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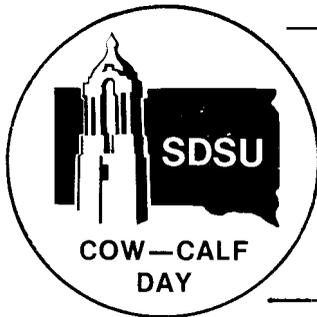
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WHAT THE BREEDER SELLS AND THE PRODUCER BUYS: BREEDING VALUE

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A breeding value is the value of an individual as a parent. This is precisely what breeding stock herds sell. It is the value of the progeny from their breeding stock in the herd of the buyer that is the issue. As specification of product becomes more important in the beef industry, breeders can be merchandizing breeding value. Beef breeders are selling a product that must transmit a sample half of its germ plasm to progeny before the result is realized. Commercial producers sell pounds, not breeding value, but they need to buy breeding value as well as combine breeds in logical combinations to obtain the crossbred advantages especially for the reproductive complex. Thus, both the commercial and breeding stock producer can benefit from understanding the concept of breeding value. The purpose of this paper is to define and describe the breeding value concept and to examine ways to use the concept in practice.

THEORY

The breeding value concept is a figment of man's fertile imagination. It was defined and developed to relate selection theory with the genetic reality that genes have their effects in pairs (one member of each pair having come from the sire and the other the dam) yet the genes are transmitted singly from parent to offspring (one gene or the other of each pair possessed by a parent is transmitted to an offspring). The basis of selection is the resemblance between parent and offspring. Since each parent transmits a sample half of its genes to an offspring, the degree of resemblance is a measure of the importance of gene effects (not gene pair effects) on the variation for a trait. The heritability of a trait is evaluated using a measure of the degree of resemblance between relatives. The sum of the gene effects, produced by the sample half of the genes transmitted from a parent, as expressed in its progeny, is a definition of one-half of the breeding value of the parent. Thus, we see from using measurable quantities obtained from performance data, it is possible to predict selection response. Heritability is the fraction of the variation in a trait that is produced by gene effects. Heritability times the superiority of the selected parents over the average is the average breeding value of the parents as well as being the response to selection expected. So the concepts tie together to give us usable theory on which to design and conduct breeding programs that maximize genetic change. Selection or the choice of parents is the only direction tool available to the breeder to bring about genetic change. There is no other.

A breeding value can be defined as twice the difference between the average performance of a large number of progeny and the population average. This is the working definition of breeding value. The difference is doubled because only a sample half of the genes of an individual are transmitted to its progeny. Several clarifications need to be stated for the definition. The other sex to which the individual is mated to produce the progeny must be a random sample from the population. If they are not, the difference measures more than just the breeding value. The population average must include progeny from the other individuals whose breeding values are to be compared. It is obvious that we are defining the basics of progeny testing and in particular that an expected progeny difference in national sire evaluation is a measure of half the breeding value of the sire. True, a progeny test of a number of sires each with a large number of progeny is the most accurate measure of breeding value, but the progeny test is costly both in resources and in time. There are alternatives. The first is the individual's own performance, if it can be measured, and the second is the performance or average performance of related individuals or groups of related individuals. The progeny in the definition are a group of related individuals since they each have the same parent. Each progeny received a sample half of his genes from the same parent. A few progeny could have received the same half and a few might have received the other half, but on the average they have one-fourth of their genes in common ($1/2$ times $1/2$). Only the parent-offspring relationship is exactly one-half. All the others are averages. However, since relatives have like genes, they have a fraction of their breeding values alike. Thus, relatives can be used to help estimate breeding values of individuals.

Consider the individual's own performance. If heritability (which as a fraction of the total variation goes from zero to one) is one, then knowing the performance of an individual as a difference from a contemporary average corresponds to its breeding value (1 times difference). If heritability is only .3 or 30% of the variation due to breeding value differences, then a difference of 20 pounds would result in a breeding value of 6 pounds ($.3 \times 20 = 6$). Now what is being done is using an average result on individuals. We say that on the average we expect only 30% of the 20 pound difference to be heritable when it is entirely possible for all or none of this difference to be heritable, but on the average 30% will be. However, if we find the average superiority of ten bulls is 20 pounds over their contemporaries, then we expect them to transmit 3 pounds (one-half their average breeding value) to their progeny on the nose.

This brings up the idea of accuracy. Accuracy is the correlation between the estimated breeding value of an individual and his true breeding value (using the definition). When using individual performance information, the accuracy is the square root of the heritability. For a trait with 50% heritability, using own performance differences has an accuracy of .71 where 1.00 is perfect accuracy. For 40% heritability, accuracy is .63. Incidentally, this is the same accuracy as evaluating six progeny, which is not bad. The point is that for highly heritable traits (50% up) individual performance, if it can be measured, is an excellent criteria to use in selecting or buying parents. This is the reason that national sire evaluation is but a means to an end. Now it is the only way to fairly compare individuals outside of the same contemporary group. But as we learn more through sire evaluation, it will be possible to use own performance to make selection more effective.

Now consider relative information. Provided the average performance of groups of relatives that are unselected and do not lengthen the generation interval can be used, they will increase the accuracy of breeding value estimation a lot for traits of low heritability and a bit even for highly heritable traits. All good cattlemen in one way or another consider the other calves of the sire and especially the calves of the dam when selecting an individual. There is logic to doing this. Each member of the group of relatives has a fraction of his or her genes in common with the individual and consequently have the same fraction of their breeding values alike. Assuming that the environmental influences are random relative to the breeding values, then some add to the value of some animals and subtract from others. If a large number are in the group, these plus and minus effects tend to cancel out leaving the group average nearly an evaluation of the fraction of the breeding values in common. This benefit is most helpful for lowly heritable traits, but it also helps for moderately heritable traits. Use of relative information is practiced in current breeding value estimation, but the concept of breeding value is not tied directly to using relative data.

RELATIVE INFORMATION

When used in concert with individual performance, paternal and maternal half-sib (calves from the same sire or dam) add to the accuracy of breeding value estimation and do not lengthen the generation interval. When the individual is a parent, the progeny average is extremely useful. Table 1 presents the various sources of relation information available in most performance programs.

Table 1. Accuracy of records on relatives for estimating breeding value of individual animal.

Relatives '	Number	Genetic relationship	Heritability		
			20%	40%	60%
Parent	1	1/2	.22	.31	.39
Midparent	2	.71	.317	.45	.55
Paternal half-sibs	10	1/4	.30	.36	.40
	40	1/4	.41	.45	.47
Maternal half-sibs	2	1/4	.15	.22	.26
	4	1/4	.21	.28	.33
Individual	1	1	.45	.63	.77
Progeny	10	1/2	.59	.72	.80
	40	1/2	.82	.90	.94

To evaluate the sources, the table gives the accuracy or correlation between the true breeding value and the estimated breeding value, using the particular relative information. Three heritability values are used. The accuracy is higher, the more heritable the trait. As the genetic relationship to the individual animal increases, so does the accuracy. When the numbers in the relative groups increase, the accuracy goes up. The rate of increase is faster for high heritability than for low, but diminishing returns for increasing

numbers set in more quickly for high than for low heritability. The accuracy of selection is influenced by heritability, relationship, and number of relatives in the average.

The primary relatives in beef records are the individual animal, his paternal and maternal half-sibs, and his progeny. If sibs are available, the parent records add little. The first three sources are available at or before reproductive maturity, while the progeny require an increased generation interval to obtain. The use of sib or progeny averages helps in breeding value estimation, since the groups are usually unselected and the averaging of several records tends to cancel out the plus and minus environmental differences, leaving more nearly a genetic value for the average.

These sources of information can be combined into a single estimate of breeding value for each animal that is the subject of selection. This is done by using the numbers in the averages, the heritability, and the relationships to develop a set of linear equations that, when solved, give proper weighting factors to the particular information available on the individual animal for the trait. Then, these weights times the records expressed as deviations will give an estimated breeding value. The value is for the particular trait, using the available information. This procedure has some desirable properties for the breeder using the values for selection. First, the correlation between true and estimated breeding value is maximum. Second, the estimate is regressed toward the average, depending on the amount of information. This latter feature makes it possible for the breeder to use these values to fairly rank individual animals that differ in the amount of information available. The computation of estimated breeding values is done easily by computer, but otherwise is extremely difficult.

Table 2 presents the percentage of attention that is paid to various combinations of information in the estimation of the breeding value of an individual. Note that 10 paternal half-sibs are about equal to the individual's own performance. When numbers of sibs are doubled in the second row, the importance of maternal sibs is doubled while paternal sibs goes up only slightly. This results because the dam side of the pedigree, from which comes half of the genes, is lacking as much information as exists on the paternal side. The last two rows indicate the importance of including progeny on the parents. When 20 progeny exist on a parent, over 70% of the attention goes to the progeny average as it should. Breeders have done something like this for a long time. The problem is that breeders are human and tend to over or under emphasize relative groups in their evaluation. The computer does what it is told and treats the special groups simply as groups.

Table 2. Relative amount of attention that should be paid to various relative groups in estimating breeding value of an individual animal.

<u>Numbers</u>				<u>Percentage attention</u>			
<u>IND</u>	<u>PHS</u>	<u>MHS</u>	<u>PROG</u>	<u>IND</u>	<u>PHS</u>	<u>MHS</u>	<u>PROG</u>
1	10	2	0	44	42	14	0
1	20	4	0	33	46	21	0
1	10	2	10	18	17	6	59
1	20	4	20	10	14	6	69

Currently several breed associations are calculating breeding values using available information on weaning and yearling weights. Because the maternal sibs are so few in number, both of these breeding values can be considered measures of growth. Growth differences pre-weaning are at least 30% heritable and post-weaning growth differences are at least 40% heritable. Thus, inclusion of relative information will increase the accuracy of breeding value estimation a bit (around 15 to 20 percent) over using only own performance.

MATERNAL BREEDING VALUES

Recently maternal breeding values have become available. As they are now calculated, they estimate the breeding value of an individual for milk production as indicated in weaning weights. In this context, breeding value estimation really comes to life as an advantage. First, the heritability for milk production is from 20 to 30%, so inclusion of relative information is an advantage in increasing the accuracy. Second, maternal performance is a generation behind in being expressed relative to growth. Either performance of daughters must be measured, which would lengthen the generation interval, or pedigree evaluation becomes necessary which does not increase the generation interval. Evaluation of maternal breeding values depend on the ability of the program to collect ratios of performance from over herds where various relatives have produced daughters. Third, milk production is a sex-limited trait being expressed only in females. Thus, only females in production must be used. If the dairy approach is used, there would be a six-year progeny testing program before calves of daughters of a sire could be used as the selection criterion of sires. This is the reason for developing maternal breeding values rather than adding on the daughter evaluation to national sire evaluation programs.

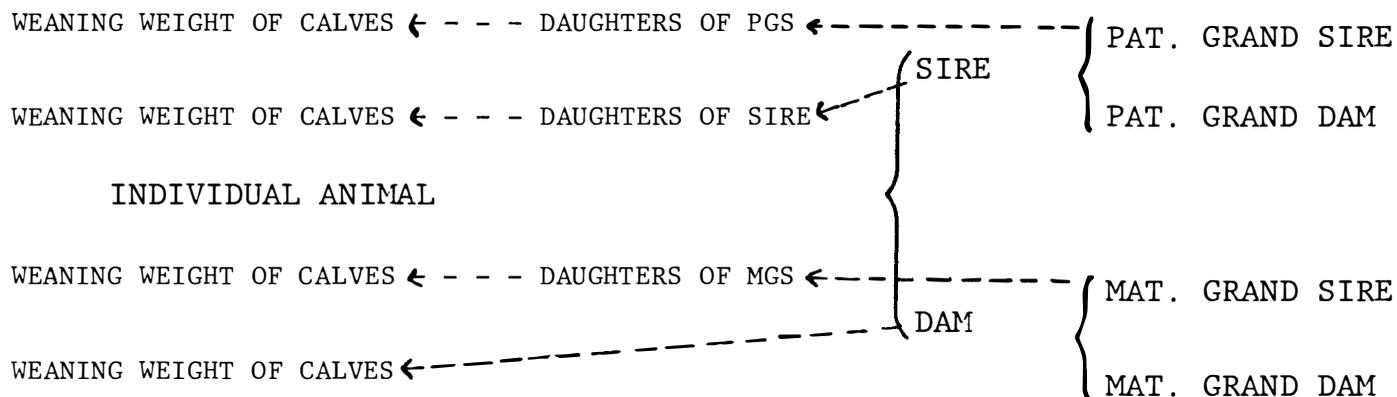
Table 3 gives the same listing of accuracy for maternal breeding values as Table 1 for growth breeding values. Heritability for milk was assumed to be .3 and repeatability .4. The accuracy values for paternal and maternal grandsires' daughters' calves are low even for a large number or progeny. Calves of the daughters of the sire have a higher accuracy, but if a breeder is turning generations, there should be little information available. The accuracy figures are low in general, but when the four relatives groups are combined, the accuracy is roughly .65 which is nearly (.67) as good an estimate on calves for their daughters' milk as in their yearling breeding value for growth using own and paternal and maternal sib information.

Table 3. Accuracy of records on relatives for estimating maternal breeding value of an individual when heritability is .3 and repeatability is .4.

Relative	No. Daughters	Calves per Daughter	Relationship	Accuracy
Calves of the Dam		2	1/2	.33
		4	1/2	.37
Calves of the Daughters of Sire	50	1	1/4	.45
	100	2	1/4	.48
Calves of the Daughters of the Paternal grandsire	100	2	1/8	.22
	200	3	1/8	.24
Calves of the Daughters of the Maternal grandsire	100	2	1/8	.22
	200	3	1/8	.24
Calves of the Individual (if a Dam)		2	1	.66
		4	1	.74
Calves of the Daughters of the Individual (if a sire)	50	1	1/2	.90
	100	2	1/2	.96

Now consider how maternal breeding values are calculated. The following is a pedigree diagram of an animal of interest.

-PEDIGREE-



Note that, with the exception of the calves by the dam, each set of weaning weights are from daughters of a sire, meaning that the maternal ability being measured is passed on a generation, so it is genetic. The maternal breeding value ratio uses four pieces of information when they are available. These are as follows:

1. The average weaning weight ratio of calves of daughters of the paternal grandsire.
2. The average weaning weight ratio of calves of daughters of the sire.
3. The average weaning weight ratio of calves of daughters of the maternal grandsire.
4. The average weaning weight ratio of calves of the dam.

When the individual is a sire that could have daughters in production, then the average performance of his daughter's calves could replace the dam information.

When the individual is a dam, then the performance of her own calves could be used in place of her dam's calves.

These averages are weighted heavily for maternal ability rather than growth rate. Any information that is available is combined into a single breeding value as was done with the regular breeding values for weaning and yearling weight. This procedure would have little information if it were not for the opportunity to look up the weaning ratios of all calves of the daughters of the paternal or maternal grandsire in the herds in which they were used.

Real problems exist in including fertility information. Use of the calf crop percentage of the dam is probably all that is practical at this time. This is unfortunate because fertility is much more important than milk production. However, this will serve to get breeders thinking about measuring maternal traits.

Table 4 gives the percentage attention paid to relative groups used to calculate maternal breeding values. The results are only approximate since the off-diagonals were ignored. The calves of the daughters of the grand sires do provide useful information.

Table 4. Relative amount of attention that should be paid to relative groups in estimating the maternal breeding value for an individual.**

IND	IND*	SIRE	PGS	MGS	IND	SIRE	PGS	MGS
Calf	2	0/0	100/2	100/2	20		40	40
	4	50/1	200/3	200/3	13	39	24	24
Dam	2	50/1	200/3	200/3	20	36	22	22
	4	50/1	200/3	200/3	23	35	21	21
Sire	50/1	100/2	200/3	200/3	46	26	14	14

*For calf the IND is calves by the dam, for dam the IND is calves by the IND, and for sire the IND is calves of the daughters of the individual. **The values were obtained ignoring the off-diagonals.

Use of maternal breeding value ratios by breeders can help breeders maintain their superior maternal performance while still improving feedlot growth rate. Without these maternal performance indications, it would be possible to lose a maternal advantage by going all out for size and growth rate. This represents another opportunity for creative breeders to develop sound breeding programs. The breeds that survive the intense competition for the commercial man's germ plasm dollar will be those breeds having an association that provides them a sound performance program and breeders willing to adopt the new technology in practical breeding programs.

TRAITS

Weaning weight, yearling weight, and milk production as indicated by weight at weaning are not all the traits on which breeding values would be useful. Fertility of daughters would be an important addition, but few data files contain complete data on each year of a cow's life. Computing breeding values on important traits to a breed might be one way of encouraging breeders to consider the trait in selection and in merchandizing their breeding stock.

PRESENTATION

There are two ways estimated breeding values can be presented for use by the breeder. The first is in the form of a selection worksheet, and the second is in the form of a performance pedigree. The first is useful in making selections in a breeding program; the second has as its purpose promotion of breeding stock.

The selection worksheet gives the animal identification, available data for that animal, and estimated breeding value, based on the records of a contemporary group of animals in a herd. The purpose is to use the selection worksheet in conjunction with common sense to select breeding stock. For example,

each time a group of calves is weaned, the breeder receives selection worksheets that give the estimated breeding values of the male and female calves separately, along with the values for the dams and sires. These are current worksheets which give all relevant weaning data for each individual animal that is on record. From this, the breeder can make his first selection on the calves and cull his cows in conjunction with a pregnancy test. When yearling selection worksheets are sent, the breeder can select his sire prospects, develop his sale bull offering, and make decisions about his herd bulls before he lots his sires for breeding. Use of the selection worksheet is a way to make effective use of records in a breeding program.

Performance pedigrees are primarily promotion, especially if the selection worksheets are being used. Using the information on a performance pedigree to estimate a breeding value for each trait of importance is a much safer procedure than trying to come up with a sound analysis of the pedigree mentally. Human nature is such that the good records get overevaluated, and the poorer ones are sometimes forgotten. The individual performance of the ancestors when expressed relative to their contemporaries provides an excellent means of determining the selection practiced in the herd. As a promotional tool, the breeding value is an estimate of what that individual animal is expected to transmit to his or her offspring. The breeding value concept is precisely what a breeding stock breeder is selling. It is what the stock of a breeder does in the herd of the buyer that makes the performance reputation.

COMBINING BREEDING VALUES

Theory is available to combine information on several traits into a selection index, so that selection could be based on the index. The additional information necessary to compute such an index is the economic value of each trait, the genetic and phenotypic correlations between the traits, and a specification by the breeder of net merit. Which traits are used and how they relate economically are individual breeder problems in the determination of goal and cannot be set for him by his performance record program.

Two logical alternatives exist for the breeder that gets estimated breeding values on his herd for several traits. First, he can weigh the estimated breeding values by appropriate economic values and use this as his selection criterion. Second, he can use an independent culling level for each trait. When the values for the first trait are available, he can select a fraction P of the animals, and when the second trait values are available, he can select a fraction Q of the remaining animals. The product $P \times Q$ must equal the number of replacements necessary.

SUMMARY

A breeding value is the value of an animal as a parent. Breeding values are what breeding stock herds sell and what commercial herds are buying. Performance data can be used to calculate breeding values for the beef industry so that specification of product at the genetic level can be enhanced. Weight breeding values offer breeders the opportunity to select and sell on all the performance information available in their program. Maternal breeding values offer breeders the opportunity to use pedigree performance data on weaning weight to select and sell animals on their potential for milk production. Letting the performance program find and weight properly the relative information allows the breeder the opportunity to devote his time to the conduct of more creative breeding programs.