Hidden Implications of Common Breeding Program Objectives And What They Can Teach Us: Part 1

A breeder has decided to focus on improving the fiber density of the alpacas on her farm, and she does this in two ways. First, she makes sure to provide optimal nutrition for her pregnant dams, to promote the maximum possible development of follicles during the development of the crias in utero. Then, she uses biopsy and adjusted fleece weight data to select breeding pairs, breeding dense animals to each other and culling from the herd animals which are less dense. As a result, the average density of animals in her herd improves markedly over time. However, when other breeders purchase these dense animals for use in their breeding programs, they often do not improve the density of the offspring produced in those programs as much as would be anticipated based on their apparent phenotypic superiority. In fact, more often than would be predicted by chance, their offspring underperform those of the less dense animals that these other breeders produced on their own farms. How could this happen?

When alpaca breeders select pairs of animals to breed, they are usually basing their decisions at least in part on criteria that they believe will result in an improved genotype of the offspring (compared to the genotype of one or both parents) for the expression of one or more phenotypic traits of interest. These attempts to favorably shift the trait-specific genotypes of the animals in a herd often have unintended but nonetheless very predictable consequences for other aspects of the animals' genotypes, some of which can be difficult to discern at first because they are not directly revealed by the animals' phenotypes. And yet, understanding what is occurring unseen in the animals' genotypes can be important to the longer-run success of a breeding program, as well as to the success of the industry as a whole.

In the serialized discussion that follows, we will present a number of less obvious genotypic implications that follow from some common approaches to alpaca breeding pair selection. These include everything from enhanced environmental sensitivity in our animals' traits to changes in trait correlations, heritability, and genetic diversity. The concepts are straightforward and interesting. We'll start with the environmental sensitivity of phenotypes, because many if not most of us are probably inadvertently enhancing this in our animals, creating a trend that may have longer-run implications for the successful development of a livestock industry.

Example 1: How Breeding and Husbandry Decisions Interact to Affect Environmental Sensitivity

You are likely familiar with the following expression:

Phenotype = Genotype + Environment

In other words, an animal's appearance is a function of both the genes it carries and the environmental conditions it has been exposed to over the course of its life. This simplified construct is a useful conceptual reminder for those of us who are not geneticists, but taken too literally can lead us to think that environmental effects on phenotype are independent of genotype, when in fact an animal's genotype determines the sensitivity of its phenotype to its environment.

Geneticists refer to the variation of phenotypic expression of a single genotype across a range of environment as the *reaction norm* for that genotype. Some animals will have genotypes that make attributes of their phenotype relatively insensitive to the environment – think, for instance, of the alpaca whose fiber stays fine no matter how rich the feed it eats. Others will have genotypes that make important aspects of their phenotypic expression more sensitive to the environment. This concept is illustrated in the graph below, where Genotype A shows greater phenotypic change than Genotype B with regard to changes in the environment. You can see how differences in environmental sensitivity can result in different genotypes being preferable in different environments.



Phenotypic Response to Environmental Change Can Vary by Genotype

In the case of the example we began this discussion with, the combination of a positive nutritional environment for the expression of follicular density and a selection process based on density resulted in an increase in the prevalence of more environmentally sensitive genotypes in the breeder's herd. It happened because the

extra nutrition that the breeder provided to her pregnant dams enhanced follicular development most in those developing crias that had, as a result of their genotypes, the greatest phenotypic sensitivity to changes in the nutritional environment. Because she used phenotypic density to determine which animals to pair for breeding, the breeder tended to keep and breed those environmentally sensitive animals with each other, increasing the phenotypic sensitivity of her herd as a whole with respect to the relationship between nutrition and density.

In the consistent husbandry environment she provided for her animals, that increased sensitivity did not matter. But when her animals went to other farms, where the nutrition programs were less optimal, the enhanced sensitivity sometimes revealed itself as a mismatch between the expected and actual phenotypic density of the offspring they produced relative to those produced by animals born and raised on the new owners' farms.

How should we manage the potential challenges presented by varying degrees of phenotypic sensitivity to environmental changes? For one, we should keep in mind that breeding animals *in* a specific environment can amount to breeding them *for* that specific environment. When other breeders purchase our animals for use in their own programs, we should help them clarify any differences in husbandry between their operation and ours that might affect the phenotype or performance of our animals in their program, so they can directly manage these factors if they wish. This will help make sure that the animals we provide to them meet their performance expectations.

Second, we may wish to consider *not* providing an overly favorable environment for the expression of a trait we are focused on, so that we select for animals that are more likely to express superiority in that trait even when exposed to less favorable environments. As most alpaca businesses succeed in part based on the phenotypic as opposed to genotypic quality of their animals – for instance, in the show ring, or when it is time to sell their annual clip – this can be a difficult goal to maintain in practice. And yet, collectively we have a very good reason to try to do so, as the long run success of our industry will depend on the provision of useful animals to livestock operations where the care standards will be very different than the pampering now provided by many "seed stock" breeding operations. If our animals' health, reproductive fitness and fiber quality are not robust to the range of more marginal environments provided by cost-constrained livestock operations, we will have poorly positioned future industry participants for success.

One final note: You may be wondering if estimated progeny differences, or EPDs, might reveal the relative environmental sensitivity of your animals or others'. The answer is no. While EPD calculations adjust for the varying environments in which genetically related animals live in order to calculate estimated genotypic values for various traits, this is not the same thing as measuring differences in the environmental sensitivity of those genotypes. Those sensitivity differences are instead "hidden" as one of several components of the estimation errors that are the

basis of the EPD accuracy estimates. That said, using EPD trait estimates and accuracies *together* indirectly incorporates into your decision-making some indirect information regarding relative environmental sensitivity.

In part 2 of our discussion, to be released soon, we will look at how breeding for correlated traits will change trait relationships within your herd.