

Beef Sire Selection Manual

T H I R D E D I T I O N — 2 0 2 1

National Beef Cattle Evaluation Consortium

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The Importance of Sire Selection

Darrh Bullock, University of Kentucky, and Dan W. Moser, Kansas State University

In commercial beef cattle operations, sire selection is the foundation of the genetic potential of the herd. The genetic merit of the herd in conjunction with the environment in which it exists, the management it is subjected to, and the underlying economic factors determine the success of the operation. Sire selection is a critical component of every cow/calf operation; it should not be practiced in isolation but rather in consideration of the other factors involved.

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) (Chapters 5 and 6), but they must accurately and objectively assess their current genetics, resources, and management (Chapter 2). Understanding breed differences (Chapter 10) and knowledge of heterosis and developing a breeding program (Chapter 9) has long been established as one of the most important means to economic success. Furthermore, advances in genomic technology (Chapter 11) have led to EPD with higher accuracy values, particularly in young bulls, which reduces the risk of selection errors due to imprecise genetic merit estimates. Selection indices and decision-support tools have the potential to enhance selection precision by assisting producers to select bulls that have the potential to improve their economic outcome (Chapters 7 and 8). Producers who stay up to date on advances in beef cattle genetics and apply that knowledge to their bull selection decisions should profit from enhanced revenue and reduced production costs.

Opportunity for Genetic Change

Sire selection represents the greatest opportunity for genetic change for several reasons. Genetic change in cow-calf operations can occur both through sire selection and through replacement female selection in conjunction with cow culling. Considering that most producers raise their own replacement heifers rather than purchasing them, 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. Even if the best half of the heifers are retained, some average heifers will be in that group. 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 EPD used primarily to select bulls. When selecting replacement heifers from within your herd, remember that the decisions you make today in sire selection will impact the future genetic potential of your cow herd.

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 relatively few bulls will service a large number of cows, producers can select bulls that target their specific needs even when using 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 usually 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 utilize multiple sources of information to give a clearer representation of cattle's genetic potential, and with increased information comes increased accuracy of selection. If AI is used, even greater accuracy is possible when selecting progeny proven bulls. Bulls used in AI may have high accuracy EPD calculated from thousands of progeny measured in many herds and environments.

Long-term Change

Genetic change tends to be slower than most management decisions, but the consequences are longer lasting. 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 generations.

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 contributions 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 his last sired calves. For this reason, purchases of bulls and semen should be viewed not as a short-term expense, but as 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 an important exercise for many areas of beef production, especially for the breeding program. These goals may be related to reproductive success, calf performance, income, cost containment, or several other targeted areas. Breeding decisions will impact each of these goals. 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. Goals that can be addressed directly through selection are typically called breeding objectives. Breeding objectives should be set to help you meet your overall farm/ranch goals. An example of a breeding objective might be to minimize calving difficulty. Breeding objectives are long-term goals; remember, 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 related to both sources of revenue and cost to determine the production potential of a herd. Data analysis may determine if a herd is performing appropri-

ately for the present level of management or if subtle or drastic genetic changes are in order to meet goals.

Determine Breed Makeup

The first step in assessing a commercial herd is to determine its breed makeup. This will help determine if changes relative to the breeding system (e.g., crossbreeding) are needed. Commercial cattlemen that have cows in the herd that are greater than 75% of one breed should consider changes to the breeding program to take better advantage of crossbreeding. 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 cow herd. 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 is drastically limited.

Determine Mature Weight of the Cows

Genetic trends for mature cow weight have been increasing for many beef breeds (Figures 1 and 2). Many beef producers have done an excellent job of moderating frame size, but this moderation has not been reflected in the mature weight. It is important to remember that cow maintenance requirements are based on cow weight, not frame size. Heavier cows require more nutrition to meet their maintenance requirements.

For most commercial cattlemen, cow maintenance costs are the major production cost for the cowherd. Heavier cattle require more nutrients just to maintain their current condition while conducting normal daily activities (grazing, walking to water, ruminating, breathing, etc.). It is critical to evaluate your cost/return balance in your management system. 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. This situation is difficult to overcome because there is

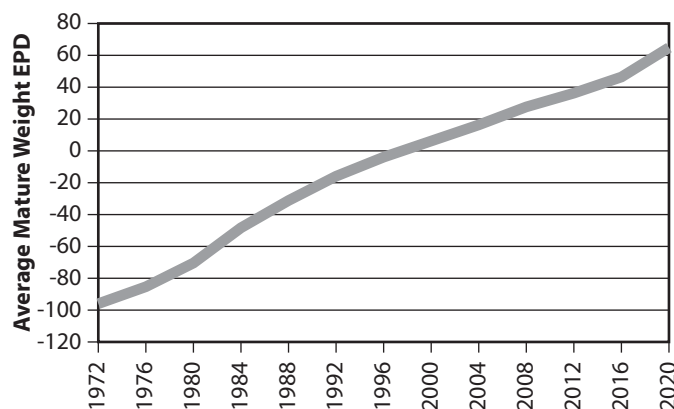


Figure 1. American Angus Association genetic trends for mature weight.

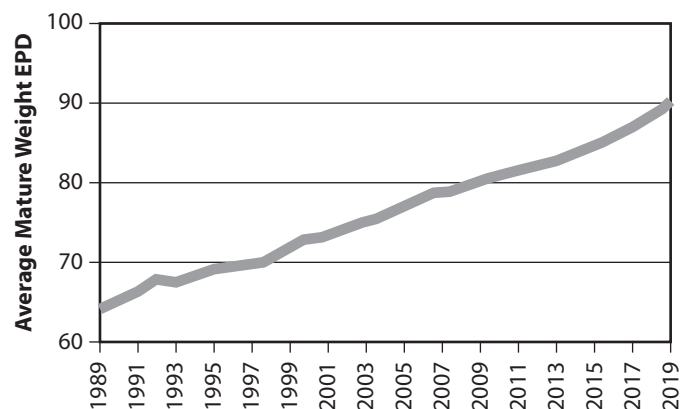


Figure 2. American Hereford Association genetic trends for mature weight.

a moderately high positive genetic correlation between early growth traits (e.g., weaning weight and yearling weight) and mature size. Therefore, it can be difficult to find a sire that has genetic potential for high early growth but moderate to lower mature size.

Management Assessment

Management is another component of an operation that should be assessed. In order to properly determine the genetic makeup 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, feed availability and quality, and unique environmental conditions (e.g., altitude, extreme heat, etc.).

Labor

Even on a family-owned and -operated farm or ranch, labor is a consideration when developing a breeding program. Manpower spent per animal, particularly during calving season, 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 sound breeding program. As an example, a full-time farmer/rancher who observes the cattle multiple times in a day may not have the same limitations for calving ease as the part-time farmer/rancher who rarely sees the cattle. Full-time farmers/ranchers usually have more available time to harvest stored feeds at the appropriate time, resulting in better quality (hay, silage, etc.), and have an increased ability to get those resources to the cattle in times of need.

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 developing your breeding program. Additionally, there is a cost that should be considered for all labor, including your own.

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 an abundance of nutrition, the larger, high-performing cattle were the most efficient at producing pounds of salable product (weaned calves) when compared to low producing cattle. Based on this information, 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. Three basic nutritional categories 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, including 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 and humidity. 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 can 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 financial 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:

Weaned calves sold at auction or by video. The only production information that is available to potential buyers is made available by the seller through the auction center's personnel.

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.

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 to offset the increased costs.

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.

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 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. Most grids pay premiums for cattle that fit specific breed-centric programs such as Certified Angus Beef or Certified Hereford Beef.
- *Formula marketing.* Cattle that are marketed during the finishing period with a specific future date and delivery point.
- *Freezer Beef.* Local marketing option where the purchase is agreed to on a live basis and delivered to a processor. Processing is custom to the purchaser.
- *Direct Marketing.* Local marketing option where processing is done at a USDA inspected processor and beef can be sold directly to consumer (restaurant, retail, farmers market, etc.).

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 that aims to meet specific breeding objectives. 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 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 pound 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 specific segment of the chromosome that codes for a precise 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 extension locus 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 classic example of a simply inherited trait in beef cattle is red/black coat color. Some genetic disorders are also simply inherited. Simply inherited traits are typically observed as either/or: either the animal is black, or they are red. 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.

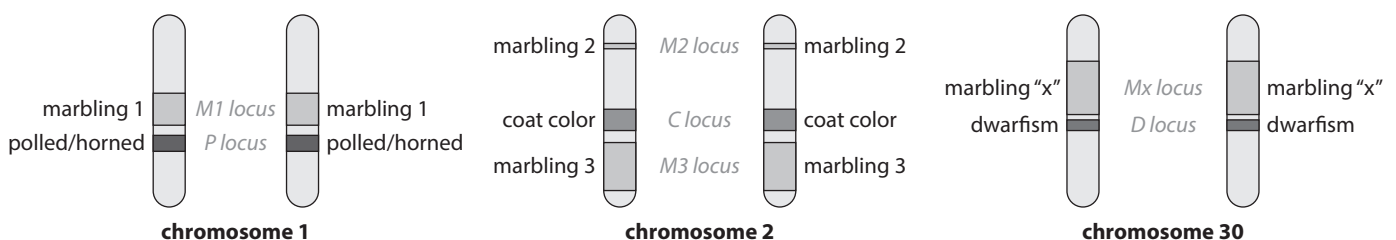
As implied in the name, polygenic traits are controlled by many genes, and most of the economically relevant traits are in this category. The number of genes involved depends on the trait, and there is currently little information on how many genes are involved for each trait. Examples of some common polygenic traits in cattle are calving ease, weaning weight, milking ability, marbling, tenderness, etc. Besides being controlled by many genes, polygenic traits are also influenced 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 influence 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 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 recessive 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.

If we were to breed these heterozygous heifers back to a Hereford bull, we would

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



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 expected ratio would be 25%:50%:25%, respectively. The expected 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 (typically hair, blood or semen), 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's phenotype is more extreme than either homozygote.

Dominance is a way to describe how alleles interact with each other at a 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 is scurs, which occur at a higher rate in males than females.

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

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 categorical traits, which mean they fit a certain discrete category. For the phenotype of horned/polled, there are only the two choices, horned or polled, which make this trait a categorical trait. Categorical 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 additive genes that influence that trait. The sum of all genes influencing a trait for an animal is called its *breeding value* for that trait. A simple case for weaning weight is illustrated in Figure 5.

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 an estimated heritability of around 0.40 in many beef cattle populations, which means that about 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

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

$$\text{Breeding Value} = 25 + 25 + 15 + (-5) + (-10) + (-15) + 0 + (-5) = 30 \text{ lb}$$

Genotype of Bull B:
AaBbCCdd

$$\text{Breeding Value} = 25 + 5 + 15 + (-5) + (-10) + (-10) + (-5) + (-5) = 10 \text{ lb}$$

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, the average of all gametes produced by an animal is half of its 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 favorable EPD tend to have higher proportion of alleles with favorable additive effects on that trait.

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 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 both simply-inherited and 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 influences 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. For example, as selections are made for increased weaning weight, yearling weight is also increased because of the positive genetic correlation between those traits. An example of a disadvantageous correlation would be that as selections are made for increased weaning weight, calving ease tends to decrease. Conversely, as selections are made to improve calving ease, weaning and yearling weights tend to decrease unless attention is paid to simultaneously select against this. 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			
CED 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 a negative genetic correlation between milk and growth. However, grand progeny would have increased WW and YW due to added milk production in the daughters.

Data Collection

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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 your genetic evaluation provider (breed association or company; GEP) to ensure the most complete and accurate genetic evaluation possible. In this chapter, the life cycles of a heifer, steer, and bull are examined to determine the records that need to be collected, how those records can be adjusted, and how to interpret these data. First, it is important to discuss several considerations when collecting and interpreting data.

Contemporary Grouping

Before collecting data, it is important to have an understanding of proper contemporary grouping. Both genetic merit and the environment to which a calf is exposed can have an effect on how well a calf performs for all 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 calves that were born within a relatively short time interval and have been managed the same. In multiple-breed genetic evaluation, calves in the same contemporary group can have different breed makeup. Regardless of the evaluation type, every calf in the contemporary group should receive an equal opportunity to express its genetic merit by receiving the same management. Once an animal has been separated from its contemporaries, it 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. However, we don't know if that calf was genetically superior for weaning weight,

or if his extra growth was due to feed and shelter. Thus, he must be placed in a separate contemporary group because he received different management and had a different opportunity to express his genetic potential. This is an extreme example, but anything that is different in the environment or management between groups of calves necessitates them being placed in different contemporary groups. Improper contemporary grouping can lead to biased and inaccurate Expected Progeny Differences (EPD). See page 19 for more information.

As an illustration of this concept, look at panel A in Figure 1. When a contemporary group is formed correctly, the environmental differences will be minimized among all animals. Thus, any differences in performance are more likely due to differences in genetic merit (light gray bars). This information is used in the generation of EPD. Figure 1 Panel B illustrates that the animal with the best genetic merit might not always have the best performance. When contemporary group information (along with pedigree) is included in EPD prediction, the resulting EPDs allow for comparison of animals across multiple environments, which was impossible with the phenotypic information alone. For more information about contemporary grouping, see the BIF Guidelines (BIF Guidelines, 2020).

Adjusting Records

Calf age and cow age are two environmental 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 because then each calf would be in its own contemporary group. As it is important to keep contemporary groups as large as possible, this scenario is not ideal let alone feasible from a management perspective. Single-animal contemporary groups do not provide any useful information for genetic evaluation. However, when all calves are weighed on the same day (when the average of the group is close to 205 days old) in the previous scenario, the younger calves will be at a disadvantage compared to the older calves. To compare them fairly, the raw weights of calves weighed on the same day will be adjusted to the same age, in this case 205 days. Basically, the adjustment uses each calf's average daily gain to predict what they will weigh (or did weigh) when they are (or were) exactly 205 days old.

The second adjustment applied is for age of dam. First-calf heifers have calves that are lighter at birth than calves from older cows,

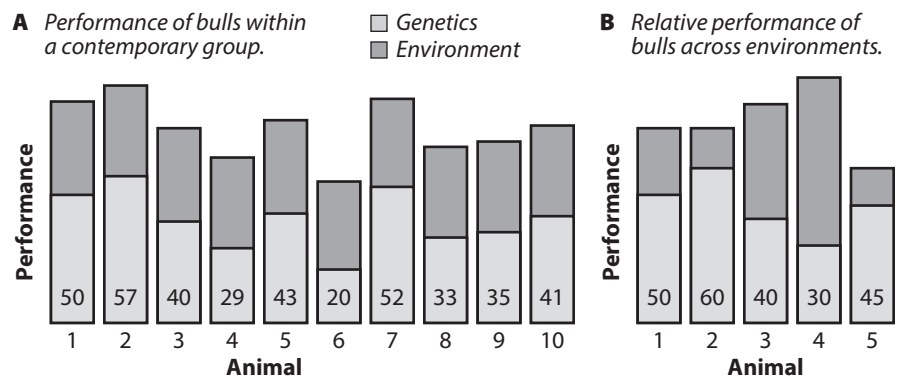


Figure 1. Variation in performance is due to variation from both genetic and environmental sources. Panel A shows a group of 10 bulls in the same contemporary group, where variation due to environment has been minimized. In panel B, one can see that EPDs (representing genetic differences) allow comparison of bulls across multiple environments to find those with the most superior genetic merit, regardless of phenotypic performance. The bull with the best phenotype is not always the bull with the best genetic merit due to the influence of environment.

and they also produce less milk throughout lactation than older cows, leading to lower weaning weights. These are not genetic factors of the calf, yet they disadvantage the calf's performance. Thus, weights for calves of first-calf heifers are adjusted to account for these effects.

The Beef Improvement Federation (BIF, 2010) publishes adjustment factors and procedures. These are general adjustment factors that are appropriate for commercial cattle. Beef Improvement Federation factors and procedures are used for illustration in this publication. Most breed associations or GEP have developed adjustment factors using their breed data. Purebred producers should use the adjustment factors and procedures derived by their respective GEP.

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 deviation from the average of its contemporary group as a percentage.

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

Because of differences in management and mean genetic level between herds, ratios should not be used to compare animals across contemporary groups. To compare the genetic merit of animals of the same breed across contemporary groups and herds, EPDs and selection indices derived from EPD are the only appropriate tools.

Whole Herd Reporting

Some breeders choose to report performance data only on calves that they want to register. However, this is not in the best interest of either the producer or their customers as this practice 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, pro-

ducers are inadvertently penalizing their highest-performing calves. In the following example (adapted from BIF Guidelines 9th ed., 2010), we will use weaning weight ratios to illustrate the effect of only reporting the best calves. Suppose we have 10 calves with an average adjusted weaning weight of 625:

Calf	Weaning weight	
	Adjusted	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 average = 625		

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

Calf	Weaning weight	
	Adjusted	Ratio
1	742	110
2	694	103
3	655	97
4	643	95
5	639	95
group average = 675		

Incomplete reporting has the same effect on EPDs that it does on ratios. Therefore, the highest performing calves (calves 1 and 2) now receive much lower ratios, and subsequently EPDs, than if they had been compared to their entire contemporary group. Calves 3, 4, and 5 were once above average (ratios of 102-105) but are now below average and receive ratios below 100, which will result in lower EPDs than if they were compared to the entire group.

Another reason to use complete reporting, sometimes referred to as whole herd reporting, is to provide the data necessary to perform genetic evaluations for cow stayability and fertility. For these traits, it is important to report data on all potential dams to determine if they are productive members of the herd and to report culling and disposal codes when they leave the herd so that an accurate and complete herd inventory is maintained and the appropriate data can be utilized for genetic evalu-

ation of these critical maternal traits. As new genetic predictions of cow efficiency, maintenance, and fertility are developed, providing accurate lifetime performance records on all cows to the GEP will be more critical than ever.

Trait-specific Data Collection

Birth Data

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

Birth weight should be collected as soon as possible after birth 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 GEP ask that breeders submit the raw data, and they will make the appropriate adjustments, using their own breed-specific adjustment factors. If you do not submit your data to a GEP, use the BIF adjustments.

Age of dam at birth of calf	Birth weight adjustment
2	+8
3	+5
4	+2
5-10	0
11 and older	+3
(BIF Guidelines, 2010)	

This is an additive adjustment, so:

$$\text{Adjusted BW} = \text{Actual BW} + \text{Age of dam adjustment}$$

(BIF Guidelines, 2020)

The following is an example using BIF adjustments:

Calf	Sex	Age of dam	Birth weight		
			Actual	Adjusted	Ratio
1	B	2	78	86	100
2	B	6	85	85	99
3	B	4	76	78	91
4	B	11	90	93	108
group average = 86					

Remember, for birth weight, a lower number is associated with less calving difficulty, so animals 2 and 3 have the most favorable weight ratios. After breeders submit actual weights, the GEP adjusts

the weights and uses them to calculate EPDs for birth weight and calving ease. It is important to note that calving ease is the economically relevant trait, not birth weight. Because calving ease EPDs include birth weight information, it is more comprehensive and a more appropriate tool for selection.

Calving ease. To record calving ease, use the scale recommended by your GEP when reporting data, or the BIF recommended scale if you are a commercial producer.

- 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 Guidelines, 2020)

Both birth weights and calving ease measurements are used to calculate calving ease direct and calving ease maternal EPDs. Calving ease is the economically relevant trait and should be used in selection. Considering both birth weight and calving ease EPD double counts birth weight in the selection program.

Weaning Weight

The next data to collect on a bull, heifer, or steer is **weaning weight**. A group of calves should ideally be weighed when the average of the group is near 205 days of age. Beef Improvement Federation 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. When splitting groups because of age range, it may be useful to try and weigh calves when the average age of the animals in each group is close to 205 days. However, each GEP's particular guidelines for age at weaning may be slightly different. Any calf that is outside the prescribed range when weighed will be in its own contemporary group and its data will not contribute to the genetic evaluation. It is beneficial to hold animals off feed and water overnight to prevent gut fill from biasing weight measurements. Contemporary groups for weaning data should be formed using the criteria used 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). Because of this, the weaning contemporary group of a calf can

never be larger than its birth contemporary group. Weaning weight should be adjusted for age of dam and for age of calf. Most GEP 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 adjustment for:	
	Male calf	Female calf
2	+60	+54
3	+40	+36
4	+20	+18
5-10	0	0
11 and older	+20	+18

(BIF Guidelines 9th ed., 2010)

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 Guidelines, 2020)

Following is an example using BIF adjustments:

Calf	Sex	Age of dam	Actual BW	Weaning age (days)	Weaning weight		
					Actual	Adjusted	Ratio
1	B	2	78	186	515	620	107
2	B	6	85	232	580	522	90
3	B	4	76	200	520	551	95
4	B	11	90	191	560	614	106

group average = 577

Weaning weights are used by GEP 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, many records can be collected on bulls, steers, and heifers. It is important to collect data when the average age of the group is near 365 days. Check with your GEP 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 GEP, 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 birth and weaning criteria, plus yearling/feeding management code, date weighed, and sex. It is beneficial to hold animals off feed and water overnight to prevent gut fill from biasing weight measurements.

Yearling weight should be collected on all animals, and adjusted for animal 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:

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

(BIF Guidelines, 2020)

Example using BIF adjustments:

Calf	Sex	Weaning weight		Days between	Yearling weight		
		Actual	Adj		Actual	Adj	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 average = 1102

Adjusted yearling weights are used to calculate yearling weight EPD. Depending on the GEP, yearling weight may also be used as an indicator trait 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 GEP use a multiple trait animal model that includes birth, weaning, and yearling weights. This approach uses genetic correlations between the trait to account for selection and avoid bias.

Hip Height

Hip height is a measurement that describes skeletal size. Many producers choose to measure hip height when collecting yearling weights because of convenience and because hip height can be used by GEP to calculate EPDs for mature weight or height. Check with the GEP for acceptable age ranges for submission of data.

Scrotal Circumference

Scrotal circumference (SC) EPD has a relationship with age at puberty; a larger SC is associated with younger age at puberty for the bull and his daughters. Measurement of SC should be at its maximal diameter, and size is often directly related to age. 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.

Adj. 365 day SC = actual SC + [(365 – days of age) x age adj factor]

(BIF Guidelines, 2020)

Breed	Age adj factor
Angus	0.0374
Red Angus	0.0324
Charolais	0.0505
Gelbvieh	0.0505
Hereford	0.0425
Limousin	0.0590
Simmental	0.0543

(BIF Guidelines, 2020)

Example using BIF adjustments:

Calf	Breed	Age (days)	Scrotal circumference		
			Actual	Adjusted	Ratio
1	Angus	354	36.2	36.6	101
2	Angus	400	38.5	37.2	103
3	Angus	368	34.6	34.5	95
4	Angus	359	36.5	36.7	101

group average = 36.3

Many GEP use 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 GEP 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. As with yearling weight, pelvic measurements should be taken between 320 and 410 days and adjusted to 365 days.

Reproductive Tract 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 currently used in national genetic evaluations, but can be a useful management tool. Heifers with immature reproductive tracts should be culled before the breeding season. (BIF Guidelines, 2020)

Carcass Data

Steers and cull heifers can be used to provide carcass data. Carcass data must be collected by trained personnel or a camera installed at a packing plant. Many GEP 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. Data should be adjusted to an age-constant or weight-constant basis. Each GEP has their own guidelines to accomplish this.

Data collected usually includes hot carcass weight, marbling score, 12-13th rib fat thickness, ribeye area, and percent kidney, pelvic and heart fat. Marbling score measures the quality grade of the carcass. Marbling score is related to quality grade as follows:

Quality grade	Marbling amount	Score	IMF%
High prime	Abundant	10.0-10.9	
Average prime	Moderately abundant	9.0-9.9	
Low prime	Slightly abundant	8.0-8.9	10.13
High choice	Moderate	7.0-7.9	7.25
Average choice	Modest	6.0-6.9	6.72
Low choice	Small	5.0-5.9	5.04
Select	Slight	4.0-4.9	3.83
High standard	Traces	3.0-3.9	2.76
Low standard	Practically devoid	2.0-2.9	

(adapted from BIF Guidelines, 2020)

Most GEP report EPDs for carcass weight, marbling, REA, 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.

Most GEP use ultrasound data collected on bulls and heifers as indicator traits in the carcass trait genetic evaluation. Each GEP 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 GEP 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. Contact your GEP to get their requirements for age of scanning. Different GEP have different requirements for ultrasound contemporary grouping. If scanning is done at 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 GEP for their contemporary grouping guidelines. The BIF Guidelines (2020) recommend that all calves in a scanning contemporary group be within 60 days of age with each other, but some GEP may allow a wider age range. Ultrasound data need to be adjusted

to a common endpoint of either age or weight. Each GEP has determined their own endpoints and adjustment factors. Some may include steer ultrasound data in their genetic evaluations. Check with your GEP for specific recommendations regarding scanning steers. It is important to use a certified technician to scan cattle if that data is to be included in a national genetic evaluation. Genetic evaluation providers have a list of certified technicians from whom they will accept data. Measurements taken at scanning include scan weight, ribeye area (REA), 12-13th rib fat thickness, rump fat thickness, and percent intramuscular fat (IMF). Expected Progeny Differences for scan weight, REA, fat thickness, and IMF 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 GEP combine weight, fat, and ribeye area into an EPD for yield or percent retail product.

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 GEP are now collecting pregnancy data on heifers and cows to calculate heifer pregnancy EPD or cow fertility EPD. At calving, birth dates, birth weights, calving ease scores, and udder scores (Figure 2) should be recorded. These are necessary to document calf performance (as discussed previously) but also to document cow performance.

It is important to record AI or exposure dates of the breeding herd. Currently there are few measures of genetic merit for reproduction, but GEP 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 (Figure 3).

Depending on the GEP, cow weights can be used to calculate mature cow weight EPDs. Also, cow weight and body condi-

tion are important components of the new EPDs being developed for cow efficiency and maintenance.

DNA Sample Collection

With the expanded use of genomic technologies in the beef industry, many producers may wish to collect a DNA sample on animals. These samples may be used for a variety of genomic testing purposes (parentage testing, SNP chip testing for development of genomic-enhanced EPD, and/or genetic defect testing) or for archival purposes.

There are many different methods for collecting DNA samples, but certain samples may be preferred by testing companies or with the labor, storage method, and supplies available. It is important to determine which sample types are accepted by your preferred testing company before collecting your sample.

We will review the most common sample types. First, blood samples may be used for DNA extraction. Blood samples can be collected and submitted using vacutainer tubes containing anticoagulant (Figure 4, Panels A and B), but are more commonly collected using FTA cards (Figure 4, Panels C and D), which bind the DNA to paper so that it is stable at room temperature. When using FTA cards, it is important not to oversaturate the card and to let it dry completely before closing the cover.

Hair samples have historically been quite common but have fallen out of favor for many companies due to the labor required in the DNA extraction process. Hair samples are collected from the switch of the animal, and the root bulb (containing the DNA) is placed on the sticky surface of the collection card (See Figure 5). Finally,

Figure 2. Udder scoring system for beef cattle.

Score	Description	
	Udder Suspension	Teat Size
9	Very tight	Very small
7	Tight	Small
5	Intermediate	Intermediate
3	Pendulous	Large
1	Very pendulous	Very large, misshapen

American Hereford Association; BIF Guidelines, 2020

the sample is sealed on the card with a clear strip of plastic and then they are ready to mail or store.

Tissue sampling tags are one of the newer options for DNA sample collection but are increasing rapidly in popularity (Figure 6). This method involves taking an ear punch while tagging the animal, which is then immediately sealed to prevent contamination. The advantage of these

Figure 3. Description of body condition scores (BCS).**Thin Condition**

1. Emaciated—Emaciated with no detectable fat over backbone, hips, or ribs. All ribs and bone structures easily visible.
2. Still emaciated but tailhead and ribs are less prominent. Backbone still sharp but some tissue on it.
3. Ribs still identifiable but not as sharp to the touch. Backbone still highly visible.

Borderline Condition

4. Borderline—Individual ribs no longer obvious. Foreribs not noticeable. However, 12th and 13th ribs may still be noticeable, particularly in cattle with big spring of rib. The backbone is still prominent but feels rounded rather than sharp.

Optimal Condition

5. Moderate—Good overall appearance. The 12th and 13th ribs are not visible unless the animal has been shrunk. Fat cover over the ribs feels spongy. Area on each side of the tailhead filled but not mounded. The transverse processes (see Figure 8-3) are not noticeable to the eye. Spaces between the processes can only be felt with firm pressure.
6. High moderate—A high amount of fat present over the ribs and around the tailhead. Noticeable sponginess over the foreribs and on each side of the tailhead. Firm pressure now required to feel the spinous processes.
7. Good—Cow appears fleshy and carries some fat. Spongy fat cover over the ribs and around the tailhead. Some “patchiness” evident around the tailhead.

Fat Condition

8. Fat—Fleshy and overconditioned. Bone structure disappearing from sight. Animal taking on a smooth, blocky appearance. Large fat deposits over ribs, around tailhead, below vulva. Patchy fat.
9. Extremely fat—Wasty, patchy, and blocky. Tailhead and hips buried in fat. Bone structure no longer visible. Animal’s movement may be impaired.



Score = 1



Score = 2



Score = 3



Score = 4



Score = 5



Score = 6



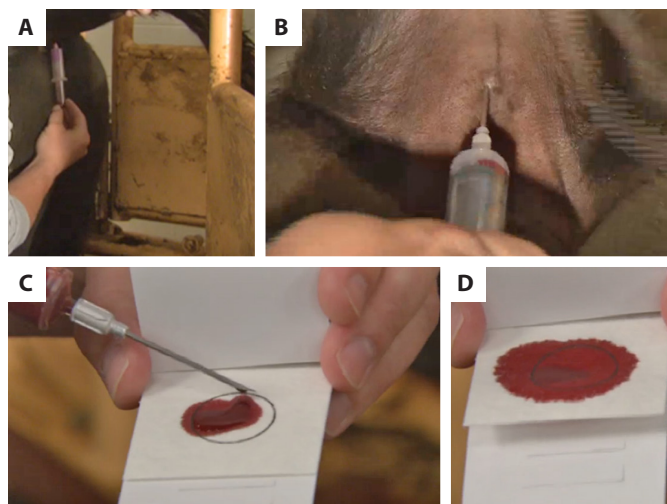
Score = 7



Score = 8 or 9

systems is that the tissue sample is directly tied to the animal ID through barcoding and identification numbers, which helps prevent sample mix-ups. Be sure to follow all label directions for proper utilization of these collection products and direction from the testing lab for storing and submitting any tissue samples for testing.

For any DNA sample collection, it is important to remember the following tips: make sure the animal ID is clearly marked on the sample, make sure samples are not contaminated by manure, dirt, or tissue and/or blood from other animals, use a different needle and syringe for each animal to prevent sample contamination, and store samples properly according to the sample type. For example, do not store samples on a vehicle dashboard or other location where heat can damage the samples. More detailed information on DNA sample collection can be found at eBEEF.org (Rolf 2016).

**Figure 4.** Blood samples collected using vacutainer tubes with anticoagulant (panel A and B) and on FTA cards (panels C and D).

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, beef producers can make more effective selection decisions and maximize genetic progress using available genetic selection tools.

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Figure 5. Hair samples collected using a collection card. Note the root bulbs adhered to the surface of the card.



Figure 6. Example of tissue sampling tags. Note the red cap on the tube where the tissue sample is stored.

Expected Progeny Differences

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It is impossible to visually determine the genetic potential of an animal as a parent for traits that are controlled by numerous genetic variants, as is the case for fertility, growth, carcass merit, and other trait complexes of economic importance. Consequently, predictions of genetic merit have evolved over the last several decades and now include phenotypic information, pedigree information, and more recently genomic information. These predictions are called Expected Progeny Differences (EPD) and have been proven to be the most reliable tool to generate change from selection.

What Are Expected Progeny Differences?

Expected Progeny Differences are predictions of genetic merit of an individual as a parent. As the name would imply, they are predictions of the differences in individuals' offspring performance. Historically, most beef breed associations conducted a genetic evaluation twice annually, meaning that EPD were updated twice a year. This schedule was due to the fact that new data were generally available twice a year, to correspond with two general calving seasons (spring and fall). However, with the advent of genomic information, new data are continually available, and producers wish to see the changes in EPD that result from the new data. This has necessitated weekly genetic evaluations, and thus updated EPD are available on a weekly basis for the majority of beef cattle breeds. In other words, more frequent genetic evaluations mean more current predictions of the genetic merit of animals.

How Do You Use EPD?

Expected Progeny Differences are tools designed to compare animals based on their genetic potential as parents and to make directional change for a particular trait. Simply knowing an animal's EPD for a given trait has no meaning without something to compare it to. This comparison can be

	Weaning Weight EPD
Bull A	50
Bull B	60

between an animal and a point of reference, such as the average of a particular breed. Breed averages are rarely 0. Rather they represent either a point in time or a set of reference animals (i.e., historic set of high accuracy sires). Knowledge of breed average is helpful in determining how an animal ranks within a given breed for a particular trait. Most breeds publish a percentile rank table which allows producers to determine how an animal ranks for a particular trait within a particular breed. Expected Progeny Differences are reported in units of the trait. For example, weight traits (e.g., birth, weaning, yearling) are reported in pounds. However, some traits are reported as percentages (e.g., heifer pregnancy, docility).

With this in mind, the interpretation of the difference in EPD between two bulls is the average difference in performance of their offspring if the bulls were mated to the same cows and the calves were reared in the same environment. Following is an example.

Based on this example, on average, we expect the offspring of Bull B to weigh 10 pounds more than the offspring of Bull A. This does not mean that every calf from Bull B will weigh more than every calf sired by Bull A. There will be variation in the weights of calves produced by both bulls, but with large enough groups of offspring the average difference will be reflected by the difference in sire EPD.

Calculating EPD

The actual calculation of EPD requires the use of sophisticated statistical approaches and modern computational resources. To put the task into perspective, larger breed organizations calculate EPD for approximately 12 to 20 traits for more than 10 million animals on a weekly basis. This is not a trivial task. However, the calculation of reliable EPD begins at the ranch level. Accurate phenotypes and correct accounting for management differences is the responsibility of the breeder. Although advancements in the use of artificial intelligence (AI) algorithms are beginning to penetrate genetic evaluations as a means of categorizing data in terms

of quality, the fundamental responsibility will always belong to the breeder to ensure that records are accurate. Records collected at the ranch level are sent to breed organizations where they are adjusted for effects such as age of the animal, age of the animal's dam, and breed composition. These adjusted records are then used in the genetic evaluation.

The genetic evaluation itself uses a system of equations referred to as the mixed model equations (MME). This system of equations uses phenotypes of animals from across the country, and in many cases internationally, to estimate the genetic value of animals. This method requires that animals are linked through relationships, either pedigree or genomic based. Given these linkages, an animal's genetic merit is informed not only by its own phenotype but also by the phenotypic records of relatives from other herds and across time. The more closely related two individuals are, the more they contribute to the other's EPD.

What Are Accuracies?

Accuracy is the theoretical correlation between an animal's EPD and their true genetic merit and can range between 0 and 1. In the U.S. beef industry, Beef Improvement Federation (BIF) accuracy is used, which is much more conservative than "true" accuracy. Expected Progeny Differences are predictions and thus are not known with complete certainty. They are updated, and become more accurate, when additional data becomes available. For example, a young non-parent animal may have a record for their own weaning weight. If the animal becomes a parent and has offspring with recorded weaning weights, their offspring inform their EPD. This increases accuracy. Another source of data that increases accuracy is genomic data. Genomic information, in the form of SNP markers, is routinely included in the genetic evaluation of all major U.S. beef cattle breeds. This enables higher accuracy predictions, particularly for non-parent animals. One way that genomic information is used to increase accuracy is by improving the estimates of relationships between animals. Instead of relying solely

on pedigree information to inform kinship, genomic data can be used to determine the relationship between animals. For example, although the expectation (pedigree) of the relationship between an individual and their grandparent is 0.25, the true relationship (genomic kinship) can range between 0 and 0.5 due to sampling of alleles inherited by different animals from their parents. By estimating relationships more accurately, EPD become more accurate.

Contemporary Groups

A contemporary group represents a set of animals that were given an equal opportunity to perform and shared a common environment. The foundation for a contemporary group includes animals born in the same year, season, herd, and who were treated equally. In other words, if a subset of animals is fed differently (given preferential treatment) they should become a separate contemporary group. Admittedly there is an optimization between accounting for environmental effects through contemporary groups and allowing contemporary group size to be large enough to compare animals (and parents). At the limit, a contemporary group size of one would perfectly account for the unique environmental effects experienced by the animal. However, single animal contemporary groups are not useful for genetic evaluation as the animal's genetic merit becomes completely confounded with the environmental effects.

It is critical to report data on all animals in a contemporary group. Not doing so leads to biased estimates of genetic merit. If only the heaviest 50% of calves have weaning weights reported, then the magnitude of the differences between each animal and the average of the contemporary group is shrunk, incorrectly suggesting that the animals reported are not as superior for pre-weaning growth as they actually are.

Direct vs. Maternal EPD

Some phenotypes are influenced by both the genetics of the individual (direct) and genetics of the dam (maternal). Examples include weaning weight and calving ease. The EPD for weaning weight direct is

simply called weaning weight whereas the maternal EPD for weaning weight is called milk. In beef cattle, milk EPD is expressed in pounds of weaning weight due to maternal influences, principally lactation. Milk EPD can be thought of as the comparison of a bull's grand-progeny that are products of his daughters. Calving ease also has a maternal genetic component. Calving ease direct EPD represent the probability of how easily a bull's calves will be born when he is bred to heifers. Calving ease maternal EPD are a misnomer in the sense that they reflect total maternal merit. Total maternal is the sum of maternal EPD and half of the direct EPD and represents the probability of unassisted births of a bull's daughters during their first parturition. Although calving ease maternal EPD are not labeled as such, the majority of beef breed associations publish total maternal calving ease.

Multiple-trait Analysis

Many traits are genetically correlated to each other. As such, knowledge of the performance of one trait informs the genetic prediction of another, correlated trait. Growth traits are a good example. Birth, weaning, and yearling weight are all genetically correlated with each other and as a consequence are evaluated in the same multiple-trait model. This has two primary benefits. First, it enables early growth traits to inform the EPD of later growth traits before the later growth traits are observed. Secondly, it mitigates the impact of selection that has occurred earlier in life (sequential selection) on EPD. In the case of yearling weight, it is conceivable that animals with low weaning weights were culled prior to the collection of yearling weight. Accounting for this selection decision is critical to avoid bias in traits measured later in life, in this example yearling weight. Using a multiple-trait model accounts for the fact that selection occurred and some animals were culled while others were not. An important caveat is that although yearling weight EPD are reported, the actual trait analyzed is post-weaning gain. Resulting EPD for weaning weight and post weaning gain (adjusted to 160 days) are then summed and reported as yearling weight

EPD. Another example of a multiple-trait model is calving ease and birth weight. Birth weight is a useful indicator of calving ease and is thus included in the same model as the economically relevant trait of calving ease. This means that resulting calving ease EPD incorporate birth weight observations, and selecting on both calving ease and birth weight EPD results in over-emphasizing birth weight.

Multi-breed Analysis

In the U.S. beef industry there is a mixture of single- and multi-breed genetic evaluations. Single breed genetic evaluations utilize data from only one breed, while multi-breed genetic evaluations utilize data from multiple breeds. Currently the largest multi-breed genetic evaluation is International Genetic Solutions (IGS). The goals of multi-breed genetic evaluations are sharing of data across breeds and the ability to report EPD across multiple breeds that are directly comparable to each other. The underpinning of a multi-breed genetic evaluation is pedigree ties across breeds and contemporary groups that include animals from more than one breed (or crossbred animals). Pedigree ties across breeds enable the sharing of data across breeds. Generally speaking, Angus and Red Angus serve as the links that tie multiple breeds together largely due to composite programs such as Lim-Flex, Balancer, and SimAngus. Having contemporary groups that contain more than one breed enable the estimation of breed differences, which are needed to conduct a multi-breed genetic evaluation. Without this, breed differences must be obtained from external sources (e.g., U.S. Meat Animal Research Center).

Summary

Expected Progeny Differences enable genetic selection decisions for multiple traits. Core to accurate EPD are well-formed contemporary groups. Expected Progeny Differences change over time as additional information is available. These changes are more frequent with weekly genetic evaluations. Genomic data that is integrated into EPD allows accuracy of non-parent animals to increase.

Interpretation and Use of Expected Progeny Differences

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Expected Progeny Differences (EPD) are the most reliable tools to generate directional change in traits. However, like all tools, they must be used correctly and require some degree of background knowledge to ensure proper use.

Breed Averages

Every breed provides breed averages for every trait with a published EPD. Breed average, as the name implies, is the average EPD for a given trait within a specific population (e.g., breed). Breed averages are rarely zero, but instead reflect a point in time or a set of historic animals. Some breeds further delineate breed average to subsets of animals, such as sires, dams, non-parent animals, and based on breed fractions (i.e., hybrids, purebreds, full bloods).

Percentile Ranks

Breed averages can serve as a barometer relative to how an animal compares to other animals in a breed. Percentile ranks serve as a more refined gauge of how an animal compares to other animals in the same breed. Like breed averages (50th percentile), percentile ranks are available for every trait with an EPD. Depending on the breed association, percentile ranks may be available for sub populations (e.g., parent animals, non-parent animals, breed makeup). Percentile ranks indicate what proportion of animals have an EPD that is better or more desirable than a given value. As an example, an animal with an EPD in the 10th percentile means that 90% of the population has an EPD for that trait that is considered less desirable than the EPD of this animal. Note that depending on specific goals of a breeding program, extreme values may not be desirable and animals that have higher percentile ranks (e.g., 50th-99th percentile) may be desirable. An example percentile rank table is presented in Table 1. Assume a bull available at auction has a calving ease EPD of +13.0. Based on the values in Table 1, this bull would be in the top 40th percentile of the breed for calving ease. If the same bull had a yearling weight EPD of 111, he would

be in the 50th percentile (breed average) for yearling weight.

Possible Change

Possible change values allow producers to construct confidence intervals or ranges around an animal's EPD. Possible change is inversely related to accuracy; as accuracy goes up, possible change goes down. As compared to accuracy, possible change represents a more tangible tool to determine the risk associated with the possibility of an EPD deviating from the animal's true genetic merit as a parent. Most breed associations publish a possible change table. Possible change values are unique to each breed and each trait. To use a possible change table, the user needs to know the correct breed, trait, and the accuracy value associated with a particular animal's EPD.

Mechanically, possible change can be thought of as a standard deviation and the EPD as a mean. Given this, the EPD +/- the possible change can provide a confidence interval in which the true genetic merit is expected to be contained. Assume a bull has an EPD of 2.0 and possible change value of 0.5. We expect his true EPD to be within the interval of 1.5 to 2.5 (EPD +/- 1 * PC) 68% of the time. Likewise, we would expect his true EPD to be within the window of 1 to 3 (EPD +/- 2 * PC) 95% of the time and from 0.5 to 3.5 (EPD +/- 3 * PC) 99% of the time. The implementation of confidence intervals allows producers to visualize both the impact of improved accuracies but also enable selection whereby an animal attains some minimum or maximum threshold with some predetermined level of confidence. Confidence intervals can be very effective genetic risk management tools.

Economically Relevant Traits and Indicator Traits

The key questions that every farmer/rancher needs to answer are:

- What are my breeding/marketing goals?
- What traits directly impact the profitability of my enterprise?

Table 1. Example percentile rank table for calving ease (CE), birth weight (BW), weaning weight (WW) and yearling weight (YW).

%	CE	BW	WW	YW
1	19.0	-5.0	100	150
5	17.0	-3.0	89	140
10	16.0	-2.5	88	133
15	15.0	-1.9	85	128
20	14.5	-1.1	82	125
25	14.0	-0.7	80	122
30	13.8	-0.5	78	120
35	13.2	-0.2	77	118
40	12.7	0.1	76	115
45	12.5	0.3	74	113
50	12.2	0.5	73	111
55	11.9	0.8	72	110
60	11.6	1.1	71	107
65	11.1	1.5	69	105
70	10.6	1.9	68	103
75	10.1	2.0	67	100
80	9.5	2.6	65	97
85	9.1	2.8	63	94
90	8.0	3.1	59	90
95	7.2	3.7	57	85

- Are there environmental constraints that dictate the minimum, maximum or optimal level of performance that is acceptable for a given trait in my enterprise?

Once these three questions are answered, sire selection becomes much simpler. The answers to these questions inherently lead a producer to the traits that are economically relevant to their enterprise. We call these traits economically relevant traits (ERT; Golden et al., 2000). Fundamentally these are traits that are directly associated with a revenue stream or a cost. All traits that are not ERTs are indicator traits, or a trait that is genetically correlated to an ERT but not an ERT itself.

Classic examples of indicator traits include ultrasonic carcass measurements and birth weight. Ultrasonic carcass measurements are a non-destructive measure of traits such as intramuscular fat percentage (IMF). Producers do not receive premiums for IMF levels, rather premiums (and discounts) are applied to quality grades.

Assuming that carcass maturity values are the same, actual carcass marbling is the driver of quality grade. Although IMF is genetically correlated to carcass marbling it is not the ERT. Birth weight is another great example of an indicator trait. Selection to decrease birth weight in an attempt to reduce the prevalence of dystocia is practiced by numerous commercial bull buyers. However, birth weight does not have a direct revenue source or cost associated with it. Calving ease is the trait that has a cost associated with it. Calving ease is related to the level of assistance needed during a calving event. Although the two are related, the genetic correlation between calving ease and birth weight is between -0.6 and -0.8, suggesting that birth weight only explains 36-64% of the genetic differences between animals for calving difficulty.

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.

Birth weight (BW)—Birth weight EPD reflects differences in birth weight and is used as an indicator of the probability of dystocia (calving difficulty). Birth weight is not an ERT.

Weaning weight (WW)—Weaning weight EPD predicts differences in the weight of bulls' calves at weaning. WW is an ERT for those producers who market calves at weaning.

Milk (MILK or Maternal Milk)—Milk EPD is actually maternal weaning weight, and thus reported in units of weaning weight. MILK is an ERT for producers who retain replacement females and who sell calves at weaning. In limited feed environments, selection for low to moderate Milk EPD would be warranted due to the added nutrient requirements for both lactation and maintenance.

Yearling weight (YW)—Yearling Weight EPD predicts differences in the weight of bulls' progeny at one year of age. YW is an ERT for cattle producers who might sell cattle post-weaning after a stocker program.

Dry matter intake (DMI)—Dry matter intake EPD predict differences in bulls' offspring for post-weaning feed intake. DMI is an ERT for cattle producers who

retain ownership of terminal calves post-weaning.

Residual average daily gain (RADG)—This is actually an index of post-weaning gain and feed intake with changes in feed intake restricted to 0. The interpretation is differences in post-weaning gain assuming feed intake is equal. RADG is not an ERT.

Residual feed intake (RFI)—This is also an index of feed intake and post-weaning gain, but assumes changes in gain are restricted to 0. The interpretation is differences in feed intake assuming post-weaning gain is equal. RFI is not an ERT.

Total maternal (TM)—The EPD is the sum of half the weaning weight EPD and the entire milk 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. YH is not an ERT.

Mature height (MH)—Similar to yearling height, the mature height EPD was also developed as a frame-size selection tool and is not an ERT.

Mature weight (MW)—The mature weight EPD is another indicator for maintenance energy requirements. On average, heavier cows are expected to require more feed energy in order to maintain themselves. Mature weight is an ERT given there is revenue derived from the sale of cull cows. Absent a genetic prediction for cow feed intake, it is also the best proxy or indicator trait for feed consumption of the cow herd related to maintenance.

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. The Scrotal Circumference EPD is expressed in centimeters with a larger number being more desirable. SC EPD is of use only in situations in which male calves are retained as bulls. Given the availability of female fertility EPD, the utility of SC as a proxy for female fertility is diminished.

Heifer pregnancy (HP)—Heifer pregnancy is an ERT. Heifer Pregnancy EPD

reports differences in the probability of bulls' daughters' ability to conceive and calve at two years of age. HP 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.

Age at first calf (AFC)—This trait is defined as the age of a female when she has her first calf. A lower value is more desirable. Differences between sires' EPD reflect differences in the average age at which their daughters will have their first calf.

Stayability (STAY)—Stayability, also called Sustained Cow Fertility (SCF), reflects the longevity of a bull's daughters in the cow herd. This EPD predicts differences in the probability of bulls' daughters having additional calves during their lifetime or remaining in the herd through extended ages.

Carcass EPD

Carcass weight (CW)—Carcass weight EPD quantifies differences in the expected carcass weight, in pounds, of a bulls' progeny when they are harvested at a constant age endpoint. CW EPD is an ERT.

Ribeye area (REA)—Ribeye area EPD are reported in square inches and indicate differences in the area of the longissimus muscle between the 12th and 13th ribs of bulls' offspring when slaughtered at a constant age endpoint. REA EPD is not an ERT, but is a component of Yield Grade which is the ERT.

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 reported in inches and depicts differences in 12th rib fat thickness of bulls' progeny when slaughtered at a constant age endpoint. FAT EPD is not an ERT but is an indicator of yield grade which is the ERT.

Marbling (MARB)—The marbling EPD indicates differences in marbling of the ribeye of a bulls' progeny when slaughtered at a constant age endpoint. Marbling is generally considered an ERT given its strong relationship to quality grade.

Yield grade (YG)—Yield Grade EPD is a prediction of differences in lean meat yield of the carcass and is an ERT given premiums and discounts are applied to YG. Phenotypically, the lower the grade, the leaner the carcass. An animal receiv-

ing 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. Yield Grade EPD are derived using component EPD of REA, FAT, and CW assuming a constant KPH.

Tenderness (WBS)—The tenderness EPD is reported in pounds of Warner Bratzler Shear Force such 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. Tenderness is an ERT from an industry perspective, although producers are not currently incentivized directly for improved meat tenderness.

Management/ Convenience Traits

Calving ease direct (CED)—The calving ease EPD, both direct and maternal, are the ERT. Calving ease direct EPD are a prediction of the differences of the ease at which bulls' calves will be born. Calving ease direct EPD are calculated using information from calvings of two-year-old females only (no calvings to older cows are included) and birth weight records. CED 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 un-

sisted calving. The majority of breeds, but not all, calculate CEM as total maternal calving ease ($\frac{1}{2}$ direct + maternal). Contrary to calving ease direct EPD, however, the calving ease maternal EPD predicts differences in the probability of a bulls' daughters calving without assistance. CEM 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.

Pulmonary arterial pressure (PAP)—Animals with higher pulmonary arterial pressure are more susceptible to brisket (or high mountain) disease. Pulmonary arterial pressure EPD are reported in millimeters of mercury with a lower value being more desirable.

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.

Docility (DOC)—Docility EPD reflect predicted differences in the temperament of bulls' offspring. 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 such that animals with a higher docility EPD will have a higher probability of producing more docile animals.

Claw set (CLAW)—Claw EPD reflect differences in the claw set of offspring.

Foot angle (ANGLE)—Angle EPD reflect differences in the angle of the foot.

Teat size (TEAT)—Teat score is measured on a 1 (very large) to 9 (very small) scale and EPD are reported in units of the subjective scale. Differences in sire EPDs predict the difference expected in the sires' daughters' udder characteristics.

Udder suspension (UDDR)—Udder scores are measured on a 1 (very pendulous) to 9 (very tight) scale and EPD are reported in units of the subjective scale. Differences in sire EPDs predict the difference expected in the sires' daughters' udder characteristics.

Summary

The list of available EPD continues to grow. To utilize EPD correctly, producers must develop a breeding objective to identify the traits on which they should select. Given more than one trait impacts profitability at the enterprise level, selecting on multiple traits is required. Tools to enable multiple trait selection including selection indices and decision support tools will be discussed in subsequent chapters.

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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 (ERT), those traits that directly influence the sources of income and/or the costs of production. To make this identification, the producer must identify a breeding objective that details how they market their animals, the performance of their animals, as well as the role of their product in the industry.

Once the breeder has identified the ERT that are appropriate for their production system, there are typically a 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. 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 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 seventies and eighties, 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 are 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 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 holistically and from a systems perspective to change many traits simultaneously and achieve the goal of improved profitability.

Multiple-trait selection, considering more than one trait at a time, is the first step towards gaining 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, 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. As an example, increasing weaning weight can increase revenue but could lead to a corresponding increase in mature cow weight of retained heifers; the latter will not be observed for several years, while the increase in sale weight could be realized in the first 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 gains 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. If the commercial producer retains ownership of the calves, the first income may not be realized until year 5. Therefore, seedstock mating decisions made today will not have an economic impact on commercial producers for at least 4 years and maybe longer depending on the trait, management practices, and marketing scheme.

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 can produce unfavorable change in correlated traits as we discussed earlier. As a result, maintaining acceptable production levels for all traits is difficult with this method.

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 calving ease direct EPD is +3. If the producer is interested in improving weaning weight but does not want to increase calving difficulty, that producer might set a minimum threshold of a +35 W/W EPD and a minimum CED EPD threshold of +3. Any potential sire not meeting both of those criteria would not be selected. Clearly, there are more than just

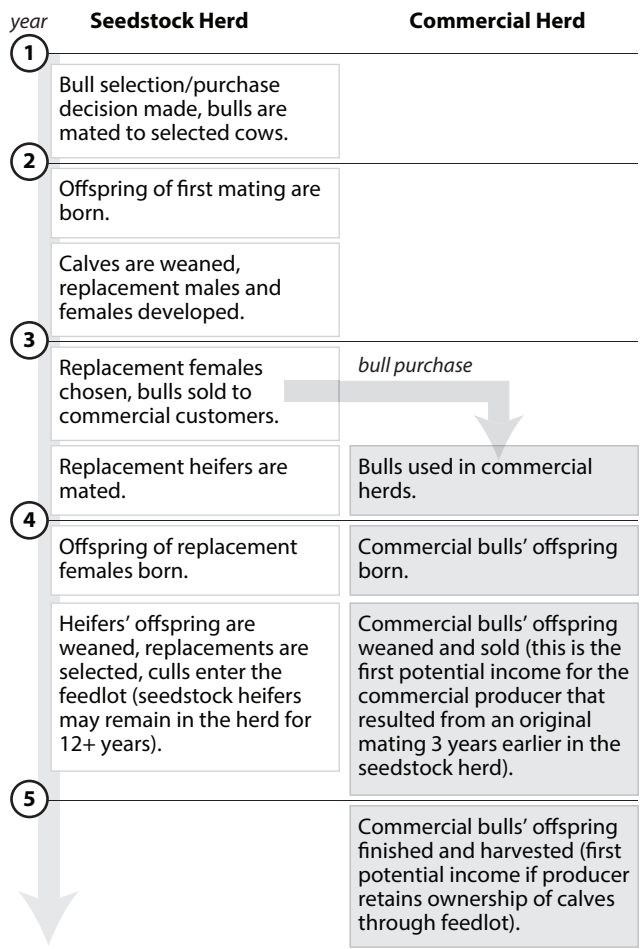
two important traits as in this example, and accordingly as additional traits are added, culling levels are set for each. This method is widely used due to the ease of implementation. Most breed association websites provide tools for sorting bulls on EPD with a user-defined set of standards (minimum 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/CED 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 calving ease lowered to +2 (from the original +3). 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 objectively incorporate the costs or income value associate with a unit change of each trait—they do not account for the economic importance of each trait, and as a result do not simplify the evaluation of potential

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.



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. It is important to differentiate between the "objective," or "goal," and the selection

criteria, or index. The goal traits represent a listing of ERT that are drivers of profit for a particular breeding objective. These may or may not have associated EPD. The selection criteria represent the traits that can actually be selected for (i.e., have EPD). These two lists of traits, the goal and the selection criteria, need not be identical. In other words, it is possible to make progress toward a specific goal without EPD for each of the goal traits. This requires that the EPD in the index, if not the goal traits, are genetically correlated or indicators of the goal traits.

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 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 residue 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 informa-

tion from surveys of groups of producers and/or governmental statistics on prices received and costs of production generally averaged over some period of time. 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: if one producer assists no heifers during calving and another has a 50% assistance rate, the former would have a relatively low economic value for improved calving ease as current levels warrant no additional genetic change, whereas the latter producer would put considerable economic value on genetic improvement of calving ease. A result of the requirement for detailed economic and herd performance information has produced low adoption rates for many breeder-specific (customizable) indexes. Although generalized indexes are a very reliable proxy, many breeders are reluctant to use them because they feel indexes remove control over the direction of genetic change in their herd and that the economic assumptions might not be germane to their production system. 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 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 birth 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 methodology is also used in many other animal industries including the pig, poultry, and dairy industries. In the swine 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, the majority of breed associations publish index values for a variety of production systems. These include general-purpose and terminal indexes. Within each category, the specificity of the available indexes varies. At one end, a “generalized” index is meant to fit the needs of all members of the group (or breed). 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.” 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 “points of consideration” to be used when evaluating strengths and weaknesses of association-provided (generalized) indexes and how 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 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 sold at weaning, sold at the end of the feedlot phase, or retained for breeding. 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, or their appropriate indicator traits of EPD for the ERT are not available. 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 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 consideration of the current genetic and production level of the herd. For instance, if replacement heifers are kept from within the herd, do they have as 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.

Use of Indexes

In comparison to how long EPD have been available, the development and application of indexes in the U.S. beef industry is relatively new and as a consequence the use of indexes in the beef cattle industry is not as widespread as in other livestock industries. Admittedly, there are other criteria to use when selecting sires. For example, there are critical thresholds that must be

met to ensure that a bull can pass on his genetics. Candidate sires should be sound, meaning that they have passed a breeding soundness exam and have adequate foot and leg structure to travel and breed cows. Once these phenotypic thresholds are met, identifying an appropriate index and using it is key.

Indexes are designed to increase net profit. In order to accomplish this, producers must select the appropriate index to use based on their own breeding objectives. Below are three critical considerations to determine which index is the most appropriate.

Retention of replacement heifers. If replacement heifers are to be retained, the index used should make this assumption. The index should include maternal traits such as calving ease maternal (or total maternal), milk, female fertility traits (e.g., heifer pregnancy, stayability or sustained cow fertility), and some proxy for feed consumed by the cowherd (e.g., mature cow weight). If replacement heifers are not retained, a terminal index should be used. A terminal index would include traits related to growth and carcass and would not include any maternal traits. Using a terminal index when replacement heifers are retained not only ignores maternal traits but could also lead to increases in mature cow size given the emphasis placed on post-weaning growth.

Sale point of terminal calves. Even if replacement heifers are retained, some fraction of calves (steers plus cull heifers) will be sold. Some producers may sell calves at weaning, while others may background calves, and others retain ownership through the feedlot phase. Ideally, the index used would mirror the sale point of the producer. Even in the case when calves are sold at weaning, post-weaning growth and carcass traits should not be ignored. Selling calves at weaning that are profitable in the post-weaning phase help to create future demand for feeder calves.

Breeding heifers. If producers are exposing bulls to heifers, some degree of attention should be directed to calving ease. The amount of emphasis placed on calving ease direct in this situation is related to both economic considerations and the producer's tolerance to risk. Regardless, an index that places some emphasis on calving ease direct should be used. If this is not possible, then calving ease EPD should be used in addition to the chosen index.

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. However, there may be economically relevant traits not in the index. For traits not in the index, the breeder will need to apply appropriate selection pressure to EPD in addition to the index. An example might be breeding heifers for the production of terminal calves. If the terminal index does not contain EPD for calving ease direct, then the breeder should use both the terminal index and calving ease direct EPD to select bulls.

Breeders often ask about the risks associated with using an index that weights traits using economic parameters that might differ from the economic values experienced by a particular breeder or enterprise. Fortunately, small errors or differences 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. Indexes are generally robust to differences in economic assumptions given it is the relationship between cost and revenue, and resulting relative importance, that are important. If two indexes include the same set of EPD but use different economic assumptions, the correlation between the two indexes (or rank of animals using the two indexes) is expected to be high.

Another issue not addressed in the above that may arise with the release of multiple, generalized indexes by a single group (i.e., breed association) 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 overemphasizing the importance of feed requirements. In this case, it would likely result in overpenalizing animals with greater growth potential. If the breeding goals are vast (i.e., raising replacement females and selling terminal offspring) then a general-purpose index that matches this objective

and includes terminal and maternal traits would be recommended. Again, selecting the single most appropriate index, is the best approach for implementation of this technology.

Conclusion

The goal of selection indexes 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 selection indexes depends upon choosing an index that most closely mirrors the breeding objective of a particular enterprise. Selection of the appropriate index is key to success.

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Decision Support Systems

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The majority of selection indexes available in the U.S. beef industry are generalized. They are generalized in the sense that they use industry-average values for costs and returns, assume industry average levels of performance, and make assumptions about common breeding objectives. Although these tools have been shown to be very robust to differences in values assigned to costs and returns, more advanced tools are available to customize selection index parameters. Breeders can also take advantage of interactive decision support tools to aid with herd-level genetic decisions. Both animal-specific and herd-level decision support tools will be discussed as they relate to systems that are available to the U.S. beef industry

Decision support systems that evaluate herd-level performance are designed to evaluate the herd's overall change in genetic merit and to aid in matching genetic potential to production environments, rather than to evaluate potential individual selection decisions. Animal, most often sire, decision support tools aid in making selection decisions that contemplate genetic potential in an economic framework. In other words, these tools help select sires that will improve net profit through advancing genetic potential.

An example of a system designed to aid in matching genetic potential to production environments is the Angus Optimal Milk Module. This decision aid is 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 recommendations for an optimal range of milk EPD for that specific operation. The remainder of this chapter will discuss animal-specific selection decision support tools.

Why Use a Decision Support Tool?

Bull purchasing decisions need to account for differing marketing goals and environmental constraints to improve profitability and sustainability, but these are unique to each herd as producer-specific production goals and inputs vary

considerably. For instance, it is well known that calving ease is more important when considering bulls that will be mated to heifers than it is when selecting bulls to be mated to mature cows. Calving ease is also more important in herds that have high levels of dystocia or that calve in extensive range environments than in herds with infrequent dystocia or readily available labor at calving. Additionally, in low-input environments where forage availability is low, selection for decreased mature size and lower milk production levels is advantageous if heifers are to be produced from within the herd. These are examples where inputs, defined as either labor or feedstuff availability, dictate optimal production levels. The targeted market endpoint also dictates traits and production levels that are economically relevant at the individual farm level. For producers who market all calves towards a quality grid (e.g. Certified Angus Beef target) without retaining replacements, survivability, disease susceptibility, sale weight, and carcass quality are primary economic drivers, and traits such as weaning weight maternal (milk) are irrelevant.

The correct bull choice is conditional on marketing objectives, environmental constraints, and value and number of offspring. Knowledge of the value of individual bulls available and the value differences amongst them would greatly enhance the profitability of commercial cow/calf enterprises. This would allow selection decisions to focus on what is economically important, and what bull price is justified to achieve the subsequent goals for a particular farm given its resource constraints. Many producers do not appear to use all of the relevant information available when making bull purchasing decisions (Weaver et al., 2014; Penton Media, 2010). The Penton Media survey (2010) revealed that producers often incorrectly include an animal's own performance record in selection decisions, and trait emphasis is in conflict with production/marketing goals. Without the aid of a decision support tool, commercial beef cattle producers, often without the technical knowledge required, are forced to attempt to combine several different pieces of information (e.g. cur-

rent herd performance, EPD of potential seedstock, accuracy of EPD, mean breed differences, projected costs and value of production, production environment constraints, etc.) to decide which bull to buy, and to determine the economic value conditional on their own needs.

Producers face the problem of obtaining the best bulls for their operation in that given setting. Implicit in this exercise is the need to account for the underlying resource base where the sire's progeny will be utilized. It is worth noting here that "best" is a relative concept. When accounting for price differentials across bulls, a "less desirable" bull may become the preferred choice over a "more desirable" bull if his sale price discount is larger than the differential in value between the two bulls. A producer armed with a decision support aid can use the estimates of "value" on different bulls to identify the relative bargains of bulls that are most underpriced relative to their value. Conversely, if the spread in bull prices does not sufficiently reflect the differences in economic value of the bulls offered, having good estimates of value should increase profitability of top seedstock producers.

Past and Current Tools

Decision support tools that address these various scenarios have been proposed before (e.g., Decision Evaluator for the Cattle Industry; DECI; Williams and Jenkins, 1998; Colorado Beef Cow Production Model; CBCPM; Shafer et al., 2005) but were not widely adopted due to the level of complexity and detail relative to firm-level inputs required to parameterize the underlying model. The American International Charolais Association offers a terminal sire index that is designed to evaluate decisions for selection of sires in the 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 tool 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 tool assumes that all calves are marketed on a carcass value basis.

It is clear that to achieve widespread use, a decision support tool that allows a tiered level of input information, with default values that are customizable from each specific user, is required. The decision process, which includes input from the user, is outlined below.

Breeding objective. This identifies which traits are economically relevant, and thus the traits that are included in the index. Critical information includes if the herd is self-replacing, at what age calves are marketed, and how value is assigned to sale animals (e.g., live weight, carcass weight).

Phenotypic values. These are the current herd averages for traits that are economically relevant. For example, average weight at time of sale, cow herd age distribution, pregnancy rates, mature cow weight, and carcass metrics could be important depending on the breeding objective. This information allows the system to establish a baseline or starting place from which to assign economic values when changing each particular trait by one unit while holding all other traits constant. A generalized index assumes that every producer has the same level of performance. A customizable index allows these values to differ. This can be important for traits whereby a threshold in costs/pricing exists. For example, a herd that has carcass weights that routinely exceed plant limits has a different economic value assigned to carcass weight than a herd that has carcass weights that fall within an acceptable window.

Values for costs and returns. In general, the relationship between costs and revenue are similar across an intermediate time span (i.e., cattle cycle). However, differences do exist between producers. These differences might exist due to differences in production environments (i.e., cost of feed).

For producers with detailed economic knowledge of their herd, such as unit cost of production, being able to customize underlying economic assumptions of an index can be helpful. However, the majority of beef cattle producers can utilize industry averages and feel comfortable in constructing an accurate index.

Cow herd breed composition. Genetic decisions relative to sire selection should be based on additive genetic effects (EPD) and non-additive genetic effects (heterosis from crossbreeding). The latter can only be determined when the breed composition of the cow herd is known to some degree. For example, if the cow herd is predominately Angus and the additive genetic merit of two bulls, Hereford and Angus, are equal, the better decision is to choose the Hereford bull given that this will lead to increased heterosis in the corresponding calf crop.

Planning horizon. This is the length of time that a producer considers for their current plan or breeding objective. For example, a terminal producer could easily change breeding objectives rapidly given no females are retained. Once females are retained, the planning horizon naturally becomes longer. Even so, some producers may think in 5-year time spans while other might consider the impact of their decisions over 10 years. This impacts the relative importance of traits that might be measured later in life (i.e., reproductive longevity).

A web-based animal selection support tool, iGenDec, has been developed by a group of researchers from the University of Nebraska-Lincoln, US MARC, Kansas State University, and Theta Solutions, LLC. This effort is funded by USDA-AFRI-CARE award number 2018-68008-27888. The iGenDec tool is designed to aid producers in combining many sources of information (EPD, herd-level data, heterosis, breed differences) toward improving net profit. This tool employs user-defined input or default values to develop a selection index that can be applied to a list of animals that are either uploaded by the user or contained in a database of participating organizations. The index is then user-specific, and accounts for differences in heterosis (if applicable).

Conclusion

The impetus for selection decision aids is not the belief that generalized selection indices are flawed but rather that improvements can be made to more closely match the selection tool with its intended use. Given that commercial producers have to make a plethora of farm-level decisions, utilizing a decisions support aid to reduce the complexity of sire selection could make this process more efficient and accurate. Producers who have greater degrees of herd-level data (past performance and costs of production) will be able to populate decision support tools with ranch-specific data rather than default values, and will derive the most benefit from these tools.

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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, popularity and perceptions of utility of some breeds and color pattern has motivated producers to stray away from sound crossbreeding systems. The primary objective of this chapter is to illustrate the economic importance of crossbreeding and to 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 straightbred 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 more distantly related

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 that is due to variation in underlying genetics between animals. 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.

Recent analysis by Schiermeister et al. (2015) estimated breed specific heterosis effects for birth, weaning, and yearling weights using records from Cycle VII and advanced generations of cattle from the US-Meat Animal Research Center (MARC) Germplasm Evaluation (GPE)

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.

project. The results of this work support the retention of heterosis in advanced generations. A common misconception is that as producers have selected breeds to be more similar in conformational and performance traits that heterosis (or opportunities to generate it) are lost or somehow diminished. The results of the Schiermeister et al. study were similar to those of Gregory et al. (1991a,b) for birth and weaning weight traits and larger for yearling weight.

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 two to three 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 crossbreeding experiments conducted in the Southeastern and Midwest areas of the U.S. Table 4 describes the expected direct heterosis of *Bos taurus* by *Bos indicus* crossbred calves, and 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 U.S.

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%

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

Trait	Heterosis	
	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 4. 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 3. Units and percentage of heterosis by trait for *Bos taurus* crossbred dams.

Trait	Heterosis	
	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 Wt., lb.	600	25.3

Table 5. Units and percentage of heterosis by trait for *Bos Taurus* by *Bos indicus* crossbred dams.^{1,2}

Trait	Heterosis	
	Units	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 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)		Weaning Weight (lb)		Postweaning Gain (lb)
	Calf Heterosis	Dam Heterosis	Calf Heterosis	Dam Heterosis	Calf Heterosis
	British x British	1.9	1.0	21.3	18.8
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; adapted from Williams et al., 2013

and an increase in longevity of more than 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.

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 marketplace.

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 these factors help determine the relative importance of traits for each production phase. A detailed discussion of breed and composite selection is contained in this manual.

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 an 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 including 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 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 is 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

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 # of Breeding Pastures	Minimum Herd Size	Number 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	1	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 F₁ 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.

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 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. All progeny produced from these matings that do not conform to the breed type of the herd should 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

Figure 1. Two-breed rotation.

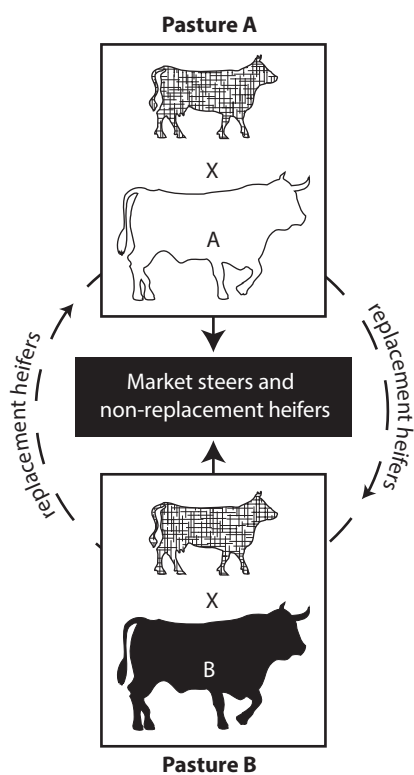
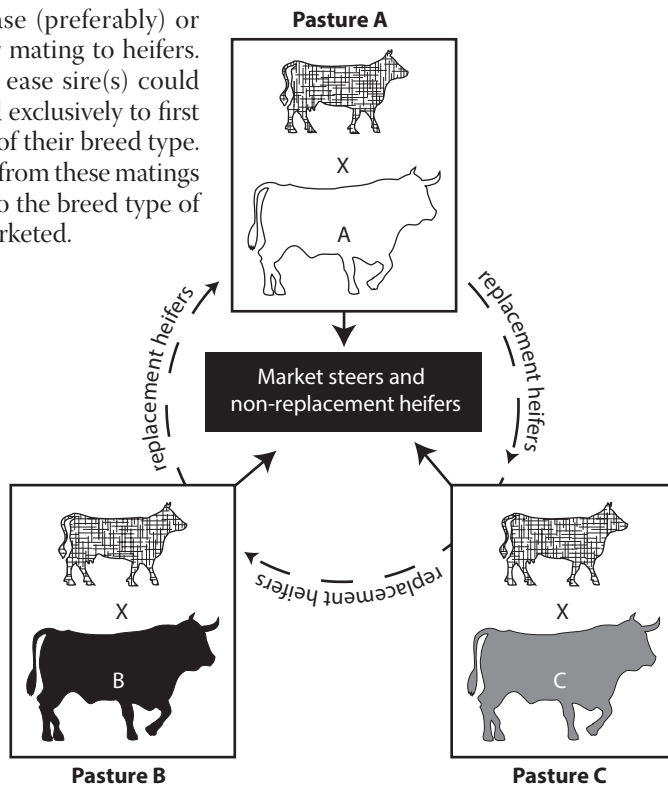


Figure 2. Three-breed rotation.



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 by 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.

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 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.

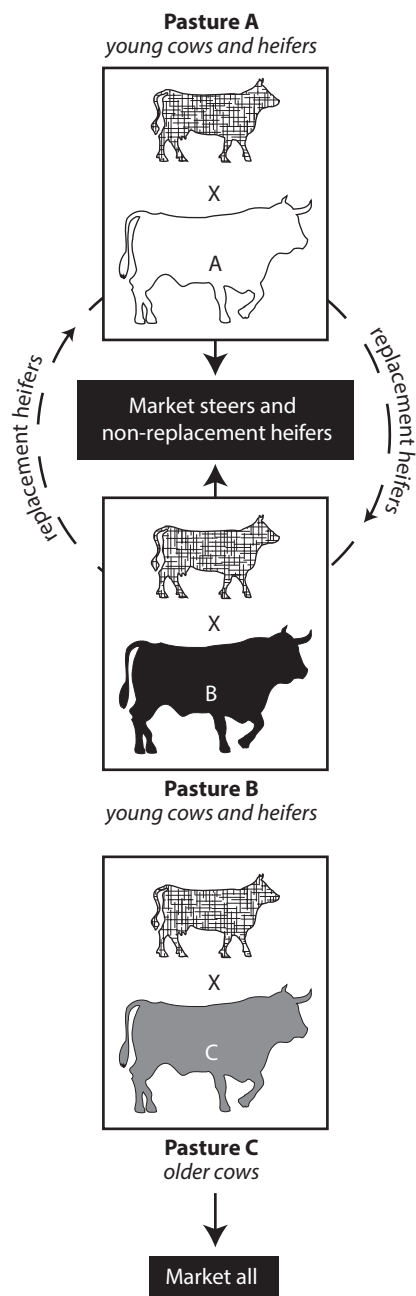
Two-breed Rotational/Terminal Sire

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 females 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 cowherd 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 of replacement females required. When fewer replacements are needed a smaller portion of the herd will be included in the rotational

Figure 3. Two-breed rotational/terminal sire.



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.

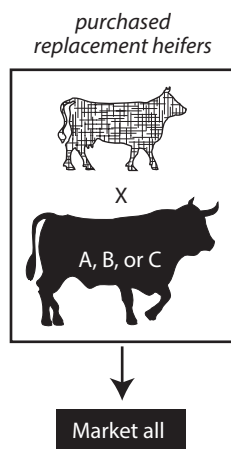
Two-breed Terminal Sire

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 F₁ 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.

Figure 4. Terminal cross with purchased F₁ females.



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 minimize dystocia problems. Alternately, three-year-old or older 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 bio-security measures are employed. Johnes, brucellosis, tuberculosis, and 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 two to five 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.

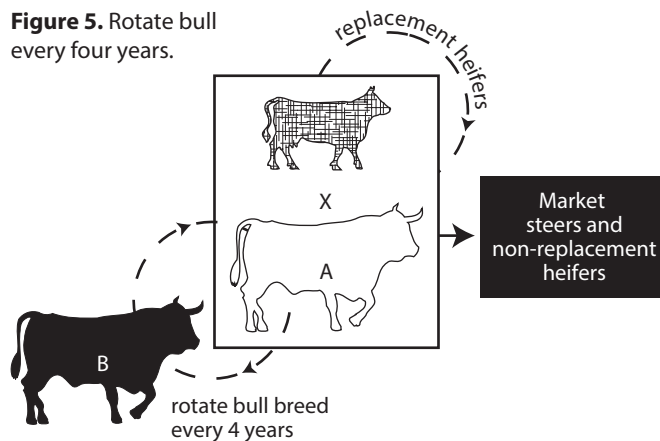
Rotate Bull Every Four Years

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 dependent 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 to 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 one third 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 three-breed rotational system. The expected improvement in weaning weight per cow exposed is a function of retained heterosis will range from 16 to 20% for at three breed system with bulls rotated every four years.

Requirements—The rotate bulls every four-year system is particularly useful

Figure 5. Rotate bull every four years.



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, makes 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.

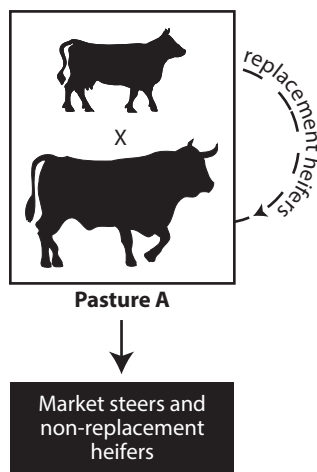
Considerations—This system does not maximize heterosis retention, but it is very simple to implement and manage. The first breed of sire should be used for five calf crops if you start with straightbred cows to optimize retention of heterosis.

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 composites 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—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

Figure 6. Composite breeding system.



the closed herd where cows are randomly mated to sires the foundation animals should represent 15 to 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. 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 F1 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 F₁ Bulls

The use of F₁, or first cross, bulls resulting from the cross of animals from two breeds is becoming more widespread. F₁ bulls provide a simple alternative to the formulation of composite breeds. Additionally, the F₁ 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 F₁ 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 F₁ 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 F₁ 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 F1 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 F1 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 straightbreeding. Additionally, they 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.

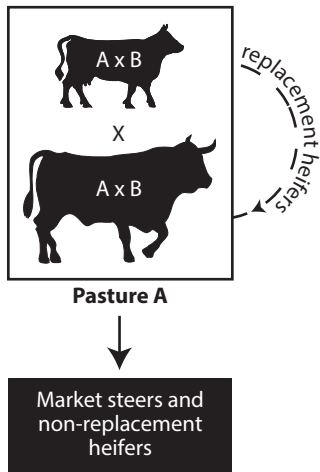
Crossbreeding Challenges

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.

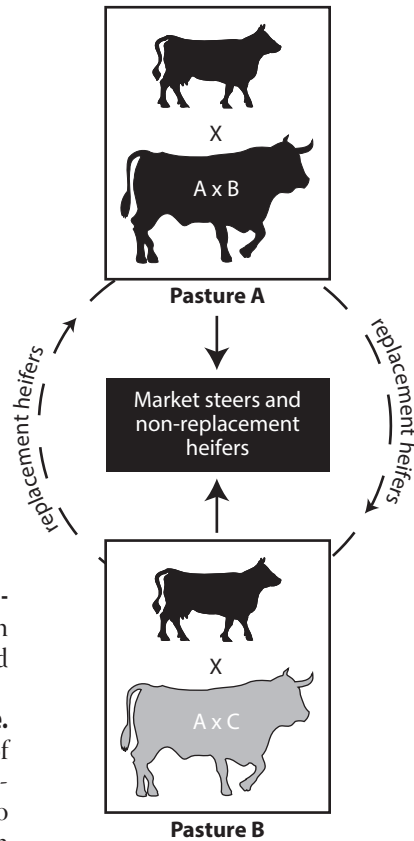
1. **More difficult in small herds.** Crossbreeding can be more difficult in small herds. Herd size over 50 cows provides the opportunity to implement a wider variety of systems. Small herds can still benefit through utilization of terminal sire, composite or F₁ systems.
2. **Requires more breeding pastures 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 F₁ bulls.**Strategy 1**

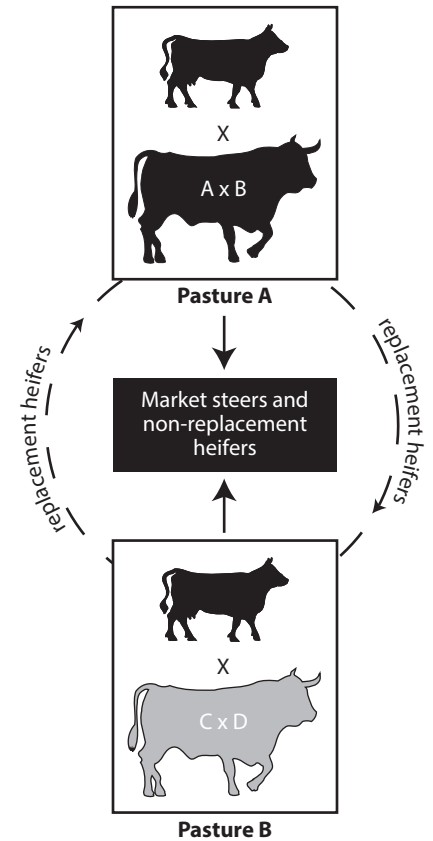
A x B bulls mated to
A x B cows.

**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 identification 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 marketplace. 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 breeds of beef cattle present in the United States, the question of “Which breed should I choose?” is difficult to answer. The top ten breeds in fiscal year 2017 reported registrations accounting for more than 90% of the pedigreed beef cattle in the U.S. These top ten breeds and their crosses represent most 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, feed intake, reproductive efficiency, 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; 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. The American breeds including Beefmaster, Brangus, Brahman, and Braford are examples of new breeds formed as composites. More recent developments include Continental by British breed crosses such as SimAngus, Balancer, and LimFlex.

Beef Breed and Composite Characterization

A great deal of research has been conducted over the last 40 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. More recently, a new sampling system was implemented at US-MARC to continuously resample the largest breeds every two years.

A popular output from the GPE program are the across-breed EPD adjustment factors that enable comparing selection candidates from different breed sources. The estimates are updated and released early in the year to provide the timeliest results in advance of the spring bull buying season. Table 1 lists the 2021 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, 2021). See www.beefimprovement.org for the most current adjustment factors. However, to gain a sense for average breed differences at a phenotypic level and to inform breed choice, producers should focus on breed of sire differences also reported from GPE data. The GPE data enables producers to compare relative breed performance in a common environment. Table 2 presents the sire breed means for 2019 born animals under production conditions similar to US-MARC (located in south-central Nebraska). The means in this table, also updated annually, represent the average phenotypes for various traits of calves produced by bulls from each breed with their respective breed average EPD. Differences in trait means in Table 2 represent genetic differences for each trait when sires are used in a common environment and mated to cows of similar genetic merit. Heterotic effects are not included here. Table 2 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 changes in the overall biological type of a breed.

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 alleles 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 allele to an offspring and dominance effects depend on the interaction of a pair of alleles, 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

Table 1. January 2021 adjustment factors to add to EPDs of eighteen different breeds to estimate across-breed EPDs.

Breed	Birth Wt. (lb)	Weaning Wt. (lb)	Yearling Wt. (lb)	Maternal Milk (lb)	Marbling Score ^a	Ribeye		Carcass Wt. (lb)
						Area (in ²)	Fat (in)	
Angus	0.0	0.0	0.0	0.0	0.00	0.00	0.000	0.0
Hereford	0.9	-16.6	-41.3	-11.1	-0.35	0.06	-0.076	-69.7
Red Angus	2.3	-21.3	-28.9	1.6	-0.11	0.29	-0.035	-7.2
Shorthorn	3.5	-23.1	-37.6	-4.9	-0.15	0.32	-0.039	-3.0
South Devon	3.1	-30.9	-57.9	2.6	-0.37	0.39	-0.042	2.2
Beefmaster	3.8	24.1	2.5	4.2				
Brahman	9.4	55.8	19.9	13.6	-0.69	0.11	-0.154	-33.9
Brangus	2.8	16.5	10.2	14.1				
Santa Gertrudis	4.9	39.7	35.1	17.5	-0.47	0.21	-0.074	-2.1
Braunvieh	2.1	-14.2	-40.6	-1.2	-0.63	1.17	-0.117	-38.9
Charolais	6.0	28.5	20.3	8.4	-0.33	0.80	-0.198	6.6
Chiangus	2.4	-23.6	-42.9	4.3	-0.40	0.53	-0.122	-26.1
Gelbvieh	3.2	-9.7	-17.2	7.1	-0.56	0.77	-0.112	-12.3
Limousin	1.7	-10.9	-35.4	-4.8	-0.39	0.61	-0.082	-4.5
Maine-Anjou	1.8	-28.5	-57.9	-7.6	-0.53	1.06	-0.169	-26.5
Salers	2.1	-17.7	-31.5	8.3	-0.78	0.53	-0.063	0.5
Simmental	1.7	-16.2	-25.5	-2.8	-0.19	0.50	-0.066	-4.5
Tarentaise	2.2	26.9	-8.1	11.1				

^a Marbling score units: 4.00 = S100; 5.00 = S500. Note that Brahman EPDs for marbling are reported on a scale where 400 = S100 and 500 = S500. When converting sires from other breeds to a Brahman basis, the adjusted EPD should be multiplied by 100. Likewise, when Brahman EPDs are adjusted to other breeds, the EPD should be divided by 100 before adding the adjustment factor.

Table 2. Breed of sire means for 2019 born animals under conditions similar to USMARC.

Breed	Birth Wt. (lb)	Weaning Wt. (lb)	Yearling Wt. (lb)	Maternal Milk (lb)	Marbling Score ^a	Ribeye		Carcass Wt. (lb)
						Area (in ²)	Fat (in)	
Angus	84.5	525.0	1050.8	506.9	5.99	13.81	0.697	935.6
Hereford	87.0	502.7	989.7	494.1	5.13	13.62	0.623	891.4
Red Angus	83.8	504.5	1012.1	509.1	5.68	13.59	0.667	908.7
Shorthorn	88.7	487.9	978.2	500.6	5.24	13.86	0.568	894.6
South Devon	87.4	495.1	974.9	502.1	5.11	13.92	0.546	879.2
Beefmaster	87.3	516.7	993.8	495.7				
Brahman	94.4	540.5	996.2	502.8	4.70	13.60	0.542	882.3
Brangus	87.0	508.1	1002.7	505.5				
Santa Gertrudis	88.4	513.6	991.9	500.6	4.93	13.45	0.615	897.9
Braunvieh	88.1	497.0	974.0	514.0	5.31	14.76	0.485	881.2
Charolais	89.6	526.8	1025.1	501.0	5.16	14.70	0.498	922.5
Chiangus	87.5	492.2	979.1	500.9	5.27	14.11	0.548	894.5
Gelbvieh	86.3	524.6	1030.4	509.2	5.11	14.55	0.559	915.8
Limousin	86.0	522.4	1011.1	498.9	5.07	14.75	0.552	917.4
Maine-Anjou	86.0	483.3	948.9	492.9	4.98	14.54	0.491	882.3
Salers	85.4	506.3	996.3	506.8	5.00	14.42	0.544	897.9
Simmental	86.8	527.0	1034.5	503.2	5.30	14.56	0.531	919.9
Tarentaise	86.0	509.5	966.7	494.3				

^a Marbling score units: 4.00 = S100; 5.00 = S500

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 selec-

tion candidates. 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 marketplace. For example, a crossbreeding system that mates Charolais bulls to Hereford-Angus crossbred 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 marketplace.

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 (i.e., Table 2). Traits are typically combined into groupings such as maternal/reproduction, growth, and carcass. When selecting animals for a crossbreeding system, breed

Table 3. Matching genetic potential for different traits to production environments¹.

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.

should be the primary consideration. Breeds selected for inclusion in a mating program will be dependent 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 3 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, dependent 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

Table 4. Units and percentage of heterosis by trait for *Bos taurus* crossbred calves.

Trait	Heterosis	
	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 5. Units and percentage of heterosis by trait for *Bos taurus* crossbred dams.

Trait	Heterosis	
	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 Wt., lb.	600	25.3

Table 6. 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.

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 two to three 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 there are more genetic differences between species than within a species. Heterosis effects reported in Tables 4 through 7 will be divided and noted into those observed in *Bos taurus* crosses or *Bos taurus* by *Bos indicus* crosses. Table 4 details

the individual (crossbred calf) heterosis and Table 5 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 U.S. Table 6 describes the expected individual heterosis of *Bos taurus* by *Bos indicus* crossbred calves, and Table 7 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 U.S.

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 presented in Table 8 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 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 than 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

Table 7. Units and percentage of heterosis by trait for *Bos Taurus* by *Bos indicus* crossbred dams.^{1,2}

Trait	Heterosis	
	Units	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 8. 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)		Weaning Weight (lb)		Postweaning Gain (lb)
	Calf Heterosis	Dam Heterosis	Calf Heterosis	Dam Heterosis	Calf Heterosis
	British x British	1.9	1.0	21.3	18.8
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; adapted from Williams et al., 2013)

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.

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 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.

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DNA-based Biotechnologies

Alison Van Eenennaam, UC Davis

Animal breeders have made incredible genetic progress by selecting animals with desirable traits as parents of the next generation. Remarkably, this selective breeding, or artificial selection, was historically accomplished based solely on outward appearances (phenotypes) and then later with genetic prediction estimates, without understanding which genes influence particular characteristics. Advances in the field of genetics enabled breeders to make more rapid progress toward their explicit breeding objectives, with modern approaches combining genomics and statistics to rank individuals based on their genetic merit (Georges et al., 2019).

During the past century, several new technologies have been incorporated into programs aimed at accelerating the rate of the genetic improvement of livestock by providing tools for breeders to maximize the genetic contributions of highly productive animals. These include artificial insemination (AI), the use of hormones to control the female reproductive cycle 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.

What Is Biotechnology?

Biotechnology is defined as technology based on biology. From this definition, it is obvious that animal breeders have been using 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 the past century.

Genetic improvement is an important component of sustainability. U.S. farmers and ranchers produced 12.725 million metric tons of beef in 2019 with approximately 95 million head of cattle (Figure 1),

approximately 40 million fewer cattle than would have been required to produce that same amount of beef using 1975 genetics and technologies. Looked at another way, in 2018 the U.S. produced 18% of the world's beef with only 6% of the global cattle population.

In the past two decades, 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 2). 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

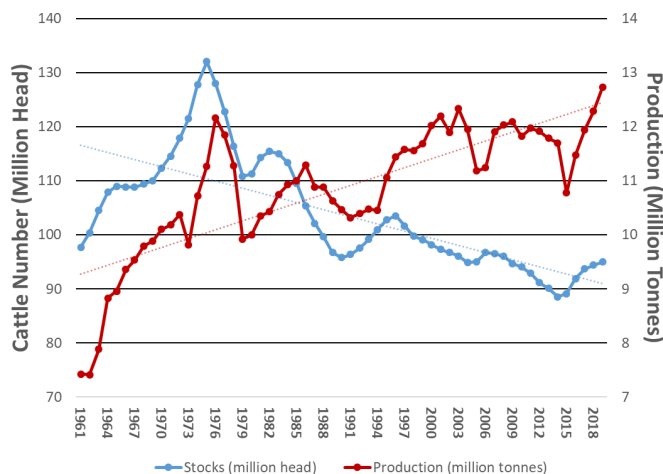


Figure 1. U.S. cattle inventory 1961-2019 (blue line; million head, left axis) and beef production (red line; million tonne, right axis). Data from USDA FAS Beef and Veal production statistics. Data derived from USDA FAS <https://apps.fas.usda.gov/psdonline/app/index.html#/app/downloads>.

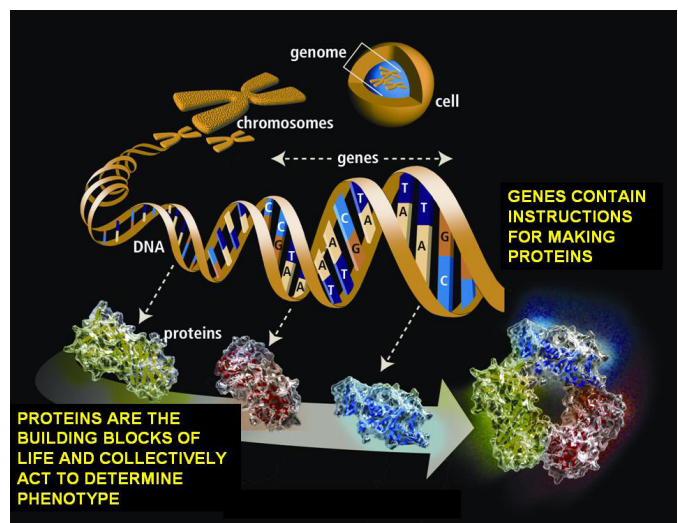


Figure 2. DNA (deoxyribonucleic acid) contains the instructions for making proteins. Differences in the nucleotide sequence of a gene's DNA can influence the type or amount of protein that is made, and this can have an effect on the observed performance of an animal. Original graphic obtained from the U.S. Department of Energy Human Genome Program, <http://www.doegenomes.org>

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. A single nucleotide polymorphism (**SNP**), pronounced "snip," is a variation at a single position in the sequence of DNA among individuals.

These alternative DNA variants 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. Coat color is a well-known example of a simple trait where the presence of the dominant black allele dictates black over the recessive red alleles.

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.

Genotyping refers to the process of using laboratory methods to determine which DNA-marker alleles an individual animal carries, usually at particular genes or locations (loci) 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 same marker allele from each parent it is referred to as homozygous, or it may inherit different alleles from each parent in which case it is referred to as heterozygous. 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 (calving ease, 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. 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.

With the advent of modern molecular genetics and the ability to sequence whole genomes, selection based on genetic information has become increasingly sophisticated. Meuwissen et al. (2001) suggested the use of genetic markers spread throughout the genome that could be used to accurately predict an individual's genetic merit, an approach known as **genomic selection** (GS). In combination with statistical methods, GS can combine phenotypic and genotypic information from ancestral populations to more accurately estimate the genetic potential of an individual animal.

By 2020, over 3.75 million dairy cattle and more than one million beef cattle had been genotyped at thousands of different loci with SNP chips (e.g. 50K or GGP-HD) in the United States. These genotypes are used in conjunction with the extensive phenotype databases that have been amassed to infer accurate genetic merit estimates of young animals based on their genotype, pedigree, and performance information (Wiggans et al., 2017). In beef cattle evaluations these are referred to as genomic or genomic-enhanced EPDs.

Genotypic information increases the accuracy of genetic merit estimates, especially of young animals.

Cloning

Cloning is defined as making a genetic copy of an individual. Cloning has been going on for a long time. Plant breeders have been using this technique to "clonally propagate" desirable plant lines for centuries. 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 into an enucleated oocyte (an egg which has had its own DNA removed). The term "cloning" became infamous following the appearance of Dolly the sheep, the first mammal cloned from DNA derived from differentiated adult somatic tissue (Campbell et al., 1996). This process is called **somatic cell nuclear transfer** (SCNT) cloning and has been successfully performed on many species including cattle.

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. 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. 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.

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. Clones are in some ways a genetic stalemate because in a well-designed breeding program every successive generation would be expected to be genetically superior to the previous one.

Cloned animals may provide a “genetic insurance” policy in the case of extremely valuable animals or can be used to 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

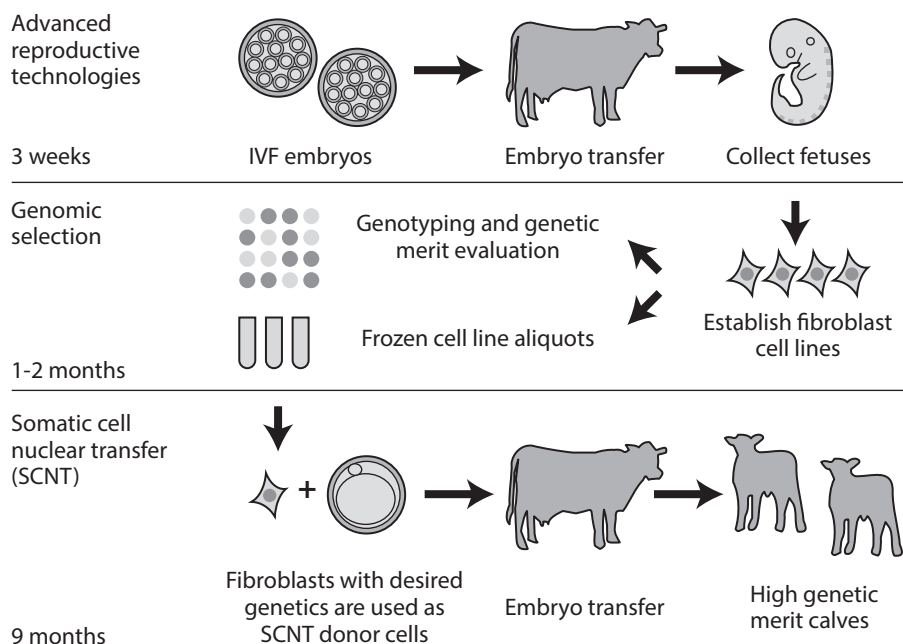


Figure 3. Production of high genetic merit calves using a range of advanced reproductive and DNA-based biotechnologies. In vitro fertilization (IVF) of multiple potentially elite embryos, followed by the brief gestation and establishment of cell lines can be used to increase the intensity of selection, genomic selection can then be used to screen cell lines for those with very best genomic breeding value, and then somatic cell nuclear transfer (SCNT) cloning can be used to realize calves from high genetic merit cell lines. Image from Kasinathan et al. (2015). Used with permission.

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. There are now companies that offer bovine (and other species) cloning as a service.

On January 15, 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 summarized 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 (FDA, 2008).

A number of advanced reproductive technologies and breeding methods are being routinely combined to accelerate the rate of genetic improvement in the cattle breeding sector. Figure 3 shows how in vitro fertilization (IVF), genomic selection, and somatic cell nuclear transfer can work to-

gether to increase the intensity of selection, the reliability of the genetic merit estimate, and potentially decrease the generation interval (Kasinathan et al., 2015).

Genetic Engineering of Cattle

Genetic engineering is the process of moving a **recombinant DNA** (rDNA) 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 a different species or even kingdom, 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 U.S. marketplace. The Food and Drug Administration (FDA) is the agency responsible for regulating genetically engineered animals (FDA, 2009).

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 containing viral antigens to vaccinate calves against disease, or beef optimized for human nutrition. 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 single genes that might be good candidates to positively influence these complex traits. Additionally, genetic improvement for most production traits can be effectively achieved using traditional selection techniques on existing genetic variation, without the expense and time involved with the production and regulatory approval of genetically engineered organisms.

The previous generation of genetic engineering tools, resulting in the first transgenic livestock 35 years ago in 1985, was limited to the insertion of foreign DNA into the genome. This DNA was generally in the form of an rDNA construct comprised of a promoter and a protein coding region (protein upregulation) or an inhibitory RNA encoding region (protein downregulation). As the insertion site of the rDNA was random, there was no way of predicting all of the possible effects that introducing the transgene would have on the animal as the epigenetic environment varies among different regions of the genome. It also meant that each genetically engineered founder animal had the gene inserted into a different location in the genome. There is only one single approved genetically engineered animal for food purposes globally, the fast-growing AquAdvantage Atlantic salmon.

The application of genetic engineering in cattle that is 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 or blood 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 (Monzani et al., 2016), although none are yet commercialized.

There have been three approvals for therapeutic proteins produced by transgenic animals. These include goats producing ATryn1[®] (human antithrombin-III) approved to treat hereditary antithrombin deficiency by the European Commission in 2006 and by the FDA in 2009, rabbits

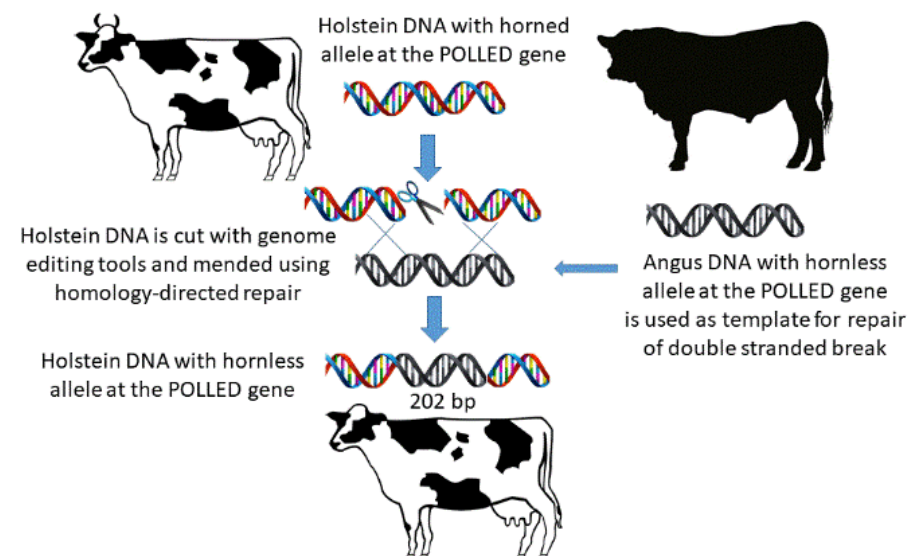


Figure 4. Genome editing induced, double-strand breaks can be repaired using a DNA template to direct the repair to mimic known, desirable genetic variants. In this example the allele that results in hornlessness was used as the homology-directed repair template to introduce a 202 bp sequence at the POLLED gene into Holstein genetics to produce dairy cattle that are naturally hornless as was described in Carlson et al. (2016).

producing Ruconest[™] (Rhucin[®] outside the EU) approved to treat hereditary angioedema in 2014, and chickens producing Kanuma[™] (sebelipase alfa) in their eggs for the treatment of patients with a diagnosis of lysosomal acid lipase deficiency in 2015. These applications have the potential to produce large amounts of human therapeutics at low cost relative to the current mammalian cell culture techniques.

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 been 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.

Genome Editing of Cattle

Genome editing involves using a nuclease (e.g. Zinc finger nuclease, TALENS, CRISPR/Cas9) which cuts DNA at a targeted, specific sequence in the genome and introduces a double-strand break (DSB) in the DNA double helix at that target site. One method that cells use to repair DSBs is non-homologous end joining (NHEJ) where the two broken ends are brought back together and the phosphodiester bonds reformed. This method is error-prone and often results in small insertions and deletions (**indels**) at the target cleavage site due to mistakes in the repair process. These alter the nuclease target site and prevent further cleavage events. An alternative repair mechanism is homology-directed repair (HDR) using homologous DNA as a repair template. A DNA repair template can be added with desired modifications between regions of homology to either side of the DSB. This method can be used to introduce a range of genome edits, from point mutations to whole-gene insertions. Genome editing was used to move the polled allele, common in beef breeds like Angus, into dairy cattle genetics (Carlson et al., 2016) without the need for crossbreeding (Figure 4).

Genome editing presents an approach to introduce targeted modifications into existing genes and regulatory elements within a breed or species, without neces-

sarily the introduction of foreign DNA, potentially avoiding concerns regarding transgenesis. It offers a new opportunity to accelerate the rate of genetic gain in livestock by precisely introducing useful extant genetic variants into structured livestock breeding programs. These variants may repair genetic defects, inactivate or knock out undesired genes, or involve the movement of beneficial alleles and haplotypes between breeds in the absence of linkage drag (genes introduced along with the beneficial gene during backcrossing.)

Genome editing research in cattle to date has focused primarily on monogenic (single gene) traits such as disease resistance (e.g. tuberculosis), production (e.g. myostatin knockout), generation of single sex offspring, elimination of allergens (e.g. beta-lactoglobulin knockout), and welfare traits (e.g. polled or hornlessness) (Table 1). Genome editing could be used to precisely introduce useful alleles (e.g. heat tolerance, disease resistance) and haplotypes into cattle breeds, thereby helping to improve their resilience while maintaining breed identity).

Data coming out of some of the large-scale genomic and sequencing projects are revealing situations where the sequence of one naturally occurring allele results in superior performance to that observed when animals inherit the alternative allele of that gene. It is envisioned that it might be possible to edit an animal's genome to the superior allele, and to do that at several genomic locations simultaneously, or for several different genes. Genome editing could be used to introduce useful alleles (e.g. heat tolerance, disease resistance) at precise genomic locations and other useful haplotypes into native locally adapted cattle

Table 1. Examples of traits that could be introduced into cattle using genome editing.

Target	Targeted Trait/Goal
Intraspecies <i>POLLED</i> allele substitution	No horns
Intraspecies <i>SLICK</i> allele substitution	Heat tolerance
Myostatin (<i>MSTN</i>) gene knockout	Increased lean muscle yield
Beta-lactoglobulin gene knockout	Elimination of milk allergen
Prion protein (<i>PRNP</i>) knockout	Elimination of prion protein
Intraspecies Calpain/Calpastatin allele substitution	Improved meat tenderness
Insertion of lysostaphin/lysozyme transgene	Resistance to mastitis
CD18 gene edit	Resistance to BRD (bovine respiratory disease)
Insertion of <i>SP110</i> , <i>NRAMP1</i>	Resistance to tuberculosis
Intraspecies <i>SRY</i> translocation onto X chromosome	All male offspring
<i>NANOS</i> gene knockout	Infertility (for germ cell transfer)

breeds, thereby helping to improve productivity while retaining adaptive traits. Simultaneous targeting of different genes has allowed bi-allelic modification of up to three genes at the same time. The advantage of gene editing over conventional selection to move these naturally occurring alleles from one animal to another is that favorable alleles rarely all occur in one single individual. Editing offers the opportunity to increase the frequency of desirable alleles in an individual or a breed more rapidly than could be achieved through conventional breeding, and in the absence of undesirable linkage drag (Rexroad et al., 2017).

One could potentially envision editing several alleles for different traits, such as

known fertility impairing haplotypes (VanRaden et al., 2011), polled, and to correct known Mendelian genetic defects that affect cattle (Casas and Kehrl, 2016) all while using conventional selection methods to keep making genetic progress toward given breeding objectives. Although monogenic traits present good targets for genome editing and can have tangible animal health, environmental and economic outcomes, nearly all economically important livestock traits are complex polygenic traits (Georges et al., 2019). These traits include milk yield and composition, carcass yield, composition and quality, feed conversion, feed efficiency, growth rate, wool yield and quality, fertility, egg yield, and disease resistance.

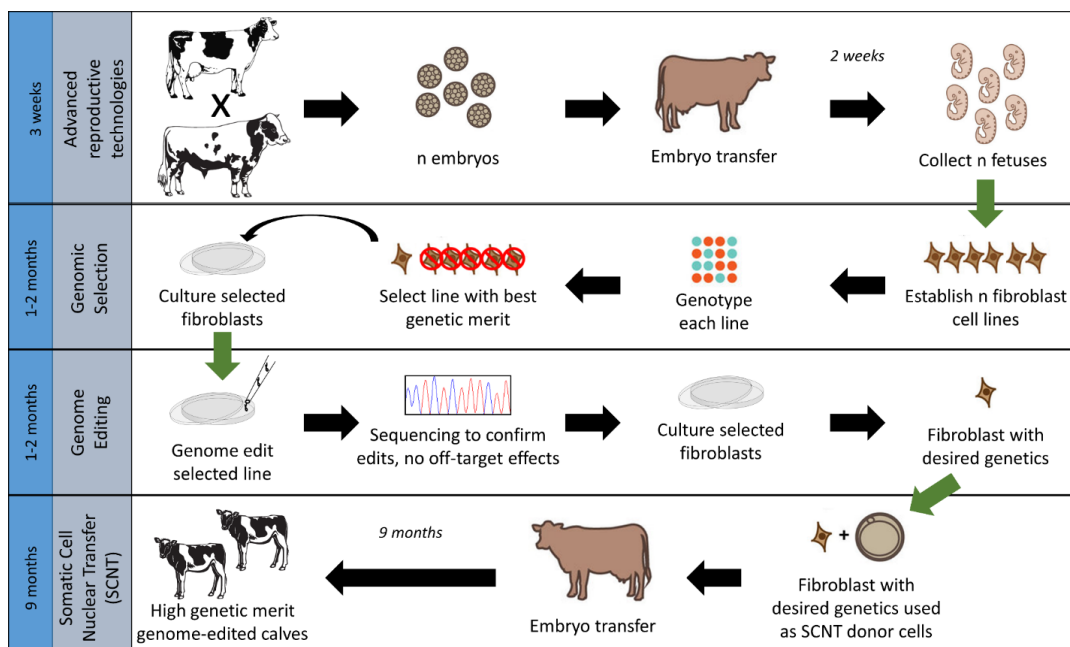


Figure 5. Production of high genetic merit calves using a range of biotechnologies and showing where genome editing might fit into the process. Gene editing was modeled as an added 1-2 month step to the elite calf production system outlined in Figure 3, which combines the use of advanced reproductive technologies and somatic cell nuclear transfer (SCNT) cloning with embryo transfer. Image from Van Eenennaam (2017). Used with permission.

Gene editing conceptually offers an approach to translate the thousands of SNP markers discovered through livestock sequencing projects, the information obtained from numerous genome-wide association studies, and the discovery of causative SNPs (Quantitative Trait Nucleotides; QTNs) into useful genetic variation for use in animal breeding programs. One modeling study reported that combining gene editing with traditional genomic selection could improve the response to selection four-fold after 20 generations (Jenko et al., 2015). It is worth noting, however, that this study modeled editing a quantitative trait that had 10,000 known QTN. In reality, breeders do not currently have a comprehensive understanding of which edits would be impactful on quantitative traits, i.e. those controlled by many genes.

It is unlikely that all of the genes affecting such traits are known, nor is it typically evident which edits might be the most desirable for these genes (i.e. what is the sequence of the desirable allele?). It is likely that, at least in the short term, editing will focus on large effect loci and known targets to correct genetic defects or decrease disease susceptibility, and conventional selection will continue to make progress in selecting for all of the many small effect loci that influence the complex traits that contribute to the breeding objective. In other words, editing will complement, not replace, conventional breeding programs.

Intersection with Conventional Breeding

To become an important driver of genetic change, genome editing methods must seamlessly integrate with conventional animal breeding programs (Figure 5). That means that they must reliably function to germline-edit animals that are selected to be the next generation of parents. Edits can be introduced through gene editing of somatic cells followed SCNT cloning, or **cytoplasm injection** (CPI) of the gene editing reagents into early stage zygotes of the next generation of selection candidates (Figure 6).

To date, SCNT has been the primary method to deliver nuclease-mediated genetic changes into livestock (Tan et al., 2016). The advantage of SCNT is that the gene edited cell line can be genotyped and/or screened prior to transfer into the

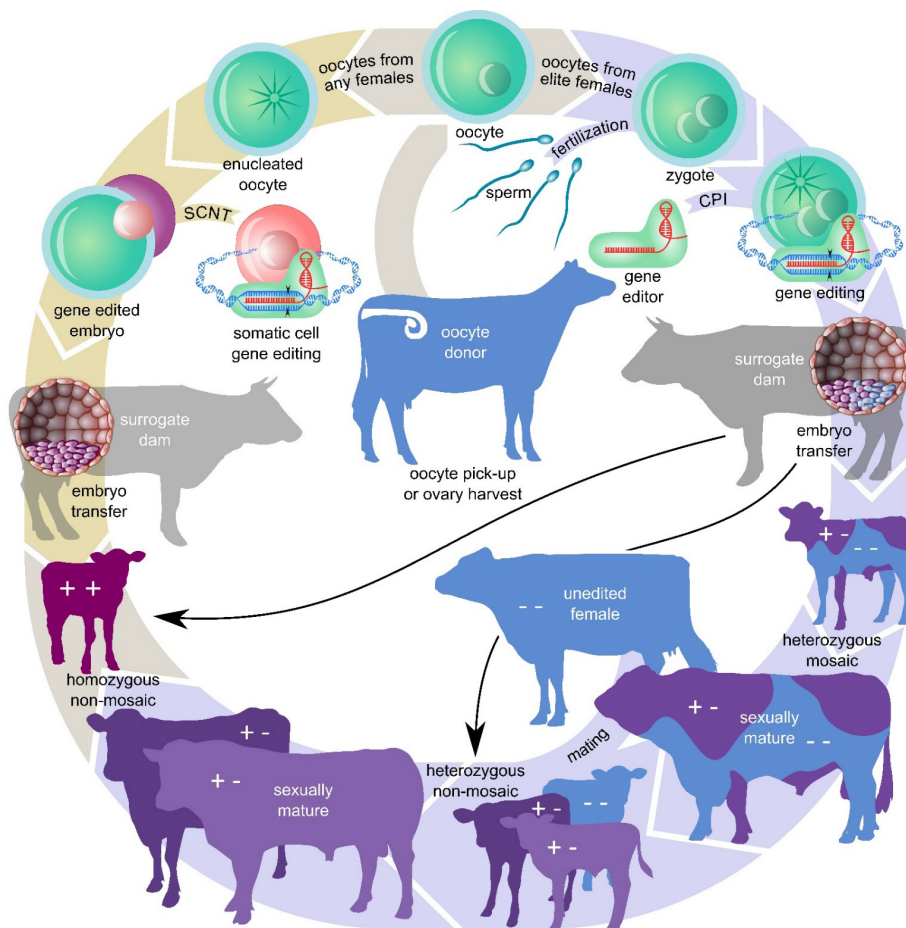


Figure 6. Steps for producing genome edited livestock through somatic cell nuclear transfer (SCNT) or zygote microinjection. Schematic showing the typical steps involved to produce homozygous, non-mosaic livestock by either somatic cell nuclear transfer (SCNT) cloning of genome-edited and screened somatic cells (yellow arrows), or cytoplasmic injection (CPI) of zygotes (purple arrows) with genome editing components. Image from Bishop and Van Eenennaam (2020). Used with permission.

enucleated oocyte to ensure that the desired edits, and no donor template integrations, have occurred. The disadvantage is that there are well-documented drawbacks and inefficiencies associated with cloning, including early embryonic losses and birth defects.

Direct editing of zygotes offers an alternative to cloning, but the disadvantage is that not all embryos will have the desired edit, and often embryos are mosaic—meaning the presence of two or more populations of cells with different genotypes in the one individual. However, on average fewer embryos are required to gene edit a pig, for example, using zygotic CPI as compared to SCNT due to the inefficiencies associated with cloning. Knock-outs using NHEJ have been achieved through CPI of zygotes from a number of livestock species and can be obtained with relatively high frequency, with some reports of 100% efficiency. Targeted gene

insertions have proven more challenging. Entire interspecies allele substitutions have been successfully knocked-in using CPI of zygotes in pigs. The birth of the first calf with a targeted gene insertion resulting from CPI of an early-stage bovine zygote occurred in 2020 (Owen et al., 2020).

Microinjection of embryos that result in mosaic offspring requires subsequent breeding to produce heterozygous or homozygous edited offspring, and this is time consuming and expensive in large food animals such as cattle (Bishop and Van Eenennaam, 2020). Many genome editing applications require homozygous modifications to ensure inheritance of one copy in the F1 generation, or for alleles with a recessive mode of inheritance. The complexity and inefficiencies associated with many of these processes makes the genome editing of livestock far from routine at the current time.

Regulations

As with earlier genetic engineering approaches, whether breeders will be able to employ genome editing in cattle genetic improvement programs will very much depend upon global decisions around the regulatory framework and governance of genome editing for food animals. The United States Department of Agriculture (USDA) has announced that genome edited plants containing genomic alterations that could have been achieved using conventional breeding methods, are not going to be treated differently from a regulatory perspective to crop varieties developed using conventional breeding.

However, the United States Food and Drug Administration (FDA) came out in 2017 with a draft guidance on the regulation of genome edited animals entitled, “Regulation of Intentionally Altered Genomic DNA in Animals” (FDA, 2017). This guidance states that “intentional genomic alterations” produced using modern molecular technologies including genome editing are going to be regulated as “new animal drugs.” It proposes that the presence of any “intentionally altered genomic DNA” would trigger mandatory, premarket new animal drug evaluation, irrespective of product risk or novelty of the genomic alteration. The draft guidance suggests the need for genotypic and phenotypic durability studies over multiple generations, including, where feasible, data on inheritance from at least two generations, preferably more, and recommends that at least two of the sampling points be from non-contiguous generations (e.g., F1 and F3). Fortunately, in 2019 the FDA determined that surrogate cows, also referred to as embryo recipients, are not considered “treated” because they are extremely unlikely to contain the “intentional genomic alteration,” through placental transfer or otherwise. Therefore, these cows may go into the food supply.

One procedural problem with the proposed guidance is differentiating between “intentional genomic alterations,” off-target genome editing alterations, and *de novo* mutations. The 1,000 Bull Genome sequencing project found that genomic sequence data among bulls of different breeds varied by more than 84 million single-nucleotide polymorphisms (SNPs), and 2.5 million small insertion/deletions (Hayes and Daetwyler, 2019). These naturally occurring genomic alterations are









Country		Additional Regulations?	Basis of trigger/regulation?
Argentina		No	Novel DNA sequence/transgene
Australia		Yes	Use of repair template
Brazil		No	Novel DNA sequence/transgene
Canada		No	Trait novelty (i.e. novel product risk)
European Union		Yes	Is a GMO if used a mutagenesis technique not in existence before 2001
Japan		No	No exogenous genes
New Zealand		Yes	Using of in vitro technique that modifies the genes/genetic material
United States		Yes	New Animal Drug

Figure 7. Regulatory approach to genome edited food animals in different countries. Chart indicating whether genome edited livestock carrying a naturally occurring allele introduced using genome editing and a homology-directed repair (HDR) donor template would be subjected to additional regulatory requirements relative to conventional breeding. Current as of 2020.

the basis for all selection programs, and evolution, and are not regulated anywhere in the world.

Further, the draft guidance recommends that all investigational animals, including offspring of genome edited animals and their biological products, be disposed of by incineration, burial, or composting. Multigenerational studies with large food animals such as cattle take years and are beyond the resources of most academic laboratories, especially if the investigational animals have to be incinerated rather than sold for food purposes. While these requirements might make some sense in the context of animals expressing a pharmaceutical protein (i.e., an actual drug), they make little sense in the context of a DNA variant or a naturally occurring allele in food. How can the absence of a small piece of DNA, or a SNP, rationally be considered a drug? Several industry and research groups have argued that the FDA’s proposed new animal drug regulatory approach for genome editing in animals is not fit for purpose (Van Eenennaam et al., 2019).

In contrast, Argentina’s regulatory approach is to treat plants and animals being genome edited for food purposes similarly. They ask two questions of the final product (i.e. food entering commerce): “Is there a new combination of genetic material in the final product?” and “Does the final product contain a transgene?” If the answer to both of these questions is no, then that product does not trigger the genetic engineering regulatory approval process. The “GMO”

regulations pertain to plants and animals containing foreign rDNA constructs containing new combinations of DNA that could potentially present a hazard in the form of a new food allergen or toxin. Figure 7 reveals the 2020 disharmonious state of proposed regulations regarding genome editing in animals globally.

Conclusions

Significant improvements in the efficiency of milk and beef production have historically been accomplished through conventional breeding of superior individuals with an eye toward specific breeding objectives. A number of biotechnologies have been used to accelerate the rate of genetic gain. These include artificial insemination, embryo transfer, and genomic selection. More recent “modern” biotechnologies that could be used in breeding programs include cloning and genetic engineering. To date no genetically engineered cattle have been approved for food purposes anywhere in the world.

Genome editing is a modern biotechnology that is well suited for modifying qualitative, single-gene traits at comparatively rapid rates in the absence of linkage drag, and could be used in conjunction with conventional selection approaches to address issues such as disease resistance and improved welfare traits. Animal breeders need regulatory certainty regarding genome editing if they are to use this technology in their breeding programs. If editing is used to introduce alterations

that are no different from those that could have been obtained using conventional breeding, it should not trigger additional layers of regulatory scrutiny and expense. Regulations should be proportionate to any novel risks inherent in the product, and not the process used to produce that product. At the current time the arbitrary trigger for regulation of genome edited livestock in the United States is the presence of “intentional genomic alterations” introduced using modern molecular techniques. This means even SNPs and deletions introduced using editing trigger a new animal drug regulatory evaluation. This new animal drug regulatory paradigm will put the United States at a competitive disadvantage when it comes to incorporating genome editing into animal breeding programs, relative to other countries (e.g. Argentina, Canada) where novel product risk-based regulatory approaches have been implemented.

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