In the last article in this series, breeding value was described as the value of an individual as a parent with respect to a given trait. Breeding values are theoretical quantities and cannot be measured directly, but they can be estimated. To learn how they are estimated, we need to understand such concepts as heritability and genetic correlation, terms that were also discussed in the last article. Equally important to breeding value estimation is a third concept, that of relationship.

**Relationship**

Relationship, in an animal breeding context, means “blood relationship.” Two animals are related if they have one or more ancestors in common. Individuals can have varying degrees of relationship with others; full sibs are quite closely related while third cousins are only distantly related.

Related animals, especially closely related animals, tend to resemble each other in a number of traits. The resemblance is due to a similarity in their breeding values for these traits. In statistical terms, this similarity can be measured as a correlation. We can say, then, that relationship is a correlation between the breeding value of one individual for a specific trait and the breeding value of another individual for the same trait, a correlation which is due to pedigree relationship alone. The correlation between breeding values of sire and son is 0.5, between half brothers and sisters 0.25, and between half first cousins 0.0625. Note that this correlation does not differ for different traits. It is strictly a function of pedigree.

Knowing the correlation between the breeding values of two animals, we can predict the breeding values of one based on information measured on the other. We can use the records of relatives to estimate the breeding values of individuals. Thus, it is possible to estimate an animal’s breeding value for birth weight by measuring the birth weights of its siblings or its calves. We
can even predict a bull's breeding value for udder conformation using measurements taken on his sisters or aunts.

The stage has been set for a full-blown discussion of breeding value estimation. However, since the concept of relationship has been introduced, I will digress and cover some associated topics of interest to cattle breeders: inbreeding, hybrid vigor and "nicking."

Inbreeding

Inbreeding is defined as the mating of related individuals—individuals that share at least one ancestor. Since all cattle are ultimately related, and since

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we don't think of all matings as producing inbred offspring, inbreeding is more precisely defined as the mating of individuals more closely related than is average for the population. (Purebred breeders can consider population to mean their breed. Commercial cattlemen can consider it to mean all commercial cattle.) The opposite of inbreeding is outbreeding or the mating of individuals less closely related than is average for the population. Linebreeding is a euphemism for inbreeding, although it usually involves the avoidance of very close matings and may be an effort to retain in the herd the genes of a particularly revered ancestor or group of ancestors.

To understand the effects of inbreeding and outbreeding, it is necessary to see what is happening to the genes themselves during the inbreeding and outbreeding processes. Genes come in pairs, one member of each pair is inherited from the sire, the other from the dam. The genes of a pair may or may not be identical in function. When they are identical, the genes are said to be homozygous, and when they are not, they are termed heterozygous. A gene may function differently depending on the gene it is paired with. Dominant genes are those which have the capability of masking to a greater or lesser degree the effects of their "partner" genes. A recessive gene, on the other hand, is one whose function can be partially or completely over-ridden when paired to a dominant gene. The gene for polledness, for example, is dominant and the gene for the horned character is recessive. When a pair contains both the polled and horned gene, the animal will be polled. With some exceptions (red coat color a notable one), dominant genes tend to be favorable while recessive genes tend to be unfavorable.

With inbreeding, a single gene that was present in an ancestor common to the sire and dam of an individual has the opportunity to be inherited by the individual from both its parents. When this happens, the genes of this particular pair in the individual are necessarily homozygous since both are replicates of the same gene. With a close mating, say between a full brother and sister, the likelihood of creating homozygous pairs in this manner is quite high because only two generations are involved; replicates of genes in the grandparents are passed to daughter and son, and from them to inbred grandson or granddaughter. Inbred animals tend to have more homozygous pairs of genes than outbred animals, and continual inbreeding within a line of animals causes a general increase in homozygosity. Sometimes this increase in homozygosity progresses to the point that certain genes become fixed within the line; in other words, those genes have a complete monopoly. The horned gene is almost, but not quite fixed in the Holstein Hereford breed (though not exclusively as a result of inbreeding).

The inbreeding coefficient is a measure of how inbred an animal is. Technically, it is the probability that two genes of a pair in an individual will be homozygous because they are replicates of a single ancestral gene. (Statistical probabilities range from zero to one, a probability of zero meaning no chance at all and a probability of one meaning absolute certainty.) The offspring from our mating of full brother and sister would have an inbreeding coefficient of 0.25 and would be considered 25 percent inbred. For comparison, half-sib matings produce offspring with inbreeding coefficients of 0.125, and the most highly inbred pedigreed cattle are about 70 percent inbred.

The increase in homozygosity resulting from inbreeding has several ramifications. One is an increase in the uniformity of the offspring of an inbred parent. This occurs because any pair of homozygous genes can only produce one type of gene to be transmitted to an offspring, and a set of these pairs will produce a consistent set of transmitted genes. To use the poker analogy, an inbred animal is like a deck of cards which contains just one suit. Every deal produces a flush. Inbreeding is commonly justified by cattle breeders as a way of increasing prepotency or breeding consistency.

Increased homozygosity can also result in the surfacing of deleterious recessive genes—hence inbreeding's bad reputation for producing undesirable traits. It should be emphasized that inbreeding does not create bad genes; they must already be present. However, inbreeding does create an opportunity for deleterious recessives to be paired in an individual, thus allowing them to be expressed. Inbreeding can, therefore, be used as a test to check for the presence of harmful recessive genes in an animal. Sire x daughter matings are an example of such a test. And highly inbred lines which show no evidence of deleterious genes are likely to be free of them.

Inbreeding works randomly with regard to what kinds of genes become homozygous. Sometimes dominant (usually favorable) genes are paired and sometimes recessive (usually unfavorable) genes are paired. An inbred animal's homozygous dominant genes give him little advantage over a non-

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inbred animal with corresponding heterozygous genes because the recessive genes of the non-inbred are masked by dominant genes. By the same reasoning, however, the homozygous recessive genes of the inbred animal are a distinct disadvantage. Because they are homozygous, they can express themselves, and although they may not be "deleterious" in the sense used above, they cause a general reduction in performance. This reduction in performance in inbred animals caused by the expression of formerly hidden recessive genes is termed inbreeding depression. It is particularly evident in reproductive traits where dominance and recessiveness seem to be especially important.
Hybrid vigor

The opposite of inbreeding depression is hybrid vigor or heterosis. Just as inbreeding depression occurs when unfavorable recessive genes are paired and therefore allowed to express themselves, hybrid vigor occurs when the recessive genes from an inbred are masked by the dominant genes from an unrelated mate. When highly inbred lines are crossed, we see great improvement in the offspring—mostly in reproduction and livability. The mechanism is no different when breeds are crossed. Breeds are really large inbred lines, and the hybrid vigor we get from crossbreeding is just an “undoing” of the inbreeding depression we take for granted in purebreds.

An important thing to remember about hybrid vigor and inbreeding depression is that they cannot be inherited. Both are consequences of the pairing of genes, but just one gene of a pair and not the entire pair is passed from parent to offspring. Only breeding value is transmitted because breeding value represents the independent effects of an individual’s genes, effects independent of pairing. Thus, there are really two quite unrelated components of genetic value: breeding value, or the value of an animal as a parent, and a value resulting from gene pairing (we might call it a “vigor value”). Because these two components are independent, it is very possible to have a depressed, unimpressive inbred bull with superior breeding values, or a flashy outcross sire with inferior breeding values.

“Nicking” is a generic term commonly used by breeders to mean the fortuitous result of crossing two lines within a breed, or of mating two particular individuals. Two lines “nick” well if the calves produced by crossing those lines are especially desirable, and a specific mating is a good “nick” if it produces a good calf.

Nicking can come about for two reasons. The first reason relates to breeding values. Since the breeding values of calves will on the average be equal to the mean breeding values of their parents, a bull with a very desirable breeding value for a trait and a cow with a similarly desirable breeding value will nick well with respect to that trait. The same goes for lines. For example, two lines that are superior in breeding value for growth will nick well with respect to growth. The combining of breeding values can result in complementarity, which can also be thought of as a form of nicking. In this case, two lines or individuals that differ widely in breeding values for one or more traits are crossed to produce intermediate, yet desirable offspring. An especially short cow can be mated to an extremely tall bull to produce medium-framed calves, or a line which is especially good milking but mediocre for growth can be crossed with a very growthy but not particularly good milking line to produce calves that are better than average for both traits. Whether or not complementarity is involved, nicking, as described above, results from the opportunistic combining of breeding values.

The second cause of nicking is hybrid vigor. It results from the mating of unrelated individuals or the crossing of unrelated lines. For hybrid vigor to occur, however, the parents or parental lines must be at least somewhat inbred relative to the general inbreeding level of the breed. Most “lines” as we think of them are not inbred lines at all; they contain animals whose sires are related, but whose dams may be total outcrosses. There is some question, therefore, whether we often get much hybrid vigor from crossing lines within a breed. If a nick does occur as a result of hybrid vigor, the mating practice which produced the nick is self-defeating from a long-term breeding standpoint. The resulting calves may be good performers themselves, but they cannot pass on their “vigor value” to their offspring. Only breeding value is passed on. The hybrid calves will perform better than they breed.

Nicking can be of value if what is meant by a good nick is simply a desirable combination of breeding values. If a good nick depends on hybrid vigor, however, its value is only cosmetic.

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NEXT:
Estimated Breeding Values and MPPA