EPDs and Heterosis - What is the Difference?

By Steven D. Lukefahr

KINGSVILLE, Texas: The value of Expected Progeny Differences or EPDs as a genetic tool of selection is widely accepted especially in the seedstock industry. On the other hand, the value of heterosis is also widely accepted but mostly in the commercial industry.

What is the basis for these genetic concepts and how do genes that relate to EPDs and heterosis manifest their effects on performance? How should breeders apply these concepts in the form of practical breeding tools? Like any breeding tool - they can be used correctly or incorrectly with either desirable or undesirable results.

First, both EPDs and heterosis involve so-called Quantitative Traits that are affected by many genes, such as traits that involve numbers like body weight or milk yield measurements are taken.

Basically, a gene expresses itself in a specific physiological manner. For example, all of the genes that an animal possesses for growth will orchestrate the expression of various hormones but at different levels due to the animal’s own genotype as compared to that of other animals. As breeders, we estimate the effect of all of these genes when the trait is measured on an animal or half of the parent’s genes if the trait is measured in its offspring. Obviously the environment also plays a role in trait performance.

**EXPECTED PROGENY DIFFERENCES**

The predictive measure of genes being transmitted from parent to offspring for a specific quantitative trait is reflected in EPDs. The animal’s Breeding Value (BV) is defined as the animal’s value as a genetic parent (Bourdon, 2000). A BV represents the numeric effects of all of the genes that the animal possesses for a quantitative trait. However, EPDs involve the transmission of only a random
sample of half of the parent's genes. This explains why there is variation among a parent's own offspring because each one received a different sample of genes for the same trait. Moreover, the parent's estimated and reported EPDs represent its average EPD. This expectation can be put to a simple formula: 1/2BV = EPD.

Hence, one-half of BV is transmissible. Most offspring will approach the average EPD value of both parents for the quantitative trait of interest. Of relevance, the amount of variation in BVs among animals for a trait in a population is the basis for determining the level of heritability. If a trait is highly heritable, rapid genetic progress can occur if EPDs are used as selection criteria. Here good caution is advised: neither single trait selection nor selection for extremism should be practiced.

Geneticists like to use models to explain gene action or behavior. The following table illustrates the numeric effects of genes and the simple relationship between BV and EPD (Table 1). The trait of interest is cow lifetime production in beef cattle, defined as the cumulative weights of all the calves that the cow has raised to weaning age.

Let's take an example of two breeds and their cross. Only three gene pairs (A, B, and C) are needed to explain the concepts of BV and EPDs, knowing that quantitative traits involve many more gene pairs.

In the table footnote are the letter codes and numeric effects for each gene (units are in pounds) because the gene effects, although different, are similar in their overall effect on the trait. In this example these two breeds have the same average for cow lifetime production. There is a difference of only one pound with respect to the breed's EPDs, referred to as across-breed EPDs.

The AxB cross has a BV of +3, which is calculated as either the sum of the EPDs of the parental breeds or as the average BV of both parental breeds. (Please note that this BV value could be worked out directly based on the sum of the numeric values for all six genes: AABBCC). The AxB cross has an EPD of +1.5, which is half the BV of +3 or the average EPD of both parental breeds. Based solely on these BVs (for the moment ignoring the potential heterosis contribution), crossbreeding would presumably do little to change the average performance of this trait. In reality, this model would explain why similar average performance results - sometimes even between distantly related breeds - have been reported in breed evaluation research studies.

In contrast, on the right-side of the table are two different breeds: C and D. The genes of these breeds impart different numeric effects than as shown for breeds A and B. As a result the BVs of -6 and +14 (EPDs of -3 and +7) are quite different.

Crossing of breeds C to D would improve the average for Breed C by a difference of 10 pounds for cow lifetime production, although it would be wise to identify other animals of Breed D with even higher EPDs if the breeding objective is improve Breed C for this trait.

Another matter, if either the AxB or the CxD cross (F1) are used as parents the EPDs of the AxB cross would range from -3 to +6 (from abc and ABC genotypes).

The range is larger for the CxD cross of -9 to +13 (from abc and ABC genotypes). Because of the genistic dissimilarity between the effects of genes between breeds C and D, the high variability of EPDs in the cross could be problematic if they are used as parents.

However, genetic variability is sometimes a good thing to have because this provides an opportunity for the breeder (as well as Nature) to practice more intense selection in choosing offspring from the very best parents to achieve more genetic progress.

**HETEROSES**

Heterosis is defined as the average performance for a trait of interest of crossbreds compared to the average performance of the parental breeds that produced the cross. "Heterosis" technically refers to a genotype being in the heterozygous state (e.g. Aa).

In fact, the amount or level of heterosis largely is a direct reflection of the extent of heterozygosity among all the gene pairs (i.e., the entire genotype) for a single quantitative trait. It goes without saying that F1 offspring from the mating of closely-related breeds (British X British cattle such as Hereford X Shorthorn) will have less heterozygosity (and express less heterosis)
In the table footnote are the letter codes and numeric effects for each gene (units are in pounds). In reality, some genes are more important than others (some are major while others have only minor effects). This hypothetical model shows that each gene can impart a different or in some cases even the same numeric value on the trait.

On the left-side of the table there are two similar breeds: A and B. (It will later be revealed why they are similar.) For animals of Breed A the BV of +4 equals the sum of the effects of all six genes ([AA: 3 + 3] + [bb: -2 + -2] + [CC: 1 + 1]). Again, half the BV of +4 equals the EPD of +2. Because the effects of genes can be summed, this type of gene behavior is called additive gene action.

Animals of Breed B have a different set of genes; however, they have a similar BV of +2 ([aa: -1 + -1] + [BB: 2 + 2] + [cc: 0 + 0]). This is
EPDs and Heterosis

Continued from p. 11

than the F1 offspring from the mating of distantly-related breeds (e.g., African X British cattle such as Tuli X Hereford).

From an evolutionary standpoint, heterozygosity is important in natural populations because this conserves genetic variation - a critical factor to better guarantee the survival of the species. Genetic variation enhances the chances that an animal population will be able to evolve by continually adapting to a changing environment. In turn, this allows Nature to be more selective for animals with the very best genotypes.

Another reason is that for a given gene pair there could be a favorable dominant gene that prevents the expression of the recessive gene that otherwise could decrease performance (e.g., a recessive gene that could lower the level of antibody production). This is called complete dominance.

Many genetic anomalies involve recessive genes; however, not all recessive genes are undesirable.

Certain recessive genes could be of value later under certain environmental conditions and hence are being conserved until this opportunity arises. Beside complete dominance, other forms of dominance exist as well.

In addition, some heterozygotes may not express any dominance at all (e.g. roan Shorthorns are heterozygous - both genes for red and white color express themselves).

In terms of practical livestock breeding, heterosis is referred to as hybrid vigor. Generally, crossbreds are more hardy or vigorous than purebreds with respect to fertility- and survival-related traits. This phenomenon explains why most livestock in the commercial industry are crossbred because the increased vigor can affect many economic traits, which translates into increased business profits.

Purebred animals that are found in the seedstock industry generally have less heterozygosity and so express less hybrid vigor, requiring better feeding and management and/or being raised in less stressful environments. (Of course there are always exceptions.)

This is why EPDs are more important to seedstock producers. However, heterosis measures the extent that there is more heterozygosity with some form of dominance expression in crossbreds relative to the purebred parental breeds, so the estimation of heterosis is the amount realized from crossbreeding.

To better understand heterosis, a basic measure known as Gene Combination Value (GCV) is used. This genetic effect will again be illustrated using a model (see Table 2).

For sake of simplicity, purebred animals of all four breeds are shown to be homozygous (two copies of the same gene for each pair). Because there is no heterozygosity in the purebred animals the GCVs are all zero. This is because there is no combination of a dominant gene with a recessive gene (i.e., the dominant gene cannot mask the possible negative effect of a recessive gene that could decrease performance).

For the AXB and CXD crosses, because there is complete dominance, only one dominant gene is needed for each pair. This makes animals that are either homozygous dominant (AA) or heterozygous (Aa) indistinguishable phenotypically in terms of what is seen or measured (depending on the trait).

For example, a bull or cow that is polled could have either the PP or Pp genotype because there is complete dominance for this simply-inherited trait. However, unlike BV (where the numeric effects of individual genes are simply summed), GCV is not so simple and is based on interaction involving heterozygous gene combinations, as well as combinations of genes among other pairs.

Therefore, GCV is non-transmissible because a parent can only transmit one gene (A or a), not both genes (Aa), from a pair. This property involves a different type of gene behavior called non-additive gene action. To put in clearer perspective, EPD is based on BV due to additive gene action whereby heterosis is based on GCV due to non-additive gene action. Potentially, for any gene pair both types of gene action could occur.

On the left-side of Table 2, as stated previously the GCVs are zero for purebred animals of breeds A and B. However, because the AXB cross is heterozygous for all three gene pairs the opportunity exists for complete dominance expression, which is measurable in terms of GCV.

The AXB cross has a GCV of +9. But how is this value calculated? For the A gene pair, if instead there was no dominance the Aa heterozygote would have a BV of +2 (from +3 + -1) and be exactly intermedi-
ate between the BVs of -2 and +6 of AA and aa genotypes.

However, because there is complete dominance the Aa heterozygote has a value of +6 which is identical to the +6 BV of AA.

This makes sense because again these two genotypes should be indistinguishable phenotypically. The numeric contribution of complete dominance for the Aa genotype is solved by taking the difference of +6 minus +2, which equals +4.

Across all three gene pairs, the AXB cross has a GCV of +9 (calculated as the sum of +4 from Aa, +4 from Bb, and +1 from Cc), which is higher than the best BV of +4 for Breed A. On the right-hand side of the table, the BXD cross has a GCV of +22, which is numerically higher than the best BV of +14 for Breed D.

Further, the Genotypic Value (GV) is the sum of BV and GCV and represents total genetic performance. The GV value of +12 for the AXB cross is higher than the value of +4 for Breed A, while the GV value of +26 for the BXD cross well exceeds the value of +14 for Breed D. (Note that the GVs for all four breeds come entirely from BV.)

In crossbreeding systems, it is important that commercial producers know that BV and GCV both contribute to total genetic performance (GV). Successful commercial producers strive to purchase bulls (or use their semen) with the best EPDs for several traits which are used in crossbreeding to produce terminal-crossbreds that will also benefit from heterosis based on GCV. Again, both BV and GCV impact GV in terms of total genetic performance.

As previously stated, traits that are greatly affected by heterosis include fertility- and survival (health)-related traits. Recall that in natural or wild populations, heterozygosity is paramount to the survival of a species where fertility and survival are critical “fitness” traits.

From a livestock breeding perspective, a commonly cited statistic used in the beef cattle industry is that the crossbred cow expresses a level of about 25% heterosis for lifetime productivity. This is a composite trait that is affected by fertility, survival, and growth component traits.

Growth- and feed efficiency-related traits usually show less but still some benefits from heterosis. Here both EPD selection and heterosis can be exploited from crossbreeding systems. However, carcass traits are influenced very little by heterosis because these traits already tend to be highly heritable. This means that BV is more important than GCV; therefore, EPDs are more useful as selection criteria.

Another important point is that heterosis expression is generally greater in unfavorable environments. In other words, in adverse environments crossbreds can be even more hardy than purebreds, the latter being more sensitive to stressful conditions. In such environments the difference in average performance between crossbreds and purebreds can be greater.

For example, in my own herd of Star composite cattle the estimate of heterosis for weaning weight is 72.1 pounds (Lukefahr, 2017). There are two reasons that could account for this large amount of heterosis.

First, the foundation breeds used in the composite - Red Angus, Scncepol, and Tull - are distantly related so there is likely more heterozygosity, boosting heterosis. And second, the composite is raised in an adverse subtropical environment so their average performance is likely higher than that of their parental breeds if they were raised in a less stressful environment.

Continued on p. 14
In summary, EPDs and heterosis are based on two different types of gene action. Some traits are influenced more, others less, by these two types of gene action. In terms of genetic performance of offspring, purebreds are affected more by EPDs than GCVs, whereas crossbreds can be affected sometimes to a similar extent by both EPDs and heterosis, depending on the trait.

This article illustrates some fundamental properties of gene effects that have practical implications to breeding management. If the breeder has an understanding and a practical grasp of these principles, he or she can apply them in practice to optimize animal performance.

Steven Lukefahr is a professor in the Dept. of Animal, Rangeland, and Wildlife Sciences at Texas A&M University-Kingsville. He teaches Agriculture students what he has learned from his own breeding and ranching experiences. Steven is available for consultation at slukefahr@gmail.com. His business web address is http://lukefahr-ranch.com.

REFERENCES