

# The Genetics Journal – Part Five

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So far, in the first four entries to the Genetics Journal, we have reviewed the Basic Mendelian Principles for the inheritance of simply inherited traits including the concepts of genes, alleles, dominant and recessive traits, the Mendelian laws of Gene Segregation and Independent Assortment, genotypes, phenotypes, Punnett squares and simple dominance. We also discussed modifications of Mendelian ratios such as partial dominance, co-dominance, epistasis and sex linked characteristics. In the fourth entry we began to discuss polygenic traits and the quantitative genetic concepts needed to make predictions about these types of traits, including the concept of breeding values. The reader may want to go back and review these entries to the Genetics Journal as this entry will continue to discuss the polygenic traits we began to look at last time.

Since so many production traits of livestock, including alpacas, are controlled by so many pairs of genes, we have to expand our thinking beyond inheritance involving one or two or even five or six genes. We don't know yet exactly how many genes alpacas have, but the number is likely to be greater than 30,000. Although each of these genes will behave according to the principles of Mendelian genetics as we have described them in the first three entries of this Journal, the large number of them involved in these kinds of traits makes it impossible for us to use Punnett squares to look at possible outcomes of different matings.

Quantitative genetics requires the use of statistical tools including statistical concepts such as heritability and accuracy. Instead of trying to identify the animal's genotype for a specific trait we try to identify breeding values and estimated progeny differences for traits of importance. These breeding values are in turn used for making breeding decisions about selection and mating. In the fourth entry to The Genetics Journal we worked through a simplified example of a polygenic trait. In our example we used five hypothetical alleles. In reality, most of the economically relevant traits, or ERTs (a useful concept I learned from Dr. Dorian Garrick) in alpacas are probably determined by hundreds or even thousands of gene loci which may each possibly have multiple alleles. Our simple example however was adequate to prove that any one given offspring from two parents has the statistical possibility of being either much better or much worse than the breeding value of both parents for any given trait. Even though these extremes are possible, they are statistically less likely. If any two animals were mated together to produce a large number of offspring, then the average breeding value of **all** of those offspring is statistically likely to be equal to the mean of the breeding value of the two parents. Any one of those offspring however could be anywhere on the continuum of possibilities. Our example, in the last journal entry, looked at two parents whose breeding values (BV) for the trait in question were +0.4 and -0.2. The offspring in our example turned out to have a BV of +0.2, slightly higher than the average of the two parents, which is +0.1. We also saw however that the range of **possible** BVs for the offspring went from -0.6 to +0.8, a wide range of possibilities! Have you ever seen a cria that was a real

show stopper that came from two average looking parents? Sure, we all have. Quantitative genetics explains how that is possible. On the other hand, we have also seen the example of two champion alpacas, with high price tags, that produced a real dog of a cria, although I admit that these occurrences are not nearly as well known because a lower quality cria is not likely to end up in the show ring or in a herdsire ad.

It is important therefore that we have a clear understanding of the difference between the concept of probabilities and possibilities. Quantitative genetics is a way of looking at all of the possibilities of a particular mating and determining what the probabilities are. There is no way the exact outcome of any mating of two animals can be predicted for any polygenic trait. Even if we could determine the **exact genotype** for each of these multiple loci, the number of possible outcomes would still preclude any accuracy of predicting the outcome from one mating of any two animals.

Unfortunately for those of us that would like to be sure of what we were going to get for our stud fee, I am about to make your uncertainty even greater! We need now to look at one of the most important equations related to determining the breeding value of any animal.

$$P = G + E$$

It is a simple looking equation, and it is easy to understand, which also makes it easy to underestimate its profound importance. What this equation says is that the phenotype (P) for any trait is the result of the combined effects the genes an animal has inherited (G) and environmental influences (E) it has been subjected to throughout its life.

**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<sup>1</sup> 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 program, 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.

Our equation then tells us that when we look at a particular animal's phenotype for a given trait, high fleece density for

instance, that what we can see and measure is a result of a combination of genetic and environmental factors. We cannot distinguish just by looking at the animal to what degree the observed phenotype is genetic and to what degree it is the result of environmental influences. Yet, if we are considering using that particular animal as a parent, breeding stock, then we would like to know what part of this phenotype is possible to be passed on to the offspring. Obviously the environmental component will not be passed on genetically. This is what we have previously looked at, breeding value. Or in other words the animal's genetic value as a parent of the next generation. Practically then what does this mean. It means we cannot just look at an animal's phenotype and determine that it is more or less valuable than another animal as breeding stock.

Environmental influences on an animal's phenotype can begin from the time it is conceived when the sperm and egg join to form a zygote, and continue throughout its lifetime. These influences can be thought of in three general categories: permanent individual environmental effects, temporary individual environmental effects, and contemporary group environmental effects.

A permanent individual environmental effect is one which would affect a particular animal's phenotypic value for a particular trait, and it would have the same effect throughout the animal's lifetime and yet would not have any impact genetically on the next generation. I can use my old herding dog, Moss, as an extreme example of a permanent environmental effect. Moss was a great border collie that helped me to herd my sheep. If you ever saw Moss on my farm, you would see that he did not have a tail. This tailless phenotype was the result of an injury that caused him to lose his tail. An environmental influence that was permanent. For the rest of his life he will have a tailless phenotype. Does that mean that some percentage of his offspring are likely to be without a tail, or partially tailless, because of Moss' genetic contribution to their phenotype? No, of course it doesn't. This is a permanent, individual environmental effect on his phenotype.

It is possible however that there could be a less obvious permanent environmental effect. For instance, in sheep it is well known that the number of secondary fiber follicles that will develop is affected by the ewe's nutrition during the last month of pregnancy. This is an environmental effect in that one individual lamb that will influence its phenotype, secondary to primary follicle ratio, throughout that sheep's lifetime. It is thus a permanent individual environmental effect. If I look at that sheep's fleece, and see that his or her fleece has a higher S/P ratio, does that help me to evaluate its breeding value? It depends on to what extent the animal's phenotype for this particular trait is due to that particular environmental effect just described and to what extent the animals underlying genetic influence determined the S/P ratio. Consider this however. Theoretically we could have two animals whose genotype for S.P ratio was identical. Genetically then, by definition, their breeding values (BV) are identical. Now, let us also hypothesize that while these two animals were in utero one dam had excellent nutrition and one had terrible nutrition. Each would then express that permanent environmental effect in

its S/P ratio. Their phenotypes would be totally different for this particular characteristic. One would have a much better S/P ratio than the other. Yet, we have just said that their breeding values would be identical. This means then that we could be totally misled as to which one we should choose to breed to, based on phenotype. What does this say to us about selecting breeding stock based on show ribbons? Or even based on hands on inspection of a particular animal? Even objective measurements such as micron tests and skin biopsies are just more reproducible ways of evaluating an animal's phenotype, not its genotype and therefore its breeding value cannot be determined by these tests alone.

Another category would be temporary individual environmental effects. Any influence that might affect an animal's phenotype at one time in its life but not be permanent could fall into this category. It is easy to think of examples of this type of environmental effect. Nutritional affects come to mind. Perhaps the animal is on a much better pasture this year than last year, or this years hay is much worse than last years, etc. I am sure you could think of many other temporary environmental affects.

If we recognize then that the phenotype for any trait is the result of the combined effects of the genes an animal has inherited and the environmental influences it has been subjected to throughout its life, how can we go about determining the breeding value of an animal? We need to find a way to relate the phenotypic characteristics which we can see or measure, such as a skin biopsy or a fleece weight, to the breeding value for those particular characteristics. This is called heritability.

The terminology used to describe just how strong the relationship is between what we can see or feel or measure on the animal and the underlying genetic breeding value for that trait is **heritability**. Heritability is extremely important to selection for polygenic traits. The object of selection is to choose animals with the best breeding values to become the parents of the next generation. The most commonly understood definition of heritability is that it measures how closely offspring resemble their parents in performance for a trait. In other words if a trait is highly heritable, high performing parents will produce high performing offspring and low performing parents will produce low performing offspring. Heritability is important because it determines our accuracy when employing phenotypic selection. In turn it affects the rate of genetic gain in our herd.

The importance of breeding values is illustrated by Bourdon's **Key Equation**<sup>2</sup>. 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. One of the four points in Bourdon's **Key Equation** is selection accuracy. Phenotypic selection for a trait of low heritability will give us poor selection accuracy and therefore a slow rate of genetic change. Accurate breeding values for the same trait on the other hand would lead to a much greater accuracy of selection. More about that will come later.

There are many misconceptions about the concept of heritability. For instance, heritability is a characteristic of a population, not an individual. Breeding value is a characteristic of an individual, not a population. This is not always intuitively obvious and requires some explanation for proper understanding. Each individual animal has its own breeding value for a particular trait, based on the genes it possesses. Each animal's BV in a population then will be different. The heritability of that trait however is the same for all animals in that population. In other words, no matter how good or bad a particular parent's genes are that it passes on to its offspring for a particular trait, the relationship between how much of what we see in the offspring compared to its parents, based on the genetics of the parent versus the environmental effects, is the same in all of the animals in that population. The heritability for a particular trait is the same for all animals in that population, whether the actual breeding values of each individual are good, bad or indifferent.

Another difficult to understand feature of heritability is that contrary to the assumptions of many breeders, heritability is *not* an immutable characteristic of a trait. That is to say, it is possible, at least to some degree, to **increase the heritability** for a trait within a **contemporary group**. The heritability for average fiber diameter could be higher or lower in my herd than it is in yours. How can that be?

A contemporary group is a group of animals that are of similar age, the same sex, and have been managed in the same way at the same farm. 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,  $\square E$  in our equation, then the more certain we can be that variations in phenotype,  $\square P$ , are the result of genetic differences,  $\square G$ . 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"<sup>2</sup>.

Since variance statistically is the square of the standard deviation the mathematical formula is then:

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

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.

What would be the point of trying to increase the heritability of any given trait in our herd? 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 are used as selection criteria. For instance, if we want to breed for fineness in fleece, and are considering if a particular female should be selected for that breeding program, only the fineness of her own fleece would be used to make the decision. The assumption in this case is that a phenotype for fineness in alpacas is somehow related to breeding value for fineness. If that is not true, then selecting the parent based on his or her phenotype for this trait would be worthless. We have already seen that phenotype is not a very accurate way of estimating breeding value, but the higher the heritability of a trait is, the greater the relationship between phenotype and breeding value, hence the more accurate our phenotypic selection is. So in summary, if we can increase heritability, we can have more accurate phenotypic selection.

#### 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 pp.