



Improving Your Herd

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In the first article of this series [see the Summer 2002 issue of *A.M.*], the three main factors that we must consider in order to produce the next generation of offspring – traits, selection, and mating – were introduced. The purpose of this article is to discuss in more detail some of the factors affecting the rate of genetic change touched on in the first article, so that we can progress toward our breeding goals by using these principles of quantitative genetics.

Breeding Value

The reader will remember that the **key equation** that determines the effectiveness of our selection process, states that the rate of genetic change is proportional to selection accuracy, selection intensity, genetic variation, and generation interval. **Selection accuracy** refers to selecting the animals with the best breeding values to be in our breeding program. What the best values are depends on the goals the individual breeder has for future generations. **Breeding value (BV)** is defined as the animal's individual value as a genetic parent – i.e., a contributor of genes to the next generation.

Our formula for phenotype:

$$P = G + E$$

says that the phenotype for any trait is the result of the combined effects of the genes an animal has inherited and the environmental influences to which it has been subjected throughout its life. We can refer to the “G” in this equation as the individual animal's “genotypic value,” but that is not the same as its breeding value (BV), which is that part of the genotypic value that can be transmitted to this individual's offspring. Some genotypic values are the result of the combination of the effects of many genes, some of which are dominant to others, some of which are additive, and some of these genes can have **epistatic effects**.

Epistasis means that the genes at one locus can have an effect on genes at other loci.

“A simply-inherited example of epistasis that is relatively easy to understand is coat color in Labrador retrievers. Labs come in three basic colors: black, chocolate, and yellow. These colors are determined by genes at two loci: the B (black) locus and E (extension of pigmentation) locus, as follows:

B_E_ => black

bbE_ => chocolate

_ _ee => yellow

The dashes in these genotypes indicate that either allele could be substituted without changing the phenotype. Black Labradors, for example, can be BBEE, BB \bar{E} e, BbEE, or BbE \bar{e} . Yellow labs can be BB \bar{e} e, B \bar{b} e \bar{e} , or b \bar{b} e \bar{e} . Note that the expression of genes at the black locus depends on the alleles present at the extension locus. So long as there is at least one E allele at the extension locus, there appears to be complete dominance at the black locus, with black being dominant to chocolate. However, if the genotype at the extension locus is ee, then genes at the black locus become irrelevant – all animals will be yellow”¹

In this example then, genes at the E locus are epistatic over genes at the B locus. Epistasis is just one type of **gene combination effect**. Dominance is another. These effects cannot be passed on by one parent, as they are due to combinations of genes, and the Mendelian process of segregation and independent assortment of genes that takes place at random when gametes (sperm and egg cells) are formed, prevents the inheritance of any particular combinations of these genes that might be present in the parent.

Because combinations of genes cannot be transmitted, then an animal's BV can only represent the independent effects of the genes they have to pass on. Therefore, we can say that an animal's genotypic value (G) is the sum of the independent gene effects that can be passed on (BV), and the gene combination effects that cannot predictably be passed on. We will call that the animal's Gene Combination Value (GCV). So in algebraic form we can say:

$$G = BV + GCV$$

Substituting into our formula for Phenotype we get:

$$P = BV + GCV + E$$

This formula is useful to keep in mind when we look at an alpaca as a potential parent. It tells us that what we can see and measure (the phenotype) is a combination of the genetic factors a parent can potentially transfer to offspring, a genetic component that cannot be transmitted to the offspring, and a component that comes from the effects that the alpaca's environment has had on its growth and development throughout its life, which of course cannot be transmitted genetically, either.

What are we doing?

As animal breeders, what are our goals and objectives? Why are we mating our animals, and why are we doing it the way we are? Is the goal to produce more alpacas and increase the size of our individual herd as well as the “national herd”? Are we breeding animals to replace our stock? Are we attempting to breed in such a way that the descendants will be “better” than the present generation? What is the “best” alpaca anyway? Is our goal a combination of all of these? If so, which outcome is the most important?

We cannot directly measure an animal's genetics. Therefore, we also cannot directly measure an animal's BV. Instead, we can estimate the breeding value based on performance data. This is what we will call Estimated Breeding Value, or EBV. The more performance data we have, the more accurate this estimate will be. This data can be from the animal's own performance records (Individual's Data); the performance of the animal's ancestors, and collateral relatives such as siblings and half-siblings (Pedigree Data); and the performance of the individual's offspring (Progeny Data).

It was stated earlier that the rate of genetic change is proportional to selection accuracy, among other factors, and that selection accuracy was based on choosing animals with the best breeding value for the traits in question. It follows then that the selection accuracy is based on the accuracy of predicting or estimating breeding values (EBV). It is important, therefore, to understand which performance data provides the most accuracy in predicting breeding values.

It is beyond the scope of this article to explain the statistical and mathematical formulas and processes that are employed to generate the following conclusions. For those who are interested in the mathematics involved in proving my next statements, please refer to the genetics and animal breeding texts listed in the references.



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progeny from which to gather performance information. It is not unusual with male alpacas to have many more than ten progeny to evaluate.

Full siblings' records have nearly the same value as progeny records when it comes to accuracy of prediction of breeding values, however it is much less common in the alpaca industry for us to have ten offspring that are full siblings than it is to have ten progeny from one parent. So, practically speaking for our purposes, full sibling data is not as valuable as progeny data. Half siblings are numerous, but since they only have 25% of their genes in common with the animal in question, they are less valuable in accurately predicting a particular parent's BV. It would take, depending on heritability, between 20 and 30 half siblings to equal the predictive value of the individual's own performance, or that of ten of the individual's offspring.

We can see then that the most accurate single source of information about the breeding value of an individual animal comes from evaluating ten or more of that individual's progeny. Fortunately, we are not required to make our decisions based on one source of information. We can look at all of the performance data of the individual, of his full siblings, half-siblings, and of his progeny all together when determining estimated breeding value. It is important to realize the relative levels of importance that each of these sources of information provide. They are not all equal in value.

Progeny records are the one best source of evaluating and predicting the breeding value of any animal, and for any trait, regardless of its degree of heritability. With enough progeny to evaluate, accuracy of predicted breeding value for a trait can be high even when heritability is low. For example, even when the heritability of a trait is as low as 5% or .05, the accuracy of an estimated breeding value for that trait could be 96% if you had 1,000 offspring to look at. With alpacas that is unlikely, but with animals such as beef and dairy cattle where AI is readily available, it is not unusual

to have records of 1,000 offspring of a particular bull. It is not unheard of, however, for a particular herd sire to have 100 known offspring, and the progeny records of all of those animals would make the EBV of a .05 heritability trait 75% accurate. For a trait that is moderately heritable, say 30%, 100 offspring's performance records could yield an EBV of 94% accuracy!

In order to make a practical example of that point, let us think of a fleece characteristic of alpacas, such as average fiber diameter. Although heritability calculations for alpaca populations are rare, most breeders believe that fleece characteristics are moderately to highly heritable. If the heritability of AFD is 30%, then measuring AFD on 100 offspring could tell us the breeding value of a particular herd sire with an accuracy of 94% or greater!

Therefore, if a hypothetical herd sire – let's call him "Mr. Studly" – has histograms showing that his average fiber diameter is 10 microns less than the mean fiber diameter of the herd, we could say that his breeding value is -10 microns for AFD, but the accuracy of that EBV would only be 55%. If, however, we can measure the AFD of 100 of Mr. Studly's offspring, and the data tells us that his EBV is -10 microns, that estimate would have an accuracy of 94%. You can see from this example how having data on a herd sire's offspring, or "Progeny Testing," can give us a much more reliable prediction of how valuable Mr. Studly might *really* be if we want to breed for lower fiber diameter. Even just 10 offspring's fiber diameter measurements will give us a much better prediction than Mr. Studly's histogram does.

The important point to remember is that ALL progeny data must be included for these numbers to be valid. As soon as any one progeny's record is intentionally left out, then the accuracy of the prediction is no longer what it should be.

Estimated breeding value, EBV, is a way of estimating the genetic value of a parent. However, we often prefer to think of what the effect of using this particular parent will be on the offspring. In other words, how much better than average will Mr. Studly's offspring be for a particular trait. This is referred to as the Estimated Progeny Difference (EPD) or some geneticists use the term Estimated Transmitting Ability (ETA). Since each parent can only contribute ½ of its genes to the offspring, then on average that parent only passes on ½ of its breeding value to the offspring. So one half of the parents breeding value is the estimated progeny difference.

EPD = ½ EBV

We must understand that a parent doesn't always pass on exactly one-half of its breeding value to each offspring. He or she always passes on exactly ½ of his or her genes, but the genes that are transmitted are always a random sampling, and are probably different for each and every child. There is no way to predict if a given individual offspring will inherit a poor, average, or superior sample of his parents' genes.

The better the production records that we have from all possible sources, individuals, siblings, and progeny, the more accurate our selection can be. Therefore, it is a fact of animal breeding that the breeder who keeps the most precise and detailed records will have the best available information on which to make selection choices and hence will have the best chance to improve the rate of genetic change in his herd.

Selection Intensity

The next factor in our key equation for affecting the rate of genetic change is **selection intensity**. This factor of the key equation tells us what percentage of a population is selected as parents. As stated in the previous article, financial considerations and the need to increase the number of alpacas in the U.S. national herd make it very difficult for North American alpaca breeders to exercise high selection intensity at this time. As the size of each individual alpaca herd and the overall national herd size increases, we will begin to see more selection intensity. We are beginning to see some selection intensity in male alpacas, but the overwhelming majority of all female alpacas are allowed to breed for as long as they are able to produce healthy crias. Therefore a detailed discussion of types of selection intensity and their effects can wait for the day to come when alpaca breeders can decide that they will only allow a certain percentage of their females to reproduce.

As we become able to select with higher intensity, we will be able to more rapidly affect genetic change in our herd. Selection intensity, a measure of how picky a breeder is in choosing which animals will be selected to reproduce, is based on one or more selection criteria. Let's go back to our hypothetical alpaca Mr. Studly. We could suppose for example that AFD again was the trait for which we wanted to select. We said Mr. Studly's EBV for AFD was -10 microns. If all available males have EBVs from -8 to -15 and we choose to breed any male with an EBV of -10 or less we are not exer-

cising a high selection intensity. If, on the other hand, all available males have EBVs of +10 to -10 microns, and we choose only those with an EBV of -10 microns to breed, we are exercising a high selection intensity and will therefore see a more rapid rate of genetic change in the herd.

Genetic Variation

Another factor in our key equation is **genetic variation**. In this context, genetic variation refers to how much difference there is between breeding values for a given trait within the population being considered. This one is important, but does not require too much discussion to understand. A given population cannot excel beyond the best genetic material present in the gene pool of that population. Genetic variation is not something that is easy to manipulate within a herd. Whatever it is, it is. The only quick way to increase the genetic variation is to bring in animals that are widely different genetically from outside of the population. If these new additions are far superior genetically, then the rate of change toward the superior position can be rapid. If the new additions are inferior genetically, then the rate of change in an inferior direction will also be more rapid. Obviously, this is not a desirable result. This is why it is dangerous to bring in "new genetics" just for the sake of breeding to animals that are not closely related to the original herd. The breeder must be certain of what the expected progeny differences are that these "new genes" will produce. Ideally, a new herd sire should be carefully progeny tested before breeding him over your herd.

Generation Interval

Generation interval, like heritability and repeatability, is a concept that is very often misunderstood, even by experienced animal breeders. The generation interval within a herd or within an entire species is defined as the amount of time necessary for one generation to be replaced by the next generation for breeding purposes. In the context of the rate at which genetic change in a closed herd occurs, the best definition of generation interval is the average age of all parents in the herd when their selected offspring are born. From a physiological standpoint, we can speak of minimum generation interval as the least amount of time for a male and female born today to produce an offspring.

For the sake of discussion, let's say that a female born today needs to reach the age of 18 months

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to conceive, and another 11 months of gestation for the cria to be born, a total of 29 months for the female. Again for the sake of discussion, let's say that a male born today needs to reach the age of 36 months to be able to settle a female, and again the cria will arrive after 11 months of gestation, a total of 47 months for this male to produce an offspring. The average age, then, between 29 months and 47 months is 38 months. Physiologically, we can say that in this example, 38 months is the physiologic generation interval. However, the genetic change in the overall herd will not be this rapid unless the parents of these offspring are no longer allowed to breed. It is unlikely that in any livestock breeding enterprise the breeding stock is culled after one offspring. Yet each time that original pair (generation) breeds again, the genetics in play are exactly the same as the first time. Therefore, if we are to have a realistic number to represent generation interval for genetic rate of change, we must average the ages of all breeding stock.

Beef cattle, for instance, usually have their first calves at age two, but some have their last calves in their teens. If we look at the average age, then, of beef cattle when their selected offspring are born, we find the average age in most herds is four to six years old. Therefore, we can say that the generation interval is four to six years for female beef cattle. I hesitate to guess what the average age for female alpacas still producing offspring is in the U.S. today. On any given farm, the average age will be different. Generation intervals tend to be less for males as they are more easily replaced, since one male can easily service upward of 50 females in a year if so desired. Females are usually kept in our breeding programs for as long as they will produce, however, for obvious economic reasons. We must understand that from a genetic standpoint, this is slowing down the rate of genetic change in our herds since it increases the generation interval substantially to have several ten- or twelve-year-old females contributing cria to the gene pool each year. The breeder who can afford to eliminate these females from his breeding program sooner will increase his rate of genetic change, all other factors being equal.

Another way to lower the generation interval is if husbandry practices and/or genetic selection leads to animals that reach maturity and are able to reproduce earlier. This must be considered carefully, however, since an advantage of decreasing generation interval may be offset by the dis-

advantage of breeding young and immature animals if it leads to dystocias, reproductive disorders, or other detrimental effects on the health of the parent or of the cria.

Other Considerations

Having discussed these four factors individually, there are other practical considerations that must be taken into account. Based on what has been written here so far, we would prefer to increase our accuracy of selection accuracy, selection intensity, and genetic variation as much as possible while at the same time decreasing the generation interval to its minimum. This would clearly give us the most rapid rate of genetic change. Is it possible to do this? Well, not exactly, because there is often a connection or linkage between two or more of these factors as well as some practical risks involved with attempting to apply the mathematical concepts above with the real practice of breeding animals.

For instance, we said that the best way to increase selection accuracy is through accurate breeding value determinations. We also showed that this accuracy is maximized by having the most abundant progeny data. Progeny testing, however, by its very nature must increase the generation interval because it takes at least one generation to collect the progeny testing data to accurately select the male we want to use over our herd. In other words, it is not possible to have a three-year-old male alpaca with a highly accurate BV (breeding value) that was calculated from 100 of his progeny if he has just become mature enough to breed!

Accuracy of selection and intensity of selection also have an adverse relationship due to practical considerations. If we want to have highly accurate breeding values to use when choosing a sire, then he must have a large number of offspring from which to garner data. The number of females available is limited, however. So if we want progeny testing on more males (so that we have more from which to choose and can thus increase our intensity of selection by choosing only the best one(s) to breed), then that means we will have fewer records on each male from which to make our choice. Increasing selection then requires decreased accuracy.

Another problem with intensity and accuracy is that if we are very intense in our selection, say choosing only one or two most promising males, there is a selection risk that these males may not be as good as predicted and we have used them

widely in our breeding program. The same risk exists when we let a sire have a high breeding impact on our herd based on his beautiful phenotype without having any progeny testing to prove his breeding value.

Summary

This article has expanded on the four factors affecting the rate of genetic change as first introduced in "Alpaca Genetics 102," - selection accuracy, selection intensity, genetic variation, and generation interval. It has touched on some of the conflicts that naturally occur when trying to optimize all four of these factors.

There are numerous other possible interactions and contradictions between separate factors of our key equation that would lead to a more lengthy discussion than allowed for in a magazine article. Suffice it to say that each breeder must take into account all of these factors, his own breeding goals, the characteristics of his particular herd, his economic considerations, and his

own comfort zone toward various risk factors in order to devise an educated breeding program. Future articles will discuss some strategies for selection; more detailed understanding of heritability and repeatability and techniques to increase them both; and multiple trait selection concepts.

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