

Genetic Alpaca Improvement 102

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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?

Of course animal husbandry, management and veterinary practices contribute greatly to the quantity and quality of alpacas in our herds. Others more experienced in these arenas than this author have written on these disciplines, and I will not be addressing any of these topics directly. These aspects of animal breeding are of inestimable importance, yet they are all under girded by each animal’s individual genetic make up, and the gene frequencies in the gene pool of the herd at large.

The purpose of this article is to describe ways that we can progress toward our goals by using the principles of genetics as they apply to animal breeding. The author assumes that the reader has some knowledge of the fundamentals of genetics and Mendelian inheritance, and this article will begin to address some of the slightly more advanced concepts.

As animal breeders there are three main factors that we must consider in order to produce the next generation of offspring: Traits, Selection and Mating.

Traits

Traits refer to the characteristics of an alpaca that we have an interest in and can observe, evaluate and/or measure. Traits can be thought of in different classes. Willis ¹ has described five classes of traits. Fitness traits; which in alpacas would be such things as conception rate, gestation length and survival ability. Production traits; one would be fleece weight. Quality traits; represented in alpacas by fiber diameter, fiber color, etc. Type traits; these include suri, huacaya, pinto, etc. Behavioral traits; these might be friendliness, aggressiveness, ease of halter training, “mothering” ability, etc. Willis also states “It is a basic principle of animal breeding that the more traits one seeks to include in a breeding programme, the harder the task will become. It is thus essential to decide which traits are crucial and include these but keep this number to manageable levels.”

Some traits are observable and subjective, such as color, gait, or head shape. Others are levels of performance and lend themselves to more objective measurement like birth weight, staple length or days of gestation. A given animal’s value for any of these traits is referred to as its **phenotype**. Sometimes traits and phenotypes are confused. One might say, “High fleece density is a common trait of this line of alpacas.” The trait, of course, is fleece density. “High” is the description of a phenotype for this trait.

The phenotype for any trait is the result of the combined effects the genes an animal has inherited and environmental influences it has been subjected to throughout its life. As a formula we could say:

$$P = G + E$$

The other two main factors, Selection and Mating, deal with decisions the alpaca breeder makes in an attempt to improve the phenotype seen in the next generation. By utilizing genetic principles and animal breeding technology to change the genetic portion of the above equation, the breeder hopes to fashion a phenotypic expression that is closer to the goal of the “best alpaca”, whatever that may be. Of course, each breeder’s visions will be different, and hence so will their breeding goals be different.

Selection

Selection, the second major factor, affects the gene frequencies of the next generation by deciding which animals will reproduce and which ones will not. Selection also implies a process referred to as **culling**, which means selecting those animals that will *not* be allowed to breed. Culling then means that the animal will not exert any genetic influence on the next generation of the herd. Males are often culled by castration, females by holding them out from mating. A breeder can cull an animal from their herd's gene pool by selling it to another breeder. While this will have its effect on that particular herd, the genetic influence of that animal is not removed from the gene pool of the breed at large if the buyer then breeds him or her with his own stock.

We want to select the animals with the best breeding values to be in our breeding program. **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.

The effectiveness of a breeder's selection decisions is measured by the resultant rate of genetic change. If we consistently select the animals with the best breeding values to be parents, we will maximize the rate of genetic change in our herd. Unfortunately we do not know the true BV of our animals, but merely some estimate of these values. The **estimated breeding values (EBV)** may not be very accurate, and often with alpacas may be all but non-existent for most traits. The author would suggest that determining accurate EBV for the traits that we want to include in our breeding programs should be possible, and it is an opportunity for us to make a quantum leap forward in the genetic improvement of our breed.

The **key equation** that determines the effectiveness of our selection process, the rate of genetic change, states that the rate of genetic change is proportional to selection accuracy, selection intensity, genetic variation and generation interval.

The most basic method of estimating breeding value, and the most commonly used in the North American alpaca industry today, is called **Phenotypic Selection**. With phenotypic selection only the observable and measurable characteristics of the candidate considered for breeding, in other words the phenotypic expression of the traits being selected for, are used as selection criteria. For instance, if we want to breed for high fleece weight, and are considering if a particular female should be selected for that breeding program, only the weight of her own fleece would be used to make the decision. Other considerations, such as the genetic merit (BV) of her sire and dam for fleece weight, and that of her siblings and offspring, would be ignored. In fact, in the case of most alpacas, those breeding values are not so much ignored as they are unknown. The assumption in this case is that a phenotype for fleece weight in alpacas is somehow related to breeding value for fleece weight. If that is not true, then selecting the parent based on his or her phenotype for this trait would be worthless.

The terminology used to describe just how strong the relationship is between a phenotype value for a trait and breeding value for that trait is **heritability**. If heritability is high, selecting a parent based on phenotype for a given trait is likely to get that phenotype in the offspring. When heritability is low, observations and measurements of the value of an alpaca's trait will not reliably predict what the offspring's value for that trait will be. For example, in most mammals fertility is not a highly heritable trait. Therefore whether or not a female conceives easily or often has little to do with her breeding value for fertility in her offspring.

Heritability is important because it determines our accuracy when employing phenotypic selection. In turn it affects the rate of genetic return in our herd. See the key equation above. Phenotypic selection for a trait of low heritability will give us poor selection accuracy and therefore a slow rate of genetic change.

Misconceptions about heritability

Occasionally someone thinks that if heritability is high, breeding value for that trait is high also. This is not so. A high heritability only tells us that the relationship between the breeding value for a trait and the

phenotypic value for that trait is a strong one. Note that heritability is a population measure, not a value associated with an individual animal. If the heritability for a trait in a given herd is high, the individual animals will still each have their own individual phenotype, good or bad, for that trait. The high heritability just tells us that the parent is likely to pass that on to the offspring. If, as an example, the heritability for fleece weight is high, an animal with a low fleece weight is likely to produce offspring with a low fleece weight; medium fleece weight parent will tend to produce medium fleece weight offspring, etc. On the other hand, if the heritability is very low, a high fleece weight parent is just as likely to produce a low fleece weight child and a low fleece weight parent could produce a high fleece weight offspring.

Contrary to the assumptions of many breeders, heritability is *not* an immutable characteristic of a trait. Heritability for a trait varies from population to population and from environment to environment. It is possible, at least to some degree, to increase the heritability for a trait within a **contemporary group**. A contemporary group is a group of animals that are the same sex, of similar age and have been managed in the same fashion at the same location. If we remember our basic equation for phenotype:

$$P = G + E$$

Then differences, or variations in phenotype are a result of changes in genetics, environment, or both:

$$\Delta P = \Delta G + \Delta E$$

The higher the genetic component of this equation, the more genetic differences will affect phenotypic differences. In other words, the heritability will be high. This illustrates two things. First, the more uniform we can make the environment, in other words the smaller we can make the variations in environment, ΔE in our equation, then the more certain we can be that variations in phenotype, ΔP , are the result of genetic differences, ΔG . This is another way of saying that heritability will be higher; or that there is a stronger correlation between phenotypic variance and genetic variance, which is breeding value. We can increase the heritability of a trait in a population by making the environmental factors as uniform as possible and by increasing the precision and accuracy of our measurements. The second point illustrated by this equation is that what we are looking at when we determine heritability is differences between animals or variances. We are comparing variances in phenotype with variances in breeding values. Mathematically defined, “Heritability = the proportion of differences in performance for a trait that are attributable to differences in breeding value for the trait”². Since variance statistically is the square of the standard deviation the mathematical formula is then:

$$h^2 = \sigma_{BV}^2 / \sigma_P^2$$

This is the most computationally useful formula for heritability. When a trait has low heritability, we cannot use our standard method of phenotypic selection to accurately determine breeding value. We need other methods of estimating BV in order to have an accuracy of selection high enough to produce an acceptable genetic rate of change. We will look at how this formula can be used mathematically to make several types of genetic predictions from different sources of information about the individual, its siblings or its progeny, and to also calculate the accuracy of those predictions, in a future article.

Selection Intensity

This factor of the key equation tells us what percentage of a population is selected as parents. If our estimation of each animal's BV is very accurate, but we allow every animal to reproduce, all we have done is shuffle the existing genes in the gene pool. There will be minimal if any genetic advancement and in general the overall genetic value of the herd cannot change. In other words, the overall gene frequencies of the herd will not change. This truth stems from the **Hardy-Weinberg** equilibrium. See the author's reference³ or virtually any other modern genetic text for a thorough discussion of the Hardy-Weinberg Law. If the **selection intensity** is high; for instance if only the top ten percent of animals, based on breeding values, are allowed to be parents, and if our accuracy of breeding value (selection accuracy) is high, then these intensely selected parents should be far better than average genetically. As a result, their offspring should be equally superior genetically and the rate of genetic change will be rapid.

Financial considerations and the need to increase the number of alpacas in the national herd make it very difficult for North American alpaca breeders to exercise high selection intensity at this time. It is the author's impression that very few females, percentage wise, are culled from breeding today. A higher percentage of males are probably kept from reproducing, but it seems that even with males there is only moderate selection intensity today. This low selection intensity means that estimating breeding values as accurately as possible is extremely important if we are to see genetic improvement in our national herd. Differences in accuracy of selection, or EBV (estimated breeding values), can be very large. Selection of each alpaca, based only on phenotypic record, is not very accurate, particularly if the heritability of the traits under consideration is low. Greater accuracy in estimating breeding values can be achieved by using more information and more sophisticated genetic prediction technology. These methods will be discussed in a future article.

Mating

Mating decisions, the third major factor, take place after selection has occurred. Selection is a herd wide process; mating is an individual process. Selection decisions determine which animals will reproduce; mating decisions determine which individual females will be bred to which individual males. There are many different mating systems based on existing stock and breeding goals. Certain mating strategies can be employed for simply inherited traits; others are necessary for polygenic traits.

Mating strategies for simply inherited traits are based on an understanding of basic Mendelian inheritance, and do not require much discussion. If one knows the number of loci involved, the number of alleles at each locus, and how the alleles are expressed, one can then determine the possible and probable genotypes of the potential parents and select mating combinations that will produce, or most likely produce the desired genotype in the offspring. Simple Punnett square diagrams can be used to plan matings that will produce certain gene combinations, homozygotes, heterozygotes, or epistatic combinations, for a simply inherited trait. Other mating strategies that can be employed for simply inherited traits are **introgression**, in which a specific allele existing in one population can be brought into another population in which it does not exist; and **topcrossing**, designed to create a purebred population or to convert a population from one breed to another.

Since most, if not all, of the traits of importance to alpaca breeders seem to be polygenic and quantitative in nature, it is more pertinent to spend our time on mating strategies for quantitative traits.

“A **mating system** can be defined as a set of rules for making mating decisions. As such, there is no limit to the number of possible mating systems. There are, however, only a few general **mating strategies**.”⁴

These general mating strategies fall into two types. One type is based on animal performance, and can be subdivided into **random mating** and **assortive mating**, which is further divided into positive and negative assortive mating. The other type is based on pedigree relationships, and includes **inbreeding** and **outbreeding**.

Random mating must be distinguished from random selection; they are not the same thing. Even very highly selected animals, once selected, can be allowed to mate with each other at random. There are numerous systems to assure that the matings are truly random. They are most useful in a large commercial operation where individual performance records are not available and the numbers of animals being dealt with are very large. Since this situation will not apply to alpaca breeders in North America for many years to come we will not spend any time on describing the systems.

Random mating can be very useful in sire evaluation. If the sire's mates are chosen for any particular reason then the results may not be a true evaluation and may give a false positive evaluation from having a particularly good set of mates or a false negative result from having particularly poor mates.

Assortive mating includes the concepts of mating two like animals together which is termed positive assortive mating or mating two animals that are dissimilar which is called negative assortive mating. Positive assortive mating could be illustrated by breeding tallest to tallest, heaviest to heaviest, finest fleece to finest fleece, etc. This increases genetic variation and tends to spread a population toward the two extremes of the characteristic for which it is practiced, and thus leads to less uniformity of the population. Since uniformity is usually desirable for most commercial animal breeders, they normally consider this increased phenotypic variation a drawback. Other breeders, attempting to create a very superior animal in some characteristic, for the purpose of the show ring, are willing to accept the loss of uniformity for the chance of producing an extreme individual, which this mating system lends itself to. For a thorough discussion of positive assortive mating see a text on animal breeding.⁵

Negative assortive mating, pairing animals that are opposites or dissimilar for a particular trait, is also sometimes called corrective mating. This is commonly seen in alpaca breeding today as breeders attempt to “correct” traits in a particular parent by selecting a mate that has a more desirable phenotype for that particular trait. It is not unusual to hear a breeder say, “I want to improve her density” or “I want to put more fiber coverage on her legs”. What they really mean is that they want to breed this female with a male that is likely to produce an offspring that has a better value for the trait in question than the mother has. They will then find a male that has better values for that trait, more fiber density, more fiber coverage on legs, etc. and assume that breeding this sire to the dam they want to “improve” will generate a cria that will be better than the dam for this trait. There are several assumptions and possibly misconceptions involved here. First, we are assuming that the trait is highly heritable, that is to say, the sire's phenotype means that his breeding value for that trait is high enough to pass it on to his offspring. We have already discussed phenotypic selection. Let us assume that for the trait in question the heritability is high enough to make phenotypic selection effective. The offspring then can be expected to be somewhere in value between the sire and the dam. So, if we have “improved” on the dam, haven't we at the same time “downgraded” the sire? We never hear a breeder say, “we want to decrease his fleece density,” or “I want to decrease his fiber coverage”, but isn't that in fact the same thing? In fact, we have “bred to the average”. This is not a good strategy if you want to maximize genetic rate of change, but it is a good strategy if you want to create uniformity of the herd. This can be advantageous for some breeding goals, but one must realize that the herd is becoming uniform around some genetic intermediate value.

Inbreeding is one of the mating strategies based on pedigree relationship. There is much difference of opinion about what constitutes inbreeding. Some would constrain the term inbreeding to the mating of full brother and sister or parent to offspring. Others would include the mating of half siblings or grandparent to grandchild. The scientific definition is the mating of two individuals more closely related than average for the population.

The primary effect of inbreeding is to increase the probability that the offspring will inherit the same thing from sire and dam. Another way of saying this is that it increases homozygosity. This can be good or bad, depending upon what the phenotypic expression of that homozygous pair of alleles is. If it is a pair of recessive genes for some detrimental defect, then the outcome is bad. If it is a pair of alleles that results in a beneficial expression, then it not only affects the offspring by improving its phenotype, it guarantees that as a parent this animal will pass on the desired allele to its offspring; it will be **prepotent**. Linebreeding is no different than inbreeding, but the term is usually reserved for matings that have a lesser coefficient of inbreeding, meaning that the common ancestor is somewhat farther back in the pedigree. Inbreeding, including linebreeding, is another tool like selection that an animal breeder can use for the improvement of livestock. Many alpaca breeders avoid inbreeding passionately, often without knowing why other than a superstitious aversion and a vague sense that it is usually associated with the appearance of genetic defects. Inbreeding does not create genetic defects any more than the pairing of any two highly unrelated animals does. If both parents pass on a recessive gene for a defect, then that homozygous recessive offspring will show the defect. It doesn't matter if the parents were related or not. Inbreeding may increase the likelihood of these recessive genes being uncovered because inbreeding increases the rate of homozygosity overall. In other words, inbreeding of itself does not create problems, but may reveal them. One upside is that it could allow breeders to identify two parents who carry that recessive allele before it is passed, hidden, throughout the entire herd over several generations. Inbreeding has been used in the past to

successfully create elite strains of livestock, and although it has its risks and dangers, is not necessarily detrimental. Lush wrote:

“Among animals, laboratory experiments have been extensive on the inbreeding of rats, mice and guinea pigs. Dr. King inbred white rats full brother and sister for more than 70 generations without finding degeneration. Mice have been inbred full brother and sister in many experiments. In at least one case this has been carried further than the 55th generation. In the United States Department of Agriculture experiments on inbreeding guinea pigs, some lines have been inbred brother by sister for more than 30 generations.”⁶

Many herds today could profit from the use of superior sires by taking advantage of inbreeding, if owners understood the effects and possible consequences of this mating system.⁷ A future article will discuss how and when to inbreed or linebreed for genetic improvement, as well as the dangers and risks of inbreeding depression .

Outbreeding or outcrossing is the opposite of inbreeding. It is the major breeding strategy used today with alpacas in North America. One of the benefits of this strategy is that it results in a gain in gene combination values and an increase in hybrid vigor. Another benefit is to take advantage of breed complementarity. Often two pure bred lines can be crossed to create a hybrid commercial animal whose vigor is high and production values are high as a result of this effect. These highly productive animals will not necessarily pass those traits along to offspring, so the commercial breeder continues to cross the two purebred parent lines of seed stock that will produce the highly productive flock animals he seeks.

In Summary

This article has highlighted the three main factors that we as alpaca breeders must consider in order to produce the next generation of offspring: Traits, Selection and Mating. Hopefully some understanding of the broad picture of these factors has been presented. In future articles, the author plans to explore some of these areas in greater detail.

About the author

Dr. Wayne C. Jarvis, in addition to being a novice alpaca breeder, lives with his wife and five daughters at Sixth Day Farm in Holley, NY where they breed Saanen dairy goats and French Angora rabbits as well as having three breeds of layer hens, four barn cats, two Labrador retrievers and a Great Pyrenees LGD dam. Dr. Jarvis studied chemical engineering, chemistry and biology, including genetics, as an undergraduate, and has been interested in genetics throughout his career as an oral and maxillofacial surgeon treating developmental deformities of the face and jaws. He lectures frequently around the world on bone graft and implant reconstructive surgery for the jaws and other scientific topics.

Footnotes

1. Malcolm B. Willis, Blackwell Science, *Dalton's Introduction to Practical Animal Breeding*, 1991, pp.1-2.
2. Richard M. Bourdon, Prentice Hall, *Understanding Animal Breeding*, 2000, p.168
3. John F. Lasley, Prentice Hall, *Genetics of Livestock Improvement*, 1978, pp. 115-117
4. Richard M. Bourdon, Prentice Hall, *Understanding Animal Breeding*, 2000, Part IV, p. 314
5. Jay L. Lush, Iowa State College Press, *Animal Breeding Plans*, 1945, pp. 341-347

6. Jay L. Lush, Iowa State College Press, *Animal Breeding Plans*, 1945, pp.288
7. John F. Lasley, Prentice Hall, *Genetics of Livestock Improvement*, 1978, pp. 207

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