

Evaluating Genetic Color Hypotheses Relative to Multi-Generational Production Results

Any proposed genetic system of coat color inheritance can be used to model the likelihood of an animal carrying a specific genotype, based on its phenotypic color and its ancestors' phenotypic colors. We acknowledge this, and even guess at these likelihoods, or probabilities, every time we look at pedigrees to try to determine the likely color of a cria from a given sire and dam. What might be less obvious, though, is that a proposed system of coat color inheritance can also be used to model the likely genomic trends within larger groups of animals that are being selected for a particular color, like an individual herd or even a national one. Those predictions can then be compared to what actually happens, the results of which may either lend support to or weaken the case for a particular hypothesized color inheritance system.

Here is a simple, if dated, example. Suppose that, as many of us were once taught, the phenotypic coat color of an alpaca is determined by a single gene, and that that gene has a dominant allele "W" that produces a white coat, and a recessive allele (or alleles), "c" that produce(s) colored coats. White animals would have either WW or Wc genotypes, and colored animals would have cc genotypes. Now, assume that you begin a white breeding program with a group of white animals which all have Wc genotypes. This group will produce 75% white animals and 25% colored animals in the next generation. Of the 75% that are white, one-third will carry a WW genotype and two-thirds a Wc genotype. If you kept and bred only the white animals from this generation to each other, the third generation of white animals produced would contain include 50% WW animals and 50% Wc animals. The fourth generation of white animals produced by the third generation whites would be 60% WW and just 40% Wc. And so on. This process of breeding whites from multiple generations of whites is, of course, exactly what we do when we build multiple generation all-white pedigrees.

You can see that this theory that a dominant white allele creates a white-coated animal implies that an animal from a multiple-generation exclusively white pedigree would have a relatively high probability of being a dominant homozygous white; that is, one which could only produce white offspring no matter what color it was bred to. A multi-generation white focused breeding program like ours should produce many dominant homozygous animals. In fact, to date, we have failed to confidently identify a single homozygous dominant white in our herd. For instance, of our 15 working white herdsires from exclusively white pedigrees (from one to four generations deep, and with no non-white ancestry,) 14 of them have produced color. (One has not yet, but has not been exposed to many colored dams, so we are not statistically confident that he cannot.)

Not surprisingly, this divergence of prediction and reality with regard to breeding for white from white, and also white from color, was so dramatic that it was noticed

over a decade ago by researchers in Australia, among others, and the existence and effect of a second gene controlling the expression of the base coat color, known as an extension gene, was proposed based on its proven existence in other more extensively studied mammals, including sheep.ⁱ They also proposed that a dominant extension allele “E” allowed the genetic base coat color to be expressed as the phenotypic color, while a double recessive “e” overrode the base coat color and produced an animal with a coat color we would call brown or fawn (because of the type of proteins produced, geneticists would refer to this color as red.) As a result, this model posited the existence of four genotypes that produce white phenotypes: WW EE, the homozygous dominant white; WW Ee; Wc EE; and Wc Ee. Because of the effects of the recessive allele of the extension gene, two other white base coat genotypes, namely WW ee and Wc ee, would not be phenotypic whites, but rather brown. This model reasonably fit one-generation breeding results and offered an answer to questions like how two colored animals could produce a white offspring if the white allele was dominant (by this theory, at least one would be “ee” at the extension gene location, and therefore “hiding” one or two dominant “W”s at the base coat location.)

Just as in the previous example, we can test these ideas by extending our projections about genotypes across multiple simulated generations, making the most conservative assumptions about the founding population relative to what we are trying to produce, and then seeing if the projected genotype trends match what we think we are seeing in reality. To assess how often this genetic basis for phenotypic coat color would produce white animals that can produce only white, therefore, we would start by assuming a founding population of phenotypically white animals with the lowest odds of producing white offspring when bred to it: namely Wc Ee whites. While it takes more generations with this two-gene color model than with the single gene model (and more of my weekend to do the math), the effect of breeding only phenotypic whites to each other causes the aggregate genetics of the group as a whole to drift towards the dominant homozygous genome WW EE, such that by the fourth generation the number of WW EE whites produced is approximately 38% of all whites in that generation. In other words, even with this model we should not have to look far to find whites from all-white pedigrees that can never produce color, even when bred to it. So this model, too, fails to describe what we see in our herd, and more broadly.ⁱⁱ

And in fact, those of you with a quantitative bent can already see that something important in our assumptions has to change to eliminate the potential -- and therefore eventual -- appearance of a homozygous dominant white. Even if more than two genes are involved in determining coat color, the aggregate genome of a white herd will drift towards the dominant, white-associated alleles in each location as the generations pass, and dominant whites will appear with increasing frequency over time.

Kylie Munyard published a paper entitled “The Inheritance of White Color in Alpacas” in 2011 that provided scientific support for revisions to not one but several

key former assumptions about alpaca coat color – and not just white.ⁱⁱⁱ In order of OMG-ness they were:

1. There is not a base coat allele for white, but rather one for “light” – white through light fawn approximately. Munyard labels it “A.”
2. That “light” allele is only *partially dominant* over the allele for brown (Ab), not completely dominant, and when paired with a brown allele at the base coat location acts in combination with it to produce a fawn, before considering the effect of the extension gene. The light allele A is fully dominant over the black allele a.^{iv}
3. It is the recessive extension gene allele “e” that, in a homozygous ee animal, acts to dilute color, not the dominant gene. And it does it by blocking production of only one of the two colors that are present in varying amounts in all base coat colors, eumelanin, which is what we non-geneticists would call black.

Munyard notes in her paper that variations in the intensity of color expressed remain to be explained, and the explanation could involve both genetic and environmental effects. It is also much more of a challenge to simulate the probability of different genetic combinations coming to prominence in a breeding program focused on a single color when one base coat allele is incompletely dominant in the manner that Munyard believes the light allele is. That said, there are certain things that logically cannot happen if the hypotheses in Munyard’s work are correct – and one of those things, interestingly, is that *we should never find a phenotypically white animal that cannot produce color when bred to it*. In fact, they will even do it a very high percentage of the time when bred to colored animals with certain genotypes, albeit with some dilution of the base coat color expressed in the phenotype in many instances

Munyard proposes that the following genotypes result in a white (or light) phenotype (ignoring for this purpose the possibility of white spots or patterns which cover the entire surface of the animal):

- AA ee – with eumelanin prevented from being expressed, this results in the bright pink-skinned white we have taken to calling “true white” around here.
- AA Ee or AA EE – these are darker skinned whites.
- Aa ee – This is a white with a recessive black allele on board and all eumelanin production blocked.
- Aa Ee or EE – this is a darker-skinned white with a recessive black allele.

Of particular interest is the AA ee genotype: pink-skinned, bright whites. This is what most white breeders, including us, select for. One very famous breeder of

white alpacas who was known to select for these traits, and did so over many generations, was Don Julio Barreda, who owned the Accoyo ranch in Peru. We show the offspring color results for some of the key males imported from his ranch to the U.S. (along with a couple of fawn males for comparison) in Exhibit 1, so that we can see how their color production results coincide with what Munyard’s research would predict for pink-skinned AA ee whites in particular.^v

Exhibit 1: Color Production Records of Key Imported Sires (from AOA records as of 11/2016)

Sire Name	Color	Number of Crias Registered	Percent White from White Dams	Percent White from Colored Dams
Caligula	WH	205	87%	44%
Vengador	WH	216	99%	43%
Elite^{vi}	WH	230	85%	39%
Pachacuti	WH	298	95%	47%
Augusto	WH	276	86%	42%
Titan	WH	270	90%	40%
Victor	MF	238	69%	13%
Camilio	MF	264	49%	9%

One prediction that flows from Munyard’s hypotheses, of course, is that none of these males would be homozygous dominant whites, because there is no dominant white allele. If there were such an allele, we would expect a number of these males to be homozygous dominant, as they came from a multiple generation, closed white breeding program. But none of these males were, so that’s one check for Munyard. Second, we would expect them to produce less than 50% white animals from colored animals, again because the light allele is hypothesized to be only partially dominant over brown. This, too, was the case for all the white imports shown here. Third, because a single light allele acts to dilute brown when combined with it in an heterozygous base coat genotype, we should find that these males produced a greater amount of white from fawn animals than from brown animals (because those fawn animals have a higher likelihood of carrying a light allele); and, because both the AA and ee parts of their genotype act to dilute color, they should tend to dilute the color of their offspring on average, relative to the color of the dams that produced them. To explore this last pair of implications, we looked at the production records of the white accoyo males above when bred to medium fawn and medium brown. These results appear below in Exhibit 2.

Exhibit Two: Color Production Records of White Accoyo Import Sires

Sire Name	% White Crias From Med Fawn Dams	% Crias Lighter Than Dam From Med Fawn Dam	% White Crias From Med Brown Dams	% Crias Lighter Than Dam From Med Brown Dams
Caligula	70%	85%	19%	100%
Vengador	56%	67%	23%	100%
Elite	36%	91%	11%	100%
Pachacuti	73%	92%	42%	88%
Augusto	39%	71%	21%	75%
Titan	38%	81%	27%	67%

The results shown here are consistent with the idea that many fawns are carrying a light allele, because a consistently greater percentage of white offspring were produced from fawn females than from brown females. The results also do not contradict the idea that light allele is partially dominant and dilutes brown when combined with it, because substantial majorities of the crias from both fawn and brown dams were lighter than their dams. Overall, therefore, the color production results of these Accoyo males do not conflict with what Munyard hypothesizes, and provides some probabilistic support.

Given the likelihood, then, that the light allele is only partially dominant and that white animals should be universally capable of producing color when bred to it, the next question that will come to mind for many breeders is whether the probability of a colored cria from any particular white/color pairing can be estimated, or whether we can better estimate the probability of *any* particular color from a specific pairing than we do now. In fact, there may well be additional clues in phenotype that we can discover with analysis of the type we have described here. We will work on it.

ⁱ See, for example, Hart, KW et al., "The Gene for White Fleece in Alpacas is Homologous to AWt, the Gene for White Fleece in Sheep," Department of Agriculture, Government of Western Australia, 2003. This article is linked on our library page.

ⁱⁱ The odds of 14 of the 15 herdsires in my herd producing color when bred to it, given the known length of their white pedigrees and the assumption that all their imported white ancestors were completely heterozygous, is just 4% assuming the base coat and extension genes and alleles worked as described in this paragraph. The true odds would likely be appreciably less as many of their ancestors came from white breeding efforts in Peru, and they presumably have longer white pedigrees than we can confirm with their U.S. registrations.

iii Munyard, Kylie; "The Inheritance of White Colour in Alpacas – Identifying the genes involved. RIRDC Publication No. 11/074, July 2011. You can find this one linked on our library page as well.

iv She also notes evidence for the existence of a fourth allele, "at," which in a homozygous animal produces a phenotype with a black body and a fawn belly. It is also completely recessive to A and because I think it is rare I have ignored it in this already-complicated discussion and let the other presumably more prevalent black allele stand in for both.

vi Elite actually has results that look a lot more like the typical male in this exhibit, as well as the one that follows, if you count his beige offspring as white. Different breeders have different standards for what constitutes a white or beige animal, which creates a real challenge in evaluating color production. With regard to this particular white/beige issue, it seems advisable to look at the data both ways – that is, beige counted as white and beige counted as not white – to see whether it makes a difference in the conclusions one draws from the data. In the case of the sires in this example, it does not, although Elite's numbers in particular change a lot.