls and semen should be viewed not as a short-term expense, but a long-term investment into the efficiency and adaptability of the beef production enterprise.

Assessing Management, Resources, and Marketing

Darrh Bullock, University of Kentucky

Goal setting is important for many areas of beef production, especially for the breeding program. These goals include reproduction, calf performance, income, herd replacements, cost containment, or a number of others. Breeding management decisions are going to impact each of these goals to varying degrees. For example, the breeding management practice that has the greatest impact on reproduction is crossbreeding; whereas selection is the best management practice for improving carcass quality. Once goals for your beef herd that are important to your family's quality of life are set, it is time to determine which management and breeding practices will be best for your cattle operation. Remember, most management decisions can be changed in an instant, but changes to your herd's genetics generally take time.

Herd Assessment

Once goals have been established, a target has been set; hence, to reach that target, it is important to determine the performance and potential of your current herd. It is very important to have complete and accurate data to determine the production potential of a herd. Data analysis may determine if a herd is performing appropriately for the present level of management or if subtle or drastic genetic changes are in order to meet goals.

Assessing the Herd

Determine Breed Makeup

The first step in assessing a commercial herd is to determine its breed makeup. This will be a reflection of the effectiveness of the crossbreeding program. If you have cows in the herd that are greater than 75% of one breed, then you may consider changes to your breeding program. Further detailed discussion will follow in the crossbreeding section.

Determine Production Level

The next step is to determine the production level of your herd. Accurate and complete records are the only method of determining the production status of a cowherd. Records allow the assessment of the date of calving for reproductive performance (including calving distribution), calving ease score, udder and teat scores, calf vigor, sickness, growth performance, cow weight and condition at weaning, and any other characteristics of importance. Herd data analyzed and summarized can become information needed to make proper management decisions. Without records, the ability of cattle producers to make best management decisions are drastically limited.

Determine Weight and Frame Size

The last step is to determine the average weight and frame size of the cowherd. Frame scores are officially determined by a calculation that includes the age and hip height of the animal. Frame score predicts the expected mature size or finished weight of market calves as shown in Table 1. The predicted mature weights assume a cow body condition score of 5, and the finished market

Table 1. Frame relationship to mature size and carcass weight.

| Frame Score | Yearling Hip Height (in) | | Expected Weight (lbs) | | |
	Bulls	Heifers	Mature Cows	Steer Harvest	Steer Carcass
3	45	43	1025	950	600
4	47	45	1100	1050	660
5	49	47	1175	1150	725
6	51	49	1245	1250	785
7	53	51	1320	1350	850
8	55	53	1395	1450	915
9	57	55	1465	1550	975

weight assumes a backfat thickness of 0.4 inches. Knowing the frame size of the cowherd will have an impact on two areas: cow maintenance and carcass weights.

Frame's Effect on Cow Maintenance

For most commercial cattlemen, cow maintenance costs are the major production cost for the cowherd. Larger-framed cattle weigh more at maturity and therefore have higher maintenance needs. These cattle will need to have additional growth genetics to generate increased income to offset the increased cow feed cost. This cost/return balance is important to determine management systems. For example, if larger feeder calves are desired and replacement heifers are retained, it may result in larger mature cows that will increase feed costs, or if feed resources are not increased, the herd's reproductive performance will suffer.

Frame's Effect on Feedlot Performance and Carcass Weight

The growth and development relationship between large- and small-framed cattle can be observed in Figure 1. The growth patterns of the different types of cattle are similar, and the circle illustrates the optimum finish point for the cattle. Feeding cattle beyond this weight will cause increased cost of production through compromised feed efficiency. Beyond this point the cattle are accumulating more body fat and less muscle. Since it requires more feed (energy) to put on a pound of fat than a pound of muscle, the cattle become less efficient. As a general rule, larger-framed cattle tend to grow at a faster rate when striving to reach their optimum heavier finish weight. Therefore, large-framed cattle require greater amounts of feed and have greater expenses due to longer growing periods in the feedyard; however, heavier finish weights will likely generate more income. As long as discounts from excessive carcass weights or inferior quality grades and yield grades are avoided, producing more pounds of salable product will be advantageous to gross income.

The real problem occurs when cattle of varying frames are fed together to a constant endpoint. The average of the group will meet industry needs, but there may be a large percentage of over- and under-finished cattle in the group. Grouping cattle according to type going into the feedyard or sorting the cattle out as they finish are essential in producing a uniform, acceptable product.

Figure 1. Comparison of growth curves of small- and large-framed cattle.

Cattle taking advantage of crop residue in Iowa.

Photo: Daryl Strohbehn
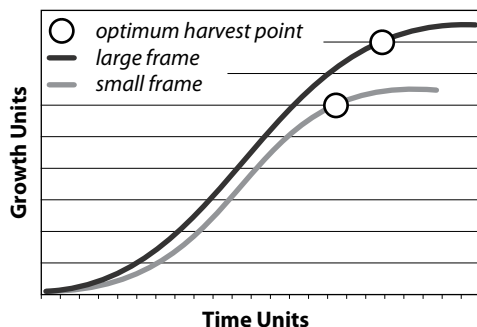
Differences in Calf Performance When Sired by a Large-Framed Bull or a Moderate-Framed Bull with the *Same EPD* for Growth: If two bulls have the same genetics for growth but differ in frame, we would expect the larger-framed bull's calves to be taller at weaning and yearling, the finished calves to be heavier and take longer to feed to optimum finish, and the females to be larger as mature cows. However, because the bulls have the same EPD for growth, we would expect the calves to weigh the same at weaning and as yearlings. If large- and moderate-framed calves weigh the same, then the larger-framed calves most likely have less muscling and/or less body capacity. To put this into perspective, visualize two men who weigh 200 pounds each, and each has the same percent body fat. One man is 6 feet 6 inches, and the other is 6 feet tall. The shorter man is likely to have a thicker build with more muscling.

Management Assessment

Management is another component of an operation that should be assessed. In order to properly determine the genetic type of cattle that is needed, it is important to know what resources will be provided and how they impact the performance of the herd. When assessing management, the primary areas of concern are labor, nutrition availability, and feed quality.

Labor

Even on a family-owned and -operated farm or ranch, labor is a consideration when developing a breeding program. Manpower spent per animal will need to be determined. In other words, is labor available over the course of the day to provide assistance when needed, or is labor limited or available on a part-time basis? Knowing this information is necessary to develop a breeding program. As an example, a full-time farmer/rancher who observes the cattle multiple times in a day may not have to pay as much attention to getting a calving ease bull as the part-time farmer/rancher who rarely sees the cattle. Additionally, a full-time farmer/rancher usually has more opportunity to provide additional nutrition during times of distress and can probably manage high-producing cattle more efficiently than a part-time farmer/rancher.

Cow/calf pair on lush pasture in South Carolina.

Photo: Lydia Yon

Another labor consideration is the physical capability of the labor. Physical limitations (age, health, handicap, etc.) will require breeding considerations for traits such as calving ease and disposition. Labor availability and capability are important components when determining your breeding program.

Effect of Performance Level and Nutrition Availability

The availability and quality of nutrition are extremely important when determining your breeding program. Cattle will perform as a response to their nutritional plane. Research has shown that under limited nutritional conditions, smaller, less productive cattle are more efficient at converting the available resources into pounds of salable product. Their calves typically weigh less, but they tend to have a greater reproductive rate, which improves the production of the herd. Under ideal nutrition, there were very little efficiency differences between high- and moderately performing cattle. In an environment that provides ample amounts of nutrition, the larger, high-performing cattle were the most efficient at producing pounds of salable product or weaned calves. Based on this information, management operations that provide exceptional nutrition should consider more productive types of cattle; however, operations with poor nutrition, either in availability or quality, should consider less-productive cattle (smaller and/or less milking ability). Quantity and quality of feed resources will be a factor in many management decisions including breeding management.

Feed Quality

Cattle are raised in every part of the United States, and conditions vary drastically. The nutritional resources that are available to cattle are also going to be considerably different depending on location and individual management practices. There are three basic nutritional categories that need to be assessed: the forage base, stored feeds, and purchased feeds.

Forage Base

The forage base assessment deals with determining the quality, quantity, and seasonality of forages that are available. This will include grass type, availability of legumes, and grazing system options (continuous, rotational, etc.). It will also include the availability of crop residues and other regional grazing practices. Because of increased production costs, intensive forage management must sustain a greater level of cattle productivity.

Stored Feeds

The best way to determine the quality of stored feeds is through lab analysis. The major factors that are going to affect that analysis will be species composition, maturity at harvest, harvesting conditions, and storage conditions. Species composition is typically influenced a great deal by the region (subtropical, high desert, fescue belt, etc.), as well as some aspects of harvesting and storage. Arid regions can typically harvest hay under better conditions than areas with large amounts of rainfall. In many regions, the window of opportunity for cutting, drying, baling, and removal is too short to avoid some exposure to rain, which affects quality. Those windows of opportunity also dictate the maturity at harvest.

Purchased Feeds

The assessment of purchased feeds should be based on the availability of economical feedstuffs and is reflected in feed tag information. The decision to purchase feeds is dictated by the deficiencies between the herd requirements and the availability of feed grown by the cattle operation. Regional situations will make certain economical feedstuffs readily available to cattle producers. The decision to purchase feed should always be based on the economic return. In other words, be certain that the cost of purchasing the feed will be offset by generated income.

Marketing Opportunities

The production of beef can be segmented so that multiple ownership of the cattle can happen before it reaches the end consumer. This type of system allows many opportunities for cattlemen, depending on the amount of risk and responsibility they are willing to take. The time of marketing (weaning, pre-conditioned, yearling, finished) and the pricing systems should be seriously considered when developing breeding programs.

The most common opportunities to market cattle intended for meat production are:

1. **Weaned calves sold at auction or by video.** Sellers provide the only production information that is available to potential buyers through the auction center's personnel.
2. **Calves sold off the farm at weaning.** Buyer has direct contact with producer and should be more aware of performance information to varying degrees, breed type, and management information.

Cattle grazing native pastures in Kansas.

Photo: Tim Marshall

3. **Calves sold either at auction or off the farm after a preconditioning period.** This marketing system is only profitable to the seller if the buyer is aware of the preconditioning. Therefore, if sold at auction, it is necessary for the preconditioning information to be provided to potential buyers to obtain price premium.
4. **Yearlings sold after a backgrounding/stocker program through an auction or off the farm.** Buyers generally have little knowledge of the cattle if the cattle have had a previous point of commerce, but yearlings tend to have better health as feeders compared to calves because of advanced age.
5. **Retained ownership through the finishing period.** Fed cattle have the following marketing options:
   - **Sell live as commodity cattle.** Cattle are priced by the average value of cattle compared to other cattle marketed at the same time.
   - **Sell in the meat.** Available options are :
     - *Grade and yield.* Carcasses are valued according to Quality Grade, Yield Grade, and dressing percentage.
     - *Value-based market through a grid or formula.* A precise marketing system that pays premiums for certain carcass traits. Some grids are better suited for high-quality grade cattle, while others are better suited for greater lean meat yield.
     - *Formula marketing.* Cattle that are marketed during the finishing period with a specific future date and delivery point.

Determining the best marketing system for an operation is difficult to determine if information about the production potential of the cattle is limited or nonexistent. Depending on resources and production potentials, differences in marketing options will determine profits. Situations that may cause re-evaluation of cattle marketing plans would be drought or other restrictions to grazing management, market and/or futures prices, alternative feed availability, facilities, ability to manage risk, or others. Although it is important to set goals and have targets, it is also important to be flexible if opportunities or adversities develop.

Summary

Evaluating the resources and opportunities of cattle operations is the first step necessary in selecting breeding stock. Once marketing goals are in place and the capacity and level of production of an operation are established, then a breeding program can be developed. The breeding program of seedstock producers should be to provide customers with cattle that fit their operations and production goals. Marketing highly productive (growth and milk) bulls in an area with limited resources may actually compromise future production. Commercial producers should consider a crossbreeding system to take advantage of heterosis and breed complementarity. After breed selection, cattle producers should then select bulls that match their resources, management, and market opportunities. Targeted selection is a must for efficient production of beef.

Genetic Principles

Darrh Bullock, University of Kentucky

To fully understand breeding management, it is important to know some basic genetic principles. Knowing the role genetics plays in each economically important trait of beef cattle can assist in making wise selection decisions. It is necessary to know which traits can be altered through breeding management (selection and/or crossbreeding) and which traits should be altered by other management techniques.

Trait is the term used to describe a characteristic in cattle. This can refer to either the appearance or performance of an animal and can also be referred to as the *phenotype;* for example, black coat color, horned, 550 lb weaning weight, etc. For most performance traits (e.g., weaning weight), the phenotype of an animal is controlled by two factors: the environment in which the animal lives and the animal's genetic makeup or *genotype.* The environment consists of not only the weather but also how the cattle are managed. Creep feed, forage quality and quantity, and health programs are examples of environmental effects. Environmental effects on economically important traits are controlled through management techniques such as nutrition and health programs.

For the purposes of this manual, the focus will be on the genetic component of the phenotype. The genetic component of all living things is expressed through the production of proteins at the cellular level. Cells can turn on or turn off the production of proteins through signals from other cells, environmental changes, age, or other factors. The code for this protein production is found in DNA (deoxyribonucleic acid), which comes in long strands that form *chromosomes.* Cattle have 30 pairs of chromosomes; humans have 23. Each animal inherits one of each pair from its sire and the other from its dam.

The term *gene* refers to the basic unit of inheritance. and it is a particular segment of the chromosome that codes for a specific protein. There are also parts of the chromosome that are thought to play no role in inheritance. The location of the gene on the chromosome is called the *locus* (Figure 1). The term *allele* refers to one of the chemical or functional possibilities that can be present at a locus (i.e., coat color has two possible alleles: red and black).

In terms of genetics, traits are usually referred to as either *simply inherited* or *polygenic.* Simply inherited traits are usually affected by only one gene. The two most commonly recognized simply inherited traits in beef cattle are red/black coat color and horned/polled. Some genetic disorders are also simply inherited.
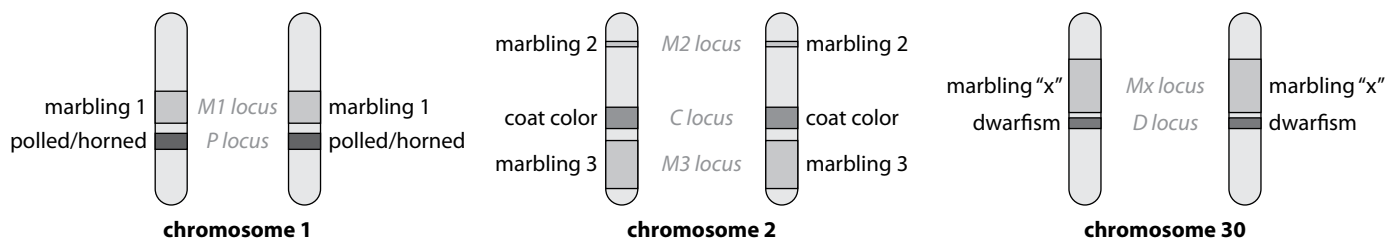
Simply inherited traits are typically observed as either/or: either the animals have horns, or they are polled. Additionally, simply inherited traits are affected little by the environment. If an animal has the genotype for black coat color, environmental conditions are not likely to make it red.

As implied in the name, polygenic traits are controlled by many genes. The number of genes involved depends on the trait, and there is currently little information on just how many genes are involved for particular traits. Examples of some common polygenic traits in cattle are birth weight, weaning weight, milking ability, marbling, tenderness, etc. Besides being controlled by many genes, polygenic traits are also controlled by the environment. We will illustrate the basic concepts of genetics using simply inherited traits and will then come back to polygenic traits.

Alleles at a locus can have an effect on the trait by themselves but can also affect the phenotype through interactions with other alleles. Alleles can interact in two ways, referred to as *dominance* and *epistasis.* There are varying degrees of dominance, and this refers to how the two alleles that an animal has at a particular locus interact. The classic form of dominance is complete dominance. With complete dominance, one allele can completely mask the expression of the other allele. This results in heterozygote animals having the exact phenotype as homozygote dominant animals. This is the type of dominance we see in red/black coat color, where black is dominant to red. Cattle that have two black alleles are black (homozygous dominant), cattle that have one black and one red allele are also black (heterozygous), and red animals are the result of having two red alleles (homozygous recessive). When dealing with traits with complete dominance, heterozygous animals are often called carriers because they are carrying the allele and can pass it to their offspring even though they do not express the trait themselves. It is possible to breed two black cattle and get a red calf because each parent was a red allele carrier.

Coat color is a good trait to demonstrate how alleles interact in a trait with complete dominance. For this example, we will mate an Angus bull to Hereford cows. The Angus bull is homozygous dominant, which means he has two black alleles (BB). The Hereford cows are homozygous recessive, which means they have two red alleles (bb). When mated, all offspring will be heterozygotes (Bb). The Punnett square in Figure 2 illustrates this mating.

Figure 1. Chromosomes with hypothetical location of genes that control some common traits in cattle.

marbling 1	*M1 locus*	marbling 1
polled/horned	*P locus*	polled/horned

chromosome 1

marbling 2	*M2 locus*	marbling 2
coat color	*C locus*	coat color
marbling 3	*M3 locus*	marbling 3

chromosome 2

marbling "x"	*Mx locus*	marbling "x"
dwarfism	*D locus*	dwarfism

chromosome 30

If we were to breed these heterozygous heifers back to a Hereford bull, we would get 50% heterozygous black (Bb) calves and 50% homozygous red (bb) calves (Figure 3.). If we were to mate the Hereford x Angus heifers to Hereford x Angus bulls, then we would get all three possibilities: homozygous black (BB), heterozygous black (Bb), and homozygous red (bb) (Figure 4). The ratio would be 25%:50%:25%, respectively. The phenotypic ratio would be 75%:25% black to red.

Traits controlled by one gene, with complete dominance, are easy to understand but can cause problems because of the possibility of carriers. For some traits, the only way to detect carriers is through progeny testing, which is costly and time consuming. However, with advancements in molecular technologies, carriers can be identified for some traits by conducting a DNA test on a tissue sample, which will be discussed in the chapter titled *DNA-Based Technologies.*

Besides complete dominance, there are other types of interactions between the two alleles at a locus, including: partial dominance, no dominance, and overdominance. As implied by their names, partial dominance means that the heterozygote favors the dominant characteristic but does not express to the full extent as the homozygous dominant. No dominance means that the heterozygote is the average of the homozygote dominant and recessive and is also referred to as additive because the phenotype of the heterozygote is the sum of the effects of the two alleles individually. Overdominance is when the heterozygote is expressed at a greater level than the homozygous dominant.

Dominance is a way to describe how alleles interact with each other at a particular locus. The term epistasis is used to describe how genes interact with genes at other loci. A classic example in cattle is the diluter genes in Charolais. When Charolais are crossed with red or black cattle, the offspring are off-white. This is the result of the diluter genes at different loci overriding the red/black genes.

Another type of inheritance interaction that can happen is sex-related inheritance. Sex-related inheritance can be categorized in three ways: sex-linked, sex-influenced, and sex-limited. Sex-linked traits are determined by genes located on the X chromosome. Sex-influenced trait expression occurs when phenotypes are different between males and females with the same genotype. An example in cattle of a sex-influenced trait would be scurs. In male cattle, the scur allele is dominant, and in female cattle it is recessive. Therefore, if a male or female are homozygous at the scur loci, then they will be scurred; if they are homozygous for the normal allele, then they will not be scurred. If they are heterozygous at the scur allele, then males will be scurred, but females will not. Sex-limited traits are those traits that can only be expressed in one sex or the other. Examples in cattle would be milking ability, which can only be expressed in females, and scrotal circumference, which can only be expressed in males.

The terms used to describe how traits are expressed are *categorical* or *continuous.* Most simply inherited traits in cattle are threshold traits, which mean they fit a certain category. For the phenotype of horned/polled, there are only the two choices, horned or polled, which make this trait a threshold trait. Cat-

Figure 2. Punnett square for coat color when mating a homozygous black bull to a homozygous red cow. The joining of the gametes shows the potential offspring and their color.

		Bull Gametes	
		B	**B**
Cow Gametes	**b**	**Bb** *black*	**Bb** *black*
	b	**Bb** *black*	**Bb** *black*

Figure 3. Punnett square for coat color when mating a homozygous red bull to a heterozygous black cow. The joining of the gametes shows the potential offspring and their color.

		Bull Gametes	
		b	**b**
Cow Gametes	**B**	**Bb** *black*	**Bb** *black*
	b	**bb** *red*	**bb** *red*

Figure 4. Punnett square for coat color when mating a heterozygous black bull to a heterozygous black cow. The joining of the gametes shows the potential offspring and their color.

		Bull Gametes	
		B	**b**
Cow Gametes	**B**	**BB** *black*	**Bb** *black*
	b	**Bb** *black*	**bb** *red*

egorical traits that are polygenic are referred to as *threshold* traits. Dystocia is typically expressed as either assisted or unassisted or is measured numerically: no difficulty = 1; easy pull = 2; hard pull = 3; caesarean section = 4; and abnormal presentation = 5. Nevertheless, it is obvious that many factors can affect dystocia including birth weight and pelvic area, which are both polygenic traits that are expressed on a continuous scale. Continuous refers to the fact that, in theory, there are infinite possibilities for the trait phenotype. Most measurement traits fall into this category.

As discussed in the beginning of this chapter, all traits are controlled by two effects: genetics and environment. In actuality, the impact of genetics can be divided into two types of action: *additive* and *non-additive.* Additive genetic action refers to the effect of genes that is independent of other genes and the environment. In other words, there is no influence of dominance or epistasis. These genetic effects are additive in nature, which means for a polygenic trait, you can take one additive gene and add it to the effect of another additive gene, and so on, for all of the additive genes that influence that trait. The sum of all of those genes for an animal is called its *breeding value* for that trait. A simple case for weaning weight is illustrated in Figure 5.

Figure 5. Simplified illustration of combining the additive genetics for weaning weight to determine the animal's weaning weight breeding value.

Allele	Effect
A	+ 25 lb
a	+ 5 lb
B	+ 15 lb
b	- 5 lb
C	- 10 lb
c	- 15 lb
D	+ 0 lb
d	- 5 lb

Genotype of Bull A:
AABbCcDd

Breeding Value =
25 + 25 + 15 + (-5) + (-10) + (-15) + 0 + (-5) = 30 lb

Genotype of Bull B:
AaBbCCdd

Breeding Value =
25 + 5 + 15 + (-5) + (-10) + (-10) + (-5) + (-5) = 10 lb

The proportion of differences we see between animals for a trait that is controlled by additive genetics is called *heritability*. For example, yearling weight has a heritability of 0.40, which means that 40% of the differences we see in yearling weights between cattle in a herd are caused by additive genetic effects. If a trait has a low heritability, this indicates that non-additive genetic effects and/or the environment have a much larger influence on that trait. High heritability indicates that additive genetics play a relatively large role in the trait. The level of heritability in a trait will have an impact on selection decisions. Progress tends to be much slower in lowly heritable traits when attempting change through selection. With higher heritability, we usually can achieve more rapid progress through selection due to greater accuracy in selection decisions.

Both the sire and the dam pass on half of their genetics to their offspring. For definition purposes, sperm and egg cells are called *gametes*. Each gamete that a parent produces gets a random sampling of that parent's genes. For a single gene, a heterozygous *Zz* animal produces 50% *Z* gametes and 50% *z* gametes. That means that there is variation in the genetic makeup of the gametes produced, which is termed *Mendelian sampling*. Mendelian sampling can be clearly observed when you compare full-sibs, and humans are perfect examples. The fact that male and female children can be born to the same parents is one example of Mendelian sampling. Now compare brother to brother and sister to sister within a family; there are often similarities because full sibs have half of their genes in common on average, but there are also differences, which can be dramatic. An example in cattle would be to compare flush-mates in an embryo transfer program; there is often variation in these full-sibs, even when raised in similar environments.

Since only half of each parent's total genetic material is in each gamete, then the average of all gametes produced is half of their breeding value. This is termed the parent's *transmitting ability*. Expected Progeny Differences (EPD) are estimates of an animal's transmitting ability and will be discussed in detail later. Selection decisions are made to change the additive genetics in the herd because additive genetics are passed on from one generation to the next; animals with high EPD tend to have alleles with positive additive effects on the trait for a larger number of loci.

Most traits are controlled to some degree by both additive and non-additive genetic action. In beef cattle breeding, we can take advantage of additive genetics through our selection decisions, but we can also take advantage of non-additive genetics. Non-additive genetic actions involve interactions between alleles at the same loci (dominance), interaction between genes at different locus (epistasis), and the interaction between genes and the environment.

Epistasis and genetic-environmental interactions are difficult to account for, but dominance can be taken advantage of through a crossbreeding program. Pure breeds or lines of cattle have been developed over time through selection and inbreeding. Both of these practices increase the level of homozygosity in that breed; i.e., animals tend to have the same alleles at a locus. But this homozygosity will be different in other breeds or lines; i.e., animals in other lines tend to have a greater proportion of other alleles. Therefore, when these breeds or lines are crossed, there is a great increase in number of loci for which the offspring will be heterozygous. For polygenic traits, the dominant alleles are often the advantageous

alleles. With complete dominance, there are no differences in performance between the homozygous dominant and heterozygous individuals. The result is that instead of the offspring performing average to the parental lines, as would be the case with additive genetics, they perform at a higher level than the average of the parental lines. The term for this increase in productivity is called heterosis. Heterosis tends to be highest for lowly heritable traits (such as reproduction) because these traits tend to have larger non-additive effects, and lowest for highly heritable traits (such as carcass traits). Crossbreeding might result in relatively small amounts of heterosis for a given trait, but these effects tend to accumulate to produce large increases in overall productivity. In some instances, a portion of this advantage is passed on to future generations, but to optimize the benefits, a crossbreeding program should be implemented (discussed in detail in the chapter on crossbreeding).

Another genetic effect that is important when making selection decisions is genetic correlations. A genetic correlation is reflected when you select for one trait and another trait is affected. There are two ways that traits can be genetically correlated: *linkage* and *pleiotropy*. Linkage is when genes that affect two traits are located close together on the chromosome. In that case, they do not segregate randomly but tend to segregate similarly (the closer together, the less random the segregation). Pleiotropy is when a gene has an effect on more than one trait. It is easy to understand that some of the genes that impact weaning weight are also going to impact yearling weight and birth weight; this is an example of pleiotropy.

The effect of one trait on the other can be either complementary or disadvantageous. Here is an example of a complementary genetic correlation: as selections are made for increased weaning weight, yearling weight is also increased. An example of a disadvantageous correlation would be: as selections are made for increased weaning weight, birth weight also increases. Genetic correlations work the same, regardless of which trait is being selected for. In other words, as selections are made to decrease birth weights, weaning and yearling weights are usually decreased, too. The implications of genetic correlations for many traits for which EPD are calculated are presented in Table 1.

The breeding management program of most seedstock producers is handled primarily through their selection practices. A sound breeding management program for most commercial cattle producers should include both selection and crossbreeding. The following chapters will go into detail about practices that are available for both selection and crossbreeding.

Table 1. Effect of genetic correlations when selecting for other traits.

	Weight			Milking Ability	Calving Ease	Mature Size
	Birth	Weaning	Yearling			
BW EPD	+	+	+	0	–	+
WW EPD	+	+	+	–	–	+
YW EPD	+	+	+	–	–	+
Milk EPD	0	–*	–*	+	0	0

+ = as EPD goes up, this trait also tends to increase.
– = as EPD goes up, this trait tends to decrease.
0 = no relationship.
* Increased milk EPD tend to decrease growth rate for the first generation. Due to added milk production, offspring of first-generation females have increased WW and YW.

The Role of Economically Relevant and Indicator Traits

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Selection is the process breeders use to produce genetic change, realizing that genetic change and genetic improvement are not necessarily the same. Producers can change many traits genetically but change does not necessarily mean improvement. Improvement implies the production of superior animals and for livestock production the definition of superior animals are those with greater profitability.

This manual explains underlying genetic mechanisms, concepts of selection, and tools that can be used to make better selection decisions to help producers meet their goals. The assumption throughout is that the goal of sire selection and beef enterprises is profitability.

The difference between indicator and economically relevant traits (ERT) and the ability to distinguish between the two are keys to improving profitability. By identifying the economically relevant traits, selection focus can be narrowed, resulting in faster genetic improvement and improved profitability. In the end, the goal of focusing selection on ERT is to increase the probability that breeders will make selection decisions that make them more profitable. This chapter establishes guidelines for identifying the economically relevant and indicator traits and provides a suggested list of ERT for commercial production systems. A subsequent chapter will discuss selection on multiple ERT and assessing the economic value of genetic improvement in those ERT.

Importance of the distinction

The rate or speed with which breeders can improve a specific trait is determined by four factors: generation interval, genetic variability, selection intensity and selection accuracy. Beef cattle producers have little control over genetic variability and limited control over generation interval. The generation interval, or the rate at which one generation of animals is replaced by the next, is largely limited by the reproductive rate (single births) and relatively late sexual maturity in beef cows and the need to generate replacements. The breeder has most control over the generation interval in males and over the remaining two factors: selection accuracy and intensity in both sexes.

Increased accuracy of selection is achieved using EPD rather than actual performance. EPD are calculated using all available performance information from animals within a database. By using all available data rather than only individual performance greater accuracy of selection is achieved and as accuracy increases, so does the rate at which genetic improvement is made. In the future as results from DNA tests are included in EPD calculations, even greater levels of accuracy will be achieved on young animals.

Use of EPD for selection decisions also improves the intensity of selection. Animals from different herds can be compared on a genetic level without sacrificing accuracy of selection because EPD account for genetic and environmental differences between contemporary groups. The ability to compare animals from different herds expands the pool from which producers can choose replacements—no longer are they limited to comparing animals from within the herd of a single seedstock producer. Another way to envision the effects of an expanded pool of potential replacement animals is to take an example from high school athletics. If a team for any sport were chosen from a high school of only 100 students, and then a team was selected from a high school of 2000 students, likely the team from the school with 2000 students would be superior. The team from the larger school would be subject to more selection pressure in forming their team. (This is why there are different classes for high school sports). The same concept is at work when making selection decisions, the use of EPD expands the pool from which to select—allowing fair comparison of animals from many different herds both small and large, enlarging the pool of animals to chose from, increasing the intensity of selection and ultimately speeding the rate of genetic improvement.

Traditionally breed associations only collected performance information on birth weight, weaning weight and yearling weight and accordingly the first EPD were produced only for those traits. Since that time, breeders and breed associations have begun collecting additional performance information on a multitude of traits such as calving ease, carcass attributes, and ultrasound measures. Once data on these new traits were available, the associations and scientists' approach has been to produce EPD for those traits as well. The production of these additional EPD was rationalized as giving a more complete description of the breeding animals (Bourdon, 1998). Unfortunately, this approach led to an ever expanding list of EPD which in some cases has increased the difficulty of making selection decisions. Many producers are simply overwhelmed by the amount of available information. In several cases, the expanding list of EPD resulted in several EPD that actually represent the same trait of interest. For instance, birth weight and calving ease EPD both address the same problem—difficult calving; and ultrasound percent intramuscular fat and marbling score both address the same characteristic—marbling of slaughter animals.

In situations where several EPD are calculated for the same trait of interest, two potential problems arise. First, if the producer uses both EPD to make a selection decision, the accuracy of that selection decision actually decreases as compared to selecting solely on the true trait of interest (a mathematical proof of this concept is beyond the scope of this manual). Second, the relative economic importance of the two becomes difficult to determine. For instance, if a BW and a CE EPD are available, where should most emphasis be placed? Or, should emphasis be placed only on one of the traits?

The rapid growth in the number of EPD exacerbates another problem inherent to any genetic improvement program--the more traits that are simultaneously selected for, the slower the rate of genetic improvement in any one of those traits. For instance, a producer that sells weaned calves and purchases all replace-

ment females likely concentrates on selecting and purchasing bulls that produce calves that are born unassisted and are heavy at weaning. If that producer decides to change the production system and begins to keep replacement females from the calf crop, heifer fertility and maternal ability become economically relevant. Rather than selecting bulls for calving ease and weaning weight; the breeder now must consider maternal ability and heifer fertility, adding two more traits to their selection criteria. This addition reduces the speed at which weaning weight (and calving ease) can be improved. As more traits are added to the list of importance, the rate of improvement in any one of those traits is decreased.

The proliferation in number of EPD and the reduced rate of improvement as more and more traits are selected for, beg for a method to simplify the selection process. So how does a producer choose those EPD that are most important to his/her production and marketing system? The distinction between economically relevant and indicator traits is the first step in simplifying the selection process.

Distinguishing Between ERT and Their Indicators

The costs of production and the income from production together determine profitability of a beef enterprise. For a commercial producer, those traits that directly influence either a cost of production or an income from production are considered economically relevant traits. For seedstock producers, the economically relevant traits are the traits that directly influence either a cost of production or an income from production for their **commercial** customers. Ultimately these commercial producers are the largest customers of the seedstock industry with approximately 830,000 cow-calf producers relying on 120,000 seedstock producers to supply genetically superior breeding animals adapted to the commercial production system (Field and Taylor, 2003). Those traits not directly related to a cost or income from production are, at best, the indicator traits and at worst superfluous.

The easiest way to distinguish between economically relevant traits and indicator traits is to ask a specific question about the trait of interest—if that trait changes one unit, either up or down with no changes in any other traits, will there be a **direct** effect on income or expense? For example, if scrotal circumference increases one centimeter, is there a direct influence on income or expense? A breeder's profitability is likely not changed if the bulls purchased for use in the herd average 1 cm larger. The profitability would come through the genetic relationship of scrotal circumference with ERTs. The primary reason for measuring scrotal circumference in yearling bulls is the relationship with age of puberty in those bulls' daughters. As yearling scrotal circumference increases, those bulls' daughters tend to reach puberty at earlier ages with the assumption that earlier age of puberty in heifers results in increased pregnancy rates at a year of age (Brinks, 1994). In a production system where replacement heifers are chosen from within the herd, one of the primary traits of interest is heifer pregnancy—do the heifers breed at a year of age in a restricted length breeding season? Age of puberty is often a large factor in determining whether a heifer becomes pregnant at a year of age, but age of puberty is only one factor involved in heifer pregnancy. In the end, heifer pregnancy is the economically relevant trait while scrotal circumference is an indicator trait for heifer pregnancy.

Table 1. Proposed economically relevant traits and suggested indicators.[a]

Economically Relevant Trait	Indicators[b]
Probability of Calving Ease	Calving ease score Birth weight Gestation length

Sale Weight[c]
   Weaning Direct
   Weaning Maternal (Milk)
   Yearling Weight
   600 day weight
   Carcass weight at finish
      endpoint[e]
   Salvage Cow Weight
	Birth weight
	205 d weight
	365 d weight
	Slaughter weight
	Carcass weight
	Cull cow weight

Cow Maintenance Feed Requirement	Mature cow weight Cow body condition score Milk production[d] Gut weight Liver weight
Stayability (or Length of Productive Life)	Calving records Days to calving Calving interval Milk production[d]
Heifer Pregnancy Rate	Pregnancy observations Scrotal circumference
Tenderness (not relevant unless increased income received for more tender beef, e.g. niche markets)	Carcass marbling score Shear Force US % intramuscular fat
Marbling Score (Quality Grade) at finish endpoint[e]	US % intramuscular fat Carcass marbling score Backfat thickness
Retail Product Weight at finish endpoint[e] (current industry standard is yield grade)	Carcass weight Rib-eye area Backfat thickness

Days to a Target Finish Endpoint
   Carcass weight endpoint
   Fat thickness endpoint
   Marbling endpoint
	Carcass weight and age at slaughter
	Backfat thickness and age at slaughter
	Quality grade and age at slaughter

Feedlot Feed Requirements	Feedlot "in" weight, Slaughter weight Dry matter intake Average daily gain Relative feed intake
Survival to Market Endpoint	Disease treatment records Disposal/death records
Health/Disease Incidence	Health treatment records
Docility	Docility Scores

[a] Portions adapted from Golden et al., 2000.
[b] Indicator traits are measured to provide information to produce EPD for the economically relevant traits thereby increasing accuracy of those EPD.
[c] Sale weight is a category of EPD. The breeder should choose the appropriate economically relevant EPD that represents when calves from a mating will be marketed.
[d] Milk production will be measured using the maternal weaning weight (milk) EPD.
[e] Current carcass EPD are typically adjusted to an age constant basis, in the future, carcass EPD that represent the value of the carcass should be delivered in a manner that allows each breeder to select animals appropriate for their target market (e.g. Quality grid, muscle grid).

Birth weight and calving ease provide another example of the distinction between an economically relevant and an indicator trait. Does a one pound change in birth weight directly influence income or expense? Likely not, as that change may or may not result in increased/decreased calving difficulty. With calving ease, a 1% decrease (meaning 1 extra animal assisted for every 100 calvings) has a direct impact on profitability. Decreased calving ease results in higher labor costs, decreased calf survival (and fewer animals to sell) and delayed rebreeding for the cow resulting in younger and hence lighter calves at weaning the following year—all of which have a direct impact on profitability. Birth weight is an indicator of the economically relevant trait, calving ease.

The final example applies to those retaining ownership or receiving additional income by producing cattle with higher marbling scores. A one unit increase in marbling score has a direct impact on profitability through increased income. So what are the indicators for carcass marbling score? The most utilized indicator is percentage intramuscular fat (%IMF) as measured by ultrasound. This measurement can be taken on both male and female breeding animals at yearling age, long before any slaughter progeny are produced and harvested. The ability to measure this trait at an early age makes collection of ultrasound information very appealing. However, a one percentage point increase in percent intramuscular fat does not directly affect the profitability of the commercial producer. The commercial producer receives additional income from increased carcass marbling (there is a strong but imperfect relationship between carcass observations and ultrasound observations—a concept that is discussed further below), not increased %IMF in a breeding animal. The economically relevant trait is carcass marbling score and %IMF is an indicator that we only measure to add accuracy to the EPD for marbling score.

A *suggested* list of the economically relevant traits and their indicator traits is shown in Table 1. Sale weight is a unique case where the economically relevant trait is actually one in a category of traits. The economically relevant trait sale weight changes depending upon the marketing system, or the age at which animals are sold. The term "sale weight" was chosen as it represents all possible sale endpoints and necessitates each producer choosing which trait in the sale weight class is most appropriate. Some producers will sell weaned calves making weaning weight the economically relevant trait. Others might sell yearling cattle making yearling weight the economically relevant trait. Those producing grass fed cattle might choose 600 day weight as their economically relevant trait. In addition, most cow-calf producers sell cull cows adding another economically relevant trait, salvage cow weight, under the class "sale weight". Again, when identifying the economically relevant traits, the producer must identify when the animals are sold. If the breeder sells weaned calves, yearling weight is not the economically relevant trait. Table 1 is merely a suggestion of economically relevant traits and is in no means meant to be all inclusive. Different environmental challenges will likely introduce other ERT.

Realize that identification of ERT also depends upon the levels of performance within the herd. Consider two producers, one that has a system where all heifers calve unassisted and another that assists 75% of the heifers. Calving ease would not be considered an economically relevant trait for the first producer—there is no better performance than 100% unassisted calvings. The second producer however, would consider calving ease an economically relevant trait worthy of improvement

There are instances where traits can be both an indicator trait and an economically relevant trait. Cow weight is one example. Cow-calf producers sell cull, open cows on a weight basis and as weight of that cow increases, the value of that cow increases—a one unit change in cow weight directly influences income. Mature cow weight is simultaneously an indicator of cow maintenance feed requirements. As mature size increases, feed requirements tend to increase but a one pound increase in mature size does not always increase maintenance requirements. For instance, two cows weighing the same but of different body condition likely have different maintenance requirements. Milk is another example of a trait that could be both an indicator and an economically relevant trait. The milk production of the cow is directly related to the pounds of calf produced at weaning and therefore income from the sale of weaned calves, but it is also an indicator of cow maintenance requirements. Cows with higher milk levels tend to have higher maintenance requirements even when they are not lactating.

Again, by identifying the economically relevant traits, producers take the first step towards simplifying selection decisions by reducing the number of EPD to consider and focusing on improving performance in traits directly related to profitability.

Application to Currently Available EPD

Many ask why there are EPD for indicator traits that are not directly related to profitability. An indicator trait is measured for two reasons. First, the trait is related to an economically relevant trait, or put another way, the two traits are genetically correlated. As discussed in the chapter on genetic principles, genetic correlations represent the strength and direction of the relationship between breeding values for one trait and breeding values for another trait. From the standpoint of selection, another way to conceptualize a genetic correlation is to ask, "when selecting for improvement in one trait, such as weaning weight, how will other traits change?" For example, if selection decisions are made with the objective to increase weaning weight alone, birth weight will increase as well, due to the positive genetic correlation between the traits. This occurs because some of the genes that increase weaning weight also increase birth weight. Second, indicator traits tend to be cheap and/or easy to measure and the data may therefore be available for the calculation of EPD.

Information on indicator traits is important because the additional information adds accuracy to the EPD for the economically relevant traits. By increasing accuracy, the rate of genetic improvement in the economically relevant traits increases as should improvement in profitability.

The value of accumulating large amounts of indicator trait data on a sire or his progeny may be limited however. Physically measuring cow feed requirements or cow intake is nearly impossible, and in situations where it is possible, the techniques are cost prohibitive; however, cow weight, body condition score, and milk production (through the milk EPD) are easily measured. These three traits are indicators of maintenance feed requirements. Given the expense associated with directly measuring cow intake, we are limited to the use of these indicators for predicting feed requirements. In this scenario indicator traits and in the future DNA tests will be combined to calculate the EPD for cow maintenance feed requirements.

In other situations, the economically relevant trait as well as the indicators can be measured. Marbling score of slaughter animals and %IMF (percentage intramuscular fat as measured by ultrasound) in breeding animals are an example. Collection of indicator trait data such as %IMF is important at early ages but for the best accuracy of selection, data on the economically relevant trait, carcass marbling score, must be collected as well. An extreme example best illustrates this concept. Assume that the focus of selection is to improve carcass marbling score and assume that within the production system, or within the breed association, no actual carcass data are collected (historically this has often been the case). All available information is from the ultrasonic measurement of %IMF on breeding animals. Given that scenario, suppose a sire has been used extensively as an AI stud and has thousands of progeny with ultrasound observations. In this scenario if an EPD were calculated for %IMF on that sire, the accuracy of that EPD would likely be .99+. The %IMF EPD is for the indicator trait, however; but because there is a positive genetic correlation between %IMF and carcass marbling score (assume the genetic correlation is .80), the %IMF information can be used to calculate an EPD for marbling score, the economically relevant trait. In this scenario, where only ultrasound data are available, the accuracy of the marbling score EPD would only be .40. To increase the accuracy of the marbling score EPD, collection of actual carcass information would be required.

The previous example dealt with a sire with many observations from ultrasound measures, and a correspondingly high accuracy %IMF EPD, but no carcass data from progeny. Collecting data on %IMF is useful in early stages of a potential breeding animal's life as it can be collected long before offspring are born. This additional indicator trait data increases the accuracy of selection of young breeding animals. To attain high accuracy EPD for the economically relevant carcass trait (in this scenario, marbling score) collection of actual carcass data is imperative.

In situations where indicator trait data are used to calculate EPD for the ERT in multiple- trait models and where EPD are published for both the indicator trait and the ERT, the indicator trait EPD should not be used to make selection decisions. In this scenario, the indicator trait data have already contributed to the calculation of the EPD for the ERT, and "double counting" of the indicator trait data occurs if the indicator trait EPD is used as well as the EPD for the ERT. For instance, if EPD for birth weight and calving ease are available, only the EPD for calving ease should be used for selection purposes. Typically, the calving ease EPD is produced using birth weight and calving ease scores and the birth weight EPD is calculated using birth weight and subsequent growth observations. Birth weight observations have already been used to calculate the calving ease EPD, so if the birth weight EPD is used along with the calving ease EPD to make selection decisions, the birth weight observations are overemphasized.

The list of economically relevant traits in Table 1 is only a suggested list. In some production systems there may be other economically relevant traits. For instance, in altitudes over 6000 feet, high-altitude or brisket disease reduces survivability of genetically susceptible animals. At that altitude, another economically relevant trait would likely be susceptibility to brisket disease. Other breeders may have unique production systems that might require additional ERT.

Final Guidelines

By focusing on the economically relevant traits, producers can reduce the number of EPD they need to consider when making selection decisions. Not all breed associations produce EPD for economically relevant traits. Some associations may only produce EPD for birth weight and not calving ease, for instance. In other cases EPD for the economically relevant traits are still under development (e.g. days to a finish endpoint). Realizing these current limitations, here are some general guidelines for sifting through all of the available performance and EPD information.

1. Identify the economically relevant traits for your production and marketing system.
2. Make selection decisions based on EPD with the following order of preference for those EPD
   1. select using EPD for the ERT when available (EPD for indicator traits should not be used to make selection decisions when the EPD for the ERT is available)
   2. select using EPD on the indicator trait when EPD for the ERT are not available

   In the rare cases where phenotypic information is available but not EPD,

   3. select from within a herd on phenotype or ratios for the ERT
   4. select on phenotype or ratios for the indicator trait

When EPD are available for a trait, these are always preferable to phenotypic measures on individual animals as they account for an individual's, its relatives, and contemporaries' performance.

Conclusion

The ability to distinguish between economically relevant and indicator traits helps breeders reduce the number of EPD to consider when making selection decisions. Reducing the number of EPD upon which to make selection decisions increases the rate of genetic progress over a program that bases selection decisions on many more EPD. The EPD in this short list of economically relevant traits are all directly related to profitability, resulting in a genetic improvement objective focused on changing profitability.

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Data Collection and Interpretation

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Collection of accurate performance records is critical to the success of genetic evaluation and selection programs. Throughout the life cycle of a beef animal, there are several points where data need to be recorded and reported to ensure the most complete and accurate evaluation. In this chapter, the life cycle of a heifer, steer, and bull is examined to determine the records that need to be collected, how those records can be adjusted, and how to interpret those data. First, it is important to discuss several concepts to consider when collecting and interpreting data. Contemporary Grouping

Before beginning data collection, it is important to have a good understanding of proper contemporary grouping. The environment that a calf is exposed to can have a large effect on how well it performs for all of the economically important traits. By using contemporary grouping, we are better able to separate genetic and environmental effects. A contemporary group for a traditional, within-breed genetic evaluation, is defined as a set of same-sex, same-breed calves that were born within a relatively short time interval, and have been managed the same ever since. In multiple-breed genetic evaluation, calves in the same contemporary group can have different breed makeup. Regardless of what type of evaluation, every calf in the contemporary group should receive an equal opportunity to express its genetic merit. Once an animal has been separated from his contemporaries, he can never be put into that group again.

For example, a producer may decide to select one particular bull calf to put into a fall or winter sale. He pulls that calf and his mother into a separate pen, where they have access to shelter and the calf gets creep feed. When weaning weights are collected on the group of bull calves, the selected calf has the highest weight. The problem is that we don't know if that calf was genetically superior for weaning weight, or if his extra growth was due to the feed and shelter. This is an extreme example, but anything that is different in the environment or management between groups of calves may give some of them an unfair advantage and make comparisons impossible. Improper contemporary grouping can lead to biased and inaccurate EPDs.

Adjusting Records

Calf age and cow age are two environment factors that are not accounted for by contemporary grouping. These effects are predictable from year to year and herd to herd, so the records can be adjusted to account for that variation. For example, all calves in the herd should not be weaned and weighed when they are exactly 205 days of age. It's important to keep contemporary groups as large as possible. If a producer weighed each calf individually when it was exactly 205 days of age, each calf would be in its own contemporary group. Single-animal contemporary groups are worthless as far as genetic evaluation goes. However, when all calves are weighed on the same day (when the average

of the group is close to 205 days old), the younger calves will be at a disadvantage compared to the older calves. To get a fair comparison, the raw weights of calves weighed on the same day will be adjusted to the same age of 205 days. Basically, the adjustment figures out how much each calf is gaining per day and predicts what they will weigh (or did weigh) when they are (or were) exactly 205 days old.

The second type of adjustment is for age of dam. First-calf heifers have calves that are lighter at birth than calves from older cows, and they also produce less milk throughout lactation than older cows, leading to lower weaning weights. These are not genetic factors of the calf, and should not be attributed to the calf's performance.

Beef Improvement Federation (BIF, 2002) publishes adjustment factors and procedures. These are general adjustment factors that are appropriate for commercial cattle. BIF factors and procedures are used for illustration in this publication. Most breed associations have developed adjustment factors using their breed data. Purebred producers should use the adjustment factors and procedures of their association.

Ratios

One way to compare calves within the same contemporary group is to use ratios. Ratios are calculated by dividing a calf's adjusted record by the average record of his contemporary group and multiplying by 100. This means that the average performing calf in the group will have a ratio of 100, poorer calves will be below 100, and better calves will be above 100 for traits where bigger is better. For traits where smaller is better, like birth weight, better (lighter) calves will be below 100, and poorer (heavier) calves will be above 100. Ratios measure an animal's percentage deviation from the average of its contemporary group. Because of differences in management and mean genetic level between herds, ratios should not be used to compare animals across contemporary groups.

$$\text{Ratio} = \frac{\text{Individual Record}}{\text{Contemporary Group Average}} \times 100$$

Complete Reporting

Traditionally, some breeders have only reported performance data on calves that they want to register. However this leads to biased and inaccurate EPDs. Complete reporting of every animal in the herd is critical to obtain the best estimates of genetic merit. By only reporting the best calves (for whatever trait), producers are not making their herd look better, they are inadvertently penalizing their highest-performing calves. In the following example (adapted from BIF, 2002), we will use weaning weight ratios to see what happens when only the best calves are reported. (Incomplete reporting has the same effect on EPDs that it does on ratios.)

Suppose we have 10 calves with an average adjusted weaning weight of 625.

Calf	Adj WW	WW Ratio
1	742	119
2	694	111
3	655	105
4	643	103
5	639	102
6	606	97
7	605	97
8	578	93
9	562	90
10	524	84
group avg	625	

Now suppose that the producer only reports the top 5 calves, which means the new average adjusted weaning weight is 675.

Calf	Adj WW	WW Ratio
1	742	110
2	694	103
3	655	97
4	643	95
5	639	95
group avg	675	

Those high performing calves (calves 1 through 5) receive much lower ratios, and subsequently EPDs, than if they had been compared to their entire contemporary group.

Another reason to use complete reporting, sometimes referred to as whole herd reporting, is to take advantage of genetic evaluations for cow stayability and fertility. As new genetic predictions of cow efficiency, maintenance, and fertility are developed, associations are going to need lifetime performance records on those cows to make the best estimates possible.

Birth

The first records to collect in a bull or heifer's life are birth weight and calving ease. Factors to consider when assigning contemporary groups are herd, year, season, sex, breed composition, management group, and embryo transfer or natural calf.

Birth weight—Birth weight should be collected as soon after birth as possible, and needs to be adjusted for age of dam before being included in a genetic evaluation. The age of dam adjustment will compare all calves on a mature-cow-equivalent basis. Most associations ask that breeders submit the raw data, and they will make the appropriate adjustments, using their own breed-specific adjustment factors. If those are not available, use the Beef Improvement Federation (BIF) adjustments.

Age of Dam at Birth of Calf	Birth Weight Adj
2	+8
3	+5
4	+2
5-10	0
11 and older	+3

(BIF, 2002)

This is an additive adjustment, so:

Adjusted BW = Actual BW + Age of dam adjustment

(BIF, 2002)

Example using BIF adjustments:

Calf	Sex	Actual BW	Age of Dam	Adj BW	BW Ratio
1	B	78	2	86	100
2	B	85	6	85	99
3	B	76	4	78	91
4	B	90	11	93	108
group avg				86	

Remember, for birth weight, a lower number is associated with less calving difficulty.

Calving ease—To record calving ease, use the scale recommended by your breed association, or the BIF recommended scale.

1	No difficulty, no assistance
2	Minor difficulty, some assistance
3	Major difficulty, usually mechanical assistance
4	C section or other surgery
5	Abnormal presentation

(BIF, 2002)

After breeders submit actual weights, breed associations adjust the weights and use them to calculate EPDs for birth weight. Both birth weights and calving ease measurements are used to calculate calving ease direct (genetic merit of the calf) and calving ease maternal (genetic merit of the dam) EPDs.

Weaning

Weaning weight—The next piece of data to collect on a bull, heifer, or steer is weaning weight. A group of calves should be weighed when the average of the group is near 205 days of age. BIF recommends that all calves be between 160 and 250 days old, or they need to be split into two contemporary groups and weighed on two different days. However, each breed association's particular guidelines for age at weaning may be slightly different. Any calf that is outside the prescribed range when weighed will not be included in a national genetic evaluation. Contemporary group criteria typically include all those for birth weight, plus birth-to-wean management code (which includes creep versus no-creep), date weighed, and sex (some calves that were bulls at birth may be steers by weaning). Weaning weight should be adjusted for age of dam and for age of calf. Most breed associations have their own age of dam adjustments, but if those are not available, the BIF adjustments are:

Age of Dam at Birth of Calf	Weaning Weight Adj for:	
	Male Calf	Female Calf
2	+60	+54
3	+40	+36
4	+20	+18
5-10	0	0
11 and older	+20	+18

(BIF, 2002)

The formula to adjust weaning weight is:

$$\text{Adj 205-d WW} = \frac{\text{WW} - \text{Actual BW}}{\text{Wean Age (days)}} \times 205 + \text{Actual BW} + \text{Age of Dam Adj}$$

(BIF, 2002)

Example using BIF adjustments:

Calf	Sex	Age of Dam	Actual BW	Actual WW	Weaning Age (days)	Adj WW	WW Ratio
1	B	2	78	515	186	620	107
2	B	6	85	580	232	522	90
3	B	4	76	520	200	551	95
4	B	11	90	560	191	614	106
group avg						577	

Weaning weights are used by breed associations to calculate weaning weight, maternal milk, and total maternal EPDs. The genetic correlation between weaning weight and other weight traits make it possible to use weaning weights to help calculate EPDs for the other weight traits.

Yearling

At a year of age, there are many records that can be collected on bulls, steers, and heifers. It is important to collect data when the average of the group is near 365 days. Check with your breed association for the acceptable range of ages to take yearling measurements. In general, BIF recommends that all animals within the group be between 320 and 410 days when yearling data are taken. If animals fall outside of the range determined by the association, the group should be split into two successive yearling dates so that all animals are within the range on the day of measurement. Contemporary grouping should include the weaning criteria, plus yearling/feeding management code, date weighted, and sex. It is beneficial to hold animals off feed and water overnight to prevent gut fill from biasing weight measurements.

Yearling weight—Yearling weight should be collected on all animals, and adjusted for age and age of dam. However, using the BIF adjustments, there is no separate age of dam adjustment. It incorporates adjusted weaning weight to account for age of dam. The formula to adjust yearling weights is:

$$\text{Adj 365-d YW} = \frac{\text{Actual YW} - \text{Actual WW}}{\text{\# Days Between Weights}} \times 160 + \text{205-d Adj WW}$$

(BIF, 2002)

Example using BIF adjustments:

Calf	Sex	Actual WW	Adj WW	Days Between	Actual YW	Adj YW	YW Ratio
1	B	515	620	168	1150	1225	111
2	B	580	522	168	1024	945	86
3	B	520	551	168	1031	1038	94
4	B	560	614	168	1175	1200	109
group avg						1102	

Adjusted yearling weights are used to calculate yearling weight EPD. Depending on the association, yearling weight may also be used as indicator traits to help calculate other EPDs, such as mature weight. Many animals that have birth and weaning records go into the feedlot, and will not contribute a yearling weight record. This could lead to selection bias for yearling weight EPDs. However, most associations use a multiple-trait animal model that includes birth, weaning, and yearling weights. This uses genetic correlations between the traits to account for selection and avoid bias.

Hip height—Frame score is a measurement that describes skeletal size. Larger framed cattle tend to be later maturing, and smaller framed cattle tend to be earlier maturing. Tables are available to convert the hip height measured in inches into a frame score (BIF, 2002). Hip height can be measured at any time from 5 to 21 months, but many producers choose to do it at yearling time because of convenience. Hip height or frame score can be used by associations to calculate EPDs for mature weight or height. Check with the association for acceptable age ranges for submission of data.

Scrotal circumference—Scrotal circumference is an indicator of a bull's fertility and it has a relationship with his daughters' age at puberty. Larger scrotal circumference is associated with younger age at puberty for the bull and his daughters. The contemporary group and age of measurement requirements are the same as those for yearling weight. Scrotal circumference measurements need to be adjusted for age with a breed specific adjustment factor.

$$\text{Adj. 365 day SC} = \text{actual SC} + [(365 - \text{days of age}) \times \text{age adj factor}]$$

(BIF, 2002)

Breed	Age Adj Factor
Angus	0.0374
Red Angus	0.0324
Brangus	0.0708
Charolais	0.0505
Gelbvieh	0.0505
Hereford	0.0425
Polled Hereford	0.0305
Limousin	0.0590
Salers	0.0574
Simmental	0.0543

(Geske et al., 1995)

Example using BIF adjustments:

Calf	Sex	Days of Age	Actual SC	Adj SC	SC Ratio
1	B	354	36.2	36.6	101
2	B	400	38.5	37.2	102
3	B	368	34.6	34.5	95
4	B	359	36.5	36.7	101
group avg				36.3	

Many breeds have their own adjustment factors, and they should be used if available. Most associations are using scrotal circumferences to calculate EPDs for scrotal circumference, and may use it as an indicator trait for heifer pregnancy EPDs.

Pelvic area—Pelvic area can be measured on bulls and heifers at yearling time. While most breed associations are not calculating EPDs for pelvic area at this time, it can be a useful culling tool within a herd. Heifers with small pelvic areas are more likely to experience calving difficulty. It may be beneficial to measure yearling bulls as well, because bull pelvic area is moderately correlated with heifer pelvic area. As with yearling weight, pelvic measurements should be taken between 320 and 410 days, and adjusted to 365 days.

Bull adj. 365 day pelvic area =
    actual area (cm2) + [0.25 x (365 – days of age)]

Heifer adj 365 day pelvic area =
    actual area (cm2) + [0.27 x (365 – days of age)]

(BIF, 2002)

Example using BIF adjustments:

Calf	Sex	Days of Age	Actual PA	Adj PA	PA Ratio
1	H	351	150	154	102
2	H	395	165	157	104
3	H	359	144	146	97
4	H	386	152	146	97
group avg				151	

Reproductive score—An experienced technician can palpate a heifer to determine the maturity of her reproductive tract and to determine if she has begun cycling. This information isn't used in national genetic evaluations, but can be a useful management tool. Heifers with immature reproductive tracts should be culled before the breeding season.

Ultrasound data—Most breed associations are now using ultrasound data collected on bulls and heifers to calculate EPDs for body composition. Each association has its own specifications for when data should be collected. In general, bulls on gain test should be measured around a year of age. Some associations will use data from forage-raised bulls that are measured later than one year of age. Developing replacement heifers are typically scanned between 12 and 15 months of age, but there is variation between associations. Contact your breed association to get their requirements for age of scanning. Different associations have different requirements for ultrasound contemporary grouping. If scanning is done the same time as other yearling measurements, contemporary grouping is often the same as for yearling weight. If done at a different time, contemporary group criteria may include weaning weight contemporary group, yearling management group, and scan date. Check with a particular association for their contemporary grouping guidelines. BIF recommends that all calves in a scanning contemporary group be within 60 days of age with each other, but some associations may allow a wider age range. Ultrasound data need to be adjusted to a common endpoint of either age or weight. Each breed has determined their own endpoints and adjustment factors. Some breeds may include steer ultrasound data in their genetic evaluations. Check with your breed association for specific recommendations regarding scanning steers. It is important to use a certified technician to scan cattle if those data are to be included in a national genetic evaluation. Breed associations have a list of certified technicians from whom they will accept data.

Measurements taken at scanning include scan weight, ribeye area, 12-13th rib fat thickness, rump fat thickness, and percent intramuscular fat. EPD for scan weight, ribeye area, fat thickness and percent intramuscular fat are produced from those measurements. Ribeye area and fat are indicators of the amount of carcass red meat yield. Percentage intramuscular fat is highly correlated with the amount of marbling in the carcass. Measurements of 12-13th rib fat thickness and rump fat thickness are combined to develop an EPD for fat. Some breeds combine weight, fat, and ribeye area into an EPD for yield or percent retail product.

Docility—Cattle behavior has been referred to as a convenience trait, but current research shows that temperament is related to growth, carcass quality, energetic efficiency, and reproductive performance, as well as having an impact on safety of both animals and handlers. Many breeds are collecting temperament scores and calculating a docility EPD. BIF recommends that scores be calculated when animal are processed through a squeeze chute at weaning or yearling measurement. Check with your breed association to determine whether to measure animals at weaning or yearling. The BIF docility scoring system is shown in the following table.

Score	Description
1 Docile	Mild disposition. Gentle and easily handled. Stands and moves slowly during processing. Undisturbed, settled, somewhat dull. Does not pull on headgate when in chute. Exits chute calmly.
2 Restless	Quieter than average, but may be stubborn during processing. May try to back out of chute or pull back on headgate. Some flicking of tail. Exits chute promptly.
3 Nervous	Typical temperament is manageable, but nervous and impatient. A moderate amount of struggling, movement, and tail flicking. Repeated pushing and pulling on headgate. Exits chute briskly.
4 Flighty (Wild)	Jumpy and out of control, quivers and struggles violently. May bellow and froth at the mouth. Continuous tail flicking. Defecates and urinates during processing. Frantically runs fence line and may jump when penned individually. Exhibits long flight distance and exits chute wildly.
5 Aggressive	May be similar to Score 4, but with added aggressive behavior, fearfulness, extreme agitation, and continuous movement which may include jumping and bellowing while in chute. Exits chute frantically and may exhibit attack behavior when handled alone.
6 Very Aggressive	Extremely aggressive temperament. Thrashes about or attacks wildly when confined in small, tight places. Pronounced attack behavior.

(adapted from BIF, 2002)

Post-Yearling

Carcass data—Steers and cull heifers can be used to provide carcass data. Carcass data must be collected by trained personnel in conjunction with a packing plant. Many breed associations have structured carcass tests in place that do much of the groundwork for producers. Contemporary grouping for carcass data includes weaning contemporary group, feeding management group, and slaughter date. Within a plant, the day, and even the shift, that the cattle are processed can have a large effect on the carcass data. Data should be adjusted to an age-constant or weight-constant basis. Each breed association has their own guidelines to do this.

Data collected include hot carcass weight, marbling score, 12-13th fat thickness, ribeye area, and percent kidney, pelvic and heart fat. Marbling score measures the quality of the carcass. Depending on market conditions, highly marbled carcasses can receive significant premiums. Marbling score is related to quality grade as follows:

Quality Grade	Marbling Amount	Marbling Score
High prime	Abundant	10.0-10.9
Average prime	Moderately abundant	9.0-9.9
Low prime	Slightly abundant	8.0-8.9
High choice	Moderate	7.0-7.9
Average choice	Modest	6.0-6.9
Low choice	Small	5.0-5.9
Select	Slight	4.0-4.9
High standard	Traces	3.0-3.9
Low standard	Practically devoid	2.0-2.9

(adapted from BIF, 2002)

Most breeds report EPDs for carcass weight, marbling, ribeye area, and fat. In addition, they may include an EPD for yield or percent retail product. These EPD are intended to indicate the amount of lean meat in the carcass and use measurements of 12-13th rib fat, kidney pelvic and heart fat, ribeye area, and hot carcass weight.

% retail product
= 65.59
– (9.93 x adj fat thickness, in)
– (1.29 x kidney pelvic and heart fat, %)
+ (1.23 x ribeye area, in^2)
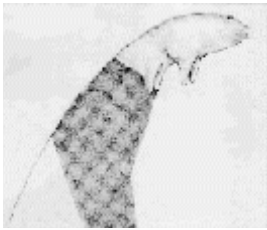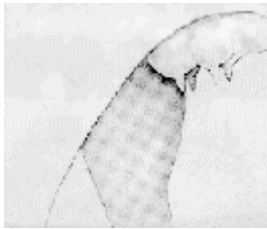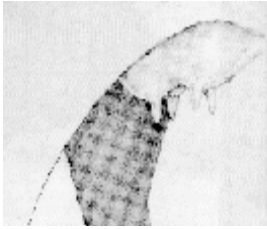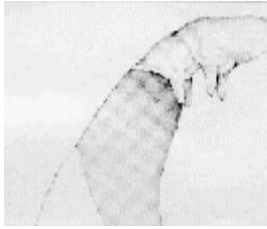– (0.013 x hot carcass weight, lbs)

(Dikeman et al., 1998)
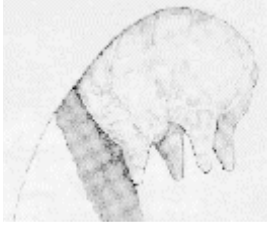
Yield grade
= 2.50
+ (2.5 x adj fat thickness, in)
+ (0.2 x kidney pelvic and heart fat, %)
+ (0.0038 x hot carcass weight, lbs)
– (0.32 x ribeye area, in^2)

(BIF, 2002)

Example using steer carcass data (adjusted for age or weight):

Steer	HCW (lb)	Fat (in)	REA (in^2)	KPH %	%RP	YG
1	735	0.35	12.8	2.0	65.7	2.5
2	690	0.40	11.5	2.0	64.2	2.8
3	845	0.45	14.4	2.0	65.3	2.6
4	905	0.60	13.5	2.5	61.2	3.6

Yearly cow herd measurements—Once a female makes it into the breeding herd, there are several records that should be collected every year. All replacement heifers and cows should be pregnancy checked after the breeding season. Besides being a management tool to cull open females, some breeds are now collecting pregnancy data on heifers to calculate a heifer pregnancy EPD. At calving, birth dates, birth weights, and calving ease score should be recorded. These are necessary to document calf performance (as discussed previously), but also to document cow performance. Stayability EPDs predict how long a cow will stay in the herd. This is based on reporting whether a cow is in the herd after 6 years of age. Udder quality is another trait that can impact herd life and calf performance. Udder suspension score and teat score should be recorded at calving.

	Description	
Score	Udder Suspension	Teat Size
9	Very tight	Very small
7	Tight	Small
5	Intermediate/moderate	Intermediate/moderate
3	Pendulous	Large
1	Very pendulous, broken floor	Very large, balloon-shaped

It's important to record AI or exposure dates on the breeding herd. Currently there are few measures of genetic merit for reproduction, but breed associations are working to provide producers with EPD for fertility traits. Having complete breeding records will allow a producer to take advantage of these EPD as soon as they are developed. At weaning, cow weight and body condition score should be collected along with calf weaning weight.

Body Condition Scoring System (BCS) for Beef Cattle

BCS	Description
1 Emaciated	Cow is extremely emaciated with no palpable fat detectable over spinous processes, transverse processes, hip bones, or ribs. Tail-head and ribs project quite prominently.
2 Poor	Cow still appears somewhat emaciated but tail-head and ribs are less prominent. Individual spinous processes are still rather sharp to the touch, but some tissue cover exists along the spine.
3 Thin	Ribs are still individually identifiable but not quite as sharp to the touch. There is obvious palpable fat along spine and over tail-head with some tissue cover over dorsal portion of ribs.
4 Borderline	Individual ribs are no longer visually obvious. The spinous processes can be identified individually on palpation but feel rounded rather than sharp. Some fat cover over ribs, transverse processes and hip bones.
5 Moderate	Cow has generally good overall appearance. Upon palpation, fat cover over ribs feels spongy and areas on either side of tail-head now have palpable fat cover.
6 High moderate	Firm pressure now needs to be applied to feel spinous processes. A high degree of fat is palpable over ribs and around tail-head.
7 Good	Cow appears fleshy and obviously carries considerable fat. Very spongy fat cover over ribs and around tail-head. In fact "rounds" or "pones" beginning to be obvious. Some fat around vulva and in crotch.
8 Fat	Cow very fleshy and over-conditioned. Spinous processes almost impossible to palpate. Cow has large fat deposits over ribs and around tail-head and below vulva. "Rounds" or "pones" are obvious.
9 Extremely fat	Cow obviously extremely wasty and patchy and looks blocky. Tail-head and hips buried in fatty tissue and "rounds" or "pones" of fat are protruding. Bone structure no longer visible and barely palpable. Animal's mobility may even be impaired by large fatty deposits.

(Richards et al., 1986)

Depending on the association, cow weights can be used to calculate mature cow weight EPDs. Also, cow weight and body condition are important components of the new EPDs being developed for cow efficiency and cow maintenance.

Summary

A successful breeding program depends on the accurate collection of performance records and the interpretation of those data. By maintaining proper contemporary grouping, adjusting the records correctly, and collecting data on every animal, the beef producer can make more effective selection decisions and maximize genetic progress.

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Expected Progeny Differences (EPD)

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Physical features, such as structure and muscling, are important for animal selection, and will be discussed further in another section of this manual. However, other important factors in beef cattle production, such as carcass, growth, maternal, and reproductive traits, cannot be adequately selected for simply by physical observation of a potential breeding animal in the pasture or sale ring. When seeing an animal once or even several times in one environment, it is difficult to determine what portion of the animal's performance is due to non-genetic factors (management, nutrition, weather, etc.), which are not passed on to offspring, and what portion is actually due to the genetics of the animal which can be passed on to its offspring. To aid producers in selecting animals based on genetic potential, genetic predictions for many traits are available. In beef cattle, these genetic predictions are referred to as Expected Progeny Differences.

What are Expected Progeny Differences?

Expected Progeny Differences, more commonly referred to as EPD, are the genetic predictions that producers can use when making selection decisions. These values are readily available on registered animals from breed associations. For most breeds, particularly those with large numbers of annual registrations, genetic evaluations are performed twice a year, but smaller breeds may perform these evaluations less frequently. For instance, breeds with fewer annual registrations may only run an evaluation once a year or only after a specific number of new registrations have been received. For specific information about your breed's genetic evaluation schedule, contact your national breed association. Contact information for many breed associations is located at www.beefimprovement.org/memberlist.html or www.beefusa.org/affibreedaffiliates.aspx.

Following each evaluation, breed associations publish EPD for active sires. Traditionally, these have been available in print in the form of sire summary books, but with the advent of the internet, most breeds have begun publishing their EPD on their websites for producers to easily access. However, it is not always necessary to look each animal up either in a sire summary or on the web in order to access its EPD.

Seedstock producers, bull studs, and anyone else wishing to market animals will often provide EPD information on their animals.

How Do You Use EPD?

By themselves, EPD on one animal have no meaning. This is because EPD are not absolute values. They are deviations from some preset value (base) that is determined individually by each breed. When EPD are used to compare two or more animals, however, the EPD have a great deal of meaning because the difference between the animals' EPD predicts the difference in performance of the future calves of the animals for a given trait.

EPD can also be used to determine how a bull ranks in the breed compared to the breed average for a given trait. Breed average EPD are rarely zero. Zero is equal to the base which is determined individually by each breed association. Many times, the base is set so that animals born in a specific year are forced to have an average EPD of zero. The breed average EPD for each trait can be found in the breed association's sire summary or on their web sites.

Table 1. Example of a beef sire summary.

Bull Name	Registration Number	Birth Weight	Weaning Weight	Milk	Yearling Weight
Bull A	98761001	-3.1	+54	+28	+108
		(0.66)a	(0.66)	(0.26)	(0.57)
Bull B	98761002	+1.0	+21	+19	+54
		(0.75)	(0.74)	(0.50)	(0.67)
Bull C	98761003	-1.9	+46	+28	+92
		(0.94)	(0.94)	(0.80)	(0.85)
Breed Average		+2.0	+28	+15	+54

a   Accuracy for the EPD

In sire summaries, EPD are reported in a format similar to what is shown in Table 1. In this example, Bull A has a weaning weight EPD of +54 lb, Bull B has a weaning weight EPD of +21 lb, Bull C has a weaning weight EPD of +46 lb, and the breed average weaning weight EPD is +28 lb. These values show that the calves of Bull A, on average, can be expected to be 33 lb heavier at weaning than the calves of Bull B and 8 lb heavier at weaning than the calves of Bull C. Furthermore, you can expect those same calves by Bull A to be 26 lb heavier than calves sired by breed average bulls.

Bull A	54 lb	Bull A	54 lb	Bull A	54 lb
Bull B	21 lb	Bull C	46 lb	Breed Avg	28 lb
Difference	33 lb	Difference	8 lb	Difference	26 lb

Using birth weight as an example, Bull A's calves are expected to be 4.1 lb lighter than Bull B's and 1.2 lb lighter than Bull C's. His calves can also be expected to be 5.1 lb lighter at birth than calves out of breed average bulls.

Bull B	1.0 lb	Bull C	-1.9 lb	Breed Avg	2.0 lb
Bull A	-3.1 lb	Bull A	-3.1 lb	Bull A	-3.1 lb
Difference	4.1 lb	Difference	1.2 lb	Difference	5.1 lb

Even though Bull A has the highest weaning weight EPD relative to the other two bulls, he also has the lightest birth weight EPD. This means that his calves could be expected to be the heaviest at weaning, but also the lightest at birth. Many times, this type of bull is referred to as being a curve bender or having a large spread because their calves are born small, but grow quickly so they are still large at weaning, contrary to the normal growth curve expectation.

Currently most EPD that are available can only be used to compare animals within a certain breed. For example, an Angus bull with a weaning weight EPD reported by the American Angus Association cannot be compared with a Charolais bull with a weaning weight EPD reported by the American International Charolais Association. This is because the two different associations report animals based on different bases and use information calculated in different analyses. The breed associations also could potentially calculate data using different models and genetic parameters. Therefore, a weaning weight EPD of +2 lb does not necessarily mean the same thing for Angus bulls as it does for Charolais bulls. Currently, there are two ways to compare bulls of different breeds. The traditional way is to use the Across Breed EPD adjustment values that are updated annually at the U.S. Meat Animal Research Center in Clay Center, Nebraska by Kuehn and Thallman (2009) and available at www.beefimprovement.org. The second way is to have multiple bulls of different breeds evaluated in the same evaluation. This could happen for a variety of reasons, such as the bulls having crossbred progeny of varying breeds or breeds running evaluations together.

What are Accuracies?

Expected Progeny Differences are predictions of the genetic merit of an animal. They are not exact known values of the true genetic merit or breeding value so there is some risk involved in using EPD. Furthermore, seldom are two EPD created with equal predictive ability because animals have varying amounts of data that contribute to the calculation of their individual EPD. The more data included in the calculation, the more accurate the EPD will be and the less risk associated with using that value. Furthermore, data are weighted differently if the data are from parents, progeny, grandprogeny, or other relatives. However, by just looking at the EPD, a producer can't tell how much or what type of data were used to calculate the prediction. Therefore, with every EPD there needs to be a measure of how confident a producer can be in the value. In beef cattle, this measure is referred to as accuracy.

In theory, accuracy can range from 0 (no information) to 1 (true genetic value known). In reality, accuracies are typically reported in sire summaries in the 0.40 to 0.99 range for traits such as the growth traits. Breed associations will not report bulls in sire summaries that have accuracy values for specific growth traits (either weaning weight or yearling weight depending on the breed) less than a predetermined number, usually the minimum is in the range of 0.40 – 0.50. Some traits, such as reproduction and carcass traits, are reported with lower accuracies due primarily to limited data available. On the high end, no animals are reported with accuracies of 1.00 because it is never known with 100% certainty what an animal's true breeding value is.

In the example sire summary that was shown previously in Table 1, below each EPD, in parenthesis, is the accuracy associated with that EPD. Based on these accuracies, it would appear that Bull A has the least amount of information included in the analysis compared to the other two bulls because his accuracies are the lowest. Similarly, it would appear that out of the three bulls reported, Bull C has the greatest amount of descendants (or progeny) with data reported, because he has the highest accuracies of the three bulls shown. The majority of information for bulls, and the information that can contribute to very high

Figure 1. Four genes control some hypothetical trait. The sire is heterozygous for all of these genes. Calf A receives all of the sire's "bad" alleles for those genes, designated by lowercase letters, and Calf B receives all of the sire's "good" alleles, designated by capital letters, for those genes. The calves in between get a sampling of good and bad genes and all calves also get alleles from their dams which will affect their performance. Over a random sampling of dams, calves should average the genetic merit of their sire.
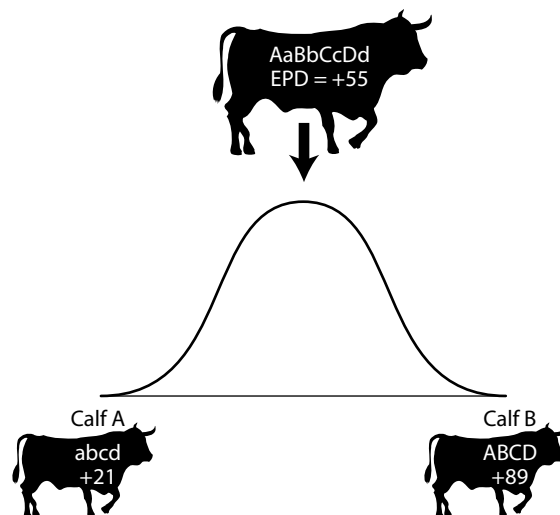
accuracies, typically comes from progeny and other descendents as opposed to ancestors.

Accuracy does not measure how close the individual progeny will perform to the EPD value, but how close the EPD prediction is to the true genetic value. By chance, a calf could receive all of its sire's undesirable genes or by chance a second calf could receive all of its sire's favorable genes (see Figure 1). The performance of these two calves can be greatly different, even if their sire has a high accuracy EPD. More often, calves will get a combination of desirable and undesirable alleles from their sire and their average performance (across many calves) will be the same as the true genetic merit which the EPD predicts if the bull is a high accuracy sire. For instance, if the bull's weaning weight EPD is 45 lb above breed average and he is a high accuracy sire, you can expect that his calves will average close to 45 lb above breed average at weaning.

Proven Sires vs. Young Sires

The difference between proven sires and young sires is simply a matter of accuracy due to data. As more data from a bull's progeny are included in the evaluation, his accuracy increases. Once the accuracy reaches a certain point, the bull is considered a "proven sire". Prior to that, the bull is included in the "young sire" category. This idea is constant, but the terminology may change from breed association to breed association.

A young sire will have a lower accuracy than a proven sire, but that does not automatically make the young sire "bad". Remember, all older, high-accuracy sires were once young, unproven, low-accuracy bulls. If a young, low accuracy bull has an extreme EPD (as shown in Figure 2), it is unlikely that his EPD will decrease enough to be less than a proven sire with a drastically smaller EPD.

Figure 2. Although both bulls will produce calves on the same bell curve (see Figure 1), the EPD of a low accuracy, young sire has more potential to change than that of a high accuracy, proven sire. However, the uncertainty of the young sire should not necessarily deter a producer from using him. In this example, the young sire has a much higher EPD than the proven sire. Even if the young sire is proven to be much worse than his current prediction, it is unlikely that his EPD will be less than that of the proven sire.

Proven Sire
high accuracy

Young Sire
low accuracy
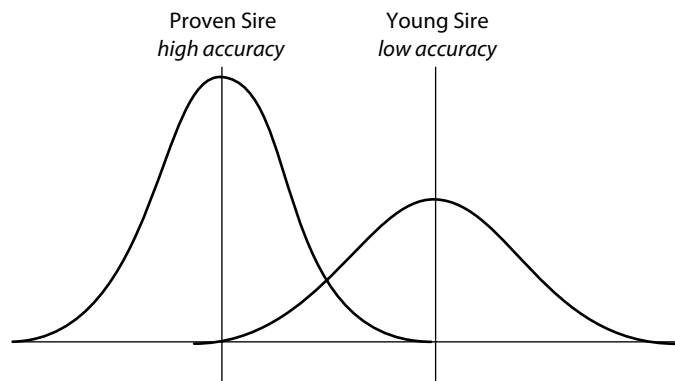
How are EPD Calculated?

Although some people think that EPD are a product of magic or someone shooting darts at a dartboard to determine the values, that really isn't the case. A large number (thousands and often millions) of calculations are performed by computers that ultimately result in an EPD.

In order to perform these calculations so that results are unbiased and predict only genetic differences, data need to be adjusted for any known non-genetic effects. This is done in two ways. The first is by preadjusting the data for environmental factors with known effects, such as age of dam and calf age. The second is through the formation of contemporary groups and using those classifications in the data analysis.

Adjustment Factors

Some non-genetic effects are assumed to have a consistent effect from year to year, farm/ranch to farm/ranch, and management style to management style. Because these effects are thought to not change, producers can adjust their own raw data in order to make selection decisions. These adjustments should never be made to data before being sent to your breed association because breed associations adjust the data themselves.

Age of Dam Adjustments

Age of dam adjustments for birth and weaning weight are necessary because heifers and young cows generally produce calves that are smaller than calves produced later in their life. This is because young females are still growing and are having to partition nutrients to not only lactation and gestation, but also their own growth. Older cows can partition the same nutrients to lactation and gestation without having to provide any nutrients for growth, providing their calves with more nourishment. Similarly, older cows (11 years and older) are usually less efficient in partitioning nutrients and therefore also tend to produce smaller calves.

Standard additive age of dam (AOD) adjustment factors for birth weight are provided by the Beef Improvement Federation in its 8th edition of the Guidelines for Uniform Beef Improvement Programs (BIF, 2002) as shown in Table 2. Not all breeds use these recommended adjustments and instead some have developed their own to fit their individual breed needs. Unique breed adjustments can be obtained by contacting your breed association.

For instance, calves out of heifers are smaller than calves out of older cows. Using the adjustments from Table 2, when making selection decisions on which calves to keep and which to cull, calves out of heifers would look more appealing as they would be, on average, 8 lb less than calves out of the same cows once they reach maturity. By adjusting the birth weights so that AOD does not have an effect, it can change the interpretation of the calf crop data considerably.

Table 2. Beef Improvement Federation recommendations for age of dam adjustments for birth weight.

AOD (yr)	Bull Calves (lb)	Heifer Calves (lb)
2	8	8
3	5	5
4	2	2
5-10	0	0
11	3	3

These standard adjustment values adjust weights to a mature cow base, adding weight to calves out of both younger and older females. With birth weight adjustments, sex is not a factor. Bull calves receive the same adjustment as heifer calves when their dams are the same age. This is not true for weaning weight adjustments. For weaning weight, heifer calf adjustments are typically less than adjustments for bull calves when their dams are the same age.

Recommendations for weaning weight AOD adjustments are also available from the Beef Improvement Federation (BIF, 2002) and are shown in Table 3. As with the birth weight adjustments, many breed associations provide their own adjustment factors for weaning weight and you should consult your specific breed association for those values. If breed specific values are not available for your breed, the Beef Improvement Federation adjustments should be used.

Table 3. Beef Improvement Federation recommendations for age of dam adjustments for weaning weight.

AOD (yr)	Bull Calves (lb)	Heifer Calves (lb)
2	60	54
3	40	36
4	20	18
5-10	0	0
11	20	18

Consider the following example:

	First Calf Heifer	6-yr-old Cow
Actual Bull Calf Birth Weight	72 lb	80 lb
Adjustment	+8 lb	+0 lb
Adj. Birth Weight	80 lb	80 lb
Actual Bull Calf Weaning Weight	480 lb	525 lb
Adjustment	+60 lb	+0 lb
Adj. Weaning Weight	540 lb	525 lb

In this case, the heifer produces a calf that could have been expected to be 8 lb heavier had the dam been older. Therefore, that calf is actually evaluated as an 80 lb calf when genetic evaluations are run, the same as the calf from the six-year-old cow. Similarly, at weaning the calf gets 60 lb added to its true weaning weight because of the decreased milk production of its heifer mother so the calf is actually genetically heavier than the calf from a six-year-old cow.

Calf Age Adjustments

In an ideal world, every calf would be born on the same day so that they are the same age when they are weighed at weaning or yearling, but that is not the case. Calves are born over a range of days and a calf crop is typically weighed for weaning and yearling weight on the same days, regardless of age. Because of this, breed associations adjust data to an equivalent calf age (see the equations below).

This allows all animals to be evaluated at a constant age and does not penalize calves born late in the calving season. It is important to remember that adjustments for AOD should be done at the end, so that it is the actual weights that are being included in the equations and not the weights that are already adjusted for AOD.

For these adjustments to be the most accurate, calves need to be within a specific age range. For weaning weight, this range is typically 160 to 250 days. For yearling weight, this range is typically 320 to 410 days. Adjustments within these age ranges are done linearly, but because the growth curve of an animal is not linear, as shown in Figure 3. Animals that are outside of these age ranges would not be adjusted correctly. Animals that are outside of these age ranges when weighed may not be included in genetic evaluations because it is harder to accurately adjust the data.

Contemporary Groups

Contemporary groups are used to account for the non-genetic effects that are not as predictable as those accounted for by adjustments, but can also alter the expression of traits. Effects such as weather, creep feed, diet, individual farm/ranch, and many other factors can affect animal performance. Unfortunately, the effects of these factors change frequently and are difficult to account for using set adjustments. Even so, the effect of these non-genetic items must be factored out so that EPD can be calculated that only account for genetic differences and not any of these other factors.

Figure 3. The growth curve of a typical calf. Weaning weight can easily be estimated by linear adjustment for the period of time in between the two dots. Linear adjustments would not be accurate for more extreme ages outside the dots.
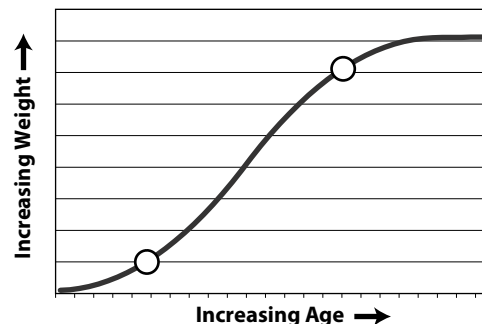
In order to do this, animals are assigned into contemporary groups for data analysis. Animals within the same contemporary group are alike for all factors that go into the formation of these groups. These factors may differ slightly from association to association and do depend on the trait being analyzed. Table 4 shows the factors that typically go into the formation of contemporary groups for the most common traits (adapted from BIF, 2002).

Breeder-Herd Code is sometimes substituted with workgroup or process date by breed associations. Workgroup or process date groups the animals that are sent into the association at the same time. If a producer splits the calf crop and sends in half of the data at a time, then the calves included in the first group will be put into a different contemporary group than the calves in the second group, regardless of whether or not they would have been included in the same group if they had been sent in together.

Breed percentage groups animals into ranges of percentages of the breed performing the evaluation so that, for instance, purebred animals are not grouped together with animals that are only 50% of the given breed.

Sex is included separately in birth, weaning, and yearling contemporary groups not only to separate males and females, but also to account for males that may not be castrated until later in life. If sex was only included in the birth weight contemporary group, which carries through to later groups, it would not be possible to separate these late castrated animals from bulls.

To adjust weaning weight, the following equation is used:

Adjusted 205d weight =

$$\left[\frac{\text{(actual weaning wt.) - (actual birth wt.)}}{\text{weaning age in days}} \times 205 \right] + \text{(actual birth wt.)} + \text{(age of dam adjustment)}$$

To adjust yearling weight, the following equation is used:

Adjusted 365d wt. =

$$\left[\frac{\text{(actual yearling wt.) - (actual weaning wt.)}}{\text{days between weights}} \times 160 \right] + \text{205d weaning wt.}$$

Table 4. Typical factors used in the formation of contemporary groups.

Trait	Grouping Factors
Birth Weight	• Breeder-Herd Code • Year • Season • Sex • Breed Composition • Birth Management Code • Service Type (Embryo Transfer Calves)
Calving Ease Direct, Calving Ease Maternal	• Same as Birth Weight
Carcass Traits	• Weaning or Yearling Weight Contemporary Group • Management/Pen/Feeding Unit • Days on Feed • Harvest Date • Grading Date • Carcass Sex • Date on Feed • Breed of Dam
Feed Efficiency	• Weaning or Yearling Weight Contemporary Group • Feed Efficiency Management/Feeding Unit Code • Days on Feed (or Date on Feed) • Date Scanned or Harvested • Sex • Breed Composition
Heifer Pregnancy	• Yearling Weight Contemporary Group • Heifer Pregnancy Management Code • Breeding Season Start and End Dates • Exposure • Breeding Pasture and/or Sire Effect
Mature Cow Body Condition Score	• Breeder-Herd Code • Year • Date Measured • Age at Measurement (Years) • Breed Composition • Birth Management Code
Mature Height, Mature Weight	• Same as Mature Cow Body Condition Score
Stayability	• Breeder-Herd Code • Birth Year • Code of the Breeder-Herd in which the cow produced a calf • Breed Composition
Ultrasound Body Composition Traits	• Weaning or Yearling Contemporary Group • Management/Feeding Unit Code • Date Scanned • Sex
Weaning Weight	• Birth Weight Contemporary Group • Management/Pasture Code • Date Weighed • Weaning Sex • Breed Composition • Service Type (Embryo Transfer Calves)
Yearling Frame Score	• Weaning Weight Contemporary Group • Management/Feeding Unit Code • Date Weighed • Yearling Sex
Yearling Weight	• Same as Yearling Frame Score

Management codes are producer defined and are a place for producers to make the association aware of management differences. Animals that are managed separately (show animals, different diets, pastures, illness, etc.) need to be identified with different codes so that they are placed in different contemporary groups. The association does not know if individual producers manage their calves together or separate them into different groups and these codes help the association group animals accordingly.

Dates that the animal is weighed are also important for contemporary grouping. For birth weight contemporary groups, birth date has to be within a predesignated range of dates, generally 90 days. The dates for the contemporary groups of other traits, however, are exact dates. So, in order to be considered in the same contemporary group for weaning weight or yearling weight, animals have to be weighed on the same day, but for birth weight, they have to be within 90 days of each other.

Additionally, in order to be in the same contemporary group later in life, animals must be in the same contemporary groups at earlier ages. So, to be in the same yearling contemporary group, animals must also be in the same birth and weaning contemporary groups.

Once contemporary groups are formed, the cumulative effects of all the non-genetic factors included in the contemporary groups can be estimated for each contemporary group. Estimation of this removes these influences on phenotype from the EPD calculation and leaves the EPD as a true genetic prediction with minimal bias. Contemporary group estimates are calculated simultaneously with the calculation of EPD, however contemporary group estimates are not reported. This is mainly because they are not repeatable and do not predict future contemporary group estimates.

Single-Animal Contemporary Groups

In order to get accurate estimates of contemporary group effects, it is important not to have single animals in a contemporary group, if possible. Producers should try to manage animals as similarly as possible so that many animals are included in each contemporary group. Obviously, there are some situations in which it is impossible to eliminate single-animal contemporary groups (i.e., show animals, sick animal, etc.), but these should be kept to a minimum. If a single animal is in a contemporary group, it is impossible to determine what portion of the performance can be attributed to the non-genetic factors and what portion of the performance is due to genetics. Because of this, the performance of calves from single-animal contemporary groups are not included in the calculation of EPD by national cattle evaluation procedures. These animals could, however, receive an EPD from pedigree estimates which will be discussed later in this chapter. If those animals go on to be parents, their descendents will contribute information even though they could not themselves.

Single-Sire Contemporary Groups

Just like single animal contemporary groups, single-sire contemporary groups should be avoided. When a single bull sires all the calves within a contemporary group, that contemporary group adds no information to a bull's genetic evaluation because it is impossible to determine how much of the performance is due to the genetics of the sire and how much of the performance is due to the non-genetic factors that are common to that contemporary

group. If a sire is only represented in single-sire contemporary groups, it is not possible to compare him with other bulls.

How Are Accuracies Calculated?

Accuracies are a direct product of not only the amount, but also the type of data that is included in the analysis. Many records from parents, grandparents, siblings, and other ancestors may be included in the evaluation, but this type of data does not add much to the accuracy of an animal. This is because these data indicate the type of genetics that the animal has the chance of inheriting, but does not indicate what genes the animal has actually inherited. With only ancestor information, two full siblings will have the exact same EPD and accuracy, but could in actuality have very different genetics (as depicted in Figure 1).

The type of data that is most important and has the largest effect on accuracy is data from descendants of an animal. These records depict the type of genetics that that animal actually possesses because it helps estimate the genetics that it has passed on to its progeny.

As more descendants have records submitted to the breed association, the higher the accuracy of the bull's EPD. Progeny data will increase accuracy faster than will grandprogeny and further descendants because the bull influences half of the genetics in his progeny (the other half come from the cow) while he only has a quarter of the genetic influence in his grandprogeny, and eighth of the genetic influence in his great-grandprogeny, and so on.

## Classification of EPD

Interim/Pedigree EPD

Expected progeny differences are an estimate of the cumulative effect of the genes that an animal has and can pass on to its offspring. Because of this, until an animal has a record of its own, or even better, progeny of its own, it is difficult to know what genes it possesses. Without this information, the only way that there is to estimate what genes an animal possesses is by averaging the parents. This means that all progeny of the same two parents will have the same EPD value until they have progeny or records of their own. These EPD that are simply averages of the parental EPD are pedigree estimates.

In most sire summaries, Pedigree EPD are easy to identify because, instead of a numerical value, their accuracy values are designated as either "I" or "P," again depending on the breed association supplying the value. Some breeds may publish actual accuracy values, but these will be extremely small in value.

An Interim EPD is a Pedigree EPD that also includes the animal's own record for that trait. In many cases, these EPD have accuracies of "I+" or "P+."

For example:

| Sire | Dam |
| WW EPD = +35 | WW EPD = +25 |

Bull Calf Progeny
WW EPD = +30
Acc. = I (or P)
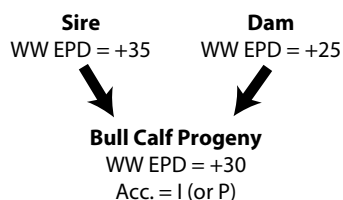
The bull calf progeny has an EPD that is the average of its parents EPD until it has a record of its own from a valid contemporary group. The accuracy is designated at "I+" (or "P+" depending on the breed association). Once the calf has its own record, the Pedigree EPD of +30 is adjusted to include the animal's own record as well., and an accuracy is reported.

For those breeds that do not report the numerical accuracy with Pedigree and Interim EPD, once the animal has progeny data reported, the accuracy value reported will be the actual numerical value. As more data are added, the accuracy of the bull's EPD will increase in value.

Direct vs. Maternal EPD

Most EPD are expressed in a direct form – meaning it predicts a bull's future progeny performance. Others are maternal EPD and predict a bull's grandprogeny through its daughters. For instance, calving ease is expressed in two different EPD, one direct and one maternal. Milk, which is known by many names including Maternal Milk, Milking Ability, Maternal, and Maternal Traits, is the most historical maternal EPD available to producers.

Direct EPD predict the performance of a bull's calves. Direct calving ease, for instance, is a prediction of calving ease when the bull's calves are born – a measure of dystocia experienced by the heifers to which he is bred. Other EPD that are not explicitly referred to as direct or maternal can usually be assumed to be direct EPD.

Maternal EPD, on the other hand, predict the performance of a bull's daughter's calves. Maternal calving ease is a prediction of calving ease when calves are born to the bull's daughters. Similarly, milk and total maternal EPD help to predict the weaning weight of a bull's daughter's calves.

Indicator Traits vs. Economically Relevant Traits

The first national sire evaluation in beef was published in the early 1970's comparing 13 sires for a limited number of traits. As time has gone on, both the number of animals and the number of traits with EPD have increased.

More recently, a more defined focus for EPD has been encouraged. This new focus has been on Economically Relevant Traits, or ERT as they are sometimes referred. Economically relevant traits, as the name implies, are those traits that have a direct economic impact to the producer. Traits such as weaning weight and carcass weight are ERT because there is a direct monetary value associated with these traits.

Other traits, such as birth weight, do not have a direct economic value associated with them. For instance, an increase in 1 lb of weaning weight increases the producer's income, but a decrease in 1 lb of birth weight does not directly affect the income or expense of a producer. Instead, birth weight is used to indicate the probability of dystocia, or calving difficulty, which does have an economic impact. For this reason, birth weight is not an ERT, but is what is called an indicator trait. Newer EPD, such as direct and maternal calving ease, are the ERT that birth weight is the indicator for. For more information on specific EPD, refer to the chapter on economically relevant traits.

Different Types of Genetic Evaluations

Genetic evaluations are different depending on the trait being analyzed. Some traits are analyzed with other traits, while some are analyzed by themselves. Some traits are expressed on a continuous scale while others are analyzed using threshold models. Traditionally, evaluations have considered one breed, but the future of evaluations includes evaluation of many breeds simultaneously.

Single-Trait Analysis

Some traits are analyzed by themselves in what is called a single-trait analysis. This means that these traits are not analyzed in conjunction with any other correlated trait. If a trait is analyzed as a single trait, data from other traits contribute no information.

Multiple-Trait Analysis

Many traits are analyzed with other traits in what is called a multiple-trait analysis. Just as it sounds, a multiple-trait analysis computes more than one trait at a time. Typically, growth traits are analyzed together as are the carcass traits. Ideally, all traits would be analyzed together in order to take advantage of all possible correlations, but this would require tremendous amounts of computing power that is not feasible.

Threshold Analysis

Most traits that producers are interested in, such as the weight traits, are expressed on a continuous scale. For instance, weight can be any positive number. Traits that are continuous usually experience a normal distribution, meaning that when the frequency of data are plotted, it forms a bell-shaped curve.

Threshold traits also follow a normal distribution, but it is not as noticeable because there are distinct categories that ranges of values fall in as shown in Figure 4. Calving difficulty, for instance, is typically scored on a scale of 1 to 4, but is actually occurring in a continuous, but unobservable phenotype.

Figure 4. Threshold traits are observed in categories, but have an underlying normal distribution.
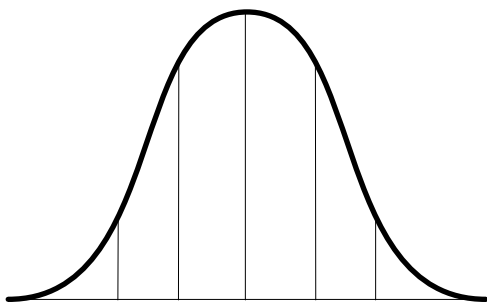
Despite the fact that threshold traits are categorically reported, when EPD are calculated, they are reported on a continuous scale. For calving difficulty (or calving ease), as an example, the EPD is typically reported as a percentage.

Multi-breed Analysis

Traditionally, genetic evaluations have been performed within breed. This means that only bulls from the same breed could be directly compared. If a producer wanted to compare two bulls of different breeds for use in his/her herd, it was impossible to do so using traditional within breed EPD.

Researchers at the USDA Meat Animal Research Center in Clay Center, Nebraska have developed Across Breed EPD adjustment factors. These additive adjustments can be used to adjust EPD from different breeds in order to compare bulls. These values are updated annually and are made available each year on the Beef Improvement Federation's website located at www.beefimprovement.org/proceedings.html.

Expected in the future is the generation of EPD bringing together animals from several breeds in a format that allows people to compare animals of several different breeds without having to additively adjust the EPD. Current research is being conducted to calculate EPD using multi-breed analyses. Results from these analyses would provide EPD for animals from all breeds included in the analyses on one common base so that animals can be directly compared.

Besides being able to compare different breeds of bulls, there are other advantages to a multi-breed evaluation. Bulls that have calves represented in several different breeds, such as Angus bulls that have sired crossbred calves from Simmental or Charolais cows, for example, can have all of that information included in one analysis to increase the accuracy of their EPD. Also, crossbred bulls, that may not typically be evaluated in a normal genetic evaluation, can be included in multi-breed evaluations.

Although there are many benefits to a multi-breed evaluation, there are also some drawbacks. Results from a multi-breed analysis may not be suitable for choosing bulls for a crossbreeding scenario as heterosis effects are taken out of the data prior to calculation of the EPD values. As an example, comparing Red Angus versus Gelbvieh bulls for use on Red Angus cows would not be a valid comparison as the Gelbvieh bulls would also introduce heterosis that the Red Angus bulls would not provide.

Summary

Expected Progeny Differences are a selection tool available to producers who want to make genetic change in their herd. With knowledge of EPD and accuracies and how to use these values, producers can improve the genetics of their herd. Details of specific EPD are provided in the next chapter.

Current genetic evaluations are limited to within breed comparisons unless the Across Breed EPD adjustment factors are used. Future genetic evaluations may result in multiple breeds being evaluated together so that producers can compare all animals on the same basis.

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Interpretation and Use of Expected Progeny Differences (EPD)

Janice M. Rumph, Pfizer Animal Genetics

Expected Progeny Differences (EPD) provide producers with a group of selection tools that specifically address the genetics of the animal. To date, EPD are the best way for producers to predict the relative performance of future progeny for a wide set of traits. EPD can be a powerful tool for the producer, and with a little knowledge of what each EPD means, they are relatively simple to use.

Statistics Associated with EPD

Calculation of EPD requires a great deal of mathematical equations and computing power, but the EPD are not the only thing these calculations generate. As a byproduct of these calculations, many other statistics are computed that are of use to the producer. These are typically shown in the first few pages of sire summaries, prior to the EPD tables or on the breed association's website. This additional information may at first appear confusing, but with a little explanation, the added information can be of great benefit to the producer.

Breed Averages

Breed average EPD provide a benchmark to compare animals to. Just as the name implies, they are the average EPD for animals included in that run of the genetic evaluation. Many associations will also split the breed averages into those for active proven sires, young sires, dams, non-parents, etc. and for specific populations of animals, such as LimFlex (Limousin), Balancer (Gelbvieh), and Simbrah (Simmental).

Traditionally, breeds had a base year and the average EPD in the base year is set to zero, so that any difference from zero would correspond to a difference from the average in the base year, not the current year. Recently, though, some breeds have varied from the base year idea, so it is not as easy to determine what an EPD of zero equates to. What is common across all breeds, however, is that zero does not automatically mean the current breed average. The 2007 breed average EPD for many U.S. beef breeds are shown in Tables 1, 2, and 3.

Genetic Trends

Genetic trends show the overall genetic change for the breed over many years. This is done by plotting the breed average EPD for each year. These trends are typically depicted in graphs similar to the one shown in Figure 1.

Figure 1 depicts a hypothetical genetic trend for weaning weight typical of most US beef breeds. It can easily be seen that weaning weight has increased over the past 40 years, most

Table 1. 2007 breed average EPD in the United States for growth traits.[a,b,c]

Breed	Growth							
	Birth Weight	Weaning Weight	Milk[d]	Yearling Weight	Total Maternal[d]	Yearling Height	Mature Height	Mature Weight
Angus	2.1	42.0	21.0	78.0		0.4	0.4	32.0
Beefmaster	0.6	7.0	2.0	12.0	6.0			
Blonde d'Aquitaine	0.0	0.0	0.0	0.0	0.0			
Braford	0.5	7.0	1.0	11.0	3.0			
Brahman	1.9	13.7	5.9	22.8				
Brangus	0.5	21.6	7.1	39.1	17.9			
Charolais	0.7	24.7	6.7	42.8	18.8			
Chianina	2.2	40.4	7.0	71.2	27.2			
Gelbvieh	1.3	41	17	74	38			
Hereford	3.5	43.0	17.0	70.0	38.0			
Limousin	2.1	42.0	20.0	77.0				
Maine-Anjou	2.95	40.09	19.75	79.81	39.75			
Red Angus	-0.1	32.0	18.0	59.0	33.0			
Red Brangus	1.4	12.5	5.6	19.8	11.8			
Salers	1.0	9.3	7.8	14.5	12.6			
Santa Gertrudis	0.5	4.0	0.0	6.0	2.0			
Shorthorn	2.0	13.4	2.4	22.3	9.1			
Simmental	1.3	32.4	4.4	57.6	20.6			
Tarentaise	1.8	13.7	26.1	1.8				

[a] Not all breeds report every trait listed here and therefore each breed will have no breed average EPD for certain traits.
[b] Index values are reported by some breed associations with their EPD values. These are not given here and will be discussed elsewhere in this text.
[c] Current as September 2005.
[d] Depending on the breed association, Milk may be referred to by a different name, such as Maternal Milk or Maternal; and Total Maternal may be referred to by a different name, such as Maternal Weaning Weight or Milk and Growth.

Figure 1. Genetic trend for weaning weight.

34
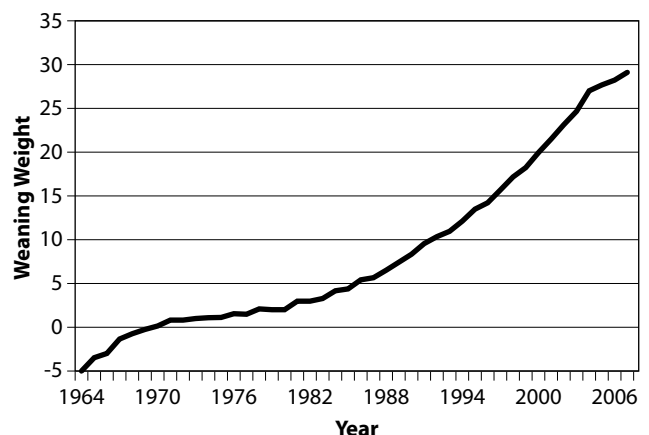
likely due to selection for weaning weight and/or yearling weight. It also appears that there has been a stronger emphasis placed on selection beginning in the mid- to late 1980's and continuing through today.

Accuracies

As discussed in the previous chapter, accuracies are a way to determine how reliable an EPD is. Accuracies that are close to 1 indicate that there is more confidence that the EPD value reflects the true genetic worth of an animal for that trait when compared to a lower accuracy.

There is an amount of risk associated with using EPD, and accuracies help to manage that risk. However, no matter how high the accuracy of an EPD, all parent animals will produce a distribution of progeny perfor- mance. Not only do non-genetic effects, such as feed, weather, stress, etc., cause this, but ran- dom Mendelian sampling also has an effect. Just by random chance, one calf may get a large proportion of its sire's favorable alleles for a particular trait and just by random chance, the next calf may get a large proportion of the undesirable alleles. More

Table 2. 2007 breed average EPD in the United States for carcass traits.[a,b,c]

| Breed	Carcass Weight	Ribeye Area[a]	Fat Thickness	Marbling	Retail Product[d]	Yield Grade	Tenderness[e]	Intramuscular Fat (%)	Ribeye Area	Fat Thickness	Retail Product[d]
	Carcass							**Ultrasound**			
Angus	11.0	0.12	0.009	0.27							
Beefmaster											
Blonde d'Aquitaine								0.0	0.0	0.0	
Braford	3.8	0.033	0.001	0.001							
Brahman	4.3	0.06	-0.003	-0.01	0.01		-0.01				
Brangus								0.010	0.33	-0.001	
Braunvieh	-15.8	-0.17	-0.108	-0.066							
Charolais	11.5	0.14	-0.003	0.01							
Chianina	0.0	-0.08	-0.01	-0.02	-0.04						
Gelbvieh	7	0.07		-0.05							
Hereford								0.03	0.19	0.002	
Limousin	14.0	0.44		-0.06		-0.10					
Maine-Anjou	2.46	0.16	0.00	0.21	0.30						
Red Angus		0.04	0.00	0.05							
Red Brangus											
Salers	12.4	0.01	0.00	0.00	0.00						
Santa Gertrudis	1.0	0.01	0.00	0.00							
Shorthorn	-0.1	0.00	0.00	0.00	0.04						
Simmental	-2.0	0.08	0.01	0.13		0.00	-0.08				
Tarentaise											

a   Not all breeds report every trait listed here and therefore each breed will have no breed average EPD for cer- tain traits.
b   Index values are reported by some breed associations with their EPD values. These are not given here and will be discussed elsewhere in this text.
c   Current as September 2005.
d   Depending on the breed association, Retail Product may be referred to by a different name, such as Percent Retail Cuts or Percent Retail Yield.
e   Tenderness is also referred to as Warner Bratzler Shear Force.

often, progeny receive some combination of a parent's desirable and undesirable alleles. Because of this, it is impossible for each calf to have the same performance (i.e., it can never be said that every progeny of a bull with a BW EPD of +2 will always weigh 2 pounds more at birth than every calf out of a bull with a BW EPD of 0). The EPD predicts the average difference over a large number of progeny.

A bull with a high accuracy will produce a group of calves with just as much variation in performance as a low accuracy sire. What changes with accuracy, however, is how close the EPD is to the actual true genetic potential of the animal. Figure 2 shows calving distributions for two bulls. Bull A (dashed line) is a high accuracy sire (acc. = 0.95) with a BW EPD of +2.0. Bull B (solid line) is a low accuracy sire (acc. = 0.50) with a BW EPD of -2.0.

As can be seen, because Bull A is a high accuracy sire, his true genetic potential is in a much more narrow range of values than the lower accuracy sire. The next time an evaluation is performed, the likelihood of Bull A's EPD falling below 0 or above 4 is very small. Bull B is a lower accuracy sire, however, so the probability of his EPD changing is larger as can be seen by his distribution curve. As new data are added and future genetic evaluations are performed, Bull B could prove to be much better (lower BW EPD is generally better) than was initially thought or, conversely, may actually have a higher BW EPD than Bull A.

Accuracies can be used to evaluate risk. Assume for every other trait, Bull A and Bull B are comparable. Bull B looks more appealing because of his BW EPD, but a producer is leery due to his low accuracy value. However, in the example shown here, the chance of Bull B's true EPD for birth weight being larger than Bull A's is small, even though the accuracy differences are large. Therefore, a producer can feel confident choosing Bull B over Bull A.

It is important to remember that even high accuracy bulls will produce calves with a wide range of phenotypes as can be seen in the lower graph in Figure 2. Accuracy helps to determine the reliance on the bull's EPD and consequently the average of his progeny, but no guarantee for every calf. This will be discussed more later in this chapter.

Breed associations do not print these bell-shaped curves for producers to use to compare bulls, but they do provide possible change values to use instead.

Possible Change

No EPD is perfect. Each EPD is the best estimate as to the true one-half breeding value of an animal. The more data that are available for calculation of this estimate, the more accurate the prediction will be, but it will never be 100% perfect. That is why accuracies are used in conjunction with EPD. Possible change is associated with accuracy. The higher the accuracy of an EPD on a particular animal, the less chance there is that it will change as more data are added. With lower accuracies, it is more likely that the EPD will change as more data are added. Because of this, breed associations provide tables of possible change. These tables show how much change should be expected in the EPD based on the current accuracy value.

Table 4 shows an example of a typical, but hypothetical, table of possible change.

In this case, if a bull had a Birth Weight EPD of +2.5 with an associated accuracy value of 0.90, it can be expected that his EPD for birth weight could change by 0.89 lb the next time an evaluation is run. This means that his EPD could be anywhere from 1.61 lb (2.50 − 0.89) to 3.39 lb (2.50 + 0.89) when EPD are calculated again. As accuracy decreases, this range increases. Additionally, as the magnitude of a trait increases, the range will also increase. For example the range for birth weight at 90% accuracy is +/- 0.89 lb, but for weaning weight, it is +/- 2.24 lb and for yearling weight, it is +/- 3.05 lb.

Possible change is not a guarantee that an animal's EPD will be within the specified range, but is an expectation that it will be within this range approximately ⅔ of the time. Approximately ⅓ of the time, it can be expected that the change in the EPD will be more extreme than the predicted possible change.

Percentile Ranks

Breed associations also provide percentile ranks for their animals. These charts are a way to see how a specific animal compares with others in the breed. Similar to the way national test scores are reported on children in schools, these percentile ranks indicate what proportion of animals have an EPD that is better than a given value. Breed average EPD are near the 50th percentile.

Because they are based on how many animals perform better than a specific EPD value, those animals with the highest rankings don't always have the largest numerical EPD values. For instance, for birth weight, animals with a lighter birth weight are thought to be more desirable. Therefore, the animals ranked in the top percentages will have negative EPD. However, higher values are thought to be more desirable for other weight traits, such as weaning and yearling weight, which means that the animals listed at the top percentages have the highest EPD for those traits.

Figure 2. Distribution of the True EPD Value for Two Bulls Differing in Accuracy (above) and the phenotypic distribution of the calves of those same two bulls (below).
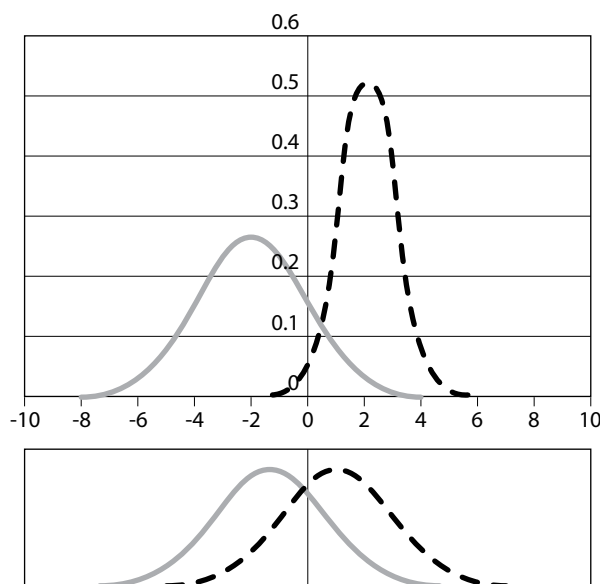
Table 3. 2007 breed average EPD for breeds in the United States.[a,b,c]

| Breed | Reproduction | | | | | Other | | | |
	Scrotal Circumference	Gestation Length	Calving Ease Direct	Calving Ease Maternal[d]	Heifer Pregnancy	Stayability	Maintenance Energy	Docility	Days to Finish
Angus	0.36		5.0	6.0					
Beefmaster	0.10								
Blonde d'Aquitaine	0.0								
Brangus	0.54								
Charolais	0.6		3.1	4.3					
Chianina									
Gelbvieh	0.4	-1.5	105	104		5			3.5
Hereford	0.6		0.0	0.7					
Limousin	0.3		7.0	3.0		17.0		15.0	
Maine-Anjou									
Red Angus			6.0	4.0	9.0	9.0	4.0		
Salers	0.2		0.0	0.1		18.4		1.2	
Shorthorn			1.2	0.1					
Simmental			6.5	2.5		18.3			
Tarentaise			-0.6	1.0					

[a] Not all breeds report every trait listed here and therefore each breed will have no breed average EPD for certain traits.
[b] Index values are reported by some breed associations with their EPD values. These are not given here and will be discussed elsewhere in this text.
[c] Current as September 2005.
[d] Depending on the breed association, Calving Ease Maternal may be referred to by another name, such as Calving Ease Daughters or Calving East Total Maternal.

Table 4. Possible change.

Accuracy	Birth Weight	Weaning Weight	Yearling Weight	Milk
0.05	4.24	17.02	24.76	14.32
0.10	4.04	16.15	23.48	13.60
0.15	3.85	15.28	22.21	12.86
0.20	3.65	14.41	20.93	12.14
0.25	3.46	13.54	19.66	11.41
0.30	3.26	12.68	18.38	10.69
0.35	3.07	11.81	17.09	9.95
0.40	2.87	10.94	15.82	9.23
0.45	2.66	10.07	14.54	8.50
0.50	2.47	9.20	13.27	7.78
0.55	2.27	8.33	11.99	7.04
0.60	2.08	7.46	10.72	6.32
0.65	1.88	6.59	9.44	5.59
0.70	1.69	5.72	8.17	4.87
0.75	1.49	4.85	6.89	4.13
0.80	1.30	3.98	5.60	3.41
0.85	1.09	3.11	4.33	2.68
0.90	0.89	2.24	3.05	1.96
0.95	0.70	1.37	1.78	1.22

Table 5. Hypothetical percentile ranks.

Top Percent	Birth Weight	Weaning Weight	Yearling Weight	Milk
1%	-4.4	69.3	120.2	33.6
2%	-3.6	63.8	111.2	31.2
3%	-3.0	60.9	105.5	29.3
4%	-2.6	58.5	101.4	27.8
5%	-2.2	56.7	98.3	27.0
6%	-2.0	55.7	96.0	26.0
7%	-1.7	54.3	93.8	25.1
8%	-1.5	53.3	91.7	24.5
9%	-1.3	52.2	89.9	23.9
10%	-1.2	51.3	88.5	23.1
15%	-0.6	47.6	81.5	20.9
20%	0.0	44.9	76.7	18.8
25%	0.3	42.3	72.2	17.3
30%	0.7	40.2	68.0	15.8
35%	1.0	38.1	64.7	14.4
40%	1.3	36.3	61.5	13.2
45%	1.6	34.4	58.4	12.0
50%	1.8	32.3	55.4	11.0
55%	2.1	30.3	52.4	9.9
60%	2.4	28.5	49.1	8.7
65%	2.7	26.6	45.6	7.5
70%	3.0	24.5	42.2	6.2
75%	3.4	22.2	38.3	5.0
80%	3.8	19.5	33.9	3.3
85%	4.2	16.4	28.5	1.5
90%	4.8	12.2	21.2	0.0
95%	5.8	5.4	10.4	-3.9

Table 5 shows a hypothetical table of percentile ranks. If a bull has a Weaning Weight EPD of 51.6 pounds, it can easily be seen that he is in the top 10% of the breed. Animals with Weaning Weight EPD of 51.3 pounds are in the 90th percentile, meaning 10% of the breed ranks higher. If that same bull had a Yearling Weight EPD of 111.2, only 2% of the breed would rank higher for yearling weight.

In addition to the percentile tables, some breeds provide producers with an added tool to compare animals with the rest of the breed. They provide a graph for each animal that shows how that animal compares to the rest of the breed for all traits evaluated. A similar, but abbreviated, graph is shown in Figure 3.

On the left hand side of the graph is listed the traits that are being evaluated and the right hand side shows which direction is the favorable direction for each EPD (i.e., lighter birth weights are better while heavier weaning weights are better). Each bar shows where the animal in question places among the rest of the breed. Bars that reach to the left indicate below average and bars that reach to the right indicate above average. The longer the bar, the farther from breed average, whether that be better or worse.

Figure 3 shows that the animal depicted is above average for weaning and yearling weight and below average for birth weight and milk. Approximately 90% of the animals in the breed have birth weight EPD that are better (lighter) than the animal depicted in this graph. Furthermore, only about 19% have better (heavier) weaning weights, about 70% have higher milk EPD values (production scenario determines if this is better or worse), and about 17% have better (heavier) yearling weight EPD.

Heritabilities and Genetic Correlations

Heritabilities are a measure of how much genetic influence there is on a particular trait. Heritability is a value between 0 and 1 and the higher the number, the more genetic influence there is on that trait. This value is critical in calculations of EPD.

Genetic correlations are important in multiple-trait analyses. When two traits are correlated, having information on one trait will aid in the calculation of EPD for the other trait. For instance, carcass and ultrasound measurements are often calculated together in multiple-trait analyses. A bull will have no actual carcass measurements on himself, but knowledge of his ultrasound measurements will provide information for his carcass EPD. The more extreme the correlation (the closer it is to -1 or +1), the more information one trait will provide for the other trait.

Figure 3. Percentile ranking of a hypothetical bull.
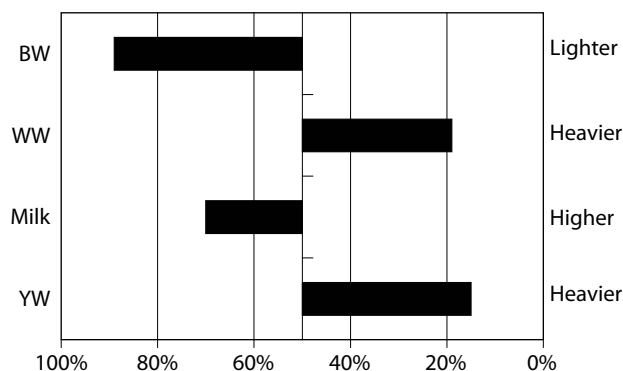
Types of EPD

Theoretically, an EPD can be developed for any quantitative trait (a trait where the phenotype can be measured on a numerical scale). Because of this, there are numerous EPD that are currently being calculated for different breeds of beef cattle and more being considered and developed. The EPD described here are those that are currently reported in the U.S. Other traits, such as 400- and 600-day weights, are common in other countries, but will not be discussed here.

In most cases, these EPD are reported in the same units as they are typically measured (i.e., birth weight is reported in pounds of birth weight), but in a few cases, the units are less obvious. The units for each type of EPD are described in the paragraphs that follow.

Both bulls and heifers/cows can have calculated EPD, but EPD are most often associated with bulls. This is mainly because:

- bulls have more progeny than cows and therefore usually have higher accuracy values;
- there is more opportunity for selection among males than among females, so EPD are of more use in bulls; and
- bulls contribute more, genetically, to the herd because as females are retained, the sires of these females are contributing half of their genetics to the cows.

Because of this, in the paragraphs that follow, EPD will be described in terms of bulls, but keep in mind that the same EPD are available on cows and could be used for female selection.

It is important to keep in mind the specific production scenario that animals are being selected for and only use those EPD that are important to that scenario. If a trait is not important to the specific production scenario or the production scenario of the customer, that EPD should not be considered in selection decisions.

For the most part, traits can be grouped into three main groups, Growth, Reproduction, and Carcass traits.

Growth Traits

The earliest developed EPD for beef cattle were for birth weight (BW), weaning weight (WW), yearling weight (YW), and milk (MILK). These are still the standard EPD that are calculated for all breeds that conduct genetic evaluations. Even those breeds that have genetic evaluations, and report no other EPD, report BW, WW, YW, and MILK.

Birth Weight (BW)—The Birth Weight EPD indicates the size of a bull's calf at birth and is used as an indicator of the probability of dystocia (calving difficulty) when that calf is born. Because birth weight EPD is expressed in pounds of birth weight, higher birth weight EPD values indicate larger calves that could result in more calving difficulty. It is normally recommended to use low birth weight EPD sires, especially when breeding heifers.

Weaning Weight (WW)—The Weaning Weight EPD is measured in pounds of weaning weight and predicts the weight of a bull's calves at weaning. Because producers selling calves at weaning are usually paid solely by pounds of calf, a higher value is more desirable.

This EPD may be of little value for producers retaining ownership of calves beyond weaning, except for its correlated response to other growth traits, such as yearling weight.

Milk (MILK)—The Milk EPD is actually a contributor to weaning weight. The Milk EPD is the maternal portion of weaning weight which is mainly determined by the milk production of the dam. The Milk EPD is measured in pounds of weaning weight of a bull's grandprogeny due to the milk production of the bull's daughters.

In areas where feed resources are abundant, selection for increased Milk EPD may not be a problem, except that it reduces the number of cows that can be maintained on a feed resource. This is because a high milking female will require more feed energy for lactation and have less energy available to put on the condition necessary to rebreed. In scenarios with limited feed resources, selection for low Milk EPD is probably warranted.

This EPD is of no use in terminal mating systems in which heifer replacements are not retained because this predicts the weaning weight of the grandprogeny.

Depending on the breed association reporting the values, sometimes the Milk EPD is referred to as the Maternal Milk, Milking Ability, Maternal, or Maternal Traits EPD.

Yearling Weight (YW)—The yearling weight EPD is measured in pounds of yearling weight and predicts the weight of a bull's progeny at one year of age. Typically, a larger value is better.

This EPD is only of use if calves are going to be retained beyond weaning. For production scenarios where calves are sold at weaning or at some point before yearling, this EPD may have little need by the producer, however its correlation with weaning weight and mature weight (if heifers are retained) can make it valuable.

More recently, other growth related EPD have been developed by some breed associations. These are not reported by all associations.

Total Maternal (TM)—Similar to MILK, Total Maternal EPD are expressed in terms of weaning weight of a bull's daughter's calves. The EPD is calculated by taking half of the Weaning Weight EPD and adding the entire Milk EPD. This accounts for the half of the weaning weight genetics that the grandprogeny will receive (the other half will come from the parents of the calf's sire) and all of the milk production of that calf's dam. Because this is an indicator of weaning weight (of grandprogeny), a higher value is usually better, similar to the Weaning Weight EPD.

Because this EPD is used to predict the performance of the bull's grandprogeny, this EPD is of no use if heifer calves are not being retained as replacements.

Depending on the breed association, this EPD is also referred to as the Maternal Weaning Weight, Maternal Milk and Growth, or Milk and Growth EPD.

Yearling Height (YH)—Yearling Height EPD were developed as a frame size selection tool. This EPD is reported in inches of hip height at one year of age. Although intermediate values are usually more desirable, this EPD could also be used to increase frame size so that a herd with mainly small framed cattle can become more moderate or decrease a larger framed herd to more moderate.

This EPD is useful for both terminal production systems and those systems where heifers are kept as replacements. Taller calves can be expected to take a longer amount of time on feed in order to reach the Choice grade. For replacements, yearling height is highly correlated with mature height (Rumph, 2002) and this EPD could be used as an indicator for mature size.

Mature Height (MH)—Similar to yearling height, the Mature Height EPD was also developed as a frame-size selection tool. In theory, selection for shorter cows will result in cows that require

less feed inputs for maintenance. Therefore, this EPD, which is reported in terms of inches of hip height at maturity, could be used as an indicator of the amount of energy required to maintain heifer calves once they reach maturity.

As a prediction of mature height, this EPD is of no use in a terminal situation where replacements are not retained. It is, however, useful as an indicator of yearling height due to the high genetic correlation between the two traits (Rumph, 2002).

Depending on the breed, this EPD is sometimes referred to as the Daughter Height EPD.

Mature Weight (MW)—The Mature Weight EPD is another indicator for maintenance energy requirements. In theory, when a cow weighs more, she should be expected to require more feed energy in order to maintain herself. Mature weight is reported in terms of the pounds of mature weight of a bull's daughters and is usually selected for reduced size.

If replacement females are not retained, this EPD is not necessary in a selection program.

Depending on the breed, this EPD is sometimes referred to as the Daughter Weight EPD.

Reproductive Traits

In addition to growth traits, breed associations have also placed an emphasis on developing EPD for reproductive traits. These traits vary from association to association and are listed below.

Scrotal Circumference (SC)—Scrotal circumference is another indicator trait. The EPD for this trait is used as an indicator for the fertility of a bull's progeny through his sons' scrotal circumference and his daughters' age at puberty which is correlated with heifer pregnancy. In theory, the larger a bull's scrotal circumference, the earlier his daughters will reach puberty and the higher probability that they will conceive to calve at two years of age. The Scrotal Circumference EPD is expressed in centimeters with a larger number being more desirable.

This EPD is of use only in situations in which male calves are retained as bulls or heifers are retained as replacements.

Gestation Length (GL)—Similar to birth weight, the Gestation Length EPD is another indicator of the probability of dystocia. This EPD is reported in terms of days in utero of a bull's calves. The longer a calf is in utero, the more that calf will weigh at birth and the higher probability of dystocia. This EPD is also used to provide cows with a longer postpartum interval before having to be rebred for the next year's calf. Therefore, the Gestation Length EPD with smaller values are more desirable.

Calving Ease Direct (CED)—The Calving Ease EPD, both direct and maternal, are the economically relevant traits (ERT) that indicator traits, such as birth weight and gestation length, are attempting to predict. Calving Ease Direct EPD are a measure of the ease at which a bull's calves will be born. This has to do mainly with size and shape of his calves. Calving Ease Direct EPD are calculated using information from calvings of two-year-old females only (no older calvings are included) and the birth weight information of the bull's progeny (Speidel et al., 2003). This EPD is reported as a percentage so that a higher value indicates a higher probability of unassisted calving.

Calving Ease Maternal (CEM)—Similar to the Calving Ease Direct EPD, the Calving Ease Maternal EPD is also an ERT for unassisted calving. Contrary to Calving Ease Direct EPD, however, the Calving Ease Maternal EPD predicts the probability of an bull's

daughters calving without assistance. This EPD is also expressed in terms of percentages with a higher value indicating that the bull's daughters are more likely to deliver a calf unassisted.

Like other EPD that are related to a bull's grandprogeny, this EPD is of no use unless heifers are retained as replacements.

Depending on the breed association, this EPD is sometimes referred to as the Calving Ease Daughters EPD or Calving Ease Total Maternal.

Heifer Pregnancy (HP)—Heifer pregnancy is an ERT that indicator traits, such as scrotal circumference, predict. Heifer Pregnancy EPD report the probability that a bull's daughters will conceive to calve at two years of age. This EPD is also reported as a percentage where a higher value indicates progeny with a higher probability of conceiving to calve at two years of age.

Carcass Traits

Carcass traits are another group of traits that have begun being included in genetic evaluations. For most breeds, these EPD are calculated on an age endpoint as if all cattle were slaughtered at a specific age. Gelbvieh EPD, however, are adjusted to a constant fat endpoint as opposed to age. Some breed associations report carcass EPD only and some report ultrasound EPD only, however, even though associations only report one type of EPD (i.e., carcass), both ultrasound and carcass information may go into the calculation of those EPD because of the genetic correlation between the traits.

For producers that are selling calves based strictly on weight with no premiums for carcass traits and not selling seedstock to customers concerned with carcass traits, both carcass and ultrasound EPD are of limited benefit in selection schemes.

Carcass EPD

Carcass EPD predict the genetic differences of a bull's progeny on the rail.

Carcass Weight (CW)—Carcass Weight EPD reports the expected carcass weight, in pounds, of a bull's progeny when it is slaughtered at a constant endpoint so that producers can select cattle that will produce calves within a certain weight range in order to avoid discounts. There is no ultrasound equivalent to this EPD.

Ribeye Area (REA)—Ribeye Area EPD are reported in square inches and indicate the area of the longissimus muscle between the 12th and 13th ribs (Boggs et al., 1998) of a bull's offspring when slaughtered at a constant endpoint. Although bigger is usually better, some grids may discount for ribeyes that are too large. The ultrasound equivalent to this EPD is the Ultrasound Ribeye Area EPD.

Fat Thickness (FAT)—Depending on the breed association reporting the estimates, the Fat Thickness EPD is also sometimes referred to as the Backfat EPD or just simply the Fat EPD. This EPD is measured in inches as the prediction of the 12th rib fat thickness of a bull's progeny when slaughtered at a constant endpoint.

A lower value is better to an extent. However, for breeds that are naturally lean, selecting against fat may result in progeny that are too lean and consequently carcass quality is reduced.

Marbling (MARB)—The Marbling EPD indicates the marbling of the ribeye of a bull's progeny when slaughtered at a constant endpoint. Table 6, adapted from the Beef Improvement Federation's Guidelines (BIF, 2002), shows how breed associations code marbling scores for analysis.

For most breeds, Marbling EPD values range from -0.50 to +0.50 which directly corresponds to the scale in Table 6. This means that the difference in marbling expected between the progeny of a bull with a +0.50 and a bull with a -0.50 would be a full grade (i.e., Low Choice to Average Choice or Select to Low Choice).

The ultrasound equivalent to this EPD is the Percent Intramuscular Fat EPD.

Retail Product (RP)—Depending on the breed association, this EPD is also called Retail Yield Percent, Percent Retail, Percent Retail Product, Percent Retail Cuts, or Retail Beef Yield Percentage. It is a prediction of the salable meat that the carcass of the progeny of an animal will yield. This EPD is roughly equivalent to the Yield Grade EPD because it takes into consideration the same component traits: fat thickness, hot carcass weight, ribeye area, and percentage kidney, pelvic, and heart fat, but weighs each component slightly different than for yield grade.

The Retail Product EPD is expressed in percentage units with a higher value indicating a greater proportion of the carcass is in the form of salable meat.

Yield Grade (YG)—Similar to the Retail Product EPD, the Yield Grade EPD is a measure of lean meat yield of the carcass. All of the same component traits are included in Yield Grade as in Retail Product, but each is weighted differently than for Retail Product.

This is because retail product is expressed in percent, while Yield Grade is expressed in grade units. The lower the grade, the leaner the carcass. An animal receiving a calculated yield grade of 1.0 – 1.9 is a Yield Grade 1, an animal receiving a calculated yield grade of 2.0 – 2.9 is a Yield Grade 2, etc. The highest Yield Grade is 5 so any animal receiving a calculated yield grade of 5.0 or more is classified as a Yield Grade 5.

There is currently no ultrasound equivalent to the Yield Grade EPD.

Tenderness (WBS)—The Tenderness EPD is measured in pounds of Warner Bratzler Shear Force so that a higher value indicates that more pounds of shear force are required to cut through the meat. Therefore a lower value indicates more tender meat and is more desirable.

There is no ultrasound equivalent to the Tenderness EPD.

Ultrasound EPD

Ultrasound EPD predict differences at ultrasound, which is an indicator of the carcass traits when it is on the rail.

Percent Intramuscular Fat (UMARB)—The ultrasound equivalent of the Marbling EPD is the Percent Intramuscular Fat EPD. Like the carcass Marbling EPD, a higher value indicates more marbling and is generally more desirable.

Table 7, adapted from the BIF Guidelines (BIF, 2002) shows how marbling score and intramuscular fat percentage are related to one another.

Unlike the carcass Marbling EPD, this EPD is measured in percentages.

Table 6. Codes for various marbling levels.

Quality Grade	Marbling	Score
Prime	Abundant	10.0 – 10.9
Prime	Moderately abundant	9.0 – 9.9
Prime	Slightly abundant	8.0 – 8.9
Choice	Moderate	7.0 – 7.9
Choice	Modest	6.0 – 6.9
Choice	Small	5.0 – 5.9
Select	Slight	4.0 – 4.9
Standard	Traces	3.0 – 3.9
Standard	Practically devoid	2.0 – 2.9

Table 7. Marbling scores and the equivalent percent intramuscular fat.[a]

Marbling Score	Intramuscular Fat %
Slightly Abundant	10.13
Moderate	7.25
Modest	6.72
Small	5.04
Slight	3.83
Traces	2.76

[a] EPD values are differences to be compared to each other. A marbling EPD of 2.76 does not indicate an animal will have a marbling score equal to Trace.

Ribeye Area (UREA)—The ultrasound Ribeye Area EPD is the ultrasound equivalent to the carcass Ribeye Area EPD. The ultrasound version is measured the same, in square inches, and it is also generally more desirable to have a higher value.

Fat Thickness (UFAT)—The ultrasound Fat Thickness EPD is comparable to the carcass Fat Thickness EPD and has the same limitations. In most cases, it is more desirable to select for less fat at the 12th rib, but selection to extremes can result in decreased carcass quality. Like the carcass equivalent, this EPD is measured in inches.

Retail Product (URP)—Similar to its carcass version, the ultrasound Retail Product EPD combines several component traits to determine the amount of salable meat in the carcass. A higher value indicates a higher proportion of the carcass is in the form of salable meat. This is measured in percent, like its carcass equivalent, but uses the ultrasound component traits.

Other Traits

A few traits don't fit into the general categories of growth, reproduction, or carcass. These, mostly having to do characteristics expressed by cows, are described below.

Stayability (STAY)—Stayability is an indicator of longevity of a bull's daughters in the cow herd. This EPD predicts the probability (in percent) that a bull's daughters will remain in the herd through six years of age. The higher the EPD value, the higher the probability that the bull's daughters will remain in the herd through six years of age.

Because this EPD is used to predict the longevity of a bull's daughters, it is of no use if replacements are not going to be retained.

Pulmonary Arterial Pressure (PAP)—Pulmonary Arterial Pressure EPD also provide another indicator for longevity in the cow herd. Animals with higher pulmonary arterial pressure are more susceptible to brisket (or high mountain) disease. Pulmonary Arterial Pressure EPD are measured in millimeters of mercury with a lower value being more desirable.

Similar to stayability, because this EPD is an indicator of longevity, it is of no use in strictly terminal situations where heifer calves are not retained. This EPD is also not necessary for cattle that are not going to be in high elevations.

The Pulmonary Arterial Pressure EPD is currently not routinely calculated by any breed association, but is calculated, by request, for some individual producers.

Maintenance Energy (ME)—The Maintenance Energy EPD is a predictor of the energy needed for a cow to maintain herself. Daughters of bulls with lower Maintenance Energy EPD values will require less feed resources than will daughters of bulls with higher values. Therefore, it is beneficial to select bulls with lower Maintenance Energy EPD values. Maintenance Energy EPD are measured in terms of megacalories per month.

This EPD is of no use if heifer calves are not retained as replacements.

Docility (DOC)—Docility EPD are a measure of the behavior of a bull's calves as they leave the chute. Animals are evaluated by producers on a scale of 1 to 6 with 1 meaning docile and 6 indicating extreme aggressive behavior. Docility EPD are reported as percentages so that animals with a higher Docility EPD value will have a higher probability of producing calm animals (Speidel et al., 2003).

Summary

Table 8 contains a listing of traits with EPD reported by each breed association for many of the breeds in the United States. Expected progeny differences provide producers with useful tools for their selection decisions. Although they are very useful,

there is a lot of information to sort through based on the breed and production scenario in question. With so many values, it can be overwhelming, so care should be taken to narrow down the information to only those values that are pertinent to the production situation that cattle are being produced.

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Table 8. Current EPD available from breeds in the United States.

Breed	Birth Weight	Weaning Weight	Milk	Yearling Weight	Total Maternal	Yearling Height	Mature Height	Mature Weight	Scrotal Circumference	Gestation Length	Calving Ease Direct	Calving Ease Maternal	Heifer Pregnancy	Carcass Weight	Ribeye Area	Fat Thickness	Marbling	Retail Product	Yield Grade	Tenderness	Itramuscular Fat (%)	Ribeye Area	Fat Thickness	Retail Product	Stayability	Mainteance Energy	Docility
	Growth								Reproduction					Carcass							Ultrasound				Other		
Angus	×	×	×	×		×	×	×	×		×	×		×	×	×	×										
Blonde d'Aquitaine	×	×	×	×	×				×												×	×	×				
Beefmaster	×	×	×	×	×				×																		
Brahman	×	×	×	×										×	×	×	×	×		×							
Brangus	×	×	×	×	×				×												×	×	×				
Braford	×	×	×	×	×									×	×	×	×										
Braunvieh	×	×	×	×	×						×	×		×	×	×	×										
Charolais	×	×	×	×	×				×		×	×		×	×	×	×										
Chianina	×	×	×	×	×									×	×	×	×	×									
Gelbvieh	×	×	×	×	×				×	×	×	×		×	×		×								×		
Hereford	×	×	×	×	×				×		×	×									×	×	×				
Limousin	×	×	×	×					×		×	×		×	×		×		×						×		×
Maine-Anjou	×	×	×	×	×									×	×	×	×	×									
Red Angus	×	×	×	×	×						×	×	×	×	×	×									×	×	
Red Brangus	×	×	×	×	×																						
Romagnola	×	×	×	×	×																						
Salers	×	×	×	×	×				×					×	×	×	×	×							×		×
Santa Gertrudis	×	×	×	×	×									×	×	×	×										
Senepol	×	×	×	×	×				×																		
Shorthorn	×	×	×	×	×						×	×		×	×	×	×	×									
Simmental	×	×	×	×	×		×	×			×	×		×	×	×	×		×	×					×		
Tarentaise	×	×	×	×	×						×	×															

Selection Decisions: Tools for Economic Improvement Beyond EPD

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Throughout this manual, the goal has been to improve the profitability of beef production through proper sire selection and genetic improvement. The first step in using genetic improvement to increase profitability is to identify the economically relevant traits, the ERT, or those traits that directly influence the sources of income and/or the costs of production. To make this identification, the producer must consider how they market their animals, the performance of their animals, as well as the role of their product in the industry. For instance, is their primary income from the sale of breeding animals, as is the case with seedstock producers, or is income primarily from the sale of animals that are ultimately destined for harvest and consumption, such as is the case with commercial producers?

Once the breeder has identified the ERT that are appropriate for their production system, typically the number of EPD of relevance has been reduced considerably, yet even after that reduction, there still remains a considerable number of EPD to consider. Given that multiple traits likely need simultaneous improvement, an objective method for determining relative importance and economic value of each trait would further ease the animal selection process. Recently, new decision support tools have been released to the beef industry to address precisely this issue—determining relative importance and economic value of each trait and ultimately easing the process for making profitable selection decisions. To fully understand the utility and application of these advanced selection tools, breeders need a basic understanding of two concepts: 1. Single-trait selection and its weaknesses, and 2. Methods for multiple-trait selection which consider the production system, but may not address the economic value of each trait. Understanding of these two concepts, provides a foundation upon which to base improvements in selection methodologies. This chapter outlines the pitfalls of single-trait selection, considers different methods for multiple-trait selection, and ends with guidelines for use and evaluation of the next generation of selection tools for improving profitability of beef production.

Single- and Multiple-Trait Selection

Single-trait selection can produce rapid genetic change. Consider how frame size has changed from the 1960's to now—originally moving from small animals to the large frame scores seen in the 70's and 80's, and back to the more moderately sized animals today. No doubt, selection works.

Unfortunately, single-trait selection typically results in undesirable changes in correlated traits as well. For instance, at the same time the industry was focused on changing frame size, mature weight and cow maintenance requirements were changing as well because they were genetically related, or correlated, to frame score. As a result the single-trait selection for increased frame size resulted in greater feed requirements and eventually in animals that were not well suited for many environments. Those not suited often ended up as thin cows, who were invariably late
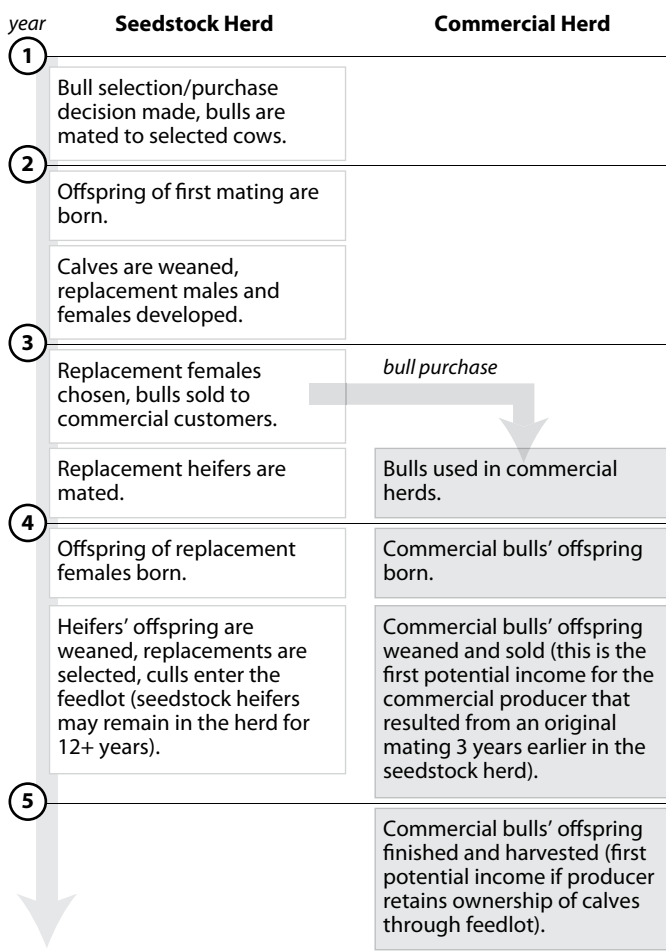
bred or not pregnant at all. Another unwanted change resulting from single-trait selection on frame score was an increase in birth weight and calving difficulty. All of these were the result of correlated response to single-trait selection on frame size. Single-trait selection is not advisable--breeders must approach genetic improvement from a systems perspective and change many traits simultaneously to achieve the goal of improved profitability.

Multiple-trait selection, considering more than one trait at a time, is the first step towards a systems perspective, but even multiple-trait selection leaves the breeder with several challenges. First, as additional traits are emphasized in a selection program, the rate of improvement in any one trait decreases. Second, the unfavorable correlations between many traits are still present. For instance, there is an unfavorable genetic correlation between calving ease and weaning weight both of which are ERT in many production systems. Calving ease tends to decrease as weaning weight is increased. This introduces a new problem—which of these two traits should be emphasized most in a genetic improvement program? These two problems are difficult to overcome without more sophisticated multiple-trait selection tools.

The best methods for evaluating a genetic improvement program's effects on profitability also consider the effects of time. The length between the selection decision and payback resulting from that decision often spans many years, and in a perfect system, the potential effect on profitability would be evaluated before the selection decision is made. Take the example of a breeder who is selling weaned calves and retaining a portion of the heifers as replacements; the sale weight ERT is weaning weight, but weaning weight is positively (and unfavorably) correlated to mature weight, an indicator of cow maintenance requirements. Selection for increased weaning weight will increase mature size and milk production, thereby potentially increasing the overall feed requirements of the herd over time and in turn, increasing costs of production. This scenario illustrates the need for selection decisions and genetic improvement goals to be evaluated in the context of the complete timespan for ramifications of the selection decision. Many producers do not consider the long-term effects of a selection decision, but rather consider what that particular sire will add to next year's calf crop.

From an industry-wide perspective, the potential impacts from a single selection decision made by the seedstock breeder requires considerable time before those superior genetics are realized by the seedstock breeder's commercial customer as illustrated in Figure 1. The seedstock breeder makes a selection and mating decision in spring, the offspring are born the following year and weaned. Bull calves are selected for development in that same year. In year 3, the bulls chosen for development are sold and used in the commercial herd. The offspring of these commercial matings are born in year 4. If those offspring are sold as weaned calves, the first income for the commercial producer arrives 4 years after the seedstock breeder's original selection decision.

Figure 1. Timeline illustrating time for the commercial producer to realize effects on profitability from a selection decision made in the seedstock supplier's herd.

year	Seedstock Herd	Commercial Herd
1	Bull selection/purchase decision made, bulls are mated to selected cows.	
2	Offspring of first mating are born.	
	Calves are weaned, replacement males and females developed.	
3	Replacement females chosen, bulls sold to commercial customers.	*bull purchase*
	Replacement heifers are mated.	Bulls used in commercial herds.
4	Offspring of replacement females born.	Commercial bulls' offspring born.
	Heifers' offspring are weaned, replacements are selected, culls enter the feedlot (seedstock heifers may remain in the herd for 12+ years).	Commercial bulls' offspring weaned and sold (this is the first potential income for the commercial producer that resulted from an original mating 3 years earlier in the seedstock herd).
5		Commercial bulls' offspring finished and harvested (first potential income if producer retains ownership of calves through feedlot).

If the commercial producer retains ownership of the calves, the first income may not be realized until year 5. So a mating in a seedstock herd made this year, may not realize income for the commercial producer until year 5.

The illustration in Figure 1 does not begin to consider the long-term effects of replacement females kept in the seedstock or the commercial herd. Assuming cows may reach 12 years of age before being culled, the original selection decision in year 1 may influence calves produced 16 years after the seedstock breeder's original decision if we consider the female replacements. As will be outlined below, good selection decision tools consider the long-term effects of selection decisions.

There are a variety of traditional methods for multiple-trait selection, many of which are implemented by producers, although they may not use this terminology to identify their methods. Each method has strengths and weaknesses.

Multiple-Trait Selection Methods

Tandem selection—Perhaps the simplest method for multiple-trait selection is tandem selection. With this method, just like a tandem axle truck or trailer, selection for one trait is followed by selection for another trait. All selection pressure is put on a single trait of interest until the performance of the herd reaches a level that the breeder desires, at which point another trait upon which to focus selection is chosen. For instance, a breeder may put all emphasis on improving marbling until a target level for percent choice is attained. At that point, the breeder realizes that performance in another trait, such as growth, needs improving and subsequently changes selection focus from marbling to growth. This method is rarely used in a strict sense because selection on one trait often produces unfavorable change in correlated traits as we discussed earlier. As a result, maintaining acceptable production levels for all traits is difficult with this method. The single scenario where this method is used considerably is for cases where some animals are culled at weaning and then the remaining group is culled further at a year of age.

Independent culling—The second and likely most common method for multiple-trait selection is independent culling. With this method, a breeder chooses minimum or maximum levels for each trait that needs to be improved. Any animal not meeting all criteria is not selected for use in the breeding program. To illustrate, consider a herd where the average weaning weight EPD is +25 and the average birth weight EPD is +1. If the producer is interested in improving weaning weight but does not want to increase birth weight, that producer might set a minimum threshold of a +35 WW EPD and a maximum BW EPD threshold of +1. Any potential sire not meeting both of those criteria would not be selected. Clearly, there are more than just 2 important traits as in this example, and accordingly as additional traits are added to the breeding objective (traits of interest), culling levels are set for each. This method is widely used due to the ease of implementation. Most breed association websites provide tools for sorting bulls on EPD with a user-defined set of standards (minimum and/or maximums). Using these web-based tools is analogous to implementing the independent culling method of multiple-trait selection.

Determining the appropriate culling level or threshold for each breeder is the most difficult aspect of this method as objective methods for identification are not widely available. Another drawback of this method is that as additional traits are added, criteria for other traits likely must be relaxed in an effort to find animals that meet all criteria. In the above WW/BW example, consider adding another trait such as marbling score EPD. If the breed/population average is +.06, the breeder might want to select only sires with a minimum marbling score EPD of +.5. To meet this marbling score standard, the weaning weight standard may have to be lowered to +30 (from the original +35) and the birth weight raised to a +2 (from the original +1). This "lowering of standards" reduces the rate of progress in any one trait, similar to other multiple-trait methods. However, once thresholds are identified, application of this method is very easy, making this method quite popular.

One major disadvantage to both tandem selection and independent culling is that neither of these methods incorporate the costs or income resulting from production—they do not account for the economic importance of each trait, and as a result do not simplify the evaluation of potential replacements based on probable effects on profit. The foundational method for overcoming this problem and for incorporating the economics of production into selection decisions and genetic improvement was developed by Hazel (1943) and is commonly referred to as selection indexes.

Incorporating Economics Into Multiple-Trait Selection

Hazel developed the concept of aggregate merit which represents the total monetary value of an animal in a given production system due to the genetic potential of that individual. Henderson (1951) reported that the same aggregate value could be calculated through weighting EPD by their relative economic value. These EPD, weighted by their relative economic values are summed to produce the aggregate value for each individual. Historically, the greatest challenge for the delivery of these indexes has been the determination of the economic values for weighting the EPD (or traits). The economic value for an individual trait is the monetary value of a one-unit increase in that trait, while other traits directly influencing profitability remain constant. For instance, the economic weight for weaning weight would be the value of a one-pound increase in weaning weight, independent of all other traits, or put another way, the value of a one pound increase in weaning weight holding all other traits constant. This may seem relatively straightforward, but problems arise in the ability to accurately assess value and changes caused by genetic correlations. Relative to assessing the value of a one pound increase in weaning weight it must be recognized that increases in weaning weight result in increased feed requirements, partially offsetting the increased income from the greater weaning weights. Accounting for these increased costs and revenue from improved weaning weight in an effort to derive the economic value is difficult at best.

The estimation of the relative economic values requires detailed economic information on the production system. Because costs of production change from producer to producer, these economic values also change from producer to producer. In some regions, breeders may have access to relatively cheap forages or crop aftermath during winter whereas others may be forced to buy relatively expensive, harvested forages to maintain the cow herd during these forage shortages. In these two scenarios, the value, or cost, associated with increases in maintenance feed requirements are not the same. The difficulty in obtaining detailed economic and production information from individual breeders has resulted in the development of generalized indexes that use information from surveys of groups of producers and/or governmental statistics on prices received and costs of production. While this is a very good alternative to breeder-specific indexes, the use of this generalized information can result in misleading economic weights from one production enterprise to the next. For instance, the relative economic value of calving ease depends upon the current levels of calving difficulty in a herd. Consider an extreme example, one producer assists no heifers during calving and another has a 50% assistance rate, the former would have a relatively low economic value for calving ease as current levels warrant no additional genetic change, whereas the last producer would put considerable economic value on genetic improvement of calving ease. A result of the requirement for detailed economic information has produced low adoption rates for many indexes. Additionally, many breeders are reluctant to use indexes because they feel indexes remove control over the direction of genetic change in their herd. Simply put, indexes take the "art" out of animal breeding.

Even with low adoption rates, those breeders and producer groups that have chosen to implement such indexes have witnessed rapid genetic and economic improvement. There are two documented examples of the genetic improvement resulting from the implementation of this technology. The first of these was reported by MacNeil (2003) and was based on an index of

$$I = \text{yearling weight} - (3.2 * \text{birth weight})$$

as proposed by Dickerson et al. (1974). This index was designed to improve the efficiency of beef production by 6% as opposed to selection on yearling weight alone. The index was calculated to reduce increases in birth weight and associated death loss resulting from the increase in yearling weight and to simultaneously reduce increases in mature weight and feed requirements usually associated with increasing yearling weight. After 11 years of selection based on this index, MacNeil et al. (2003) reported positive genetic change in direct and maternal effects on 365-day weight and a negligible, slightly positive change in birth weight. MacNeil also implemented independent culling levels for birth weight and yearling weight in another selection line. The independent culling line exhibited no increase in birth weight, but the increase in yearling weight was only half of that achieved with index selection (MacNeil et al., 1998).

Selection index technology was also implemented in 1976 by a New Zealand ranching firm, Landcorp Farming, Ltd. In that year, the company began selecting animals in their Angus seedstock herd for an economic breeding objective developed by Morris, Baker and Johnson and described by Nicoll, et al. (1979). The breeding objective was defined as

$$H \text{ (Net Income (\$ per cow lifetime))} = 0.53*L*D_P*(4.8*F-1)+0.06*M*D_M$$

Where:

0.53	=	the net income (1976NZ\$/kg carcass) from the slaughter of young stock;
0.06	=	the net income (1976NZ\$/kg carcass) from the slaughter of cull cows;
L	=	slaughter weight (kg) of surplus progeny at 30 months of age;
D_P	=	dressing percentage (x 0.01) of slaughtered progeny;
D_M	=	dressing percentage (x 0.01) of the culled cow;
F	=	net fertility; and
M	=	weight (kg) of cow at disposal.

(All of the above dollar values are in 1976 New Zealand dollars, but in the end, currency does not matter—the systems work the same).

The value for $4.8*F$ represents the total number of saleable calves per cow lifetime. One was subtracted from this total to account for the cow's replacement in the herd. Costs of production and income were based on data from the New Zealand Meat and Wool Boards' Economic Service and are reported in New Zealand dollars. Selection on this breeding objective resulted in simultaneous improvement in direct and maternal weaning weight, yearling weight, number of calves weaned per cow, and overall aggregate merit (Figure 2). As in the previous index where birth weight remained relatively stable and yearling weight increased, in this breeding system mature weight was remained relatively constant while early growth increased.

In both of the examples above, breeding programs that implemented selection indexes achieved rapid genetic gain and were able to hold traits of particular importance relative to costs, birth weight and mature weight, relatively stable.

Figure 2. Genetic trend in aggregate breeding value (New Zealand $) during 17 years of index selection.

Selection index technology is also used in many other animal industries including the pig, poultry, and dairy industries. In the hog industry, application of these technologies in one breeding program has resulted in nearly $1 more profit per head marketed per year (Short as quoted in Shafer, 2005).

Application of Selection Index Methods in North America

In North America, several breed associations publish index values for a variety of production systems. These include maternal, terminal, and pre-identified finish endpoint indexes. Within each category, the specificity of the available indexes varies. At one end a "generalized" index, usually developed by a group of producers or a breed, is meant to fit the needs of all members of the group. At the other end of the spectrum are indexes designed for use in specific production systems with specific production costs, revenue streams, and performance levels. At the extreme, this end of the continuum results in a specialized index for each breeder's specific production system, so that a seedstock producer might have a different index appropriate for each of their customers' production systems, hence the term "specialized". While specialized indexes represent the best implementation, development of specialized indexes for every producer or customer is likely cost and time prohibitive. Because of these difficulties, most published U.S. beef breed association indexes are generalized--some more than others. Hereafter the term "generalized" index will be used to refer to an index that is designed for use across multiple breeders for specific marketing situations. It is beyond the scope of this manual to review every index currently published and with the anticipated release of more indexes by several associations, such a discussion would be outdated very quickly after publication. This discussion will be limited to suggested "points of consideration" to be used when evaluating strengths and weaknesses of association-provided indexes or to decide whether to implement selection on a particular index or not.

The first step is to identify the most appropriate index for a particular breeder or production system (or your production system). To successfully execute this step the breeder must have identified the primary use of their market animals (breeding or harvest). If the breeder is a seedstock producer, they should be considering how their customers, the commercial producers, will be marketing the offspring of the animals the seedstock breeder wishes to sell. If the breeder is a commercial producer, they must

consider how the offspring of those sires will be marketed. The age at which those offspring will be marketed, and the end purpose of those market animals are also important considerations. For instance, different traits will likely be emphasized if animals are marketed at an auction, through private treaty, or on the rail for quality or yield grids. A cow/calf producer selling weaned calves anonymously through an auction would likely select a weaned calf index as opposed to an index that assumes that animals will be marketed on a grid basis. Similarly, a producer retaining ownership on calves and subsequently marketing those on a muscle (yield) grid, would not base selections on an index which assumes marketing on a quality grid, nor would that producer use a weaning index. Essentially identification of the appropriate index starts with the identification of the economically relevant traits for that producer's production system (as outlined in the previous chapter) and is followed by selection of the index that includes those economically relevant traits. Just like using the ERT to reduce the amount of information that must be considered when making a selection decision, the goal of any index is to combine information on individuals in the form of EPD to make selection more straightforward. Use of an inappropriate index may not produce genetic improvement that yields greater profit.

The other important component necessary to choose the appropriate index is considerations of the current genetic and production level of the herd. For instance if replacement heifers are kept from within the herd, do they have high conception rates as yearlings? What percentage of calving difficulty does the herd experience? Knowledge of these production characteristics helps determine the appropriate index and helps determine whether (as will be discussed below) other criteria should be included in making selection decisions beyond the index.

Criteria for Evaluating Indexes

Many indexes are produced by breed associations and may or may not include all of the traits that are economically relevant to a particular production system. When deciding on the use of generalized indexes several criteria must be available for the breeder to evaluate utility of each index in their production system. If these criteria are not available then application of those indexes should be limited at best. At minimum a description of every index should at a minimum include the first 3 items below and preferably the 4th:
1. Traits included in the index,
2. Description of information used in the index, such as EPD from a breed evaluation or individual phenotypic performance,
3. Source of economic information and performance levels used to calculate economic weights, and preferably
4. Relative economic emphasis of each trait to the overall index.

The reasons behind the first requirement are obvious, without knowing the traits included in an index, a producer can not decide whether it's use is appropriate or not. In a perfect world, the index would contain all of the traits that are economically relevant for the breeder's system. Unfortunately, this scenario is unlikely and the breeder should identify the index with the most traits in common with their list of economically relevant traits. The second item above is needed as use of EPD is always a more accurate form of selection than use of phenotypic information.

The reasons behind third and fourth requirements are less obvious and best explained with an example. Consider two breeders where one has access to relatively cheap crop aftermath to graze cows during the winter while another producer is limited to purchasing rather expensive harvested forages. The cost associated with increased maintenance requirements is different for the two breeders and similar economic values on maintenance requirement (or mature weight) would not be appropriate. Point 4 further refines the selection of the appropriate index. For instance, a typical index for selecting animals to produce slaughter progeny that are marketed on a quality grid would include marbling score in the index. For a producer whose slaughter cattle consistently grade 95%+ choice, more selection pressure on marbling score is unwarranted and marbling score should receive less emphasis if any. This producer would likely rather hold marbling score constant while improving other traits such as growth rate or time on feed. Point 4 provides information on the relative importance of traits in an index—which trait is most emphasized, which is second, and so on down to the least emphasized trait. Economic weights can be expressed as a dollar value or as a relative weight indicating the emphasis placed on each trait. A breeder would not likely choose an index that puts most emphasis on a trait that is of little value to that production system, or is already at an optimum level in their own herd.

In comparison to how long EPD have been available, the development and application of indexes in the U.S. beef industry is in its infancy. As more indexes are developed and released, however; the producer will also want to consider the relative importance of each trait in the index (points 3 and 4). This is one of the deficiencies of generalized indexes—rarely are they appropriate for every breeder due to the differences between the relative importance emphasized in the index and reality for the breeder. They are typically most appropriate for the overall genetic improvement of a breed as a whole. Until more specialized indexes are developed, the producer likely can not consider the source of data used to calculate the economic weights or the relative importance of each trait in the index. Additionally, most indexes released as of this writing do not have published relative economic weights for each trait as there have been concerns voiced over the proprietary nature of that information.

Once the appropriate index has been selected, strict application of the index system would necessitate that sire selection decisions be made solely on this information. Realistically, there are other issues to be concerned with such as breeding soundness, structure, and economically relevant traits not in the index. For traits not in the index, the breeder will need to apply appropriate selection pressure in addition to that on the index.

The successful application of generalized indexes relies upon the logical implementation as outlined below:

1. Identify your production and marketing system
   a. When will the animals be marketed (at what age)?
   b. How will the animals be marketed (private treaty, public auction, etc)?
   c. What is the current performance and genetic level of your herd?

2. Identify an index appropriate to the production system outlined in #1
   a. Questions to be addressed
      • What traits are included in the index?
      • What are the relative economic values used to weight the traits (or at least what data is used to estimate cost of production and value of income sources)
3. Decide on the appropriate index for evaluation based on the most similarity between points 1 and 2.
4. Evaluate index based on past performance and economic data (very difficult, so is listed as "optional")

For those skeptical of index selection, item number 4 provides a measure of confidence in a particular index, answering the question "Does this index produce results consistent with my production system?" A "cowboy" evaluation of an index's usefulness would include using historical performance and income data from sire-identified animals in the herd. The sire-identified animals chosen should have been marketed in a manner similar to that in the chosen index. The producer could then calculate an average value for each sire's progeny within a contemporary group. Once these averages are calculated, determine the difference in gross income between the sires' progeny averages. If available, calculate the costs of production for each sire's progeny groups and the net income for each sire group. The difference in net income (or gross income) should rank sires similarly to the rankings provided by the index value. The actual differences in profitability may not be as exact as those predicted but rankings should be similar. As with EPD, small contemporary groups or relatively few animals available for comparison reduce the confidence in this "cowboy" method. Larger contemporary groups are more informative and provide higher levels of confidence in the comparisons. This type of ad hoc evaluation becomes more difficult and less precise for cow/calf producers who retain female replacements. The primary difficulty is in evaluating changes in cow feed requirements and in length of productive life. To appropriately evaluate such indexes our recommendation is at least 6 years of cow data, and preferably more, be used to evaluate the applicability of any index where replacement heifers are retained. Admittedly, this method does not satisfy the requirements of strict academicians, but if validated with performance and economic information from contemporary animals, confidence should increase in the use of a specific index.

Breeders often ask what are the risks associated with using an index that incorrectly weights traits. Fortunately, small errors in economic weights are likely to have little effect on overall genetic improvement provided no single trait dominates the index (Smith, 1983; Weller, 1994). Problems arise when a single trait dominates an index and large changes occur in the importance of that trait.

Another issue not addressed in the above that may arise with the release of multiple, generalized indexes by a single breeding group is the potential for "double counting" and overemphasizing a particular trait. For instance, let's assume an index is being used that is appropriate for a cow/calf operation marketing weaned calves, and retaining replacement females and the index accounts for changes in feed requirements in the cow herd. If the breeder then also selects on another index that also accounts for genetic changes in feed requirements, the breeder could be overem-

phasizing the importance of feed requirements. In this case, it would likely result in over-penalized animals with greater growth potential. Again, selecting the single most appropriate index, is the best approach for implementation of this technology.

There are problems inherent with selection indexes as outlined above. Most of these deal with the use of generalized indexes rather than specialized indexes and incorrect economic values for each trait. In the ideal situation all economically relevant traits will be included in an index. Not including an economically relevant trait in an index is the same as assuming the value of improving that trait is zero unless the producer includes that trait in selection decisions along with the index values. The next section discusses other options for sire selection that overcome many of the problems with generalized selection indexes.

Beyond Indexes—Advanced Decision Support Systems

The development and use of selection indexes is increasing rapidly and is a considerable improvement over any other multiple-trait selection method previously available. Yet, indexes still have weaknesses. Of the currently available indexes most are generalized for overall breed improvement and use average costs and incomes from production rather than accounting for specific producer's marketing and production systems. More advanced selection support tools that offer breeders increased flexibility through interactive computer systems are becoming increasingly available. This "next generation" of selection tools is rapidly being released by various breed associations, but currently only several options exist for North American production systems. Each of these will be briefly discussed, but given the brisk pace at which new tools are being developed and improved, the majority of the following will focus on application and appropriate use of these tools.

Interactive decision support tools overcome the weaknesses inherent in generalized indexes. The term "interactive" refers to systems that allow the producer to input parameters specific to their production systems. These interactive systems offer increased flexibility to simulate individual breeders' production systems, and allow evaluation of the long-term effects of selection decisions and evaluation of the risks associated with particular selection decisions.

There are two general classes of interactive decision support systems. The first are herd-level systems that require herd-wide biological inputs and costs and incomes of production and in turn, return herd-wide results. These systems are designed to evaluate overall change in genetic level rather than to evaluate potential individual selection decisions and to uncover important interactions between genetic level and environment. Systems of the second type are animal based and predict outcomes of individual selection decisions and the potential consequences of using an animal (or animals with similar EPD) over the long term scenario. Because the former do not evaluate individual selection decisions they will only be briefly discussed here.

The first class of decision support systems includes the Decision Evaluator for the Cattle Industry or DECI and the American Angus Association's Optimal Milk Model. The DECI system is available through the website, http://www.ars.usda.gov/services/software/software.htm. The tool was developed for managers to

"evaluate strategic decisions affecting productivity and profitability through multiple marketing endpoints for an individual herd of breeding females." This system does not evaluate the consequences of individual selection decisions but rather evaluates the overall effects of changing genetic levels of a herd between three options: low, medium, and high. (The system will also evaluate changes in management of the herd such as changing supplementation levels or calving seasons). For instance, the system was designed to compare the option of using moderate growth sires versus high growth sires in a production system where feed resources are limited and heifers are retained from within the herd as replacements. In this system a baseline herd that represents the current herd structure, performance, and costs and product value is parameterized. Once the base herd is parameterized modifications to the genetic level and/or management procedures are evaluated through their overall effect on herd profitability. Additionally, specific herd production parameters such as weaning weight, calving weight or cow body condition score can be monitored over the course of the simulation.

The Angus Optimal Milk Module (www.angus.org/Performance/OptimalMilk/OptimalMilkMain.aspx) takes a similar approach, providing a tool designed specifically for producers to decide the appropriate range of milk EPD given the mature weight of their cows, annual cow costs, and variability in feed resources. The system produces output estimating cost of feed energy per Mcal and useful recommendations for an optimal range of milk EPD for that specific operation. Additionally, graphical outputs are available that illustrate the effect of increasing/decreasing milk EPD on net income per cow as shown in Figure 3.

Individual-Sire Decision Support

The second class of decision support systems is designed for evaluating individual animal selection decisions, and the impact of those decisions on profitability. These systems are based on breeder-specific production and economic data. Currently, only two systems exist with this flexibility and that are available to all commercial producers. These are located via the web at www.charolaisusa.com (Terminal sire profitability index) and ert.agsci.colostate.edu. The latter will be known as the ERT tool and the

Figure 3. Example of graphical presentation of results from the Angus Optimal Milk Module.

Economic Value of Varying Milk EPDs

X-axis: Milk EPD. Y-axis: Impact on Net Income per Cow ($).
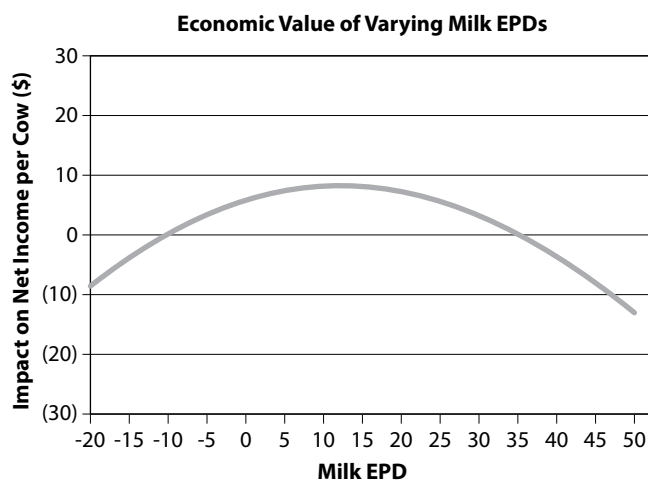
former as the terminal system (TS). Both systems are designed so that the breeder need only input critical performance, cost and product value (income) data (Table 1). These limited data ensure that the tool is as easy to use as possible while retaining flexibility to simulate different production systems.

The TS is designed to evaluate decisions for selection of sires in the American International Charolais Association database based on their relative impact on profitability in a terminal sire mating system. By definition no replacements are kept from within a terminal mating system. The TS allows input of current herd production characteristics and sources of income by the producer including options for weaned calves, backgrounded calves, and grid pricing models. Sires are then ranked by their index values given the producer's production values. This system offers increased flexibility over selection indexes by allowing producers to select animals based on their specific production system. The terminal system accounts for increased feed requirements for animals sired by bulls with greater levels of growth, but does not account for differences in costs of production. The TS also assumes that are calves are marketed on a carcass value basis.

Table 1. Example input information required for use of terminal sire and ERT (cow/calf) decision support systems

Category	Terminal Sire	ERT (cow/calf)	
		Observed Performance	EPD
Animal performance	• Cow Size • Weaning weight • Backgrounding phase ADG • Growing phase ADG • Finishing phase ADG • Marbling Score • USDA Yield Grade	• Herd Size • Mature cow calving rate • Heifer calving rate • Mature Cow Weight • Calf Survival Weight • Yearling weight • Weaning weight • Birth Weight • Heifer calving difficulty	• Birth weight • Weaning weight • Yearling weight • Milk • Calving Ease Direct • Heifer Pregnancy • Calving Ease Total Maternal • Stayability • Maintenance
Management Information	• Length of Backgrounding phase • Length of growing phase • Length of finishing phase	• Input goal • Replacement source • Cows per bull • Breeding system • Maximum cow age	
Economic Information	• Cull cows, $/cwt • Weaning Price $/lb (sliding scale) • Backgrounding Price, $/lb	• Non-feed cow costs • Value of bred heifers • Value of bred cows • Value of herd sires • Heifer price • Cull cow price • Calf price • Replacement heifer price • Cost of additional feed • Discount Rate	
Carcass Grid Information	• Base price, $/cwt • Light and heavy carcass, weight breaks and discounts • Quality grade discounts and premiums • Yield grade discounts and premiums		

The current ERT system is designed to evaluate selection decisions for the cow/calf producer marketing weaned calves. This system requires inputs on the production system, management specifications, genetics, and economics of production. The tool has been designed for both commercial and seedstock breeder with basic data requirements that should be readily available for most producers. The system produces data for evaluating the consequences of a particular selection decision both on a performance basis and on an economic basis. The outputs are based upon the current genetic level of the herd and changes resulting from selection of a particular sire. The system relies on a database of EPD from participating breed associations and allows comparison of animals within breeds.

Given advances in flow of performance data between industry sectors and advances in the development of decision-support systems, more of these decision tools will likely be released to the industry in the near future. As with any new technology breeders must have faith in the tool and also have some method to evaluate the technology. When EPD were originally delivered to the industry, that tool also needed such scrutiny and eventually became widely accepted. From a scientific standpoint, the ultimate testing of any decision-support product, whether selection index or interactive decision support, would be peer-reviewed studies on the utility of each system in a research setting. Research herds typically are able to record much more detailed information than is cost effective for the average producer. The deficiency of such studies is that they represent the environment and production system in which they were validated. Additionally, these studies take time to generate and publish. Given the dynamic beef industry, producers need some method to evaluate the utility of these for their own production system.

The following is a suggested protocol for evaluation of these systems for specific production systems. The points outlined below are much like those outlined for evaluation of selection indexes. Realize that some decision support systems will account for production changes that are not readily quantified by every breed association genetic evaluation. For instance, these systems will likely account for change in feed requirements, something not easily measured by most commercial producers, and therefore difficult to translate into profitability. Each point will be discussed subsequently.

An outline of steps for evaluation of interactive decision support tools (discussion follows):

1. Identify production and marketing system
   a. When will the animals be marketed (at what age)?
   b. How will the animals be marketed?
   c. What is the current performance and genetic level of your herd?
   d. Gather historical cost and income data on the herd of interest (relative to the required inputs for step 2)
2. Enter herd parameters into decision support system
3. Simulate your current herd
4. Evaluate results
   a. Consider the following:
      • Does the system accurately predict animal performance (may or may not be an outcome of an interactive system)
      • Does the system accurately predict economic performance (may or may not be produced—interpret carefully as most producers will likely not have all performance information needed to precisely evaluate the system)
5. Enter EPD for currently used bulls (or select those bulls) and calculate results of those selections.
6. Compare results for bulls used in number 5 to actual results.
7. Use system to identify potential sire selection decisions.

Step 1 is similar to that used for evaluation of selection indexes. As with any decision support tool, specifying the production and marketing system is critical for evaluation and successful use of selection tools. Selection of the appropriate selection tool begins with identification of a system that closely resembles the producer's production and marketing system. For instance, a producer would not want to use a selection tool that assumes marketing finished animals on a carcass basis, if that producer actually markets weaned calves through an auction system. Step 2 is self-explanatory. Steps 3 through 4, may or may not be available depending upon the system. Some systems such as DECI and ERT provide performance and outputs on the current herd structure. The TS requires input of bulls used in the past if the user wishes to evaluate the system's representation of a current production system (Step 5). In theory, a terminal-sire breeder could input the terminal sires they have used in the past, and then compare the actual performance of those bulls' progeny to the differences predicted by the TS system (Step 6). Step 6 is critical for evaluation of the selection system—does the tool rank animals and profitability similarly to historical performance? If the system closely resembles past performance (using historical inputs), the user has much more faith in the system and can proceed to Step 7. Step 6 must be implemented with the realization that the producer may not have all of the needed information to fairly evaluate the decision support tool. The economic and animal performance data available for the producer may not be as detailed or as accurate as required for a "fair" evaluation of the system. As previously mentioned, values for changes in feed requirements will very

likely be missing. If retaining replacement heifers, likely data on female lifetime productivity will be lacking, making appropriate evaluation of the decision support system difficult. If the data to evaluate the system are suspect or deficient, then the producer should not lose confidence in the system. Similarly to when EPD were first introduced, the most detailed analysis of the results of these systems and the verification of their utility will be performed through research facilities. Several studies with the primary goal of validating these systems are currently underway.

Conclusion

The goal of both selection indexes and interactive decision-support systems is to ease the process of multiple-trait selection and to combine the economics of production with selection to improve profitability. The successful use of either selection indexes or interactive decision- support systems depends upon selection of a system that simulates a specific production and marketing system. Selection of the appropriate index or interactive system is key to success. With the application of one of these systems both the commercial and seedstock producer should increase profitability. Two studies described within showed great progress using only phenotypic data, not the much more accurate EPD available today. Use of these systems will also make selection and marketing of animals more straightforward and simple.

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Crossbreeding for Commercial Beef Production

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Improvement of the economic position of the farm or ranch is an ongoing process for many commercial cow-calf producers. Profitability may be enhanced by increasing the volume of production (i.e. the pounds of calves you market) and/or the value of products you sell (improving quality). The reduction of production costs, and thus breakeven prices, can also improve profitability. More and more producers are finding that a structured crossbreeding system helps them achieve the goals of increasing productivity and reducing production costs. Indeed, pricing differences, popularity and perceptions of utility of some breeds and color pattern have motivated producers to stray away from sound crossbreeding systems. The primary objective of this chapter is to illustrate the economic importance of crossbreeding and diagram a number of crossbreeding systems.

Why Crossbreed?

The use of crossbreeding offers two distinct and important advantages over the use of a single breed. First, crossbred animals have heterosis or hybrid vigor. Second, crossbred animals combine the strengths of the parent breeds. The term 'breed complementarity' is often used to describe breed combinations that produce highly desirable animals for a broad range of traits.

What is Heterosis?

Heterosis refers to the superiority of the crossbred animal relative to the average of its straight bred parents. Heterosis is typically reported in percentage improvement in the trait of interest. For example, bulls of breed A, which have an average weaning weight of 550 pounds, are mated to cows of breed B, which have an average weaning weight of 500 pounds. The average weaning weight of the straightbred parents is then $(550 + 500)/2 = 525$. The F_1 (first cross) calves that result have an average weaning weight of 546 pounds. The percentage heterosis is 4% (0.04) or $(546 - 525)/525$. Heterosis percentage is computed as the difference between the progeny average and the average of the straightbred parents divided by the average of the straightbred parents.

Heterosis results from the increase in the heterozygosity of a crossbred animal's genetic makeup. Heterozygosity refers to a state where an animal has two different forms of a gene. It is believed that heterosis is the result of gene dominance and the recovery from accumulated inbreeding depression of pure breeds. Heterosis is, therefore, dependent on an animal having two different copies of a gene. The level of heterozygosity an animal has depends on the random inheritance of copies of genes from its parents. In general, animals that are crosses of unrelated breeds, such as Angus and Brahman, exhibit higher levels of heterosis, due to more heterozygosity, than do crosses of more genetically similar breeds such as a cross of Angus and Hereford.

Generally, heterosis generates the largest improvement in lowly heritable traits. Moderate improvements due to heterosis are usually seen in moderately heritable traits. Little or no heterosis is observed in highly heritable traits. Heritability is the proportion of the observable variation in a trait between animals

Table 1. Summary of heritability and level of heterosis by trait type.[a]

Trait	Heritability	Level of Heterosis
Carcass/end product	High	Low (0 to 5%)
Skeletal measurements		
Mature weight		
Growth rate	Medium	Medium (5 to 10%)
Birth weight		
Weaning weight		
Yearling weight		
Milk production		
Maternal ability	Low	High (10 to 30%)
Reproduction		
Health		
Cow longevity		
Overall cow productivity		

[a] Adapted from Kress and MacNeil, 1999.

that is due to the genetics that are passed between generations and the variation observed in the animal's phenotypes, which are the result of genetic and environmental effects. See Table 1 for grouping of traits by level of heritability. Traits such as reproduction and longevity have low heritability. These traits usually respond very slowly to selection since a large portion of the variation observed in them is due to environmental factors and non-additive genetic effects, and a small percentage is due to additive genetic differences. Heterosis generated through crossbreeding can significantly improve an animal's performance for lowly heritable traits. Crossbreeding has been shown to be an efficient method to improve reproductive efficiency and productivity in beef cattle.

Improvements in cow-calf production due to heterosis are attributable to having both a crossbred cow and a crossbred calf. Differing levels of heterosis are generated when various breeds are crossed. Similar levels of heterosis are observed when members of the *Bos taurus* species, including the British (e.g. Angus, Hereford, Shorthorn) and Continental European breeds (e.g. Charolais, Gelbvieh, Limousin, Maine-Anjou, Simmental), are crossed. Much more heterosis is observed when *Bos indicus*, or Zebu, breeds like Brahman, Nelore and Gir, are crossed with *Bos taurus* breeds. The increase in heterosis observed in British by *Bos indicus* crosses for a trait is usually 2-3 times as large as the heterosis for the same trait observed in *Bos taurus* crossbreds (Koger, 1980). The increase in heterosis results from the presence of greater genetic differences between species than within a species. Heterosis effects reported in the following tables will be divided and noted into those observed in *Bos taurus* crosses or *Bos taurus* by *Bos indicus* crosses. Table 2 details the individual (crossbred calf) heterosis and Table 3 describes the maternal (crossbred cow) heterosis observed for various important production traits in *Bos taurus* crossbreds. These heterosis estimates are adapted from a report by Cundiff and Gregory (1999) and summarize cross-

breeding experiments conducted in the Southeastern and Midwest areas of the US. Table 4 describes the expected direct heterosis of *Bos taurus* by *Bos indicus* crossbred calves, while Table 5 details the estimated maternal heterotic effects observed in *Bos taurus* by *Bos indicus* crossbred cows. *Bos taurus* by *Bos indicus* heterosis estimates were derived from breeding experiments conducted in the southern United States.

The heterosis adjustments utilized by multi-breed genetic evaluation systems are another example of estimates for individual (due to a crossbred calf) and maternal (due to crossbred dam) heterosis. These heterosis adjustments are present in Table 6 and illustrate the differences in expected heterosis for various breed-group crosses. In general the Zebu (*Bos indicus*) crosses have higher levels of heterosis than the British-British, British-Continental, or Continental-Continental crosses.

Why Is It So Important to Have Crossbred Cows?

The production of crossbred calves yields advantages in both heterosis and the blending of desirable traits from two or more breeds. However, the largest economic benefit of crossbreeding to commercial producers comes from having crossbred cows. Maternal heterosis improves both the environment a cow provides for her calf as well as improves the reproductive performance, longevity and durability of the cow. The improvement of the maternal environment, or mothering ability, a cow provides for her calf is manifested in the improvements in calf survivability to weaning and increased weaning weight. Crossbred cows exhibit improvements in calving rate of nearly 4% and an increase in longevity of more that one year due to heterotic effects. Heterosis results in increases in lifetime productivity of approximately one calf and 600 pounds of calf weaning weight over the lifetime of the cow. Crossbreeding can have positive effects on a ranch's bottom line by not only increasing the quality and gross pay weight of calves produced but also by increasing the durability and productivity of the cow factory and reducing replacement heifer costs.

Table 2. Units and percentage of heterosis by trait for *Bos taurus* crossbred calves.

Trait	Heterosis Units	Heterosis %
Calving rate, %	3.2	4.4
Survival to weaning, %	1.4	1.9
Birth weight, lb	1.7	2.4
Weaning weight, lb	16.3	3.9
Yearling weight, lb	29.1	3.8
Average daily gain, lb/d	0.08	2.6

Table 3. Units and percentage of heterosis by trait for *Bos taurus* crossbred dams.

Trait	Heterosis Units	Heterosis %
Calving rate, %	3.5	3.7
Survival to weaning, %	0.8	1.5
Birth weight, lb	1.6	1.8
Weaning weight, lb	18.0	3.9
Longevity, years	1.36	16.2
Lifetime Productivity		
Number of calves	.97	17.0
Cumulative weaning weight, lb	600	25.3

Table 4. Units and percentage of heterosis by trait for *Bos Taurus* by *Bos indicus* crossbred calves.[a]

Trait	Heterosis Units
Calving rate, %	4.3
Calving assistance, %	4.9
Calf survival, %	-1.4
Weaning rate, %	1.8
Birth weight, lb	11.4
Weaning weight, lb	78.5

[a] Adapted from Franke et al., 2005; numeric average of Angus-Brahman, Brahman-Charolais, and Brahman-Hereford heterosis estimates.

Table 5. Units and percentage of heterosis by trait for *Bos Taurus* by *Bos indicus* crossbred dams.[a]

Trait	Heterosis Units	Heterosis %
Calving rate, %	15.4	--
Calving assistance rate, %	-6.6	--
Calf survival, %	8.2	--
Weaning rate, %	20.8	--
Birth weight, lb	-2.4	--
Weaning weight, lb	3.2	--
Weaning weight per cow exposed, lb[b]	91.7	31.6

[a] Adapted from Franke et al., 2005; numeric average of Angus-Brahman, Brahman-Charolais, and Brahman-Hereford heterosis estimates.
[b] Adapted from Franke et al., 2001.

Table 6. Individual (calf) and maternal (dam) heterosis adjustments for British, Continental European, and Zebu breed groups for birth weight, weaning weight and post weaning gain.

Breed Combinations	Birth Weight (lb) Calf Heterosis	Birth Weight (lb) Dam Heterosis	Weaning Weight (lb) Calf Heterosis	Weaning Weight (lb) Dam Heterosis	Postweaning Gain (lb) Calf Heterosis
British x British	1.9	1.0	21.3	18.8	9.4
British x Continental	1.9	1.0	21.3	18.8	9.4
British x Zebu	7.5	2.1	48.0	53.2	28.2
Continental x Continental	1.9	1.0	21.3	18.8	9.4
Continental x Zebu	7.5	2.1	48.0	53.2	28.2

Wade Shafer, American Simmental Association, personal communication.

How Can I Harness the Power of Breed Complementarity?

Breed complementarity is the effect of combining breeds that have different strengths. When considering crossbreeding from the standpoint of producing replacement females, one should select breeds that have complementary maternal traits such that females are most ideally matched to their production environment. Matings to produce calves for market should focus on complementing the traits of the cows and fine tuning calf performance (growth and carcass traits) to the market place.

There is an abundance of research that describes the core competencies (biological type) of many of today's commonly used beef breeds. Traits are typically combined into groupings such as maternal/reproduction, growth and carcass. When selecting animals for a crossbreeding system, their breed should be your first consideration. What breeds you select for inclusion in your mating program will be dependent on a number of factors including the current breed composition of your cow herd, your forage and production environment, your replacement female development system, and your calf marketing endpoint. All of these factors help determine the relative importance of traits for each production phase. A detailed discussion of breed and composite selection is contained in the following chapter.

If you implement a crossbreeding system, do not be fooled into the idea that you no longer need to select and purchase quality bulls or semen for your herd. Heterosis cannot overcome low quality genetic inputs. The quality of progeny from a crossbreeding system is limited by the quality of the parent stock that produced them. Conversely, do not believe that selection of extremely high quality bulls or semen or choosing the right breed will offset the advantages of effective crossbreeding system. Crossbreeding and sire selection are complementary and should be used in tandem to build an optimum mating system in commercial herds. (Bullock and Anderson, 2004)

What are the Keys to Successful Crossbreeding Programs?

Many of the challenges that have been associated with crossbreeding systems in the past are the result of undisciplined implementation of the system. With that in mind, one should be cautious to select a mating system that matches the amount of labor and expertise available to appropriately implement the system. Crossbreeding systems range in complexity from very simple programs such as the use of composite breeds, which are as easy as straight breeding, to elaborate rotational crossbreeding systems with four or more breed inputs. The biggest keys to success are the thoughtful construction of a plan and then sticking to it! Be sure to set attainable goals. Discipline is essential.

Crossbreeding Systems

Practical crossbreeding systems implemented in a commercial herd vary considerably from herd to herd. A number of factors determine the practicality and effectiveness of crossbreeding systems for each operation. These factors include herd size, market target, existing breeds in the herd, the level of management expertise, labor availability, grazing system, handling facilities and the number of available breeding pastures. It should be noted that in some instances the number of breeding pastures

Table 7. Summary of crossbreeding systems by amount of advantage and other factors.[a]

Type of System		% of Cow Herd	% of Marketed Calves	Advantage (%)[b]	Retained Heterosis (%)[c]	Minimum No. of Breeding Pastures	Minimum Herd Size	No. of Breeds
2-Breed Rotation	A*B Rotation	100	100	16	67	2	50	2
3-Breed Rotation	A*B*C Rotation	100	100	20	86	3	75	3
2-Breed Rotational/ Terminal Sire	A*B Rotational	50	33			2		
	T x (A*B)	50	67			1		
	Overall	100	100	21	90	3	100	3
Terminal Cross with Straightbred Females[d]	T x (A)	100	100	8.5	0[e]	1	Any	2
Terminal Cross with Purchased F$_1$ Females	T x (A*B)	100	100	24	100	1	Any	3
Rotate Bull every 4 years	A*B Rotation	100	100	12-16	50-67[f]	1	Any	2
	A*B*C Rotation	100	100	16-20	67-83[f]	1	Any	3
Composite Breeds	2-breed	100	100	12	50	1	Any	2
	3-breed	100	100	15	67	1	Any	3
	4-breed	100	100	17	75	1	Any	4
Rotating Unrelated F$_1$ Bulls	A*B x A*B	100	100	12	50	1	Any	2
	A*B x A*C	100	100	16	67	1	Any	3
	A*B x C*D	100	100	19	83	2	Any	4

[a] Adapted from Ritchie et al., 1999.
[b] Measured in percentage increase in lb. of calf weaned per cow exposed.
[c] Relative to F$_1$ with 100% heterosis.
[d] Gregory and Cundiff, 1980.
[e] Straightbred cows are used in this system which by definition have zero (0) percent maternal heterosis; calves produced in this system exhibit heterosis which is responsible for the expected improvement in weaning weight per cow exposed.
[f] Estimates of the range of retained heterosis. The lower limit assumes that for a two breed system with stabilized breed fractions of 50% for each breed; three breed rotation assumes animals stabilize at a composition of 1/3 of each breed. Breed fractions of cows and level of maternal heterosis will vary depending on sequence of production.

required can be reduced through the use of artificial insemination. Additional considerations include the operator's decision to purchase replacement females or select and raise replacements from the herd. Purchasing healthy, well developed replacement females of appropriate breed composition can be the simplest and quickest way for producers, especially small operators, to maximize maternal heterosis in the cowherd. Regardless of the crossbreeding system selected, a long-term plan and commitment to it are required to achieve the maximum benefit from crossbreeding. A variety of crossbreeding systems are described on the following pages. These systems are summarized in Table 7 by their productivity advantage measured in percentage of pounds of calf weaned per cow exposed. Additionally the table includes the expected amount of retained heterosis, the minimum number of breeding pastures required, whether purchased replacements are required, the minimum herd size required for the system to be effectively implemented, and the number of breeds involved.
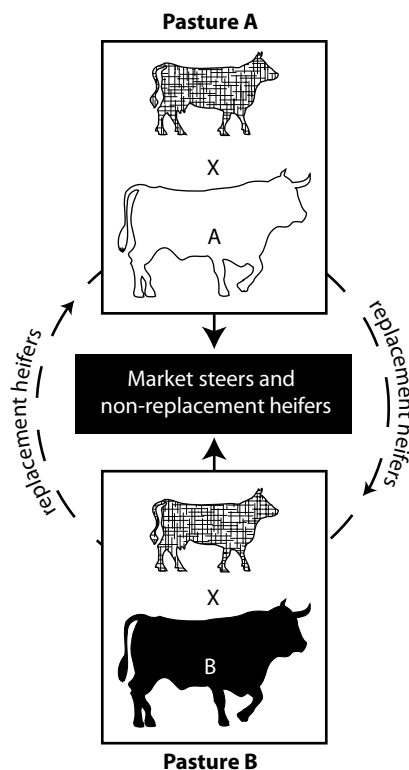
Two-Breed Rotation

A two-breed rotation is a simple crossbreeding system requiring two breeds and two breeding pastures. The two-breed rotational crossbreeding system is initiated by breeding cows of breed A to bulls of breed B. The resulting heifer progeny (A*B) chosen as replacement females would then be mated to bulls of breed A for the duration of their lifetime. Note the service sire is the opposite breed of the female's own sire. These progeny are then ¼ breed A and ¾ breed B. Since these animals were sired by breed B bulls, breeding females are mated to breed A bulls. Each succeeding generation of replacement females is mated to the opposite breed of their sire. The two-breed rotational crossbreeding system is depicted in Figure 1. Initially only one breed of sire is required. Following the second year of mating, two breeds of sire are required. After several generations the amount of retained heterosis stabilizes at about 67% of the maximum calf and dam heterosis, resulting in an expected 16% increase in the pounds of calf weaning weight per cow exposed above the average of the parent breeds (Ritchie et al., 1999). This system is sometimes called a crisscross.

Requirements— A minimum of two breeding pastures are required for a two-breed rotational

Figure 1. Two-breed rotation.

Pasture A

X

A

Market steers and non-replacement heifers

replacement heifers

replacement heifers

X

B

Pasture B

system if natural service is utilized exclusively. Replacement females must be identified by breed of sire to ensure proper matings. A simple ear tagging system may be implemented to aid in identification. All calves sired by breed A bulls should be tagged with one color (e.g. red) and the calves sired by bulls of breed B should be tagged with a different color (e.g. blue). Then at mating time, all the cows with red tags (sire breed A) should be mated to breed B bulls, and vice-versa.
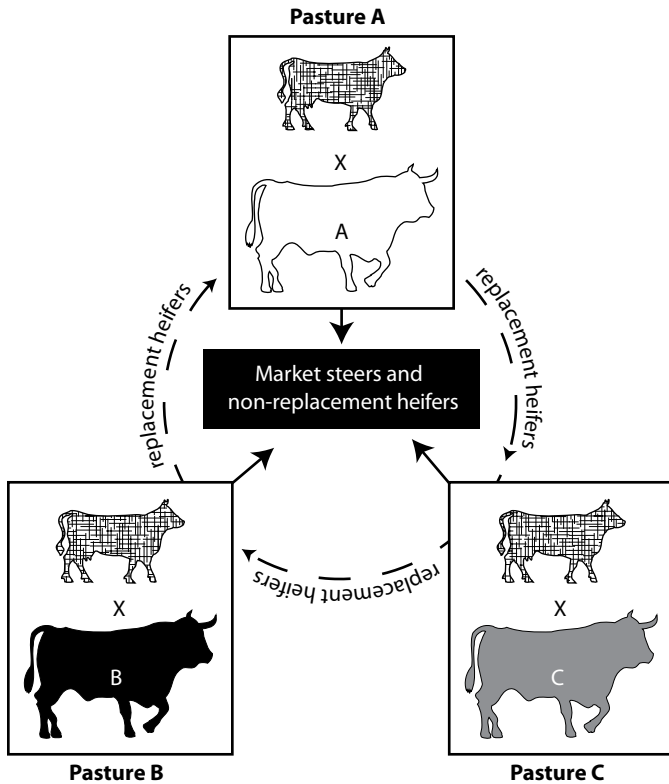
Considerations—The minimum herd size is approximately 50 cows with each half being serviced by one bull of each breed. Scaling of herd size should be done in approximately 50 cow units to make the best use of service sires, assuming 1 bull per 25 cows. Replacement females are mated to herd bulls in this system so extra caution is merited in sire selection for calving ease to minimize calving difficulty. Be sure to purchase bulls or semen from sires with acceptable Calving Ease (preferably) or Birth Weight EPDs for mating to heifers. Alternately, a calving ease sire(s) could be purchased to breed exclusively to first calf heifers regardless of their breed type. The progeny produced from these matings that do not conform to the breed type of the herd should all be marketed.

Breeds used in rotational systems should be of similar biological type to avoid large swings in progeny phenotype due to changes in breed composition. The breeds included have similar genetic potential for calving ease, mature weight and frame size, and lactation potential to prevent excessive variation in nutrient and management requirements of the herd. Using breeds of similar biological type and color pattern will produce a more uniform calf crop which is more desirable at marketing time. If animals of divergent type or color pattern are used, additional management inputs and sorting of progeny at marketing time to produce uniform groups may be required.

Three-Breed Rotation

A three-breed rotational system is very similar to a two-breed system in implementation with an additional breed added to the mix. This system is depicted in Figure 2. A three-breed rotational system achieves a higher level of retained heterosis than a two-breed rotational crossbreeding system does. After several generations the amount of retained heterosis stabilizes at about 86% of the maximum calf and dam heterosis, resulting in an expected 20% increase in the pounds of calf weaning weight per cow exposed above the average of the parent breeds (Ritchie et al., 1999). Like the two-breed system, distinct groups of cows are formed and mated to bulls of the breed which represents the smallest fraction of the cows breed makeup. A cow will only be mated to a single breed of bull for her lifetime.

Requirements—A minimum of three breeding pastures are required for a three-breed rotational system. Replacement females must be identified by breed of sire to ensure proper matings. A simple ear tagging system may be implemented to aid in identification. All calves sired by breed A bulls should be tagged with one color (e.g. red), the calves sired bulls of breed B should be tagged with a different color (e.g. blue), and the progeny of bulls of breed C tagged a third color (e.g. green). Then at mating time, all the cows with red tags (sired by breed A) should be mated to breed B bulls, cows with blue tags (sired by breed B) should be mated to breed C bulls, and, finally, all cows with green tags (sired by breed C) should be mated to breed A bulls.

Figure 2. Three-breed rotation.

Considerations—The minimum herd size is approximately 75 cows with each half being serviced by one bull of each breed. Scaling of herd size should be done in approximately 75 cow units to make the best use of service sires, assuming 1 bull per 25 cows. Replacement females are mated to herd bulls in this system so extra caution is merited in sire selection for calving ease to minimize calving difficulty. Be sure to purchase bulls or semen from sires with acceptable Calving Ease (preferably) or Birth Weight EPDs for mating to heifers. Alternately, a calving ease sire(s) could be purchased to breed exclusively to first calf heifers regardless of their breed type. The progeny produced from these matings that do not conform to the breed type of the herd should all be marketed.

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2-Breed Rotational/Terminal Sire

The two-breed rotational with terminal sire system is sometimes called a rota-terminal system. It includes a two-breed rotational crossbreeding system of maternal breeds A and B. This portion of the herd is charged with producing replacement fe-males for the entire herd, so maternal traits of the breeds included are very important. The remainder of the cow herd is bred to a terminal sire of a different breed as illustrated in Figure 3. In this system approximately half of the cow-herd is committed to the rotational portion of the breeding system and half to the terminal sire portion. This system retains about 90% of the maximum calf heterosis plus capitalizes on 67% of the maximum dam heterosis; it should increase weaning weight per cow exposed by approximately 21%.

Requirements—This system requires a minimum of three breeding pastures. Females in the rotational portion of the system must be identified by breed of sire. Minimum herd size is approximately 100 cows. Given the complexity of the breeding system and identification requirements, this system requires more management and labor to make it run effectively than some other systems do. The trade off in systems that are easier to manage is that they typically yield lower levels of heterosis. If management expertise and labor are readily available this system is one of the best for maximizing efficiency and the use of heterosis.

Considerations—The females in the rotational portion should consist of the youngest females, namely the 1-, 2-, and 3-year-olds. These females should be bred to bulls with both good calving ease and maternal traits. Calving ease and maternal traits are emphasized here because the cows being bred are the youngest animals where dystocia is expected to be highest. Additionally, replacement females for the entire herd will be selected from the progeny of these cows so maternal traits are important. The remainder of the cow herd consists of mature cows that should be mated to bulls from a third breed that excel in growth rate and muscularity. The proportion of cows in each portion of the breeding system should be adjusted depending on the number

Figure 3. Two-breed rotational/terminal sire.
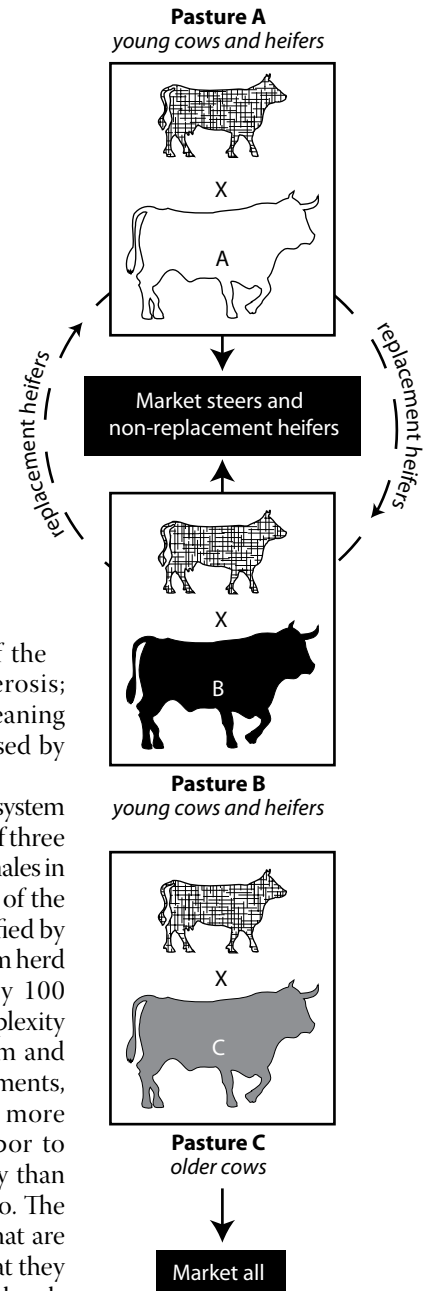
of replacement females required. When fewer replacements are needed a smaller portion of the herd will be included in the rotational system. Be sure to keep the very youngest breeding females in the rotational system to avoid dystocia problems. If ownership of calves will be retained through harvest some consideration should be given to end product traits such as carcass weight, marbling, and leanness. One drawback of the system is that there will be two different types of calves to market: one set from the maternally focused rotational system and one from the terminal sire system. Sorting and marketing can typically help offset this problem. The benefits of the rota-terminal system are usually worth the limitations.

Two-Breed Terminal Sire

A two breed terminal cross system uses straightbred cows of one breed and a sire(s) of another breed. No replacement females are kept and therefore, must be purchased. Since all calves are marketed it is a terminal sire system. Charolais or Limousin sires used on Angus cows would be a common example. Implementations of two breed terminal sire systems are not desirable or recommended as they do not employ any benefits of maternal heterosis as the cows are all straightbred. Remember most of the benefits of heterosis arise from the enhancement of reproduction and longevity traits of crossbred cows. A slight improvement in pounds of calf weaned per cow exposed will be observed due to individual heterosis in the calves produced by this system.

Terminal Cross with Purchased F_1 Females

The terminal cross system utilizes crossbred cows and bulls of a third breed as shown in Figure 4. This system is an excellent choice as it produces maximum heterosis in both the calf and cow. As such, calves obtain the additional growth benefits of hybrid vigor while heterosis in the cows improves their maternal ability. The terminal-cross system is one of the simplest systems to implement and achieves the highest use of heterosis and breed complementarity. All calves marketed will have the same breed composition. A 24% increase in pounds of calf weaned per cow exposed is expected from this system when compared to the average of the parent breeds.

Requirements—The terminal cross system works well for herds of any size if high quality replacement females are readily available from other sources. Only one breeding pasture is required. No special identification of cows or groups is required.

Considerations—Since replacement females are purchased care should be given in their selection to ensure that they are a fit to the production environment. Their adaptation to the production environment will be determined by their biological type, especially their mature size and lactation potential. Success of the system is dependent on being able to purchase a bull of a third breed that excels in growth and carcass traits. If virgin heifers are selected as replacements, they should be mated to an easy calving sire to

Figure 4. Terminal cross with purchased F_1 females.

purchased replacement heifers

X

A, B, or C

Market all

minimize dystocia problems. Alternately, three year-old cows may be purchased as replacements and mated to the terminal sire breed. Disease issues are always a concern when introducing new animals to your herd. Be sure that replacement heifers are from a reputable, disease-free source and that appropriate biosecurity measures are employed. Johnes, brucellosis, tuberculosis, bovine viral diarrhea (BVD) are diseases you should be aware of when purchasing animals. Another consideration and potential advantage of the terminal-cross system is that replacement females do not need to be purchased each year depending on the age stratification of the original cows. In some cases replacements may be added every 2-5 years providing an opportunity to purchase heifers during periods of lower prices or more abundant supplies. Heifers could also be developed by a professional heifer development center or purchased bred to easy calving bulls.

Rotate Bull Every Four Years

This system requires the use of a single breed of sire for four years then a rotation to a second breed for four years, then back to the original breed of sire for four years, and so on. This system is depicted in Figure 5. Breed fractions of cows and level of maternal heterosis will vary depending on sequence of production. Estimates of the range of retained heterosis are dependant on the number and breed make-up of females retained in the herd. Several assumptions are made when estimating the expected performance improvement and retained heterosis. In a two-breed rotation of bulls the minimum retained heterosis is 50% and assumes that over time the average breed fractions represented in the herd are equal (50% breed A, 50% breed B) with random selection of replacement females. However, depending on culling rate and replacement selection, this retained heterosis maybe as high as 67%, similar to a true two-breed rotation. The expected improvement in weaning weight per cow exposed is a function of retained heterosis will range from 12-16% for at two breed system with bulls rotated every four years.

Likewise, in a three-breed rotation of bulls every four years, the minimum expectation of retained heterosis is 67% assuming the animals stabilize at a composition of 1/3 of each breed. Again, depending on culling rate and replacement selection the retained heterosis may be as high as 83% which is similar to a true 3 breed rotational system. The expected improvement in weaning weight

Figure 5. Rotate bull every four years.

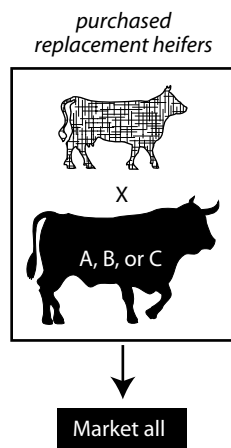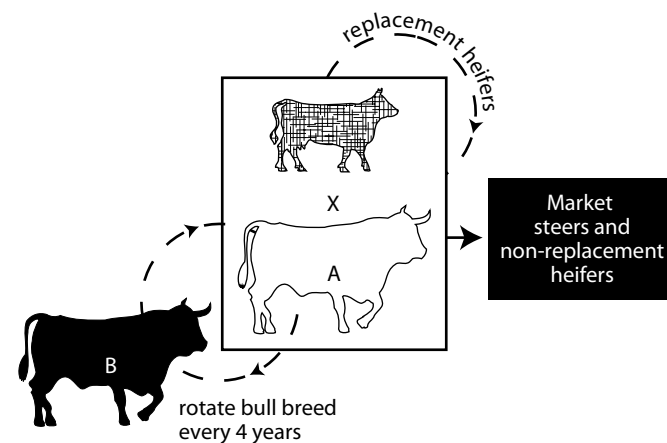*replacement heifers*

X

A

B

rotate bull breed every 4 years

Market steers and non-replacement heifers

per cow exposed is a function of retained heterosis will range from 16-20% for at three breed system with bulls rotated every four years.

Requirements—The rotate bulls every four years system is particularly useful for small herds or herds with minimal management or labor inputs as only one breeding pasture is required and cows are not required to be identified by breed of sire. Replacement females are kept in this system but should only be kept from the first two calf crops of a bull breed cycle. Some sire-daughter matings will occur in this system during years three and four of a sire breed cycle. Sire-daughter matings increase inbreeding and over represents the breed of sire in the resulting calves. Both decrease heterosis and these calves desirability as replacement females. Bulls may be replaced after two breeding seasons to minimize sire-daughter matings. This strategy, however, make less efficient use of capital investments in bulls given their useful life is longer than two years. This decreased efficiency has to be balanced against the limitation of retaining replacements during two of every four years in a sire-breed cycle. This limitation may be of little consequence in small herds, but large fluctuations in cow inventory may result if this system is utilized in large operations.

Considerations—This system does not maximize heterosis retention, but it is very simple to implement and manage. The first breed of sire should be used for five calf crops if you start with straightbred cows to optimize retention of heterosis.

Composite Breeds

The use of composite populations in beef cattle has seen a surge in popularity recently. Aside from the advantages of heterosis retention and breed complementarity, composite population breeding systems are as easy to manage as straightbreds once the composite is formed. The simplicity of use has made composites popular among very large, extensively managed operations and small herds alike. When two-, three- or four-breed composite are formed they retain 50%, 67%, and 75% of maximum calf and dam heterosis and improve productivity of the cowherd by 12%, 15%, and 17%, respectively. Thus, these systems typically offer a balance of convenience, breed complementarity and heterosis retention. A composite breeding system is presented in Figure 6.

Requirements—This requires either a very large herd (500 to 1000 cows) to form your own composite or a source of composite bulls or semen. In closed populations inbreeding must be avoided as it will decrease heterosis. To help minimize inbreeding in the closed herd where cows are randomly mated to sires, the foundation animals should represent 15-20 sire groups per breed and 25 or more sires should be used to produce each subsequent generation (Ritchie et al., 1999). Similar recommendations would be made to seedstock breeders wishing to develop and merchandize bulls of a composite breed. In small herds, inbreeding may be avoided through purchase of outside bulls that are unrelated to your herd.

Figure 6. Composite breeding system.

Pasture A

Market steers and non-replacement heifers

replacement heifers
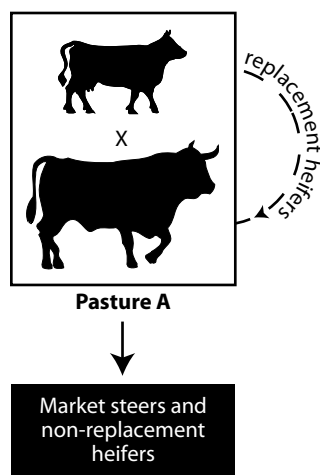
Due to the ease of use once the composite is established, composite systems can be applied to herds of any size or number of breeding pastures.

Considerations—Clearly, availability of outside seedstock is the limiting factor for most producers. However, with emerging popularity of structured, stabilized half blood systems (inter se mated F_1 animals) such as SimAngus, Balancer and LimFlex, availability is much easier for these British x Continental crossbreds. Other composites have been formed and include: MARC I, MARC II, MARC III, Rangemaker, Stabilizer, and others.

Rotating Unrelated F_1 Bulls

The use of F_1, or first cross, bulls resulting from the cross of animals from two breeds is becoming more wide spread. F_1 bulls provide a simple alternative to the formulation of composite breeds. Additionally, the F_1 systems may provide more opportunity to incorporate superior genetics as germplasm can be sampled from within each of the large populations of purebreds rather than a smaller composite population. The use of unrelated F_1 bulls, each containing the same two breeds, in a mating system with cows of the same breeds and fractions will result in a retention of 50% of maximum calf and dam heterosis and an improvement in weaning weight per cow exposed of 12%. A system that uses F_1 bulls that have a breed in common with the cow herd (A*B x A*C) results in heterosis retention of 67% and an expected increase in productivity of 16%. While the use of F_1 bulls that don't have breeds in common with cows made up of equal portion of two different breeds (A*B x C*D) retains 83% of maximum heterosis and achieves productivity gains of 19%. This last system is nearly equivalent to a three breed rotational system in terms of heterosis retention and productivity improvement, but much easier to implement and manage. These three systems are depicted in Figure 7.
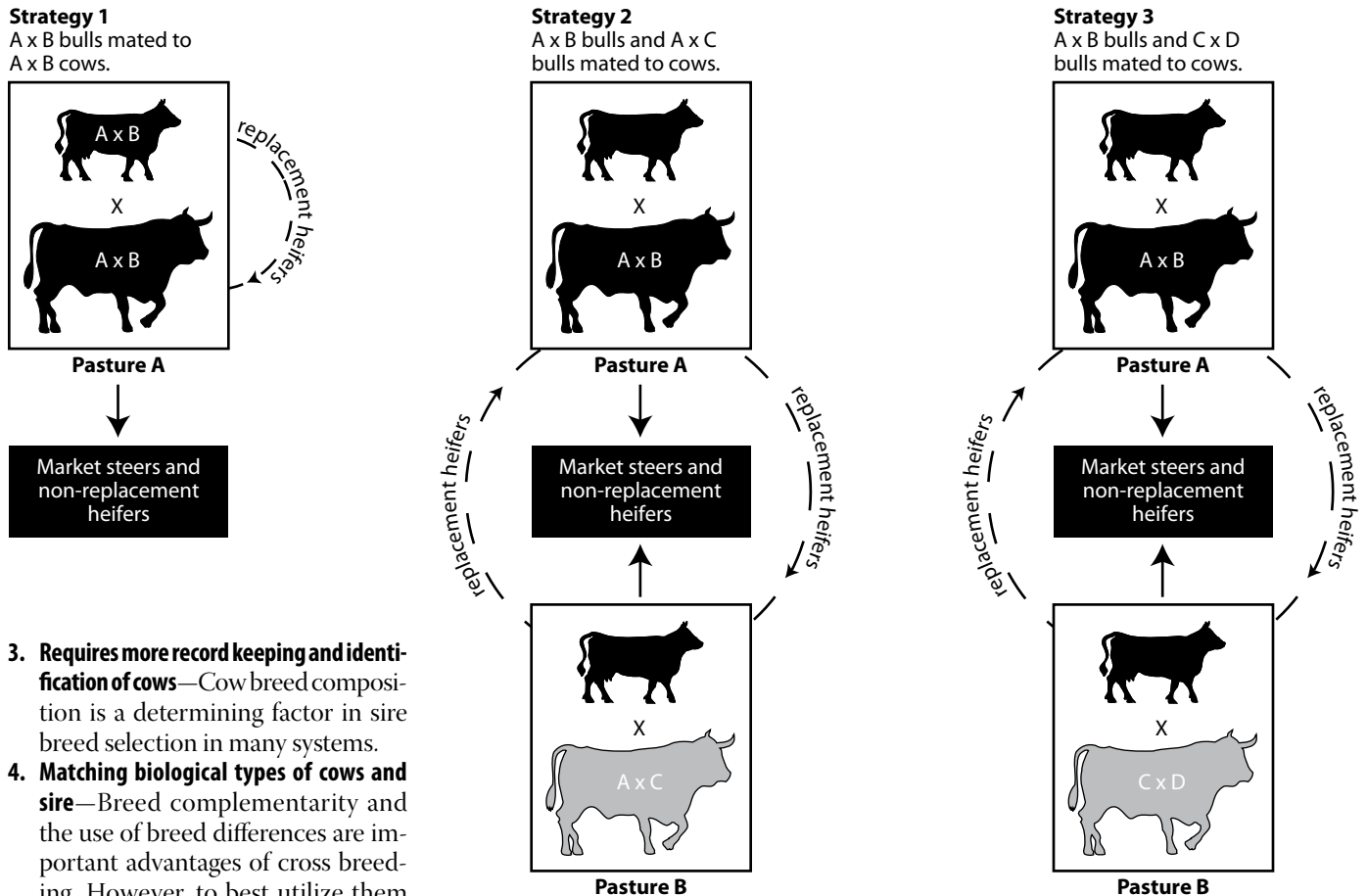
Requirements—The use of F_1 bulls requires a seedstock source from which to purchase. The bulls will need to be of specific breed combinations to fit your program. These programs fit a wide range of herd sizes. The use of F_1 bulls on cows of similar genetic make-up is particularly useful for small herds as they can leverage the power of heterosis and breed complementarity using a system that is as simple as straight breeding. Additionally, operators of this system can keep their own replacement females.

Considerations—The inclusion of a third or fourth breed in the systems takes more expertise and management. To prevent wide swings in progeny phenotype, breeds B and C should be similar in biological type, while breeds A and D should be similar in biological type.

Crossbreeding Challenges

Although crossbreeding has many advantages, there are some challenges to be aware of during your planning and implementation as outlined by Ritchie et al., 1999.

1. **More difficult in small herds**—Crossbreeding can be more difficult in small herds. Herd size over 50 cows provides the opportunity to implement a wider variety of systems. Small herds can still benefit through utilization of terminal sire, composite or F_1 systems.
2. **Requires more breeding pastures and breeds of bulls**—Purchasing replacements and maximum use of A.I. can reduce the number of pastures and bulls. However, most operations using a crossbreeding system will expand the number of breeding pastures and breeds of bulls.

Figure 7. Rotating F$_1$ bulls.

Strategy 1
A x B bulls mated to
A x B cows.

Strategy 2
A x B bulls and A x C
bulls mated to cows.

Strategy 3
A x B bulls and C x D
bulls mated to cows.

3. **Requires more record keeping and identi-fication of cows**—Cow breed composition is a determining factor in sire breed selection in many systems.
4. **Matching biological types of cows and sire**—Breed complementarity and the use of breed differences are important advantages of cross breeding. However, to best utilize them care must be given in the selection of breeds and individuals that match cows to their production environment and sires to market place. Divergent selection of biological type can result in wide swings in progeny phenotype in some rotational systems. These swings may require additional management input, feed resources, and labor to manage as cows or at marketing points.
5. **System continuity**—Replacement female selection and development is a challenge for many herds using crossbreeding systems. Selection of sires and breeds for appropriate traits (maternal or paternal traits) is dependent of ultimate use of progeny. Keeping focus on the system and providing labor and management at appropriate times can be challenging. Discipline and commitment are required to keep the system running smoothly.

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Breed and Composite Selection

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With more than sixty (60) breeds of beef cattle present in the United States, the question of "Which breed should I choose?" is a difficult question to answer. The top ten breeds in fiscal year 2007 reported registrations accounting for 93% of the pedigreed beef cattle in the U.S. These top ten breeds and their crosses represent the majority of the genetics utilized in commercial beef production, providing a hint at the breeds that possess the most valuable combinations of traits as recognized by beef producers. The breed, composite or combination of breeds employed in a breeding program can have a large impact on the profitability of a commercial beef operation and the value of animals it produces as they move through the beef complex. The breed or biological type of an animal influences economically important production traits including: growth rate, mature size, reproductive efficiency, milk yield, and carcass merit.

Large differences exist today in the relative performance of various breeds for most economically important traits. These breed differences represent a valuable genetic resource for commercial producers to use in structured crossbreeding systems to achieve an optimal combination of traits matching the cowherd to their production environment and to use sire selection to produce market-targeted progeny. As such, the selection of the 'right' breed(s) to use in a breeding program is an important decision for commercial beef producers. The determination of the 'right' breed(s) to use is highly dependent on a number of characteristics of a farm or ranch such that not every operation should use the same breed or combination of breeds.

Breed and Composite Defined

A common definition of a breed is a genetic strain or type of domestic livestock that has consistent and inherited characteristics such as coat color or pattern, presence or absence of horns, or other qualitative criteria. However, one can also consider performance traits as common characteristics shared by individuals of a breed. In simple terms, these common characteristics are the performance traits that are often associated with a breed as its reputation has grown over time and represent the core traits for which a breed of livestock has been selected for over time. Breeds differ in the level of performance for various traits as a result of different selection goals of their breeders.

A composite is something that is made up of distinct components. In reference to beef cattle, the term composite generally means that the animal is composed of two or more breeds. A composite breed then is a group of animals of similar breed composition. Composites can be thought of as new breeds and managed as such.

Beef Breed and Composite Characterization

A great deal of research has been conducted over the last 30 years at various federal and state experiment stations to characterize beef breeds in the U.S. These studies have been undertaken to examine the genetic merits of various breeds in a wide range of production environments and management systems. During this time, researchers at the U.S. Meat Animal Research Center

(MARC) have conducted the most comprehensive studies of sire breed genetic merit via their long term Germplasm Evaluation (GPE) project. This project evaluated over 30 sire breeds in a common environment and management system. The data summarized by the MARC scientists consisted of records on more than 20,000 animals born between 1978 and 1991, with a re-sampling of the most popular sire breeds in 1999-2000. The various sire breeds evaluated were mated to Angus, Hereford and crossbred cows. Thus, the data reported were for crossbred progeny. During the study, Angus-Hereford crossbred calves were produced in the study as a control for each cycle of the GPE project.

One of the major outcomes of the GPE project was the characterization of sire breeds for a wide variety of economically important

Table 1. Breeds grouped into biological type by four criteria.[a,b]

Breed Group	Growth Rate and Mature Size	Percent Retail Product	Age at Puberty	Milk Production
Jersey	X	X	X	XXXXX
Longhorn	X	XXX	XXX	XX
Angus	XXX	XX	XX	XXX
Hereford	XXX	XX	XXX	XX
Red Poll	XX	XX	XX	XXX
Devon	XX	XX	XXX	XX
Shorthorn	XXX	XX	XXX	XXX
Galloway	XX	XXX	XXX	XX
South Devon	XXX	XXX	XX	XXX
Tarentaise	XXX	XXX	XX	XXX
Pinzgauer	XXX	XXX	XX	XXX
Brangus	XXX	XX	XXXX	XX
Santa Gertrudis	XXX	XX	XXXX	XX
Sahiwal	XX	XXX	XXXXX	XXX
Brahman	XXX	XXX	XXXXX	XXX
Nellore	XXX	XXX	XXXXX	XXX
Braunvieh	XXXX	XXXX	XX	XXXX
Gelbvieh	XXXX	XXXX	XX	XXXX
Holstein	XXXX	XXXX	XX	XXXXX
Simmental	XXXXX	XXXX	XXX	XXXX
Maine Anjou	XXXXX	XXXX	XXX	XXX
Salers	XXXXX	XXXX	XXX	XXX
Piedmontese	XXX	XXXXX	XX	XX
Limousin	XXX	XXXX	XXXX	X
Charolais	XXXXX	XXXX	XXXX	X
Chianina	XXXXX	XXXX	XXXX	X

[a] Adapted from Cundiff et al. 1993.
[b] Increasing number of X's indicate relatively higher levels of trait.

traits. Because all of the animals were in a common management system and production environment, the average differences observed in performance were due to genetic differences. Following the analysis of progeny data, the breeds can be divided into groups based on their biological type for four criteria: 1) Growth rate and mature size 2) Lean to fat ratio 3) Age at puberty, and, 4) Milk production. The breeds evaluated at MARC are grouped by biological type in Table 1. British breeds such as Hereford, Angus, Red Angus and Shorthorn are moderate in growth and mature size, relatively higher in carcass fat composition, reach puberty at relatively younger ages and are moderate in milk production. Continental European breeds, with a heritage that includes milk production, including Simmental, Maine-Anjou, and Gelbvieh tend to have high growth rates, larger mature sizes, moderate ages at puberty and relatively high levels of milk production. Another group of Continental European breeds, with a heritage of meat and draft purposes, including Charolais, Chianina and Limousin tend to have high growth rate, large mature size, older ages at puberty, very lean carcasses and low milk production.

Another way to compare the relative genetic merit of breeds for various performance traits is through conversion of their EPD to a common base. This can be accomplished using the across breed EPD adjustments published each year in the proceedings of the Beef Improvement Federation's annual meeting. These adjustments are generated by researchers at MARC. Table 2 lists the across breed adjustment factors that are added to the EPD of an animal of a specified breed to put that animal's EPD on an Angus base (Kuehn and Thallman, 2009). Table 3 presents the average across breed EPD of animals born in 2007 as reported from 2009 genetic evaluations from the most widely used breeds on a common genetic base (Angus). Differences in across breed EPD averages represent genetic differences for each trait. Table 3 provides a more contemporary look at the differences in breed genetic potential for various traits and accounting for genetic trends occurring in each breed due to selection. Due to selection pressure placed on growth and maternal traits over time, many breeds have made considerable gains in those traits. In some cases, the large gains in performance have resulted in subtle changes in the overall biological type of a breed.

Table 2. 2009 adjustment factors to add to EPD of fifteen different breeds to estimate across breed EPD[a].

Breed	Birth Wt.	Weaning Wt.	Yearling Wt.	Maternal Milk	Marbling Score	Ribeye Area	Fat Thickness
Angus	0.0	0.0	0.0	0.0	0.00	0.00	0.00
Beefmaster	7.7	44.2	44.0	2.6			
Brahman	11.2	36.3	2.2	29.0			
Brangus	4.7	21.9	19.9	2.4			
Braunvieh	7.5	21.4	12.8	30.6	-0.26	0.78	-0.149
Charolais	9.7	38.2	51.9	5.6	-0.50	0.63	-0.244
Chiangus	4.1	-19.6					
Gelbvieh	4.5	1.7	-12.6	9.9			
Hereford	2.9	-2.8	-16.1	-17.5	-0.36	-0.24	-0.057
Limousin	4.2	-3.4	-28.6	-14.2	-0.80	0.93	
Maine-Anjou	5.5	-10.7	-22.8	-0.8	-0.92	1.07	-0.197
Red Angus	2.9	-5.4	-4.4	-3.0	-0.01	-0.21	-0.045
Salers	3.4	22.7	52.3	13.1	-0.11	0.78	-0.224
Santa Gertrudis	8.1	17.1					
Shorthorn	6.1	19.9	52.8	23.1	0.06	0.12	-0.133
Simmental	5.5	25	22.4	13.7	-0.60	0.92	-0.193
South Devon	4.5	6.9	-1.4	-6.5	-0.32	0.39	-0.131
Tarentaise	2.5	29.7	17.9	22.2			

[a] Kuehn and Thallman, 2009.

Table 3. Average Across-Breed EPD for animals born in 2007 by breed from 2009 genetic evaluations and 2009 USDA-MARC Across-Breed EPD adjustment factors[a].

Breed	Birth Wt.	Weaning Wt.	Yearling Wt.	Maternal Milk	Marbling Score	Ribeye Area	Fat Thickness
Angus	2.2	43.5	80.0	20.5	0.31	0.15	0.01
Beefmaster	8.2	51.5	56.5	4.6			
Brahman	13.0	49.9	24.4	34.8			
Brangus	5.3	43.8	60.1	9.7			
Braunvieh	7.3	22.3	14.3	30.9	-0.25	0.79	-0.15
Charolais	10.3	61.5	93.1	12.1	-0.47	0.80	-0.24
Chiangus	5.3	24.6					
Gelbvieh	5.8	42.7	61.4	27.9			
Hereford	6.4	38.2	51.9	-1.5	-0.33	-0.07	-0.06
Limousin	5.9	39.2	50.5	7.1	-0.80	1.33	
Maine-Anjou	7.4	29.4	56.3	19.2	-0.71	1.23	-0.20
Red Angus	3.2	25.8	50.5	13.1	0.05	-0.16	-0.05
Salers	4.3	40.5	81.9	21.5	-0.11	0.80	-0.22
Santa Gertrudis	8.6	21.1					
Shorthorn	8.3	34.2	76.2	25.6	0.06	0.10	-0.13
Simmental	6.8	57.4	79.9	17.9	-0.47	1.00	-0.18
South Devon	7.1	46.6	74.1	14.9	-0.06	0.49	-0.12
Tarentaise	4.0	33.7	28.9	23.2			

[a] Adapted from Kuehn and Thallman, 2009 and Kuehn et al., 2009

Use of Breeds and Composites for Genetic Improvement

Inclusion or exclusion of germplasm from a breed (or composite) is a valuable selection tool for making rapid directional changes in genetic merit for a wide range of traits. Changes in progeny phenotype that occur when breeds are substituted in a breeding program come from two genetic sources.

The first source of genetic impact from a substitution of a breed comes through changes in the additive genetic effects or breeding values that subsequent progeny inherit from their sire and dam. Additive genetic merit is the portion of total genetic merit that is transmissible from parent to offspring and on which traditional selection decisions are made. In other words, additive genetic effects are heritable. EPD are estimates of one-half of the additive genetic merit. The difference in average performance for a trait observed between two breeds is due primarily to differences in additive genetic merit.

The second source of genetic change is due to non-additive genetic effects. Non-additive effects include both dominance and epistatic effects. Dominance effects arise from the interactions of paired genes at each locus. Epistatic effects are the interaction of genes across loci. The sum of these two interactions result in heterosis observed in crossbred animals. Since each parent only contributes one gene to an offspring and dominance effects depend on the interaction of a pair of genes, a parent cannot transmit dominance effects to its progeny within a breed. However, the selection of which breeds and how much of each breed to incorporate into progeny has a large impact on dominance (or heterosis) effects which affect phenotype. Because epistatic effects arise from the interaction of genes at different loci, independent segregation of chromosomes in the formation of gametes causes pairings of genes not to always stay together from one generation to the next. Like dominance effects, epistatic effects are not impacted by mate selection but by the frequency of different alleles and their dominance effects across breeds.

Both additive and non-additive genetic effects can have a significant impact on a particular phenotype; therefore, it is important that both are considered during breed selection. Due to their different modes of inheritance, different tactics must be employed to capture the benefits of each.

Additive genetic merit may be selected for in two distinct ways. First, by the selection of individuals *within* a breed that have superior genetic merit for the trait under selection. Typically this is achieved through the use of EPD to identify selection candidates, although it can also be done through selection for specific alleles using DNA markers. The rate of improvement in phenotypes due to selection within breed is limited by the heritability of the trait. Heritability describes the proportion of phenotypic variation that is controlled by additive genetic variation. So, for traits with moderate to high heritability, considerable progress in progeny phenotype may be achieved through selection of superior animals within the breed as parent stock. The second approach to change additive genetic merit is through the selection of animals from a different breed(s) that excels in the trait under selection. *Across* breed selection can provide rapid change in progeny phenotype given that large differences exist between breeds in a number of economically relevant traits. Selection of superior parent stock from a different breed that excels in a trait is often more effective than selection within a breed (Gregory et al., 1999) as the breed differences have a heritability of nearly 100%.

The use of breed differences to achieve the best overall results across multiple traits may be achieved through the implementation of the concept of breed complementarity. Breeds are complementary to each other when they excel in different traits and their crossbred progeny have desirable levels of performance in a larger number of traits than either of the parent breeds alone. Making breed and mating selections that utilize breed complementarity provide an effective way to aggregate the core competencies of two or more breeds in the progeny. Moreover, use of breed complementarity can be a powerful strategy to genetically match cows to their production environment and progeny to the market place. For example, a crossbreeding system that mates Charolais bulls to Hereford-Angus crossbreed cows utilizes breed complementarity. The Charolais bull contributes growth and carcass yield to progeny genetics while the Hereford-Angus crossbred cows have many desirable maternal attributes and contribute genetics for carcass quality. When considering crossbreeding from the standpoint of producing replacement females, one could select breeds that have complementary maternal traits such that females are most ideally matched to their production environment. Matings to produce calves for market should focus on complementing traits of the cows and fine tuning calf performance (growth and carcass traits) to the market place.

There is an abundance of research that describes the core competencies (biological type) of many of today's commonly used beef breeds as described earlier and listed in Table 1. Traits are typically combined into groupings such as maternal/reproduction, growth and carcass. When selecting animals for a crossbreeding system, breed should be the primary consideration. Breeds selected for inclusion in a mating program will be dependant on a number of factors including current cow herd breed composition, forage and production environment, replacement female development system, and calf marketing endpoint. All of these factors help determine the relative importance of traits for each production phase.

One of the challenges of breed selection is the interaction of the animal's genotype with its production environment. Table 4 describes common production environments by level of feed availability and environmental stress and lists optimal levels of a variety of performance traits (Bullock et al., 2002). Here, feed availability refers to the regular availability of grazed or harvested forage and its quantity and quality. Environmental stress includes parasites, disease, heat and humidity. Ranges for mature cow size are low (800 to 1,000 lb.), medium (1000 to 1,200 lb.), and high (1,200 to 1,400 lb.) Clearly, breed choices should be influenced by the production environment in which they are expected to perform.

Crossing of breeds or lines is the primary method to exploit beneficial non-additive effects called heterosis. Heterosis refers to the superiority of the crossbred animal relative to the average of its straightbred parents and heterosis results from an increase in heterozygosity of a crossbred animal's genetic makeup. Heterozygosity refers to a state where an animal has two different forms of a gene. It is believed that heterosis is primarily the result of gene dominance and the recovery from accumulated inbreeding depression of pure breeds. Heterosis is, therefore, dependant on crossbred animals having a greater percentage of heterozygous animals than is present in straightbred animals. The level of heterozygosity an animal has depends on the random inheritance of copies of genes from its parents. In general, animals that are crosses of unrelated breeds, such as Angus and Brahman, exhibit higher levels of heterosis due to more heterozygosity, than do crosses of more genetically similar breeds such as a cross of Angus and Hereford.

Generally, heterosis generates the largest improvement in lowly heritable traits. Moderate improvements due to heterosis are seen in moderately heritable traits. Little or no heterosis is observed in highly heritable traits. Traits such as reproduction and longevity have low heritability. These traits respond very slowly to

selection since a large portion of the variation observed in them is due to environmental effects and non-additive genetic effects, and a small percentage is due to additive genetic differences. But, heterosis generated through crossbreeding can significantly improve an animal's performance for lowly heritable traits, thus the importance of considering both additive and non-additive genetics when designing mating programs. Crossbreeding has been shown to be an efficient method to improve reproductive efficiency and pre-weaning productivity in beef cattle.

Improvements in cow-calf production due to heterosis are attributable to having both a crossbred cow (called maternal or dam heterosis) and a crossbred calf (called individual or calf heterosis). Differing levels of heterosis are generated when various breeds are crossed. Similar levels of heterosis are observed when members of the *Bos taurus* species, including the British (e.g. Angus, Hereford, Shorthorn) and Continental European breeds (e.g. Charolais, Gelbvieh, Limousin, Maine-Anjou, Simmental), are crossed. Much more heterosis is observed when *Bos indicus*, or Zebu, breeds like Brahman, Nelore and Gir, are crossed with *Bos taurus* breeds. The increase in heterosis observed in British by *Bos indicus* crosses for a trait is usually 2-3 times as large as the heterosis for the same trait observed in *Bos taurus* crossbreds (Koger, 1980). The large increase is especially true with heterosis observed in the crossbred cow. The increase in heterosis is sensible as the there are more genetic differences between species than within a species. Heterosis effects reported in the following tables will be divided and noted into those observed in *Bos taurus* crosses or *Bos taurus* by *Bos indicus* crosses. Table 5 details the individual (crossbred calf) heterosis and Table 6 describes the maternal (crossbred cow) heterosis observed for various important production traits in *Bos taurus* crossbreds. These heterosis estimates are adapted from a report by Cundiff and Gregory, 1999, and summarize crossbreeding experiments conducted in the Southeastern and Midwest areas of the US. Table 7 describes the expected individual heterosis of *Bos taurus* by *Bos indicus* crossbred calves, while Table 8 details the estimated maternal (dam) heterotic effects observed in *Bos taurus* by *Bos indicus* crossbred cows. *Bos taurus* by *Bos indicus* heterosis estimates were derived from breeding experiments conducted in the southern US.

The heterosis adjustments utilized by multi-breed genetic evaluation systems are another example of estimates for individual (due to a calf) and maternal (due to a crossbred dam) heterosis. These heterosis adjustments are present in Table 9 and illustrate the differences in expected heterosis for various breed-group crosses. In general the Zebu (*Bos indicus*) crosses have higher levels of heterosis than the British-British, British-Continental, or Continental-Continental crosses.

The production of crossbred calves yields advantages in both heterosis and the blending of desirable traits from two or more breeds. However, the largest economic benefit of crossbreeding to commercial producers comes from the crossbred cow. Dam heterosis improves both the environment a cow provides for her calf as well as improves her longevity and durability. The improvement of the maternal environment a cow provides for her calf is manifested in improvements in calf survivability to weaning and increased weaning weight. Crossbred cows exhibit improvements in calving rate of nearly 4% and an increase in longevity of more that one year due to heterotic effects. Heterosis results in increases in lifetime productivity of approximately one calf and 600 pounds of calf weaning weight over the lifetime of the cow.

Table 4. Matching genetic potential for different traits to production environments.[1]

Production Environment		Traits					
Feed Availability	Stress[2]	Milk Production	Mature Size	Ability to Store Energy[3]	Resistance to Stress[4]	Calving Ease	Lean Yield
High	Low	M to H	M to H	L to M	M	M to H	H
	High	M	L to H	L to H	H	H	M to H
Medium	Low	M to H	M	M to H	M	M to H	M to H
	High	L to M	M	M to H	H	H	H
Low	Low	L to M	L to M	H	M	M to H	M
	High	L to M	L to M	H	H	H	L to M
Breed role in terminal crossbreeding systems							
Maternal		M to H	L to H	M to H	M to H	H	L to M
Paternal		L to M	H	L	M to H	M	H

L = Low; M = Medium; H = High.
[1] Adapted from Bullock et al., 2002.
[2] Heat, cold, parasites, disease, mud, altitude, etc.
[3] Ability to store fat and regulate energy requirements with changing (seasonal) availability of feed.
[4] Physiological tolerance to heat, cold, internal and external parasites, disease, mud, and other factors.

Table 5. Units and percentage of heterosis by trait for *Bos taurus* crossbred calves.

	Heterosis	
Trait	Units	Percentage (%)
Calving Rate, %	3.2	4.4
Survival to Weaning, %	1.4	1.9
Birth Weight, lb	1.7	2.4
Weaning Weight, lb	16.3	3.9
Yearling Weight, lb	29.1	3.8
Average Daily Gain, lb/d	0.08	2.6

Table 6. Units and percentage of heterosis by trait for *Bos taurus* crossbred dams.

	Heterosis	
Trait	Units	Percentage (%)
Calving Rate, %	3.5	3.7
Survival to Weaning, %	0.8	1.5
Birth Weight, lb	1.6	1.8
Weaning Weight, lb	18.0	3.9
Longevity, years	1.36	16.2
Lifetime Productivity		
Number of Calves	.97	17.0
Cumulative Weaning Weight, lb	600	25.3

Crossbreeding can have positive effects on a ranch's bottom line by not only increasing the quality and gross pay weight of calves produced but also by increasing the durability and productivity of the cow factory.

The effects of dam heterosis on the economic measures of cow-calf production have been shown to be very positive. The added value of maternal heterosis ranges from approximately $50/cow/year to nearly $100/cow/year depending on the amount of maternal heterosis retained in the cowherd (Ritchie, 1998) Heterosis expressed by dams accounted for an increase in net profit per cow of nearly $75/cow/year (Davis et al., 1994) Their results suggested that the benefits of dam heterosis on profit were primarily the reduced cost per cow exposed. Crossbred cows had higher reproductive rates, longer productive lives, and required fewer replacements than straightbred cows in their study. All of these factors contribute to reduced cost per cow exposed. Further, they found increased outputs, including growth and milk yield, were offset by increased costs.

When it comes to crossing breeds with the goal of producing high levels of maternal or individual heterosis, not all breeds are equal. Heterosis depends on an animal having two different alleles or alternate forms of a gene at a locus. The likelihood of having different copies of genes at a locus is greater in breeds that are less related than when the breeds crossed are closely related. For instance Angus and Hereford, both British breeds, are more similar than Angus and Simmental (a Continental European breed) which are more similar than Angus (a *Bos taurus* breed) and Brahman (a *Bos indicus* breed). Since heterosis offers considerable advantages to commercial producers in terms of reproductive efficiency, productivity and economic returns, care should be given when selecting breeds for inclusion in a crossbreeding system. Just as breeds differ in the amount of heterosis generated when crossed, crossbreeding systems achieve differing levels of heterosis depending on the number of breeds and their fractions represented in each animal. A more complete discussion on crossbreeding and crossbreeding systems appears in a separate chapter in this manual.

When comparing two breeds for inclusion in a crossbreeding system that offer similar strengths, select the breed that offers the most heterosis when mated to animals of other breed(s) in your system. Table 10 provides estimates of the percentage increase in pairs of alleles at a locus that are different (heterozygosity) when various purebreds are crossed to form F1 progeny. These estimates were developed using the input data and procedures suggested by Roughsedge et al., 2001. It is easy to see that not all breeds offer the same increase in heterozygosity, and therefore, heterosis when crossed. Expected percent heterosis for cow fertility, birth weight,

Table 7. Units and percentage of heterosis by trait for *Bos Taurus* by *Bos indicus* crossbred calves.[1]

Trait	Heterosis Units
Calving Rate, %[1]	4.3
Calving Assistance, %[1]	4.9
Calf Survival, %[1]	-1.4
Weaning Rate, %[1]	1.8
Birth Weight, lb[1]	11.4
Weaning Weight, lb[1]	78.5

[1] Adapted from Franke et al. 2005; numeric average of Angus-Brahman, Brahman-Charolais, and Brahman-Hereford heterosis estimates.

Table 8. Units and percentage of heterosis by trait for *Bos Taurus* by *Bos indicus* crossbred dams.[1,2]

Trait	Heterosis Units	Heterosis Percentage (%)
Calving Rate, %[1]	15.4	--
Calving Assistance Rate, %[1]	-6.6	--
Calf Survival, %[1]	8.2	--
Weaning Rate, %[1]	20.8	--
Birth Weight, lb[1]	-2.4	--
Weaning Weight, lb[1]	3.2	--
Weaning Wt. per Cow Exposed, lb[2]	91.7	31.6

[1] Adapted from Franke et al. 2005; numeric average of Angus-Brahman, Brahman-Charolais, and Brahman-Hereford heterosis estimates.
[2] Adapted from Franke et al. 2001.

Table 9. Individual (calf) and maternal (dam) heterosis adjustments for British, Continental European, and Zebu breed groups for birth weight, weaning weight and post weaning gain.

Breed Combinations	Birth Weight (lb) Calf Heterosis	Birth Weight (lb) Dam Heterosis	Weaning Weight (lb) Calf Heterosis	Weaning Weight (lb) Dam Heterosis	Postweaning Gain (lb) Calf Heterosis
British x British	1.9	1.0	21.3	18.8	9.4
British x Continental	1.9	1.0	21.3	18.8	9.4
British x Zebu	7.5	2.1	48.0	53.2	28.2
Continental x Continental	1.9	1.0	21.3	18.8	9.4
Continental x Zebu	7.5	2.1	48.0	53.2	28.2

(Wade Shafer, Am. Simmental Association, personal communication)

survival to weaning and weaning weight was computed according to the procedure outlined by Roughsedge et al., 2001. Table 11 provides the expected heterosis percentage for cow fertility observed in F1 females. Similarly, Tables 12, 13 and 14 provide the expected heterosis percentage for birth weight, survival to weaning and weaning weight, respectively. Note that this study provided no estimates of heterosis for *Bos indicus* breeds such as Brahman, Nelore or Gir as only *Bos taurus* breeds common in the United Kingdom and continental Europe were sampled for biologic material.

Summary

Selection of appropriate breeds for a particular production system can be a challenging task. Consideration during the selection process should be given to a number of criteria (Greiner, 2002) including:
Climate (frost-free days, growing season, precipitation).
Quantity, quality and cost of feedstuffs available.
Production system (availability of labor and equipment).
Market end points and demands.
Breed complementarity.
Cost and availability of seedstock.

The selection of breeds and the genetics they contribute to the cowherd can have a large impact on profitability through the aggregate effects on each of the above criteria. Clearly, breeds need to be selected to fit a specific production system, whether that is selling replacement females, weaned feeder calves, or carcass

Table 10. Increase in heterozygosity of F1 animals when respective breeds are crossed.[a]

Breed	A	C	Ch	G	H	PH	L	MA	Sa	Sh	S	SD
Angus (A)	0.000	0.110	0.193	0.116	0.136	0.110	0.103	0.061	0.151	0.057	0.071	0.088
Charolais (C)	0.110	0.000	0.134	0.093	0.148	0.141	0.050	0.096	0.048	0.096	0.059	0.148
Chianina (Ch)	0.193	0.134	0.000	0.128	0.262	0.268	0.139	0.165	0.160	0.183	0.162	0.238
Gelbvieh (G)	0.116	0.093	0.128	0.000	0.183	0.189	0.110	0.151	0.114	0.137	0.063	0.149
Hereford (H)	0.136	0.148	0.262	0.183	0.000	0.011	0.172	0.163	0.195	0.110	0.151	0.183
Polled Hereford (PH)	0.110	0.141	0.268	0.189	0.011	0.000	0.166	0.139	0.198	0.089	0.148	0.172
Limousin (L)	0.103	0.050	0.139	0.000	0.172	0.166	0.000	0.081	0.057	0.094	0.071	0.112
Maine-Anjou (MA)	0.061	0.096	0.165	0.151	0.163	0.139	0.081	0.000	0.151	0.057	0.104	0.116
Salers (Sa)	0.151	0.048	0.160	0.114	0.195	0.198	0.057	0.151	0.000	0.175	0.069	0.211
Shorthorn (Sh)	0.057	0.096	0.183	0.137	0.110	0.089	0.094	0.057	0.175	0.000	0.115	0.093
Simmental (S)	0.071	0.059	0.162	0.063	0.151	0.148	0.071	0.104	0.069	0.115	0.000	0.139
South Devon (SD)	0.088	0.148	0.238	0.149	0.183	0.172	0.112	0.116	0.211	0.093	0.139	0.000

[a] Adapted from Roughsedge et al., 2001.

Table 11. Cow fertility expected heterosis (%) for F1's (first cross).

Breed	A	C	Ch	G	H	PH	L	MA	Sa	Sh	S	SD
Angus (A)	0.00	7.32	12.87	7.76	9.05	7.32	6.87	4.05	10.04	3.77	4.77	5.85
Charolais (C)	7.32	0.00	8.97	6.21	9.89	9.43	3.35	6.43	3.21	6.43	3.91	9.89
Chianina (Ch)	12.87	8.97	0.00	8.51	17.50	17.85	9.27	10.97	10.66	12.23	10.82	15.90
Gelbvieh (G)	7.76	6.21	8.51	0.00	12.23	12.63	7.32	10.04	7.61	9.12	4.20	9.96
Hereford (H)	9.05	9.89	17.50	12.23	0.00	0.74	11.44	10.89	13.03	7.32	10.04	12.23
Polled Hereford (PH)	7.32	9.43	17.85	12.63	0.74	0.00	11.05	9.27	13.19	5.92	9.89	11.44
Limousin (L)	6.87	3.35	9.27	0.00	11.44	11.05	0.00	5.41	3.77	6.29	4.77	7.47
Maine-Anjou (MA)	4.05	6.43	10.97	10.04	10.89	9.27	5.41	0.00	10.04	3.77	6.95	7.76
Salers (Sa)	10.04	3.21	10.66	7.61	13.03	13.19	3.77	10.04	0.00	11.68	4.62	14.08
Shorthorn (Sh)	3.77	6.43	12.23	9.12	7.32	5.92	6.29	3.77	11.68	0.00	7.69	6.21
Simmental (S)	4.77	3.91	10.82	4.20	10.04	9.89	4.77	6.95	4.62	7.69	0.00	9.27
South Devon (SD)	5.85	9.89	15.90	9.96	12.23	11.44	7.47	7.76	14.08	6.21	9.27	0.00

Table 12. Birth weight expected heterosis (%) for F1's.

Breed	A	C	Ch	G	H	PH	L	MA	Sa	Sh	S	SD
Angus (A)	0.00	2.64	4.65	2.81	3.27	2.64	2.48	1.47	3.63	1.36	1.72	2.11
Charolais (C)	2.64	0.00	3.24	2.24	3.57	3.41	1.21	2.32	1.16	2.32	1.41	3.57
Chianina (Ch)	4.65	3.24	0.00	3.08	6.32	6.45	3.35	3.96	3.85	4.42	3.91	5.75
Gelbvieh (G)	2.81	2.24	3.08	0.00	4.42	4.56	2.64	3.63	2.75	3.30	1.52	3.60
Hereford (H)	3.27	3.57	6.32	4.42	0.00	0.27	4.13	3.94	4.71	2.64	3.63	4.42
Polled Hereford (PH)	2.64	3.41	6.45	4.56	0.27	0.00	3.99	3.35	4.77	2.14	3.57	4.13
Limousin (L)	2.48	1.21	3.35	0.00	4.13	3.99	0.00	1.96	1.36	2.27	1.72	2.70
Maine-Anjou (MA)	1.47	2.32	3.96	3.63	3.94	3.35	1.96	0.00	3.63	1.36	2.51	2.81
Salers (Sa)	3.63	1.16	3.85	2.75	4.71	4.77	1.36	3.63	0.00	4.22	1.67	5.09
Shorthorn (Sh)	1.36	2.32	4.42	3.30	2.64	2.14	2.27	1.36	4.22	0.00	2.78	2.24
Simmental (S)	1.72	1.41	3.91	1.52	3.63	3.57	1.72	2.51	1.67	2.78	0.00	3.35
South Devon (SD)	2.11	3.57	5.75	3.60	4.42	4.13	2.70	2.81	5.09	2.24	3.35	0.00

components. For most producers, that production system should employ a structured crossbreeding system that utilizes two or more breeds. The breeds (and/or composites) chosen should produce calves that are appropriate for the market targeted. Moreover, the system and breeds included should provide a mechanism for the use of crossbred cows that are matched to the production environment in terms of mature size and lactation potential so as to capture the benefits of maternal heterosis. Selection of breeds that are too large and/or produce too much milk for the forage environment in which they are expected to produce may result in lower reproductive efficiency and increased supplemental feed costs. Selection of breeds provides an opportunity for the beef producer to impact both additive and non-additive genetics of the cowherd. Optimization of these two genetic components requires a disciplined approach to breed selection.

Table 13. Survival to weaning expected heterosis (%) for F1's.

Breed	A	C	Ch	G	H	PH	L	MA	Sa	Sh	S	SD
Angus (A)	0.00	1.90	3.34	2.01	2.35	1.90	1.78	1.05	2.60	0.98	1.24	1.52
Charolais (C)	1.90	0.00	2.33	1.61	2.56	2.44	0.87	1.67	0.83	1.67	1.02	2.56
Chianina (Ch)	3.34	2.33	0.00	2.21	4.54	4.63	2.41	2.85	2.77	3.17	2.81	4.12
Gelbvieh (G)	2.01	1.61	2.21	0.00	3.17	3.28	1.90	2.60	1.98	2.37	1.09	2.58
Hereford (H)	2.35	2.56	4.54	3.17	0.00	0.19	2.97	2.83	3.38	1.90	2.60	3.17
Polled Hereford (PH)	1.90	2.44	4.63	3.28	0.19	0.00	2.87	2.41	3.42	1.54	2.56	2.97
Limousin (L)	1.78	0.87	2.41	0.00	2.97	2.87	0.00	1.40	0.98	1.63	1.24	1.94
Maine-Anjou (MA)	1.05	1.67	2.85	2.60	2.83	2.41	1.40	0.00	2.60	0.98	1.80	2.01
Salers (Sa)	2.60	0.83	2.77	1.98	3.38	3.42	0.98	2.60	0.00	3.03	1.20	3.65
Shorthorn (Sh)	0.98	1.67	3.17	2.37	1.90	1.54	1.63	0.98	3.03	0.00	1.99	1.61
Simmental (S)	1.24	1.02	2.81	1.09	2.60	2.56	1.24	1.80	1.20	1.99	0.00	2.41
South Devon (SD)	1.52	2.56	4.12	2.58	3.17	2.97	1.94	2.01	3.65	1.61	2.41	0.00

Table 14. Weaning weight expected heterosis (%) for F1's.

Breed	A	C	Ch	G	H	PH	L	MA	Sa	Sh	S	SD
Angus (A)	0.00	1.94	3.42	2.06	2.40	1.94	1.82	1.08	2.66	1.00	1.26	1.55
Charolais (C)	1.94	0.00	2.38	1.65	2.62	2.50	0.89	1.71	0.85	1.71	1.04	2.62
Chianina (Ch)	3.42	2.38	0.00	2.26	4.65	4.74	2.46	2.91	2.83	3.25	2.87	4.22
Gelbvieh (G)	2.06	1.65	2.26	0.00	3.25	3.35	1.94	2.66	2.02	2.42	1.11	2.64
Hereford (H)	2.40	2.62	4.65	3.25	0.00	0.20	3.04	2.89	3.46	1.94	2.66	3.25
Polled Hereford (PH)	1.94	2.50	4.74	3.35	0.20	0.00	2.93	2.46	3.50	1.57	2.62	3.04
Limousin (L)	1.82	0.89	2.46	0.00	3.04	2.93	0.00	1.44	1.00	1.67	1.26	1.98
Maine-Anjou (MA)	1.08	1.71	2.91	2.66	2.89	2.46	1.44	0.00	2.66	1.00	1.84	2.06
Salers (Sa)	2.66	0.85	2.83	2.02	3.46	3.50	1.00	2.66	0.00	3.10	1.23	3.74
Shorthorn (Sh)	1.00	1.71	3.25	2.42	1.94	1.57	1.67	1.00	3.10	0.00	2.04	1.65
Simmental (S)	1.26	1.04	2.87	1.11	2.66	2.62	1.26	1.84	1.23	2.04	0.00	2.46
South Devon (SD)	1.55	2.62	4.22	2.64	3.25	3.04	1.98	2.06	3.74	1.65	2.46	0.00

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Visual and Phenotypic Evaluation of Bulls

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While a majority of the emphasis in bull selection should be placed on objective performance information, visual and phenotypic evaluation of bulls remains important for two reasons. First, bulls must be evaluated for traits that affect their physical ability to breed cows. In addition, some traits of economic relevance are not included in genetic evaluation programs. Successful commercial cow-calf operators should strive to select bulls that combine the genetic potential to improve profitability with the physical ability to work and survive in their production environment.

Breeding Soundness Traits

Likely the most important reason to evaluate prospective herd sires visually is to ensure they have the physical characteristics necessary to serve a large number of cows for a number of years. Typically, bulls offered for sale will have been subject to a breeding soundness exam (BSE), conducted by a veterinarian using guidelines set by the Society for Theriogenology (Spitzer, 2000). A BSE consists of three steps, as follows;

1. A generalized physical examination and thorough examination of both internal and external portions of the reproductive system;
2. A scrotal circumference measurement; and
3. Collection and evaluation of a semen sample.

The Society of Theriogenology has established minimum acceptable thresholds for scrotal circumference, sperm motility and sperm morphology. Bulls are classified as either satisfactory (achieves minimum thresholds and is free of problems that may compromise fertility), unsatisfactory (fails to meet minimum thresholds and has a poor prognosis for improvement), or deferred (cannot be classified as satisfactory but are likely to improve with time or therapy). It is not uncommon for younger yearling bulls (less than 15 months old) to be deferred at their first examination, but bulls that are deferred should be retested before being turned out to service females. In studies conducted at university-sponsored bull testing programs, 70 to 80% of all bulls were classified as satisfactory potential breeders (Coulter et al., 1997).

While structural soundness of feet and legs is included in the BSE, producers would be wise to make their own evaluation of a bull's skeletal structure before making a purchase. The ability of a bull to walk freely and without discomfort is critical for both breeding and grazing behavior. The most critical details of soundness are correct slope and angle to the joints of the front and rear limbs. Bulls that are excessively straight-legged travel with short strides, and are somewhat prone to stifle injuries during mating (Boggs et al, 1998). Sound structured bulls, walking on smooth, level ground, will set their rear hoof down in the track of their front hoof. Straight-shouldered, straight-legged bulls will set their hind foot down in a position well behind where the front foot was set. Hocks and knees should be free of any swelling or inflammation. Structural problems in yearling bulls tend to become more severe as the bulls age and increase in weight.

Body condition, or fatness of bulls is also an important consideration. Bulls need to be in moderate body condition at the beginning of the breeding season, as most will lose weight during periods of active breeding. However, excess body condition can adversely affect fertility. Research has shown that excessively fat bulls on high-energy diets tend to deposit fat in the neck of their scrotum, interfering with temperature regulation of the testicles and lowering fertility (Coulter et al., 1997).

Visual Estimation of Breeding Value

Prior to the advent of performance testing, producers used visual evaluation to predict the breeding value of bulls for traits like growth rate and carcass composition, with variable success. The first performance-tested herds provided adjusted weights and in-herd ratios to their bull buyers, increasing accuracy of selection within one herd's offering. But only with the availability of expected progeny differences (EPD) were bull buyers able to accurately compare animals from different herds. Nonetheless, some bull buyers continue to emphasize actual weights or in-herd ratios when selecting a herd sire.

Bull buyers often incorrectly assume that the animal with the most desirable actual performance will produce the most desirable progeny. While individual and progeny performance are related, the relationship is far from perfect. The relationship between an individual's performance and their progeny's performance depends on the heritability of the trait. For highly heritable traits, like carcass traits, relatives generally resemble each other closely, and an individual's measurement is a reasonable estimator of their progeny's performance, after adjustment for environmental effects. For moderately heritable traits, like weaning weight, the relationship weakens, and data on relatives of the prospective sire add considerable information used in calculating the animal's EPD. When dealing with traits of low heritability, like maternal weaning weight or reproductive traits, considerable information on relatives and progeny is needed to evaluate animals accurately. Regardless, EPD calculations account for the heritability of the trait, and the EPD is the single best estimate of progeny performance.

When EPD are available, using the actual weights or ratios with or without the EPD decreases the accuracy of selection for several reasons. When the most recently calculated EPD (including interim EPD) are available, they are the most accurate estimate of the animal's genetics for the measured traits. The animal's actual weight or measurement for the trait has already been included in the EPD calculation. The EPD calculation appropriately weights all the relevant information, including performance of ancestors and other relatives, and progeny when available. If producers use both the EPD and the actual weight in selection, they overemphasize the animal's own performance, and underemphasize the performance of relatives and progeny. If an animal has a favorable EPD for a trait, but a less favorable actual weight or measurement for the same trait, either there are significant environmental effects influencing the actual observation that are accounted for in the EPD calculation, or there is an overwhelming amount of

evidence from relatives that the animal in question has superior genetics.

However, there may be a few instances where traits of economic importance are not included in genetic evaluations, usually because the traits are subjectively measured. For example, bull buyers may evaluate feet and leg structure, not only to ensure the bull can service cows, but also to maintain feet and leg soundness in the bull's daughters. Again, the degree to which a sire's conformation for such traits will be reflected in their progeny depends on the heritability of the trait in question. For feet and leg conformation, limited data have been collected in beef cattle. One example of such a scoring system is the Genetic Trait Summary provided by ABS Global (Kirschten, 2002a). A sample of heritability estimates for type scores in Simmental appears in Table 1.

Table 1. Heritability estimates for type traits in Simmental cattle (Kirschten, 2002b).

Trait	Heritability	Trait	Heritability
Stature (height)	.60	Rear legs (hock set)	.12
Body length	.39	Foot/pastern angle	.13
Muscling	.42	Udder attachment	.23
Capacity	.44	Udder depth	.35
Femininity	.32	Teat size	.39

Heritability above 0.40 is considered high, while heritability of 0.15 or less is considered low. From the table above, height in this population is highly heritable, indicating that selecting sires that are taller or shorter in height than their contemporary group mates should result in daughters with somewhat similar characteristics. Rear leg and pastern set, in contrast, is low in heritability; so post legs and weak pasterns are more likely the result of environmental effects rather than genetics. Udder depth and teat length are moderate in heritability, offering some opportunity for improvement through visual selection. However, those traits can only be observed in females. While it may be possible to observe a bull's dam for her udder characteristics, only half of her genetics for those traits are passed to any one son, and only half of that passed from the son to his daughter. Culling the cowherd on udder traits is more likely to improve those traits than is sire selection. The exception would be when selecting AI sires that have a large number of daughters in production, if many of those daughters can be visually evaluated.

One of the traits most commonly evaluated visually by bull buyers is muscling. Koch et al. (2004) selected Hereford cattle for 20 years based on weaning weight alone, yearling weight alone, or a combination of yearling weight and muscle score. Visual muscle score was shown to be at least as heritable as carcass ribeye area (0.37 vs. 0.26, respectively). The authors reported a genetic correlation of 0.54 and a phenotypic correlation of 0.19 between ribeye area and retail product percentage, a favorable result. The correlation of visual muscle score with retail product percentage was near zero (genetic=0.06, phenotypic=-0.10), indicating visual selection for muscling would have little impact on cutability. While cattle selected on both yearling weight and muscle score had larger ribeye area compared to those selected on yearling weight alone, the differences between selection lines

for retail product percentage were insignificant. Selection on ribeye area EPD, based on carcass measurements, ultrasound measurements or both will likely result in greater improvement in both carcass muscling and retail product percentage, compared to visual selection for muscling.

Obviously, bulls with overly aggressive, nervous or flighty dispositions can create management problems for producers, and should be avoided for that reason. Docility in Limousin cattle has been shown to have moderate to high heritability (0.40; Kuehn et al., 1998), indicating that the resemblance between sires and their daughters for disposition should be fairly strong. However, behavior may also be influenced by sex characteristics of males versus females. So while bulls with poor dispositions are themselves a problem, there is some likelihood that their daughters will inherit similar dispositions.

Another area in which producers might use visual evaluation or phenotypic measurement in predicting a sire's breeding value is in the area of calving difficulty, either direct or maternal. For example, a bull buyer might observe that a bull appears wider and more muscular through his shoulders, and wrongly conclude that his calves might require greater assistance at birth. Two studies at Virginia Tech evaluated the relationships between calf shape and calving difficulty, and concluded that once birth weight was considered, any measurements of the calf's dimensions or shape provided no additional information on the ability of the calf to be born unassisted (Nugent et al., 1991; Nugent and Notter, 1991). Also, pelvic area in females, measured at a year of age, has been shown to be a useful predictor of their ability to calve unassisted (Bellows et al., 1971). However, Kriese (1995) showed that using pelvic area of yearling bulls to predict their daughter's calving ease is not useful. First, pelvic area is moderately heritable, so a sire with a larger pelvic area should transmit some but not all of that advantage to his offspring. Also, pelvic area seems to be significantly affected by developmental differences between males and females (Kriese et al., 1994), so genetics that result in large pelvic area in males might not have the same effect in females.

Summary

In summary, buyers of bulls or semen should focus on genetic evaluation results in the form of EPD for selection whenever possible. Using the most current EPD will most likely result in the desired genetic change. Some traits that affect the ability of natural service sires to successfully breed cows, like breeding soundness and skeletal structure, must be visually evaluated. However, "adjusting" EPD for the actual performance data or visual characteristics of the sire biases selection, and results in less than maximum genetic progress with no reduction in risk.

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DNA-Based Biotechnologies

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Biotechnology is defined as technology based on biology. From this definition, it is obvious that animal breeders have been practicing biotechnology for many years. For example, traditional selection techniques involve using observations on the physical attributes and biological characteristics of animals to select the parents of the next generation. One only needs to look at the amazing variety of dog breeds to realize the influence that breeders can have on the appearance and characteristics of animals from a single species. Genetic improvement through selection has been an important contributor to the dramatic advances in agricultural productivity that have been achieved in recent times (Dekkers and Hospital, 2002).

During the past century, several new technologies have been incorporated into programs aimed at accelerating the rate of the genetic improvement of livestock. These include, but are not limited to, artificial insemination (AI), sire testing programs that use data from thousands of offspring, the use of hormones to control the female reproductive cycle so as to allow for synchronization and superovulation, and embryo transfer. Prior to their eventual widespread adoption, some of these new technologies (e.g. AI) were initially controversial and their introduction met with some resistance. In the past decade, applied DNA-based technologies have become available as a tool that livestock producers can use to aid in making their selection decisions. The intent of this chapter is to provide the necessary background to create an understanding of DNA-based technologies, and to discuss some of the recent developments and future applications in cattle production systems.

What is DNA ?

Living organisms are made up of cells, and located inside each cell is deoxyribonucleic acid, or **DNA** for short. DNA is made up of pairs of four nucleotides abbreviated as "A", "C", "G" and "T" (Figure 1). The entire genetic makeup, or **genome,** of an organism is stored in one or more chromosomes located inside each cell. DNA has two important functions; first, it transmits genetic information between generations during reproduction, and second, it continually spells out the identity and the rate of assembly of proteins. **Proteins** are essential to the structure and function of plants and animals. A **gene** is a distinct sequence of DNA that contains all of the instructions for making a protein. It is possible for the DNA sequence that makes up a gene or **"locus"** to differ between individuals. These alternative DNA sequences or forms of a gene are called **alleles,** and they can result in differences in the amount or type of protein being produced by that gene among different individual animals. This can affect the performance or appearance of animals that carry different alleles. Alleles can be **recessive,** meaning that an animal must inherit the same allele (i.e. the same sequence) from both parents before there is an effect, **additive** meaning that the effect is proportional to the number of an allelic variants inherited by the animal (i.e. carrying two copies of a particular allele produces double the effect of carrying one copy), or **dominant,** meaning that the presence of one allele is sufficient to result in an effect on the trait or attribute of interest. Gender-

determination is a well-known example of a simple trait where the presence of the dominant Y-chromosome dictates maleness.
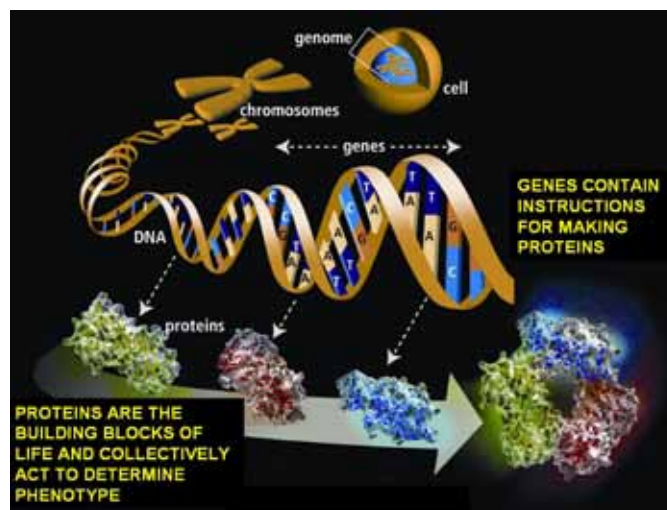
Scientists have started to identify regions in chromosomal sequence of DNA that influence production traits. They have used the techniques of molecular biology and quantitative genetics to find differences in the DNA sequence in these regions. Tests have been developed to identify these subtle sequence differences, and so identify whether an animal is carrying a segment of DNA that is positively or negatively associated with a trait of interest. These different forms of a genetic marker are known as DNA-marker alleles. There are several types of genetic markers. **Microsatellites** are stretches of DNA that consist of tandem repeats of a simple sequence of nucleotides (e.g. "AC" repeated 15 times in succession). The tandem repeats tend to vary in number such that it is unlikely two individuals will have the same number of repeats. To date, the DNA markers used to determine parentage have primarily utilized microsatellite markers. Another type of genetic marker is referred to as a **single nucleotide polymorphism** or SNP (referred to as "snip") where alleles differ from each other by the sequence of only a single nucleotide base pair. SNP genetic tests focus on detecting precise single nucleotide base pair differences among the three billion nucleotide base pairs that make up the bovine genome (Figure 2).

Genotyping refers to the process of using laboratory methods to determine which DNA-marker alleles an individual animal carries, usually at one particular gene or location (locus) in the genome. The **genotype** identifies the marker alleles an animal carries. Because an animal gets one allele of each gene from its sire, and one allele of each gene from its dam, it can only carry two alleles of any given marker locus or gene. If an animal gets the

Figure 2. A section of DNA output generated by a DNA sequencer. At the indicated site, this individual inherited a "T" nucleotide from one parent, and a "C" nucleotide from the other parent. This site represents a single nucleotide polymorphism. *Original graphic obtained from Michael Heaton, USDA, ARS, Meat Animal Research Center (MARC). Used with permission.*
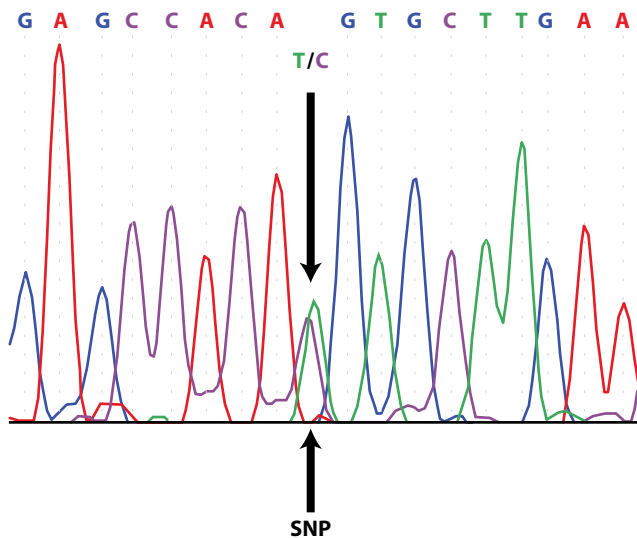
same marker allele from each parent it is referred to as **homozygous** (e.g. "**" or "TT" or "140, 140"), or it may inherit different alleles from each parent in which case it is referred to as **heterozygous.** (e.g. "*-" or "TC" or "144, 136"). DNA testing can be used to distinguish between animals carrying different marker alleles and this information can also be used for tracking parentage.

Most of the economically relevant traits for cattle production (birth weight, weaning weight, growth, reproduction, milk production, carcass quality, etc.) are **complex traits** controlled by the protein products of many genes, and also influenced by the production environment. The protein produced by different alleles of genes may influence the observed performance or **phenotype** of the animal carrying those alleles. The genetic component of phenotypic variation is the result of DNA sequence differences between chromosomes of individuals. When an animal has an EPD above the base year average for a certain trait, it means the animal has inherited a higher than average proportion of alleles for genes that favorably affect the trait. In other words, selection based on EPDs results in an increase in the average number of favorable alleles an animal can pass on to its offspring, without knowing which specific genes are involved. This contrasts with DNA-based selection which is based on the use of genotyping to identify animals carrying specific DNA variants that are known to be associated with the trait of interest. It should be noted that traditional EPD-based selection methods inherently tend to increase the frequency of DNA markers associated with the alleles of genes that have beneficial effects on selected traits.

Parentage Analysis

Commercial herds using multiple-sire breeding pastures often have no way of identifying the paternity of calves. DNA markers can be used to assign calves to their individual sires based on the inheritance of markers. Sires pass on only one of the two marker alleles that they carry for each gene locus. If a calf does not have a marker allele in common with a sire at a particular locus, then that

sire is excluded as being the parent of that calf. Paternity "identification" involves examining each calf's genotype at multiple gene loci and excluding as potential sires those bulls that do not share common alleles with the calf. Because paternity identification is a process of excluding potential sires on the basis of their genotype, it is therefore important that DNA from all possible sires be included in paternity tests. While parents can be excluded using this process, results cannot be used to "prove" parentage. Parentage testing identifies individuals that, due to a specific combination of marker alleles, could qualify as a parent for a particular offspring. Paternity testing is complicated by genetic relationships between the bulls. If bulls are closely related then they are more likely to carry the same marker alleles. Consequently, it will be more difficult to definitively make paternity assignments on closely related bulls in a multiple-sire breeding pasture. Forming multiple-sire groups for each pasture from unrelated animals, i.e. putting full-brothers in with different groups of cows, will help to minimize this problem. If there is only one potential sire for a calf (e.g. an A.I. calf), then paternity can be "assigned" by confirming that the calf's genotype shares a marker allele in common with the alleged sire at all of the genetic loci that are tested. Although microsatellites have typically been the marker of choice for paternity analysis, the use of SNP markers is becoming more common for a number of reasons including their abundance, high potential for automation, low genotyping error rates, and ease of standardization between laboratories (Figure 2).

Example. How does parentage assignment work?

	Bull A	Bull B	Bull C	Bull D
Genotype	A/A, C/C	A/T, C/G	T/T, G/G	T/T, C/C

A calf with the genotype "A/T, C/G" could have received one allele from any of these bulls and so none of these bulls can be excluded as the possible sire. Additional markers would need to be used to uniquely assign one of the bulls as the sire of the calf.

A calf with genotype "A/A, C/C" could not have been sired by Bulls C or D, but could have been sired by either Bull A or B.

A calf with genotype "T/T, G/G" could not have been sired by Bulls A or D, but could have been sired by Bull B or C.

Uses of parentage testing include identifying the sire(s) of outstanding or poorly performing calves and ascertaining whether one particular bull is routinely siring progeny that require calving assistance. To identify the sire(s) of a select group of calves (e.g. calves that have difficult births or top 10% of carcass quality animals) the costs of DNA analysis are minimized by sampling and DNA testing the herd bulls and only a targeted subsample of the calves. Yet another use of parentage testing would be to identify which sire is responsible for contribution of a genetic defect. More extensive sampling of the entire calf crop can allow for a determination of the proportion of the calf crop attributable to each bull in the herd. It is generally assumed that each bull contributes equally to the calf crop. However, studies have shown that some bulls sire more than their "fair share" of the progeny, while other bulls sire none of the progeny (Figure 3; Van Eenennaam et al. 2007b).

Matching individual sires with the performance records of their entire calf crop also provides the data required to develop

within-herd EPDs for herd sires (Van Eenennaam et al., 2007b). The use of progeny testing to develop within-herd EPDs for herd sires on economically-relevant traits has the potential to generate value by improving the response to selection for targeted traits.

In practice it is preferable to collect DNA samples from all potential sires at the beginning of the breeding season. It is also important to try to keep young sires and mature bulls in separate breeding pastures as dominant mature bulls will tend to keep young bulls from siring any calves (see Figure 3).

Missing identification of sires can occur for a variety of reasons (neighboring bulls jumping the fence, precocious bull calves, or inadvertent omission of sire(s) from sample collection). Missing sire DNA samples when using DNA marker-based parentage for genetic evaluation decreases the rate of genetic gain. The frequency of sire misassignment can be minimized by using a powerful marker panel; or by simple management practices that include: dividing large herds into smaller multiple-sire breeding groups with fewer sires while maintaining the same bull:female ratio; sorting bulls into sire groups with divergent genotypes; and minimizing relatedness among bulls. It is also important to try to keep young sires and mature bulls in separate breeding pastures as dominant mature bulls will tend to keep young bulls from siring any calves.

The return on investment that results from such progeny testing has been found to be greatly influenced by the cost of genotyping (Pollak, 2005). New SNP genotyping platforms continue to drive down the cost to generate SNP genotypes, and the future will undoubtedly see the introduction of less expensive genotyping assays using high resolution SNP parentage panels. As with any new technology, the value associated with the parentage information must be estimated to determine if it outweighs the expense of collecting and genotyping the DNA samples.

Marker-Assisted Selection (MAS)

Marker-**A**ssisted **S**election (MAS) is the process of using the results of DNA-marker tests to assist in the selection of individuals to become the parents in the next generation of a genetic improvement program. Selection may be based on test results associated with simple traits such as coat color, horned status, or simply inherited genetic defects. Such traits are determined by the inheritance of specific alleles at known genes and so tests are able to accurately assess whether an animal is a "carrier" (i.e.

heterozygous) or will "breed true" (homozygous) for that trait (e.g. red versus black).

The test for Arthrogryposis Multiplex (AM) is an example of this type of test. The genetic test for this recessive lethal genetic defect also known as "curly calf," identifies an animal as a carrier of the AM mutation (AM**C**) or a non-carrier (AM**F**), meaning that an animal that has been determined to be free of the AM mutation. Of course, the genotype of an AM affected (AM**A**) animal is obvious on the basis of its appearance and lethality. Irrespective of its pedigree, an animal that has been tested and found to be a non-carrier (AMF) did not inherit the mutation and will not carry or transmit this genetic defect to its progeny. If a cow has an AM calf, it means that the cow is a carrier of the AM mutation and that the sire she was bred to also carries the AM mutation.

Example. Determining the proportion of offspring that will inherit a genetic defect.

From a breeding standpoint there are several possible scenarios when considering the inheritance of a recessive genetic defect. In the case of AM, if both parents are carriers (AMC), then there is a one in four chance of producing a dead AMA calf, a one in two chance of having a normal-appearing AM carrier (AMC) calf, and a one in four chance of having a normal AM free (AMF) calf.

AMC x AMC = ¼ affected (AMA):
½ normal-appearing carrier (AMC): ¼ AM free (AMF)

If only one parent is a carrier, then all of the offspring will be normal appearing, but half of them will be carriers (AMC).

AMC x AMF = ½ normal-appearing carrier (AMC):
½ AM free (AMF)

Naturally-occurring recessive genetic defects are common in all species, and only become evident when certain lines of cattle are used very heavily, such that both cows and bulls have common ancestors in their pedigree, thereby allowing a rare genetic defect to become homozygous in their offspring. The widespread use of the superior carcass-trait bull Precision 1680, an AM carrier (AMC), increased the probability of this bull showing up on both sides of many Angus pedigrees, and this uncovered the presence of the recessive lethal AM mutation.

Figure 3. Calf output of 27 herd bulls of varying ages in a single multiple-sire breeding pasture. Five of the 27 herd sires produced over 50% of the calves. The leading digit of the sire identification number denotes the age of the bull at the time of breeding, and it can be seen that of the ten natural-service herd bulls that sired no progeny, nine were yearlings. *Modified from Journal of Animal Science, 85, Van Eenennaam, A. L.; R. L. Weaber; D. J. Drake; M. C. T. Penedo; R. L. Quaas; D. J. Garrick; E. J. Pollak. DNA-based paternity analysis and genetic evaluation in a large, commercial cattle ranch setting., pages 3159-3169. (2007), with permission from American Society of Animal Science.*
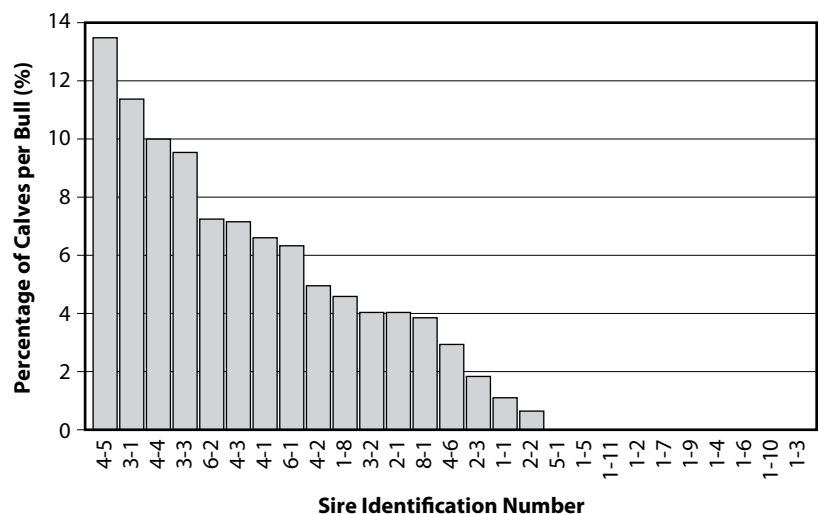
The rapid development of a commercial DNA test for this genetic defect by Dr. Jonathan Beever and colleagues over a period of approximately 4 months was made possible by the availability of the bovine genome sequence. It represents one of the most compelling examples of the power and utility of this sequence information for the cattle industry. In the absence of a DNA test, there would have been no way to determine the AM-status of animals with affected pedigrees, and in the process of proactively eliminating potential carriers, many AMF animals would have been needlessly culled. It is likely that the bovine genome information will accelerate the development of DNA tests for other genetic defects as they become evident in the population.

MAS also holds great promise for selection based on complex production traits, both those that are in existing genetic evaluation programs, and those for which no genetic merit estimate currently exists. In order of greatest to least degree of benefit, the following categories of traits are likely to benefit the most from marker-assisted selection:

Greatest	1.	simply inherited genetic defects,
	2.	carcass quality and palatability attributes,
	3.	fertility and reproductive efficiency,
	4.	carcass quantity and yield,
	5.	milk production and maternal ability,
Least	6.	growth traits and birth weight.

This ranking is due to a combination of considerations including: 1) relative difficulty in collecting performance data, 2) relative magnitude of the heritability and phenotypic variation observed in the traits, 3) amount of performance information available, and 4) when performance data become available in the life cycle.

The first commercial test for a quantitative production trait in beef cattle was a single marker test for marbling (Barendse et al., 2001). This was soon followed by other tests involving a small number (1-3) of markers associated with marbling (Buchanan et al., 2002) and tenderness (Casas et al., 2006; Schenkel et al., 2006). Early methods of marker discovery focused on finding SNP markers in regions of the genome that were experimentally known to have a relatively large effect on the trait of interest. Rarely are DNA markers the actual DNA sequence causing the effect, rather markers are closely situated or "linked" to the causative sequence. Markers therefore flag the location of sequences that directly have an effect on the trait (Figure 4).

However, it is important to understand that any one marker will identify the alleles for only one of the many genes that are associated with complex traits. Put another way, any single marker is only going to account for a fraction of the genetic variation associated with a complex trait. This is distinct from the situation for simple traits (e.g. coat color, horned status, lethal recessive mutations) where one or two markers may be sufficient to accurately predict an animal's phenotype and carrier status. Conflicting reports about some of these first commercially-available markers (Barendse et al., 2005; Casas et al., 2005), and the recognized occurrence of well-proven bulls with a high EPD for a given trait but carrying two copies of the "wrong" (unfavorable) marker allele for that trait made some producers understandably wary of investing in DNA-based testing. Genetic tests for complex traits

are likely to require hundreds or even thousands of markers to effectively track all of the genes influencing complex traits.

Example. Making selection decisions based on DNA marker test results.

Consider the following two scenarios where you are choosing between two bulls. One carries two copies of a marker allele that is associated in a positive way with a trait that you are interested in improving, while the other bull carries no copies of the favorable marker allele.

1. Two full brothers produced by embryo transfer that have identical, low-accuracy EPDs based on their pedigree data.
This is a simple choice and it would clearly be the animal carrying two copies of the marker allele. The DNA test tells you with a high degree of certainty that one bull is carrying two favorable alleles for one of the genes associated with the trait of interest. Subsequent progeny testing may prove the other bull superior based on the chance inheritance of "good" alleles for the many other genes associated with the trait, but the markers provide some definitive information to enhance your chances of choosing the better of the two bulls at an early age.

2. Two well-proven bulls have identical, high-accuracy EPDs based on progeny testing.
This is a more difficult scenario. The marker test tells you that the bull with the two copies will transmit a favorable form of the gene associated with the marker to all of his progeny. If the marker allele accounts for a large proportion of the additive genetic variance, then using him as a herd sire will ensure that all of his calves get this desirable form of the gene. Using this bull may make sense if your herd has a low frequency of the marker allele. However if your herd already has a high frequency of the favorable marker allele, then using the bull that carries desirable alleles of all of the other genes that contribute to trait, as evidenced by an EPD equal to the homozygous marker bull's EPD, will likely accelerate genetic progress more rapidly by bringing in new sources of genetic variation. Seedstock breeders need to be particularly careful not to inappropriately discriminate against bulls that have well-ranked, high-accuracy EPDs but that are found to carry no favorable alleles of a single marker associated with a given trait, especially if such bulls are relatively common or have desirable EPDs for other traits. These bulls represent a valuable source of alleles for all of the unmarked genes associated with the trait of interest. Offspring that inherit both the marker-allele from their dam and desirable alleles of unmarked genes from high-rank EPD bulls carrying no copies of the marker, are likely to inherit the greatest number of favorable alleles for both the unmarked and marked genes that affect the trait.

Once a decision has been made to use marker-assisted selection, the actual application of the technology is fairly straightforward. DNA samples should be collected from all animals to be tested. Common collection methods include a drop of blood blotted on paper (make sure to let the sample dry well before storing), ear tag systems that deposit a tissue sample in an enclosed container with bar code identification, semen, or hair samples (including the DNA-rich follicle or root). To increase the frequency of a marker that is positively associated with the trait of interest, select for animals that are carrying one or two copies of the marker, and against those carrying no copies of the marker. All of the offspring from a parent carrying two copies of the marker (homozygous) will inherit a copy of the marker from that parent. In a typical herd, selection for homozygous sires will probably be the most rapid way to increase the frequency of the
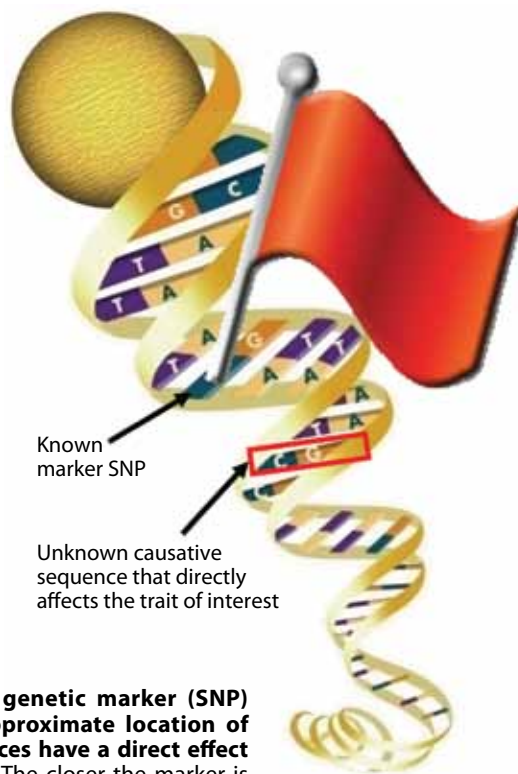
Known marker SNP

Unknown causative sequence that directly affects the trait of interest

Figure 4. A genetic marker (SNP) flags the approximate location of DNA sequences have a direct effect on the trait. The closer the marker is to the causative locus the more likely it is that they will be inherited together and so the marker acts as a proxy for the causative sequence. If the marker is a long way from the causative sequence then it may become uncoupled from the sequence, and so selecting for the marker will no longer lead to genetic improvement for the trait of interest.

marker, although this may severely limit your choice of sires and hinder progress in other traits. Marker-assisted pre-selection of young sires with equivalent EPDs is an excellent way to rapidly increase the proportion of animals carrying a specific genetic marker and increase the frequency of that marker allele in the population.

Marker-Assisted Management (MAM)

Marker-Assisted Management (MAM) is the process of using the results of DNA-marker testing to predict the future phenotype of the animal being tested and sort individual cattle into management groups that are most likely to achieve specific end points (e.g. Quality grade Choice or better). The word "assisted" implies that markers can be used in conjunction with other information on the individual animal such as breed composition, age, weight, condition score, and ultrasound measurements, to assist in sorting animals into groups that can then be managed in a uniform manner to target a specific performance goal or market.

It is possible for a test to be useful for MAM but not for MAS. For example, if all of the animals in a given breed carry two copies (fixed), or no copies, of a marker allele, then that marker will be of no use for within-breed MAS as the marker accounts for none of the genetic variability seen for the trait in that breed, even though that marker may be associated with a big effect on the trait in breeds where it is not fixed. In cattle of unknown origin or mixed breeds however, marker frequencies may be of use in sorting animals with similar genetic backgrounds into

management groups. For example, if a set of markers was fixed in *Bos taurus* cattle and absent in *Bos indicus* cattle, then the allele frequencies of these markers would give some indication as to the proportion of *Bos taurus* influence in a mixed population of cattle. This information may be of use to help sort animals into more uniform groups that target a specific market or end point.

Validation

Prior to moving genetic markers from discovery populations to commercialization, it is important to validate their purported effects on the trait of interest in a different population, and assess them for correlated responses in associated traits (Barendse, 2005). As mentioned previously, genetic markers are usually closely associated or "linked" to the DNA sequence that is actually having an effect on the trait of interest (Figure 4). However, the relationship between the marker and the causative sequence may differ among breeds, and even between subpopulations within a breed. For one breed, a marker might be linked to the DNA sequence causing the desirable effect on the trait, whereas in other breeds there may be no effect of that marker on the trait or the opposite might be true such that the marker flags the "bad" sequence. The predictive value of a DNA test decreases (that is it does not "work" as well) when markers are incorrectly associated with the trait of interest in a given breed or animal. Therefore, once an association has been found between a DNA marker and a trait in a discovery population, that association needs to be validated in a different population. This validation will be most effective when the validation population is representative of the population where the test will ultimately be used.

The U.S. National Beef Cattle Evaluation Consortium (NBCEC) has been involved in the process of independently validating commercial DNA tests for quantitative beef quality traits since their first appearance on the U.S. market in the early 2000s (validation results are posted at www.NBCEC.org; Accessed 3/09/10). The term "having validated" was originally defined as finding a significant association "between genetic tests and traits as claimed by the commercial genotyping company based on phenotypes and genotypes derived from reference cattle populations" (Van Eenennaam et al., 2007a). Validation is a critical activity to test the strength of support for the genotyping company's published claims based on independent data. This process sometimes revealed that tests did not perform as expected, and in certain cases companies chose to withdraw those tests from commercialization.

During the past decade, the DNA testing industry matured from single gene tests to panels involving an ever-increasing number of markers with purported effects on multiple traits and/or in specific cattle populations. As marker panels grew in size and there were increasing intellectual property concerns regarding disclosure of the specific marker loci involved in a genetic test, validation moved from testing the effect of individual loci towards testing a single marker score, sometimes called a molecular breeding value (MBV), based on a panel of SNP markers.

The NBCEC and DNA testing companies sometimes struggled to find appropriately-phenotyped populations that were not involved in the discovery process for validation studies. Additionally, results from different validation populations genotyped with the same SNP panel were often inconsistent with respect to the significance of the association between the test and the trait(s),

and sometimes even with respect to the direction of the association (i.e. the test predicted the worst animals, not the best). This complicated the interpretation of validation results, and created confusion as to whether "validation" meant a test "worked" (i.e. was significantly associated with the trait) in one or more of the test populations, or had simply been tested by an independent third party.

At the current time the data that are reported on the NBCEC validation website include the direction of the effect ("b" value; regression coefficient), and the significance ("p" value; associations are typically considered significant if $p < 0.05$) of that effect. A positive regression coefficient means that the test was associated with the trait in a positive way, i.e. one unit of test increase was associated with an increase of (1 x regression coefficient) unit of the trait.

Example. If two animals have a DNA-based tenderness score that differs by 2 units and the regression coefficient of phenotype on the genetic score is 0.3, then it would be predicted that there would be a (2 x .3) = 0.6 lb difference in Warner Bratzler Shear force between steaks derived from these two animals.

A common criticism of the currently-available DNA tests for quantitative traits in beef cattle is that their ability to predict genetic merit is limited. The accuracy of a DNA test at predicting the true genetic merit of an animal is primarily driven by the proportion of additive genetic variation accounted for by the DNA test. Current estimates suggest this proportion is generally low (0-0.10) in existing tests, although this number is not readily available for all tests. The exception is tenderness DNA tests where available estimates for the proportion of genetic variation range from .016-0.299 (http://www.beefcrc.com.au/Aus-Beef-DNA-results; Accessed 3/09/10). Over time it is envisioned that genetic tests will have many more markers which will be associated with the majority of important genes influencing a trait. A January 2010 press release announced the availability of greater than 50,000 marker DNA test for Angus cattle (http://www.pfizeranimalgenetics.com/Pages/HD50KRelease.aspx, Accessed 3/09/10). It is hoped that in the future DNA tests will be highly predictive of the true genetic value of an animal. Future NBCEC validations will report the accuracy and proportion of genetic variation accounted for by DNA tests. Obtaining estimates of these values is an important step in moving the focus of validation from whether a test "works", towards developing the information that will be needed to incorporate DNA testing into cattle genetic evaluations. Publishing traditional EPDs and marker information separately, as is currently the case, is confusing and can lead to incorrect selection decisions when emphasis is placed on marker scores that predict only a small proportion of the genetic variation. Developing an approach to develop marker-assisted EPDs seems to be a logical next step in the implementation of DNA tests into national genetic evaluations. In fact some breed associations are already moving in that direction as indicated in a July 2009 press release (http://www.angus.org/Pub/Newsroom/Releases/AGI_Igenity_EPDs.html; Accessed 3/09/10).

Web Sites of US Companies Providing Genotyping Services for Beef Cattle
(current as of 3/2010)

A listing of available tests is maintained at the following web address: http://animalscience.ucdavis.edu/animalbiotech/Biotechnology/Companies/index.htm

AgriGenomics, Inc. (http://www.agrigenomicsinc.com) Arthrogryposis Multiplex (AM), Tibial Hemimelia (TH), Pulmonary Hypoplasia with Anasarca (PHA), Black/Red Coat Color (CC), Dilution (DL), Idiopathic Epilepsy (IE), Arthrogryposis Multiplex (AM) or Curly Calf Syndrome analysis

Biogenetic Services (http://www.biogeneticservices.com) Parentage, freemartin, coat color, leptin, meat quality, BSE resistance, Johne's disease, Bovine Virus Diarrhea (BVD)

GeneSeek (http://www.geneseek.com) Arthrogryposis Multiplex (AM), Parentage, coat color, Seek-Black, Seek-Tender, Bovine viral diarrhea (BVD-PI), identity tracking, 50,000 SNP CHIP genotyping

Genetic Visions (http://www.geneticvisions.net) Coat color, Prolactin (CMP), BLAD, Citrullinemia, DUMPS, Kappa-Casein, Beta-lactoglobulin, Complex Vertebral Malformation (CVM), Calpain 316/530, Freemartin

Igenity (http://us.igenity.com) Arthrogryposis Multiplex (AM), Neuropathic Hydrocephalus (NH) , Coat Color Dilution (DL), Idiopathic Epilepsy (IE), Osteopetrosis (OS), Pulmonary Hypoplasia with Anasarca (PHA), and Tibial Hemimelia (TH), Parentage, Myostatin, Breed-specific horned/polled, BVD-PI diagnostic test, Igenity Profile Analysis (tenderness, marbling, quality grade, fat thickness, ribeye area, hot carcass weight, yield grade, heifer pregnancy rate, stayability, maternal calving ease, docility, residual feed intake, average daily gain), DoubleBLACK coat color, identity tracking

MMI Genomics (http://www.metamorphixinc.com) Arthrogryposis Multiplex (AM), Neuropathic Hydrocephalus (NH), Osteopetrosis (OS) or "marble bone disease", Parentage, Tru-Marbling™, Tru-Tenderness™, MMIG Homozygous Black, polled/horned

Pfizer Animal Genetics (previously Bovigen) (http://www.pfizeranimalgenetics.com) Arthrogryposis Multiplex (AM) or Curly Calf Syndrome analysis, Neuropathic Hydrocephalus (NH), Osteopetrosis (OS), Tibial Hemimelia, Pulmonary Hypoplasia with Anasarca, Idiopathic Epilepsy GeneSTAR® MVP™ (feed efficiency, marbling, tenderness), HD 50K for Angus (Calving ease direct, birth weight, weaning weight, average daily gain, dry matter intake, net feed intake, calving ease maternal, mature weight, milking ability, carcass weight, backfat thickness, ribeye area, marbling score, tenderness), GeneSTAR® Elite Tender, GeneSTAR® BLACK, parentage, identity tracking

Quantum Genetics (http://www.quantumgenetics.ca) Leptin

Repro Tec Inc. (http://www.reprotec.us) Fertility Associated Antigen (FAA)

Veterinary Genetics Laboratory (UC Davis) (http://www.vgl.ucdavis.edu) Parentage, freemartin, coat color, Dexter Cattle: Dexter Dun, Extension (Red/Black), Bulldog Dwarfism (Chondrodysplasia), freemartin karyotyping

Viagen (http://www.viagen.com) Breed identification (AnguSure™)

Whole Genome Selection

Recent developments in genotyping technologies and SNP discovery methods (Van Tassell et al., 2008) have led to the development of panels that allow a single DNA sample to be simultaneously genotyped for tens of thousands of SNPs (e.g. the 50,000 SNP bovine panel). It is hoped that cumulatively these markers will be associated with a large proportion of the genetic variation associated with various traits of importance to the beef cattle industry. This may pave the way for producers to select animals to become parents of the next generation based on breeding values calculated from DNA marker data, a process called whole genome selection (**WGS**) or genomic selection.

WGS is a form of marker-assisted selection (MAS) that uses thousands of markers that are distributed throughout the genome. With WGS, the approach is to genotype thousands of SNPs on animals that have phenotypes for a given trait, and then use these data to determine a prediction equation that predicts how well an unknown animal will perform for that trait based on its SNP genotype alone (Meuwissen et al., 2001). There are three populations required for WGS; a training population, a validation population, and the application or selection population (i.e. animals where the test will be applied to make selection decisions; (Goddard and Hayes, 2007). WGS effectively derives an EPD estimate for thousands of individual SNPs based on phenotypes in the training population. An overall measure of the merit of an animal is then obtained by summing the EPD estimates to generate a molecular breeding value (**MBV**). The accuracy of the prediction equation is then assessed by applying it to an independent group of animals that have been genotyped and measured for the trait to estimate the correlation between the MBV and the true breeding value. Ideally validation populations should have a similar genetic makeup to the application population where the prediction equation will be applied (Figure 5).

The potential benefits of whole genome selection are likely to be greatest for traits that:
- have low heritability (reproductive traits).
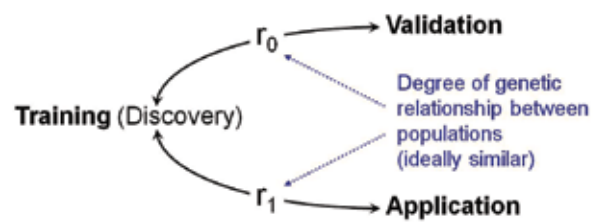- are difficult or expensive to measure (e.g. disease resistance).

Figure 5. Populations involved in Whole Genome Selection. *Original graphic obtained from Mark Thallman, USDA, ARS, Meat Animal Research Center (MARC). Used with permission.*

- cannot be measured until after the animal has already contributed to the next generation (e.g. stayability).
- are currently not selected for as they are not routinely measured (e.g. product composition, tenderness, or nutritional value).

It is envisioned that whole genome selection will accelerate genetic progress by increasing the accuracy of selection, and allowing selection decisions to be made at a younger age (Schaeffer, 2006). The prediction of breeding values at an early age removes many of the limitations of current phenotype-based breeding programs and provides a clear time advantage in developing genetic estimates for sex-limited traits, or traits that are not available until late in an animal's life, such as fertility or longevity. Additionally this approach may open the way to develop genetic predictions on difficult to measure economically-relevant traits, such as disease resistance and feed efficiency, which are not currently included in beef cattle genetic evaluations. It may also allow for selection on traits that have never been previously considered in genetic evaluations such as the compositional makeup and nutritional value of meat for human consumption.

SNP-based Fingerprinting for Cattle

"SNP fingerprinting" may also play a role in individual animal identification (Figure 6). After an animal has been slaughtered, DNA remains a stable, identifiable component to track the origin

Table 1. Possible progression of DNA testing technologies over the next decade.

2003	2008	2013	2020
Single marker/single trait tests	Multimarker tests become available for a small number of traits	Panels with 100-1000s of markers for multiple traits	Testing costs are low
Actual genotyping results reported	Results reported in a variety of formats although move towards reporting numeric scores	Results consistently reported in unit of the trait	Large SNP panel used by worldwide beef cattle community for a large number of traits
Low accuracy			
Limited adoption	Tests account for <10% additive genetic variation	DNA information starting to be routinely incorporated into genetic evaluation	Seamless submission of genotype data into national genetic evaluation schema
Technology oversold			
	No tie in between results and national genetic evaluation	DNA-based evaluations begin to improve accuracy of EPDs	EPDs available on many economically relevant traits
	No way to determine appropriate emphasis to place on test result	Larger numbers of genotyped populations start to become available for validation	DNA information greatly increases the accuracy of genetic evaluations
	Technology not in form producers could easily use		Industry routinely uses DNA information for herd management, and breeding decisions

Figure 6. SNPs may offer a permanent and traceable fingerprint for cattle and beef in the future. *Original graphic obtained from Michael Heaton, USDA, ARS, Meat Animal Research Center (MARC). Used with permission.*

of beef products. Genotyping 30 SNP loci that exhibit variability across all common beef breeds would be sufficient to uniquely identify 900,000 cattle (Heaton et al., 2002). The odds that two individuals coincidentally possess identical 30-SNP loci genotypes is less than one in a trillion! And 45 highly-informative SNP loci are estimated to be sufficient to identify all of the cattle in the world (estimated to be approximately 1 billion). In the future, SNPs may also be used as a tool to counter inbreeding by maintaining genetic diversity at many sites on the genome (Daetwyler et al., 2007), and to allow for the transmission of beneficial alleles from rare breeds into commercial breeds of cattle.

Cloning

The term "cloning" became infamous following the appearance of Dolly the sheep, the first mammal cloned from DNA derived from differentiated adult tissue, in 1997. In fact, cloning has been going on for a long time. Plant breeders have been using this technique to "clonally propagate" desirable plant lines for centuries. Cloning is defined as making a genetic copy of an individual. Identical twins are clones, but more commonly the term is now used to refer to an individual that results from the transplantation of the DNA contained in a single cell of somatic tissue derived from an adult organism into an enucleated oocyte (an egg which has had its own DNA removed). This process is called somatic cell

Figure 7. Two somatic cell nuclear transfer (SCNT) cloned Holstein calves, Dot and Ditto. *Original photo taken by Alison Van Eenennaam, UC Davis. Used with permission.*

nuclear transfer or **"SCNT"** and has been successfully performed on many species including cattle (Figure 7). It is important to note that prior to SCNT, two other well-established procedures were available and used to make cattle clones. Splitting or bisecting embryos, a process in which the cells of a developing embryo are split in half and placed into empty zona (the protective egg coat around early embryos) prior to transfer into different recipient mothers, was commonly used in the 1980s. Likewise, cloning by nuclear transplantation from embryonic cells was developed in the 1970s and introduced into cattle breeding programs in the 1980s, well before the appearance of Dolly. From an animal breeding perspective, the importance of the SCNT procedure that created Dolly is that it allows for the replication of adult animals with known attributes and highly accurate EPDs based on pedigree, progeny, and their own performance records.

Although clones carry exactly the same genetic information in their DNA, they may still differ from each other, in much the same way as identical twins do not look or behave in exactly the same way. In fact, it has been found that SCNT clones differ more from each other than do contemporary half-siblings (Lee et al., 2004). Clones do not share the same cytoplasmic inheritance of mitochondria from the donor egg, nor the same maternal environment as they are often calved and raised by different animals. It is also important to remember that most traits of economic importance are greatly influenced by environmental factors, and so even identical twins may perform differently under varying environmental conditions. In the case of SCNT there is an additional complicating factor, and that is the requirement for "reprogramming" of the transferred nuclear DNA as it goes from directing the cellular activities of a somatic cell, to directing the development of an entire new embryo. Currently this process is not well understood, and there appears to be an increased rate of perinatal and postnatal loss and other abnormalities in SCNT clones relative to offspring conceived in the traditional way. It may be that SCNT clones differ from the original DNA-donor in the way that their nuclear genes are expressed. These problems are not seen universally in SCNT cloned cattle, and there are reports of apparently healthy cattle that have gone on to conceive and have healthy calves (Lanza et al., 2001; Pace et al., 2002). Studies comparing the performance of SCNT and other types of dairy cattle clones to their full siblings found that there were no obvious differences in performance or milk composition (Norman and Walsh, 2004; Walsh et al., 2003). Although the performance records of SCNT clones may be different from their DNA-donor, as far as we currently know they would be expected to have the same ability as their progenitor to transmit favorable alleles to their offspring. More research is required to determine if the offspring of SCNT clones perform as well as would be expected based on the predicted genetic potential of the original DNA-donor animal.

Cloned animals may provide a "genetic insurance" policy in the case of extremely valuable animals, or produce several identical bulls in production environments where AI is not a feasible option. Clones could conceptually be used to reproduce a genotype that is particularly well-suited to a given environment. The advantage of this approach is that a genotype that is proven to do especially well in a particular location could be maintained indefinitely, without the genetic shuffle that normally occurs every generation with conventional reproduction. However, the disadvantage of this approach is that it freezes genetic progress at

one point in time. As there is no genetic variability in a population of clones, within-herd selection no longer offers an opportunity for genetic improvement. Additionally, the lack of genetic variability could render the herd vulnerable to a catastrophic disease outbreak, or singularly ill-suited to changes that may occur in the environment. On January 15th, 2008 the FDA published its final 968-page risk assessment on animal cloning which examined all existing data relevant to 1) the health of clones and their progeny, or 2) food consumption risks resulting from their edible products, and found that no unique food safety risks were identified in cloned animals. This report, which summarizes all available data on clones and their progeny, concludes that meat and milk products from cloned cattle, swine and goats, and the offspring of any species traditionally consumed as food, are as safe to eat as food from conventionally bred animals (http://www.fda.gov/cvm/CloneRiskAssessment_Final.htm; Accessed 3/09/10).

Although cloning is not genetic engineering per se, there is a logical partnership between the two technologies. Cloning offers the opportunity to make genetically engineered or transgenic animals more efficiently from cultured somatic cells that have undergone precise, characterized modifications of the genome. The first genetically engineered mammalian clones were sheep born in 1997 carrying the coding sequences for human clotting factor IX, which is an important therapeutic for hemophiliacs (Schnieke et al., 1997). Cloning has also be used to generate genetically engineered cows that produce human polyclonal antibodies (Kuroiwa et al., 2002). It is envisioned that these unique cows will make it possible to create an efficient, safe, and steady supply of human polyclonal antibodies for the treatment of a variety of infectious human diseases and other ailments including organ transplant rejection, cancer and various autoimmune diseases, such as rheumatoid arthritis. Cloning also offers the possibility of producing animals from cultured cells that have had selected genes removed. This "gene knockout" technique, commonly used in research with mice and the subject of the 2007 Nobel Prize in medicine, enables selective inactivation of specific genes in livestock with applications for both agriculture and biomedicine. For example, cloning has been successfully used to produce cattle from cells lacking the gene for the prion protein responsible for mad cow disease (Kuroiwa et al., 2004).

Genetic Engineering of Cattle

Genetic engineering is the process of stably incorporating a recombinant DNA sequence (i.e. a DNA sequence produced in a laboratory by joining pieces of DNA from different sources) into the genome of a living organism. What this means is that new genes, possibly derived from different species, can be directed to make novel proteins in genetically-engineered organisms. Genetically engineered organisms are commonly referred to as "transgenic", "genetically-modified", "GMO", or simply "GE". Genetic engineering has been successfully used to make transgenic cattle, although none have been approved for commercialization or entry into the US marketplace (Table 2). The Food and Drug Administration (FDA) is the agency responsible for regulating genetically engineered animals.

Genetic engineering might find a place in agricultural production as a way to change the nutritional attributes or improve the safety of animal products in ways that are not possible through traditional selection techniques. Such applications might include milk lacking allergenic proteins or containing viral antigens to vaccinate calves against disease, or beef optimized for human nutrition. Genetic engineering in conjunction with SCNT cloning could also be used to remove or "knock out" certain proteins from the genome of cattle. Genetic engineering could conceptually be used to improve production traits in cattle. It is unlikely that this will be implemented in the near future due in part to the difficulty in identifying genes that might be good candidates to positively influence these complex, multigenic traits. Additionally, genetic improvement for most production traits can be effectively achieved using traditional selection techniques, without the expense and time involved with the production and regulatory approval of genetically engineered organisms.

The application of genetic engineering in cattle that is the most likely to be cost-effective, at least in the near future, is the production of useful protein products – such as human hormones or blood proteins—in the milk of genetically engineered cows. Such animals would not be destined, or permitted, to enter the food supply. Several human therapeutic proteins have been produced in cattle (Salamone et al., 2006; van Berkel et al., 2002; Wang et al., 2008). The first human therapeutic protein,

Table 2. Existing and potential genetically engineered cattle applications for agriculture.

EXISTING TRANSGENIC CATTLE	Target Gene	Approach	Reference
BSE resistance	Prion	Knockout	(Richt et al., 2007a; Richt et al., 2007b)
Mastitis resistance	Lysostaphin	Transgene overexpression	(Wall et al., 2005)
Mastitis resistance	Lactoferrin	Transgene overexpression	(van Berkel et al., 2002)
Increase cheese yield from milk	β-casein, κ-casein	Clone/Transgene overexpression	(Brophy et al., 2003)
CONCEPTS UNDER DEVELOPMENT	**Target Gene**	**Approach**	**Reference**
Increased lean-muscle growth	Myostatin	RNAi /Knockout	(McPherron and Lee, 1997)
Suppressing infectious pathogens	RNA viruses (eg. foot and mouth, fowl plague, swine fever)	RNAi	(Clark and Whitelaw, 2003; Whitelaw and Sang, 2005)
Coronavirus-resistance	Aminopeptidase N	RNAi /Knockout	(Schwegmann-Wessels et al., 2002)
Low lactose milk	Lactase	Transgene overexpression	(Jost et al., 1999)
Low lactose milk	α-lactalbumin	RNAi /Knockout	(Stacey et al., 1995)
High omega-3 fatty acid milk	n-3 and n-6 fatty acid desaturase	Transgene overexpression	(Morimoto et al., 2005)
Resistance to Brucellosis	NRAMP1	Transgene overexpression	(Barthel et al., 2001)

Antithrombin III (ATryn®, GTC Biotherapeutics, Framingham, MA), derived from the milk of genetically engineered goats has been approved by the European Commission and the FDA for the treatment of patients with hereditary antithrombin deficiency. These "biopharming" applications have the potential to produce large amounts of human therapeutics at a low cost relative to the current mammalian cell culture techniques. It remains to be seen whether any of these potential benefits are sufficient to outweigh the considerable time and expense involved in the development and approval of genetically engineered cattle.

Conclusion

DNA-based technologies are developing at a rapid pace. It is likely that these technologies will play a progressively important role in beef production and marketing in the future. DNA-based tests can be used for various purposes; for example selection and breeding decisions, feedlot sorting, pedigree verification, and as a marketing tool. Estimates of DNA test performance (e.g. proportion of genetic variation accounted for by a DNA test panel) and accuracy in representative populations will be required to evaluate their use for selection, and also for incorporation of DNA data into the existing genetic evaluation infrastructure. Whole genome selection has the potential to improve traits that are currently intractable (feedlot health, feed efficiency, palatability). As a result of experiments with the 50,000+ SNP chip in cattle, it is likely that the number and accuracy of DNA-based marker tests will increase in the coming years, and eventually "DNA-adjusted EPDs" will become a reality. In the meantime, however, the increased economic returns from using DNA-marker tests and ultimately incorporating them into the national cattle evaluations must outweigh the costs (DNA sampling, genotyping, phenotyping) associated with obtaining the additional genetic information.

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Utilizing Molecular Information
in Beef Cattle Selection

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Molecular sources of information represent a rapidly developing technology with regards to beef cattle selection. Given the rapid commercialization of DNA marker panels, producers have been able to see changes first hand in reporting styles, panel sizes, and traits for which panels are available. Unfortunately, the power of this technology will only be fully exploited when it is seamlessly integrated into National Cattle Evaluations (NCE).

Utilization of Molecular Information to Date

DNA information has been effectively utilized to identify animals that are carriers of recessive alleles. This has been of particular interest for genetic defects, color, and horned/polled status. Prior to the advent of this technology the only way to test if a sire was a carrier of a particular genetic defect was to mate him to a given number of known carriers of the defect or an even greater number of his own daughters of unknown genotype. Even then definitive conclusions could only be drawn if he sired an afflicted calf. If all corresponding offspring were free of the defect, then it would be possible to assign a certain probability to the sire being a non-carrier with the probability being dependant on the number of calves born from a particular mating. DNA-marker technology has also proven very beneficial in determining parentage. More recently, SNP panels have been developed to test for a portion of the genetic merit of an animal for a variety of traits ranging from fertility and longevity, to growth and carcass merit.

Methods of Reporting (past and present)

Many of the early recording systems to relay marker panel results were categorical in nature. For instance, systems existed that provided one star for each favorable allele regardless of the proportion of variation explained by the marker. Others provided a 1-10 scale where genotypes were categorized by the impact they had on the trait of interest. Neither of these systems allowed for the inclusion of these results in NCE. More recently marker panel results have been reported as Molecular Breeding Values (MBVs). Although MBV is the term that is being used by the scientific community, DNA testing companies have created unique names to identify their respective products in the market place (i.e. Molecular Value Prediction [MVP] and Genetic Prediction Difference [GPD]).

Differences between MBVs and EPDs

EPDs provide an estimate of the genetic potential of an animal as a parent based upon ancestral information; his/her own records, and the records of his/her progeny. With this in mind, an EPD accounts for all the genes that affect a particular trait, regardless of the magnitude of their affect. While an EPD accounts for all of the additive genetic variation, the specific sources of the variation (genes) are unknown. Conversely, DNA marker tests reveal the genotype of an animal for specific DNA markers for a particular trait but, to date, do not account for all of the genetic variation. This is simply due to the fact that the markers or genes with the largest effects are the easiest to identify and become the logical candidates for inclusion in marker panels. The potentially infinite number of markers or genes with much smaller effects are more difficult to identify, and consequently have not been included in the development of marker panels.

The other caveat is the inherent difference between an EPD and an estimated breeding value (EBV). An EBV is the genetic merit of an animal whereas an EPD is the genetic merit of an animal as a parent given that an animal can only pass on a sample half of its alleles to the next generation. The relationship between the two is as follows:

$$EPD = 1/2(EBV)$$

Although some DNA companies report results in a form that looks similar to an EPD in that it is reported in units of the trait, the values are EBVs based on molecular information. To determine how much better one animal is versus another as a parent, EBVs must be divided by two.

It is critical to understand that a desirable genetic test result with current commercially available panels is not always associated with a desirable EPD. For instance, it would be possible for an animal to be homozygous for the favorable allele for a DNA marker for marbling but still have a marbling EPD that is below breed average. This could occur because, although the animal has the favorable form of both alleles of one of the genes affecting marbling, it may have unfavorable alleles for numerous other unknown genes that affect marbling as well.

Accuracy

When DNA from an animal is submitted for a DNA-test, there is an accuracy associated with that result. Accuracy has multiple meanings. One definition is "degree or extent of freedom from mistake or error". Genotyping generally has a high level of technical accuracy or precision, meaning that there are rarely errors in the actual results of the DNA test. However, in animal breeding, accuracy refers to how well an estimate of the genetic merit (e.g. EPD, or DNA-test result) predicts the true genetic merit of an animal. One measure of this genetic prediction accuracy is the correlation (r) between a genetic merit estimate and the true genetic merit of that animal. Accuracy values can range from 0 (in which case the estimate has no relationship to an animal's true genetic merit) to 1 (in the theoretical situation where the estimated breeding value is equal to the true breeding value). In practice accuracy values never reach the theoretical limit of 1, although very high accuracy of extensively used AI sires can reach 0.99.

In some countries, the accuracy of a genetic prediction (EPD in the U.S.) is reported as the correlation between the estimated value and the "true" value. With progeny test information, this accuracy measure quickly attains a high value as progeny numbers exceed 20, especially for traits with moderate to high heritability. Traits that are lowly heritable, such as reproductive traits, require more progeny records to attain the same level of accuracy as a trait that is moderately to highly heritable.

The U.S. beef industry reports accuracy using standards suggested by the Beef Improvement Federation (BIF). The BIF accuracy scale is based on minimizing Prediction Error Variance (a measure of the magnitude of errors in predicting breeding values), rather than using *the correlation* between the estimated and true breeding value. BIF accuracies are more conservative than the simple correlation, in that they require more data (e.g. progeny records in the case of a bull evaluated from a progeny test) to achieve high accuracy values. Table 1 illustrates this point.

Table 1. Accuracies of estimated breeding values based on (A) the correlation with true breeding values (r), and (B) the BIF standard, and the number of progeny test records required to obtain these accuracy values for traits of low (0.1) and moderate (0.3) heritability.

Correlation (r)	BIF Accuracy	Number of Progeny Records Required	
		Low Heritability (0.1)	Moderate Heritability (0.3)
.1	.01	1	1
.2	.02	2	1
.3	.05	4	2
.4	.08	8	3
.5	.13	13	5
.6	.20	22	7
.7	.29	38	12
.8	.40	70	22
.9	.56	167	53
0.99	.93	1921	608
0.995	.99	3800	1225

The accuracy associated with EPDs increases as more information becomes available. Initially EPDs are derived from the average of animals' parents (called a pedigree estimate). Once an animal has a record, the accuracy of the EPD increases and continues to do so as the animal has recorded progeny. Unfortunately this takes time and for some economically relevant traits (ERTs) it is not possible for animals to have a record themselves or the record may occur very late in life (i.e. stayability). New metrics for estimating the "accuracy" of DNA tests have been developed based on the relationship between MBVs and the trait of interest, some of which are published by DNA testing companies to accompany marker panel results. It is critical to understand that at present, these values are not directly comparable to the BIF accuracy values associated with EPDs.

Example. Assume that a DNA test has a genetic correlation of 0.8 with the trait of interest. This would equate to a BIF accuracy of 0.40. For traits that are hard to measure or measured late in life this would be very beneficial. Seedstock producers could identify superior animals earlier in life and commercial producers who purchase unproven sires could reduce the risk associated with low accuracy values. However, if the genetic correlation between the molecular test and the trait of interest is low (0.02) then the value of using only the genetic test score for the purposes of selection is dramatically decreased, especially in the context of having available EPDs for the trait of interest. The greatest benefit in accuracy should come from the integration of DNA tests scores along with phenotypic records in the calculation of EPDs.

The reason that DNA tests are able to increase the accuracy of EPDs is that they have the ability to account for a phenomenon called "Mendelian sampling". This term is used to describe the random sampling that occurs when parents pass on a random sample of half of their DNA to their offspring. Every allele, good or bad, has an equal likelihood of being inherited. One could envision a scenario where an animal could receive only the most desirable alleles from both parents resulting in a large favorable Mendelian sampling effect or the exact opposite which could result in a large unfavorable sampling effect. Perhaps the best example of this is a set of flush mates. Although all of them have the same pedigree estimate, they may differ considerably in terms of their performance and ultimately their EPDs due to Mendelian sampling. This effect can be quantified using contemporary group deviations and is a measure of how much better or worse an animal is compared to the average of its parents. Mendelian sampling is the reason that performance records on the individual and its progeny are required to obtain accurate genetic predictions. Individual records provide some information on the sampling of alleles inherited by an animal, and progeny information provides even greater insight as to the sum of the additive effects that the animal is passing to the next generation. DNA tests have the potential to view into the black box of Mendelian sampling at birth and reveal what alleles an animal inherited.

The accuracy of a DNA test at predicting the true genetic merit of an animal is primarily driven by the amount of additive genetic variation accounted for by the DNA test. Thallman et al. (2009) found that the best predictor of this proportion was the square of the genetic correlation between the MBV and the trait of interest. The first generation of DNA tests for complex traits in beef cattle did not have high accuracies because the small number of markers included in these tests were associated with only a small proportion of the additive genetic variation for the trait of interest (Allan and Smith, 2008). As the number of informative markers in a DNA test increases so will the proportion of additive genetic variation explained by the test.

Since the first marker tests were developed, a large number of SNP markers have been identified in the bovine genome. As a result, companies have started to develop tests using multiple (10-200) SNPs to develop marker panels to predict an animal's genetic merit. In January 2010, Pfizer Animal Genetic announced the availability of a 50,000 marker DNA test for Angus cattle (http://www.pfizeranimalgenetics.com/Pages/HD50KRelease.aspx). As marker panels grow they track the inheritance of an increased number of genes, and if these genes are associated with genetic variability in the trait under selection then these tests will explain a larger proportion of the overall genetic variation for that trait.

What is the benefit of higher accuracy values on young sires? For the seedstock producer, it enables the selection of truly superior animals earlier in life and potentially decreases the number of animals to place on test. It also allows seedstock producers to supply clientele with a product that has less risk of change associated with it. The benefit to commercial producers lies in the ability to buy yearling bulls with more certainty surrounding their EPDs.

Example. Assume a commercial producer wants to purchase a calving ease bull for use on heifers. If a bull does not have a record of calving ease himself, the BIF accuracy might be 0.20.

Assume that the possible change[1] value associated with this accuracy level is 6 and that his published EPD is +5 (breed average in this case). In this situation, we would be 68% confident that this bull's "true" EPD for calving ease is between -1 and +11 realizing that for calving ease a larger number is more desirable since it is interpreted as the percentage of unassisted births. However, if the accuracy were higher (0.5) this would mean a small possible change value (4) so we would then be 68% confident that his true EPD would be between +1 and +9.

Increased accuracy values can aid in the selection of truly superior animals. For instance, if calving ease is a concern for a commercial producer who buys yearling bulls then there is an inherent risk that the bull's true genetic merit and his predicted genetic merit are not close. It would be advantageous to have more information from which to predict the genetic merit of yearling animals so that the predicted value was a closer estimate of the true value.

Example. Assume that two yearling bulls both have a calving ease direct EPD of +5 and that the possible change values associated with them are +6. In this scenario both bulls would be equally likely to be candidates for selection. However, assume that we were able to garner more information, in the form of a marker panel test, and thus increase the accuracy values of both bulls by joining the results of the marker panel and the information included in the EPD. Perhaps we would find that one bull is actually a -1 and the other bull's is a +11. In this case the two bulls seemed equally valuable based on their low accuracy EPDs but as the accuracy values increased and we were able to get a clearer picture of their true genetic potential as parents we found one bull is actually superior over the other. In this example, the difference between the two bulls is actually 12 or one bull is likely to have 12% fewer assisted births than the other. If multiple bulls were purchased with the same low accuracy EPDs (in this case +5) it could be argued that the average of the "true" values would still be close to +5 even though some are likely to be higher and some lower. However, for a trait like calving ease, it is advantageous to eliminate bulls that may create calving difficulty even if the average of an entire bull battery is acceptable.

Shorter Generation Interval

Combining phenotypic and molecular data, particularly for traits that cannot be measured early in life, can lead for faster genetic change. The factors that impact the rate of genetic change are the accuracy of selection, the genetic standard deviation, the selection intensity, and the generation interval. Generation interval is defined as the average parental age when the offspring

are born. Typically this is six years of age in beef cattle. Genetic change per year can be derived by:

$$\frac{(\text{Accuracy of Selection})*(\text{Selection Intensity})*(\text{Genetic Standard Deviation})}{\text{Generation Interval}}$$

It is clear that if the generation interval were to decrease then the rate of genetic change would increase. For seedstock producers, the ability to use a yearling sire heavily due to increased confidence in his EPD could reduce generation interval and thus lead to faster genetic progress.

The benefits of including molecular information in the calculation of EPDs for yearling bulls will depend on the marker panel itself. The more genetic variation that is explained by the panel the larger the increase in accuracy. Marker panel results should be thought of as another phenotype, correlated to the trait of interest, which can be included in the genetic prediction. In other words, the addition of the DNA panel phenotype adds to the amount of information and consequently provides an increase in accuracy proportional to the amount of variation explained by the panel.

Paradigm of Disjointed Pieces of Information

Differences in reporting styles, between EPDs and molecular test results and even between DNA companies, have led to a plethora of confusion. There are seemingly two distinct pieces of information, marker panel results and EPDs, which due to the sources of information included in them can potentially be in disagreement. This has often begged the question of which to use. Sometimes it has led to the belief that one must be incorrect.

Benefits of Combining Molecular and Phenotypic Data

An obvious benefit of combining traditional phenotypic based EPDs and the results from marker panel results is less confusion. No longer would there be a question as to which one to use. However there are other, more quantitative benefits such as the potential to increase the accuracy of EPD predictions in young animals thereby potentially enabling a decrease in the generation interval leading to more rapid genetic change.

Methods of Combining MBVs and EPDs

Rather than thinking of DNA-marker panel results as being separate and disjointed pieces of information, test results should be thought of as an indicator trait that is correlated to the trait of interest. As such, the MBVs can be included in NCE as a correlated trait. In this scenario it will be important to estimate the heritability of the marker score and the genetic correlation between it and other production traits as well as the phenotypic variation of the marker score. Kachman (2008) suggested that marker scores (MBVs) have a number of advantages over using the marker panel data (genotypes) directly. Three primary advantages are:

1. It reduces the amount of data that must be processed when conducting a genetic evaluation.

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[1] Possible change values are standard deviations and are a measure of risk associated with different accuracy values. Possible change values differ between breeds and between traits. Updated possible change values can be found on breed association websites.

2. Markers used in the test (panel) do not have to be identified.
3. It allows for advances in DNA tests and statistical methodology to be taken advantage of in a timely manner.

One major caveat to this approach is the need to clearly identify evolutions in marker panels. For instance, if company X has a marker panel for some trait that includes 50 SNPs and the panel is later updated to include 100 SNPs it is important to be able to identify which panel was used. Futhermore, the covariances between marker scores generated by different tests within a company and for tests between companies will need to be estimated given that there are likely differences in the amount of additive variance explained by the variety of tests that are either currently available or that will be available in the future. Other methods have been proposed including adjusting the additive variance of the trait of interest and the appropriate (co)variances for the amount of variation explained by the molecular source of information (Spangler et al., 2007), and using large (50,000+) SNP panels to form a genomic relationship matrix in place of the traditional pedigree based relationships that are currently used.

MacNeil et al. (2010) utilized Angus field data to look at the potential benefits of including both ultrasound records and MBVs for marbling as correlated traits in the evaluation of carcass marbling score. MacNeil and colleagues used a 114-SNP marker panel that was developed using 445 Angus animals and calculated to have a genetic correlation (r) of 0.37 with marbling score (i.e. the test explained $(0.37)2 = 0.137$ or 13.7% the additive genetic variation). For animals with no ultrasound record or progeny data, the marker information improved the BIF accuracy of the Angus marbling EPD from 0.07 to 0.13. Assuming a heritability of 0.3 for marbling, a BIF accuracy of 0.13 is equivalent to having approximately 5 progeny carcass records on a young animal (Table 1) or an ultrasound record on the individual itself. In this particular study, both ultrasound records and MBVs were found to be beneficial indicators of carcass marbling. The genetic correlation between MBVs and ultrasound was found to be 0.80, suggesting that these two were not explaining the same sources of variation and thus were both beneficial when included as correlated traits in the model.

In the context of utilizing marker panels that explain less that 100% of the additive genetic variation, collecting phenotypes is beneficial particularly at the nucleus level. Garrick (2007) illustrated an example of different selection schemes to improve carcass marbling using combinations of phenotypes and molecular information. Five possible selection schemes illustrated were as follows:
1. Measure carcass marbling scores on progeny test offspring of young bulls bred in the nucleus herd prior to their widespread use in the bull breeding herd (prior to use to produce seedstock for the multiplier and commercial levels).
2. Measure ultrasound IMF% on all yearling males in the bull breeding herd (nucleus herd).
3. Measure ultrasound IMF% on all offspring bred in the nucleus herd.
4. Genotype all young bulls in the bull breeding herd.
5. Genotype and measure IMF% on all males in the bull breeding herd.

In his example, Garrick assumed that the heritability of carcass marbling was 0.54 and the phenotypic and genetic standard deviations were 0.88 and 0.65, respectfully. Finally it was assumed that the heritability of IMF% was 0.50 and the genetic correlation between carcass marbling and IMF% was 0.72. Under these assumptions using a marker panel that accounted for 10% of the additive variation in place of collecting ultrasound information was less beneficial than collecting ultrasound information and even a panel that accounted for 50% of the variation was not more profitable than collecting IMF% in both sexes.

The American Angus Association has announced that they are going to develop "genomic-enhanced EPDs" by integrating IGEN-ITY profile for Angus DNA marker results for carcass traits into their NCE (http://www.angus.org/Pub/Newsroom/Releases/AGI_Igenity_EPDs.html; Accessed 3/09/10). This development, along with the integration of DNA markers into tenderness breeding values reported by the Animal Genetics and Breeding Unit of the University of New England in Australia (Johnston et al., 2009), represent important milestones in the application of DNA testing in beef cattle.

A Model for the Flow of Data

Tess (2008) detailed a model for the evaluation of commercial marker panels (Figure 1) and the incorporation of different sources of information including DNA test information from multiple companies into NCE on an ongoing basis (Figure 2). In this model the National Beef Cattle Evaluation Consortium (NBCEC) serves as the independent source of validation. The evaluation of DNA tests includes:
1. The delivery of DNA samples from reference populations to the DNA testing company that developed the test.
2. The company genotypes the samples and calculated the molecular score.
3. The company communicates the molecular score to the independent validation entity.
4. The validation entity performs the statistical evaluation of the molecular scores using pedigree and phenotypic information from the reference population.
5. The results of the statistical analysis are communicated to the DNA testing company and to the public.

This model would allow for the calculation of covariances between the DNA test and the target trait, covariances between competing DNA tests, and covariances between the DNA test and non-target traits and finally the calculation of EPDs and associated accuracy values on the BIF scale.

Economics

DNA testing presents a marketing opportunity for bull sellers. Early adopters, those who have panel information sent to breed associations for inclusion in genetic evaluations, may have a competitive advantage over other seedstock producers who do not. This assumes that bull buyers are willing to pay more for yearling bulls with higher accuracy values. The process of collecting DNA samples and then paying for a diagnostic test for a particular trait represents an additional cost to the breeder. Some seedstock producers are currently DNA-testing their bulls to provide potential buyers with DNA information. The value of that information to the buyer is will be determined by the market.

If the value is deemed to be more than the cost of testing and is reflected in the bull purchase price, then the seedstock producer will have improved his/her bottom line.

DNA testing also presents an opportunity accelerate the rate of genetic progress through marker-assisted selection (MAS). The important question to ask regarding this application is "Does DNA testing increase the accuracy of the genetic prediction (e.g. EPD) of young animals sufficiently to justify its cost?" There is undoubtedly value associated with increasing accuracy. This is perhaps best reflected by the higher price of a straw of semen from a well proven AI bull, versus the price of semen from a low-accuracy, unproven bull with the same EPD values and by the risk associated with selecting an unproven bull by commercial producers. High accuracy of selection can almost always be achieved for a highly heritable trait like marbling, but accumulating the necessary data takes time, lengthening the generation interval, and is associated with increased costs. Likewise, generation interval can be shortened by the use of younger, less proven sires, but accuracy typically suffers under that scenario. Genetic tests have the potential to decrease the generation interval by improving the accuracy of genetic merit estimates associated with young sires.

The value of increasing accuracy will also depend on whether the trait in question is an economically relevant trait (ERT), and the availability and accuracy of existing genetic merit estimates. It may be that DNA-based approaches allow for the development of genetic merit predictions for economically relevant traits that are not currently part of beef cattle genetic evaluation programs (e.g. adaptability, feed efficiency). If these traits are ERTs, meaning traits that directly affect profitability by being associated with a specific cost of production or a revenue stream, then some estimate of genetic merit is better than none. However, the aggregate economic value of including that trait in selection decisions must outweigh the costs of obtaining the genetic estimate and associated effects on other economically relevant traits.

The economic benefits associated with MAS relative to the costs involved in running a small number of markers accounting for a modest amount of the genetic variance in a limited number of complex traits in beef cattle have not been well characterized from a scientific viewpoint, as evidenced by the lack of published results on this topic. However, the joint analysis of both phenotypic and molecular information has the potential to enhance the bottom line of both DNA testing companies and producers. Similar to ultrasound in the early 1990's, DNA technology is at a critical point. It seems reasonable to expect that if marker panels are included in NCE, they will eventually become a regular part of information collection for the seedstock industry, as has become the case for ultrasound data (Moser, 2008).

Other Considerations

There are other considerations associated with the use of DNA tests in beef cattle breeding that have not yet been fully addressed. One is the issue of breed differences with regard to allele frequency (Johnston and Graser, 2010). If a marker is found to have a large effect in one breed, but to the close to fixation (frequency close to 1) in another breed, then it is probably not worth applying selection pressure to increase the frequency of that marker in the second breed since most animals will already be homozygous for it.

Gene markers effects have also been found to vary between independent datasets and in breeds outside of those used for discovery (i.e. population where the markers were discovered). Marker panels are likely to work best in discovery populations and be less predictive of genetic merit in more genetically distant populations or breeds. Johnston and Graser (2010) found that markers which worked well in temperate breeds did not always work well in tropical breeds. This suggests that a test developed in an Angus discovery population, as in the following example, might be expected to work well in an Angus target population, but not in a Bos indicus target population.

1. Angus (discovery) -> Angus (target)
2. Angus (discovery) -> Charolais (target)
3. Angus (discovery) -> *Bos Indicus* (target)

This premise has yet to be thoroughly tested in beef cattle populations, although there are existing projects that are working to, at least in part, answer this question (Pollak et al., 2009). Another important consideration is genetic correlations that may exist between marker panels and secondary traits (i.e. non-target traits). Prior to using marker information for selection, it should be confirmed that the marker panel does not have undesirable correlations with other non-target traits.

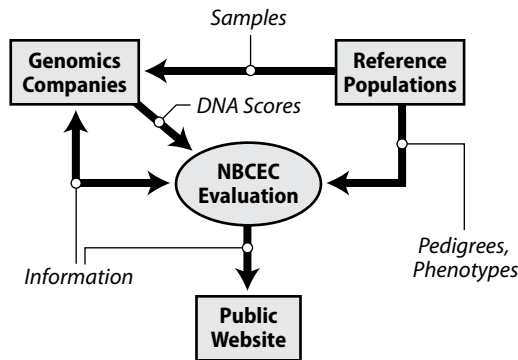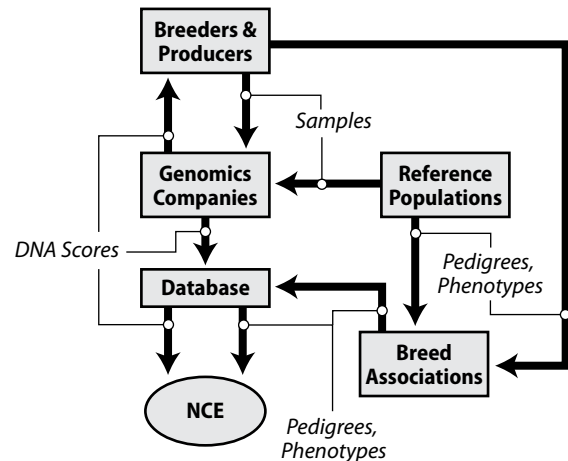**Figure 1.** Model for the evaluation of commercial DNA tests (Tess, 2008).

Figure 2. Model for the incorporation of DNA test information into national cattle evaluations (Tess, 2008).

The Future

Marker panels are likely to continue to grow in size and in the future it may even become cost-effective to obtain whole genome sequence on individual animals, i.e. sequence all 3 billion base pairs! These technology advances could enable selection decisions to be made solely on the basis of DNA information, an approach entitled "whole genome selection" (WGS). WGS is a form of MAS that uses thousands of markers distributed throughout the genome to make selection decisions. With WGS, thousands of animals that have phenotypes for a given trait are genotyped, and these data are then used to develop a prediction equation that predicts how well an unknown animal will perform for that trait based on its DNA genotype alone (Meuwissen et al., 2001). Currently genome selection in beef cattle is in its infancy. Although preliminary data coming from the dairy industry look promising (VanRaden et al., 2009), evaluation and validation of the technology for the beef industry will be required before adoption.

Some of the significant hurdles for the successful implementation of WGS in the beef industry include data suggesting large discovery populations (i.e. thousands) of genotyped and phenotyped cattle are going to be needed to make WGS prediction equations accurate in unrelated animals (Goddard, 2009). Additionally, it has been shown that DNA tests developed in one breed are considerably less predictive (i.e. do not work as well) when used in a different breed (de Roos et al., 2008). Given that there are numerous important beef cattle breeds with dozens of traits of economic importance, it is conceivable that beef cattle discovery populations for WGS will need to be very large. It is also likely that populations of animals will be needed to continually update the association between markers and traits of interest. The selection of young animals as parents based on their genotype will likely result in some SNP alleles becoming fixed. This will effectively decrease the proportion of genetic variation explained by a panel of DNA markers over time. In the absence of periodic reevaluation of SNP effects, it is possible that selecting young animals over several generations would have the effect of decreasing the accuracy of selection.

Summary

The advent of molecular information in the form of both tests for simply inherited traits and complex traits has created both excitement and confusion. The lag between discovery and application has been decreased, allowing for technology to be rapidly delivered to industry. In some cases this has caused confusion surrounding the methods for incorporating this technology into breeding schemes. DNA marker tests results should not be used to replace traditional selection based on EPDs and economic index values, but rather should be seen as providing an additional source of information from which to predict genetic merit. When included in the estimation of genetic predictions DNA information provides valuable information on young animals which could improve the accuracy of genetic predictions. DNA testing holds the greatest promise for economically-relevant traits which are too expensive to measure, and for which no good selection criteria exist (e.g. residual feed intake). Commercial companies have started to offer genetic tests for such traits. Meaningful incorporation of these traits into national cattle evaluations will be required to make the best use of DNA information, and such efforts will call for collaboration between DNA companies, producers, scientists, and breed associations.

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Summary

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As discussed throughout this manual, a producer's decision-making skills in herd genetics can greatly impact bottom-line economics. Through the dedicated hard work and immense economic investment of countless seedstock producers, university geneticists, and breed association staffs, our current generation of cattle producers has at their disposal the greatest tools for selecting bulls ever imagined. The work at hand is the incorporation of these tools into beef herd management schemes.

Genetic change in the past has been slow due to selection technique methodology with low accuracy. However, in today's beef systems, directional and actual change can come about quickly because of improved accuracy of breeding value prediction. The key element for cattle producers is to be certain of the direction taken with selection decisions. This correct direction is ascertained by within-herd measurement and realization of attaining market goals while utilizing farm/ranch resources in an optimal and sustainable manner.

Genetic and economic research has shown that cattle producers are working with an animal that has heritable and economically important traits that will respond to the general principles of genetic selection. Additionally, research clearly shows that production traits vary in their level of heritability, so traditional methods of culling and selecting superior animals, while working in certain lowly heritable trait areas, will yield very limited gains. Fortunately, Mother Nature and dedicated breeders of the past have given us breed diversity, which allows us to utilize crossbreeding programs for strengthening trait areas through complementarity and hybrid vigor.

Professional sire selection is not going to be done with the same technique and with the same emphasis of traits by every producer in this country, nor in a state or, for that matter, within a rural community. Each producer has his or her own: 1) type of operation (seedstock versus commercial), 2) unique micro-environment to deal with, 3) unique set of economic circumstances, 4) marketing plan, 5) end product customer needs, and 6) unique set of family and operational goals. All of these unique factors call for different methods in defining a product for the marketplace and approaches in genetic selection. Would one expect a commercial producer selling calves right off the cow to have the same selection goals as a commercial producer retaining ownership all the way to the harvest plant? Would one expect a commercial producer in the desert southwest or in the humid, high rainfall area of the southeast United States to have the same selection goals and methodologies as one in the Corn Belt? In addition, would one expect seedstock producers to have the same selection goals if they are servicing commercial operations with this type of variation?

As pointed out in this manual, there are economically relevant traits for all operations and the selection of seedstock for superiority in a trait area can and will impact performance and economic returns within the operation. Keep in mind that for every selection action, there is a performance reaction. While our intention is that this first performance reaction is profitable, we may find some negative performance reactions may occur that may reduce or completely eliminate any economic gain. For instance, selection for superior growth can lead to increases in mature size and females too large for the forage resources existing on the operation. This in turn leads to either greater supplementation needs or lowered reproductive rates, which potentially have negative connotations to an operational bottom line. Our only solution to improving the likelihood of moving the operation ahead economically is to incorporate decision-making tools into the selection process, thus reducing judgment errors. With the proliferation of EPD availability, producers will be utilizing economically weighted selection indexes that incorporate many EPD and the economic relationships that exist on their operation.

While we can get completely wrapped up in assessing genetic performance in reproduction, growth, and end product traits, it is imperative that we not forget that beef cattle are a means of harvesting forages and manufacturing co-products for the production of a high-quality protein source for human consumption. This can only be done efficiently if cattle are structurally sound, have longevity, and are easy to handle. The culling of females or bulls early in their lives due to disposition problems, lameness, unsound udders, or other abnormalities is too costly. Critical judgment in this area is important.

The beef industry has an exciting genetic future. As one reflects on what has happened in DNA-based technology and genetic marker additions to the selection tool chest, one has to be excited for what lies in our future. At the end of the first decade of the new millennia enormous breakthroughs have occurred with the addition of a 50,000 plus SNP chip panel which is allowing advancements in whole genome prediction of molecular breeding values for currently utilized traits with other traits being added at this writing. Just as computers have advanced at a rapid pace it is likely that much larger and more economical SNP panels will be developed allowing scientists to better define breeding values with this advanced DNA technology. Will these new technologies muddy selection decisions or enhance them? A role of the National Beef Cattle Evaluation Consortium (NBCEC) is to assist breed associations in incorporating DNA technology into their genetic predictions; thus, the end product of future genetic evaluations will be EPDs enhanced with DNA technology allowing for more accurate genetic predictions earlier in an animal' life. Our future in beef cattle selection and mating will definitely be changing; it is our challenge to learn to make wise decisions and capitalize on these advancements.

Sire selection is one of the most important and economical activities in a beef operation. This will not diminish in the future. Producers need to continuously improve their knowledge base in herd evaluation, nutrition and health management, and genetic selection for improved economic returns. Reading and understanding information from this NBCEC Beef Sire Selection Manual is a significant step in achieving an improved knowledge base for managing the beef operation.

Author Biographies

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Originally from Muscatine, Iowa, Dr. Jennifer Minick Bormann, grew up working on a small purebred cattle and horse operation. She earned a B.S. in animal science from Iowa State University in 1997, a M.S. in animal science from Oklahoma State University in 1999, and a Ph.D. in animal breeding and genetics from Iowa State University in 2004. She joined the faculty at Kansas State University in 2004 as an assistant professor with a 75% teaching and 25% research appointment. Jenny specializes in beef cattle breeding and has worked on a number of projects including collaborations with the NCBA and the American Angus Association. Currently she teaches or co-teaches genetics, animal breeding, advanced animal breeding, equine genetics, equine lab, and freshman honors seminar, as well as advises undergraduate students and the KSU Pre-Vet Club.

Darrh Bullock
Extension Professor
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Darrh Bullock grew up on his family's commercial cattle/watermelon farm in north-central Florida. He received his Bachelors degree from Auburn University and started his career as herdsman at Auburn's Lower Coastal Plains Experiment Station. He returned to school and received his Masters degree from Auburn University and Doctorate from the University of Georgia. Darrh joined the faculty at the University of Kentucky in 1992 as an Assistant Extension Professor and currently holds the rank of Extension Professor. His responsibilities are for statewide education in beef production with an emphasis in breeding management. Darrh has served as Eastern Region Secretary of the Beef Improvement Federation, represented the US on the International Committee for Animal Recording Beef Working Group and is currently a member of the Scientific Council for the National Beef Cattle Evaluation Consortium where he serves as co-coordinator of educational programs.

R. Mark Enns
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Mark grew up working on the family's 4th generation wheat and cattle operation in northwest Oklahoma. He received his undergraduate degrees from Tabor College, and Masters and Doctorate degrees in Animal Breeding and Genetics from Colorado State University. He then worked two years in New Zealand for Landcorp Farming Ltd, the largest ranching company in that country, where he was charged with developing and implementing genetic evaluation and selection procedures to improve the profitability of the company. Upon his return to the United States, he spent 4 years at the University of Arizona, before returning to Colorado State University in 2001. Mark teaches both undergraduate- and graduate-level courses in animal breeding and integrated resource management. His research focuses on methods for the genetic evaluation and selection of animals that are adapted to their production environments and will increase profitability. These interests include genetic improvement of female fertility, cow maintenance requirements, feedlot finishing time, and susceptibility to disease. Mark serves on the Scientific Council for the National Beef Cattle Evaluation Consortium and the Board of Directors for the Beef Improvement Federation.

Dan W. Moser
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A native of northeast Kansas, Moser received his B.S. in 1991 from Kansas State University, then earned his M.S. (1994) and Ph.D. (1997) from the University of Georgia in Beef Cattle Breeding and Genetics. He currently serves as Associate Professor in the Department of Animal Sciences and Industry at K-State. He teaches courses in genetics and animal breeding, and serves as advisor to undergraduate and graduate students. His recent research has focused on the use of ultrasound measures in national cattle evaluation for carcass traits, and the impacts of selection for carcass traits on cow reproduction and efficiency. He served as Breed Association Liaison for the National Cattlemen's Beef Association's Carcass Merit Project, a research project studying the genetics of beef tenderness and other carcass traits in fourteen breeds of cattle. Formerly, he served on the board of both the National Beef Cattle Evaluation Consortium and the Ultrasound Guidelines Council. He is a consulting geneticist for the American Hereford Association, and faculty coordinator for the K-State Purebred Beef Teaching Unit. He remains active in his family's Hereford seedstock operation.

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Senior Scientist
PFIZER ANIMAL GENETICS

Janice Rumph is a native of southeast Michigan where she grew up on a small livestock and fruit operation. Janice received her B.S. degree in Animal Science from Michigan State University and her M.S. and Ph.D. degrees from the University of Nebraska-Lincoln, also in Animal Science. While in graduate school, Janice completed research internships with the U.S. Meat Animal Research Center, the North American Limousin Foundation, and the Red Angus Association of America. Since attainment of her doctoral degree, Janice has been an Assistant Professor in the Department of Animal and Range Sciences at Montana State University and Livestock Extension Educator and Adjunct Associate Professor in Animal Science at Michigan State University. She currently is a Senior Scientist with Pfizer Animal Genetics in Kalamazoo, Michigan.

Matt Spangler
Assistant Professor
University of Nebraska-Lincoln

Matt Spangler grew up on a diversified crop and livestock farm in south-central Kansas where his family still farms and has a cow/calf operation. After receiving his B.S. degree in Animal Science from Kansas State University (2001) he attended Iowa State University and received his M.S. degree in Animal Breeding and Genetics in 2003. He received his Ph.D. at the University of Georgia in Animal Breeding and Genetics (2006) and is currently an Assistant Professor and Extension Beef Genetics Specialist at the University of Nebraska-Lincoln. Matt focuses on developing and delivering extension material related to the genetic improvement of beef cattle, within Nebraska and nation wide. The majority of this effort is centered on the use of genomic tools. From a teaching perspective, he coordinates the Nebraska Beef Industry Scholars program and is responsible for the UNL teaching herd and annual bull sale. His research interests include the integration of molecular data into national cattle evaluations. He has served on the Ultrasound Guidelines Council, is a member of the National Beef Cattle Evaluation Consortium Producer Education Team, and serves as a member of the Editorial Board for the Journal of Animal Science.

Daryl Strohbehn
Professor Emeritus
Iowa State University

Daryl Strohbehn was raised on a family-owned cattle and grain farm in northeast Iowa. He received his bachelor's degree from Iowa State University in animal science, and his master's and doctorate degrees from Michigan State University. Strohbehn joined the faculty at Iowa State University in 1974 and retired in 2010 and is currently Professor Emeritus of Animal Science. Strohbehn coordinated outreach efforts in cow-calf production in Iowa for over 36 years with assistance from field staff specialists and other central staff members. He was recognized in the Corn Belt for his work in cow-calf production systems that utilized on-farm resources and correct genetic systems to yield profit. In addition, regional and national educational efforts were done with the National Cattlemen's Beef Association, National Beef Cattle Evaluation Consortium, Beef Improvement Federation, and the Forage and Grassland Council.

Alison Van Eenennaam
Cooperative Extension Specialist
University of California-Davis

Alison Van Eenennaam joined the faculty of the Department of Animal Science as a Cooperative Extension Specialist in Animal Genomics and Biotechnology at the University of California in Davis in 2002. She received her B.S. degree in agricultural science from the University of Melbourne in Australia, and an M.S. in animal science and Ph.D. in genetics from U.C. Davis. Her Animal Genomics and Biotechnology Extension program examines the various pros and cons associated with animal biotechnology, broadly defined as "the application of science and engineering to living organisms". She has focused her program on generating research information and educational materials on the use of DNA information in livestock production systems. Her research interests include the application of DNA-based biotechnologies to the beef cattle industry, and the transgenic modification of milk lipids for the improvement of human health. She has developed a variety of extension programming for beef cattle producers on topics ranging from cloning to marker-assisted and whole-genome enabled selection. Since 2005 she has served as the extension representative on the National Beef Cattle Evaluation Consortium (NBCEC) Industry Council.

Bob Weaber
Assistant Professor
University of Missouri

Bob Weaber, Ph.D., joined the faculty of the Division of Animal Sciences at the University of Missouri in 2004. He serves as the Missouri Extension Specialist-Beef Genetics and is responsible for the development and delivery of innovative educational programming in the area of beef cattle genetics. His recent research has focused on modeling of selection strategies using DNA markers, use of high-density DNA marker data for construction of genomic relationship structures, discovery of markers associated with feed intake and efficiency, and exploration of the phenotypic and genetic relationships between measures of temperament and production/health traits in beef cattle. He serves as Central Regional Secretary of the Beef Improvement Federation, is co-coordinator of the National Beef Cattle Evaluation Consortium education programs and has served on the National Cattlemen's Beef Association Policy Division Board of Directors. He serves as a consultant for several breed associations and beef cattle genomics companies. Weaber grew up on a cow-calf operation in southern Colorado, earning a B.S. and M.S. at Colorado State University. He completed his doctoral studies at Cornell University. While there, he served as the Interim Director of Performance Programs for the American Simmental Association for three and a half years. He earlier was Director of Education and Research at the American Gelbvieh Association.