

Some Educated Guesses on Color Genetics of Alpacas.

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Only a very few studies have been published on alpaca color, and those were generally undertaken before some of the really key concepts had been worked out in other species such as sheep, mice, and other species. This may sound like a trivial detail, but color genetics within any species works best when viewed through the consistencies that are present across species. Since comparative data are not present for alpacas, the following thoughts are largely my own, and come mainly from working with color genetics in horses, dogs, sheep, and goats. In addition I have tried to analyze data from alpacas whenever possible. Those data have been few, but have supported the outline presented here. In short - this is an educated guess but all the hard evidence I have seen does support this guess.

It is important to realize that genetics is not a science of prediction of specifics, but is more a science of the prediction of the range of possibilities. Genetics does a great job of predicting general characteristics included among the next 100 crias, but only rarely will it pinpoint the exact characters in the next individual cria. Genetics becomes extremely useful when used to predict a range of possibilities, which in this case means trying to pinpoint the range of colors an individual alpaca can produce in its crias.

One of the difficulties of color genetics in a fleece-bearing species, such as alpacas, is that most investigators focus only on the fleece color. This approach overlooks details of color in nonfleeced portions of the animals, and can result in some critically important details being overlooked. A prerequisite for any good investigation of alpaca color genetics is going to include a very accurate and detailed classification of the color of the animals involved. The main problem with the simpler classing of animals by fleece color alone is that multiple genotypes (genetic combinations in an individual animal) can lead to the same final color phenotype (external appearance), and likewise, single genotypes can lead to multiple final color phenotypes depending on all the modifiers present. This sounds clear as mud, but color genetics is inherently complicated, and unless it is viewed in its detail it is not going to provide many answers that can help breeders.

The basic approach that I find most useful in approaching color genetics is to first separate color from white. White is the absence of color. White results when color is taken off of animals, even though these still have an underlying directive for color production. By separating white and color it is possible to understand the cause of each better. I will first discuss color, and then patterns that add white. Overall whiteness can be problematic, since the Michell charts list multiple types of white. Lumping these whites together is not going to impede this discussion, and is a valid first step in trying to sort out the “big picture” of color genetics.

Basic principles of genetics are critically important for this discussion. The underlying concept for most of genetics is that genes control nearly all the biochemical processes that occur in animals. These genes occur as pairs, one inherited from the sire and one from the dam. When an animal reproduces it passes along only one of the pair, the resulting offspring getting the other member of the pair from its other parent. The pairing of the genetic information is what makes genetics “work”, with different combinations possible at each generational step.

Genes can interact in different ways, and the nomenclature reflects this. Recessive genes

are only expressed when present in two doses (both members of the pair are the same, referred to as homozygous). Dominant ones are expressed whether one (heterozygous) or two (homozygous) are present, and therefore “dominate,” or hide, the recessive genes if they are paired with them (heterozygous). The result of this is that recessive genes can pop up as surprises when the pair up from two parents that carry them masked by dominant genes in the heterozygous state. Dominant genes rarely occur as surprises. My basic approach in this article will be to go through the various genetic loci (addresses, or sites) that are likely to control alpaca color, and to discuss what each is doing. These will be added together to yield a final color. After discussing color, the discussion will focus on white or patterns of white superimposed over the color. This approach goes through genes first rather than color classification, and at the end a retrospective from color back to genes will be given.

Color terms are also going to be controversial in any discussion of color genetics.

Pigments come in two types: eumelanin and pheomelanin. Each is distinct biochemically, and the classification of color as to one or the other basic pigment is important. Eumelanin is basically black or a derivative of black such as slate blue or flat chocolate brown. Pheomelanin is basically tan, which includes any brown with a red shade to it. Pheomelanin in alpacas appears to vary from very light fawn, through all the fawn shades, to red brown, and even to a very dark mahogany. At the very darkest end of the variation of pheomelanin it is possible to confuse it with chocolate brown eumelanin. This may be a trivial distinction in alpacas, where nearly all the browns/tans/fawns appear to be pheomelanin and not eumelanin.

Determination of color class is difficult at certain ages because color can change. The age at which to determine color class can therefore be important. The initial coat of crias can be lighter than the subsequent coat, so classification is most accurate at first shearing.

Control of color

Agouti locus

The Agouti locus is very important as a major determinant of color in several species, and appears to be so in alpacas. The Agouti locus controls the distribution of black versus tan pigment throughout the coat. The result is usually a symmetrical distribution of pigment, so that the animal is the same side to side. Alpacas appear to have relatively few variants at this locus, but still do have enough so that the Agouti locus appears to be a major determinant of color variation in alpacas. It is therefore the most important locus to understand.

Dominance relationships among Agouti locus alleles are consistent in that all tan areas are expressed. The result is that patterns that are more tan are dominant to patterns that are less tan. Several of the Agouti locus patterns also appear to be shaded so that the ventral part of the animal is paler than the dorsal part. These are the easiest patterns to ascribe to the Agouti locus, since the symmetrical interplay of black, tan, dark, and light is very typical of patterns controlled by this locus.

Colors that are probably determined by Agouti locus alleles include:

pale shaded fawn. These animals are very pale, but are subtly darker over the topline than on the sides, belly, and legs. Few if any black hairs are present, even around eyes, nose, nailbeds, and leg scent glands.

shaded fawn/vicuña pattern. This pattern is somewhat darker than the pale shaded fawn, and tends toward redder and brighter on the back, with shading to cream or nearly white

on sides, belly, and legs. Very little black pigment is present, usually at the nail beds, eyerims, eyelashes, and around the mouth.

red with minimal black trim. These animals are bright clear red, and lack the shading of the previous two patterns. They have minor black trim at the nail beds, around the eyes, and around the mouth.

red-brown with black trim. This pattern is darker than the previous one, and also has more obvious black areas including the lower leg and face. This pattern is sometimes called “bay”, and the fleeced areas are generally a medium to dark reddish brown.

shaded mahogany. These animals are dark brown to nearly black, with very distinct lighter regions on the lower sides and belly. The light regions are generally red rather than the cream or nearly white of the previous shaded patterns.

black with tan belly. I have seen only one of these, and this was a black animal with a very distinctly cream belly. This is expected, from homology with other species, to be an Agouti locus allele.

black. As the name suggests, these animals are solid black with no tan or red areas. Some black animals fade, others do not, and the control for that is probably not at the Agouti locus.

The summary for the Agouti locus, if nothing else were controlling color, is that the paler shades should on occasion be producing the darker shades. This is due to their being dominant to them and able to hide them. Each pattern should only be able to reproduce itself, or one of the darker members of the series (since these darker members can be masked as recessives). The patterns should only be able to produce a paler member of the series following mating to an animal with a pale variant. That is, black to black should only yield black. Pale shaded fawn mated to pale shaded fawn should (across a population) produce mainly pale shaded fawns, but also should produce just about everything else at least rarely.

It is important to note that each animal can have only two of these variants, and generally only expresses the paler of the two. So, an animal with a “pale shaded fawn” allele and a “red-brown with black trim” animal will appear pale shaded fawn visually, but could produce red-brown with black trim crias if mated appropriately. This animal could not produce blacks, no matter how mated, since it simply does not have the genetic machinery to allow for that.

At the Agouti locus black is the best “test cross” to see what recessives are lurking in the other colors. Black is recessive to all the others, and so whatever they are carrying will eventually come to light following mating to a black mate. This strategy could be overdone throughout a population, though, and would so drastically increase the frequency of black that other interesting and useful colors could become more rare within the population.

Extension locus

The Extension locus has an intricate, predictable, and complicated interaction with the Agouti locus. Some small amount of evidence does indicate that this locus accounts for some results, and so it is important to include some discussion of it. I do suspect that in most cases the Agouti locus is the main determiner of color. Where the Extension locus comes into play it will make color predictions more confusing and difficult, and the reason for this is that some Agouti and some Extension colors are visually identical but genetically distinct.

Extension acts somewhat opposite to Agouti in that black is dominant, and red/tan is recessive. The black and the red variants at the Agouti locus are also epistatic to Agouti. “Epistatic” means that they completely mask any expression of Agouti. This is complicated, but is essential to understand if color genetics is to make any sense. The most likely alleles at Extension are:

dominant black. This is, as the name suggests, dominant. It is dominant to other members of this locus, and also masks any of the Agouti patterns behind the black color. Strangely, dominant black in most species is somewhat “weaker” than the Agouti recessive black, and is frequently off black or very dark brown instead of true black. This is subtle but can help in some cases to detect these animals. The main significance of a dominant black allele is that black to black could indeed result in some segregation of other Agouti patterns. This allele is therefore responsible for some very confusing results in a otherwise orderly system, since distinguishing all recessive blacks from dominant blacks on visual inspection is impossible. Each behaves very differently in a breeding program, which can be a source of breeder headaches. Fortunately this dominant black allele appears to be rare, if it exists at all, so that blacks can generally be assumed to be an Agouti locus phenomenon, and therefore easy to understand.

wild type or neutral. This is an intermediate allele, and can be considered as “neutral”. This allele allows the expression of the Agouti locus. This sounds confusing, but is simple to remember because every animal with an Agouti pattern must be expressing this allele. The “wild type” name is a convention since this is the allele of the guanaco and vicuña, although only results in those colors when the appropriate Agouti locus allele is also present.

uniform fawn (recessive red/tan). This allele is recessive, and results in a completely and uniformly tan coat with no black hairs. This includes no black hairs anywhere, although skin can be black. Most alpacas of this color are a uniform (as opposed to shaded) fawn. This color, though recessive, also masks the Agouti locus, so that surprises are easily possible with these animals. As an example, a uniform fawn could have “red with trim” and “red-brown with black trim” at the Agouti locus. Mating this animal to a black animal that is “wild type” at Extension and “black” at Agouti will result in “red with trim” or “red-brown with black trim” crias.

Table 1. Alleles at the Agouti and Extension loci
locus allele symbol range of fleece colors

Agouti pale shaded fawn Apf beige, light fawn

vicuña A+ light fawn, medium fawn

red with black trim Ar medium fawn, dark fawn, light brown

bay AA light brown, medium brown, dark brown

shaded mahogany Am dark brown, bay black

black with light belly At black

black Aa black

Extension dominant black ED black, bay black

wild type (neutral) E+ as determined by Agouti

uniform fawn Ee medium fawn

The Agouti and Extension loci probably account for most of the color variation in alpacas. My suspicion is that the Agouti locus is the main determiner of color in colored alpacas. Extension appears to be important in only a very few blacks, and in uniform

fawns. These two can make color breeding predictions difficult in some cases.

Other Genes That Might Affect Color

A few other rare phenomena also can affect color, at least theoretically. Whether these are important, or even occur, in alpacas is debatable. However, as more and more alpacas are produced it is likely that a few “new” colors will emerge, and discussing the mechanisms for these will help breeders to identify and use these when that time comes. One mechanism that is important in many species is called “dilution” as a general phenomenon. Dilution factors in many species include several different loci with a number of different alleles. This means that the overall topic of dilution is complicated, although if taken apart component by component it is possible to tease out some potentially useful trends. Dilution factors appear to be reasonably rare in alpacas.

Dilution genes in other species have a variety of actions, and each pattern of action can give clues as to the genetic cause of the dilution. Some dilution loci affect only eumelanin, the result generally being chocolate brown with some genes, and uniform slate blue/grey in others. These colors are very distinctive in species in which they occur. The biggest clue that one of these diluters is present is that all the eumelanin in an animal is affected - face, body, short hair, fleece. Diluters with action only on eumelanin leave pheomelanin untouched, and so it is fully and intensely expressed.

Some other dilution factors, in other species, affect only pheomelanin. These diluters usually take the typical tan or red-brown of pheomelanin and lighten it to gold, “yellow”, cream, or even to ivory or white. These diluters fail to act on eumelanin, which remains fully black. It is very unlikely that any diluters of these classes exist in alpacas. The evidence for this is a general lack of gold fleece types that have black points. This combination would be expected from a diluted bay, and simply does not seem to occur. Other dilution factors affect both pigment types. These would result in an overall lightening of both eumelanin and pheomelanin. These animals, regardless of underlying base pattern, are lightened to more pale colors.

These distinctions in the action of any potential diluters are helpful in ascertaining whether multiple dilution mechanisms are at work. This is because each pattern of action is usually consistent with a specific dilution gene. In species where multiple dilution factors exist they can sometimes combine in individual animals to yield some unusual results. Such combinations also act in unusual ways in a breeding program if the breeder is unaware that multiple dilution factors are present.

A few colors in alpacas are candidates for dilution. Certainly dilution of pheomelanin might be present in some of the fawn types, since these are basically light pheomelanin colors. A powerful argument against this, though, is the fact that a real black-pointed bay does not seem to exist in a gold or fawn type. This combination should occur if dilution of pheomelanin is the mechanism for fawn color. It is therefore more likely that the fawns are simply Agouti locus alleles, and most breeding results point in that direction.

One rare color that might indeed be due to dilution is dark charcoal grey with no intermixture of white or other colors. That is, these animals have a uniformly dark grey color throughout the fleece, with some slight dilution of the face and leg hair as well. The overall result is a dark charcoal color that is distinctly bluer than black, and yet is very dark. This color is likely to be due to the action of a dilution gene. An educated guess is that it is a dominant gene, so that charcoal x black matings should produce about 50% black and 50% charcoal crias. The action on pheomelanin is not determined, but it is

doubtful that it does act much on pheomelanin.

Another locus that is sometimes postulated is the Brown locus. In other species this locus has alleles that change all black to a flat, chocolate brown. This is the brown of chocolate Labrador retrievers. The key to this locus is that the appropriate alleles change all the black to brown, leaving no black. The few alpacas I would classify as “chocolate brown” all had black trim, so that the Brown locus could not have been responsible for these. Variation at this locus may indeed not occur in alpacas, although breeders should always be alert to it popping up somewhere as it could lead to an interesting array of fleece colors.

Since dilution effects in alpacas are very rare (if they exist at all) it is difficult to make breeding recommendations on these. If breeders have animals that are candidates for dilution then certainly they can be mated to maximize the potential for reproducing the dilute colors. The safest recommendation is to mate to a fully intense animal with the same Agouti phenotype as the diluted animal. So, for example, mate charcoal grey to black. This provides for expression of the potential dilution gene without much extraneous color variation so that breeders can more likely determine the genetic mechanisms at work.

A rare phenomenon in alpacas is what is termed “appaloosa” in llamas. I prefer “harlequin” for this, since the pattern has important differences from the patterns of the Appaloosa horse. Harlequin alpacas generally have dark, generally round, spots scattered over the body. The background to the dark spots is usually a lighter color, but not white. The result is a subtle interplay of dark and light areas, and usually results in a very distinctive face color. The harlequin effect is expected to be different on different background colors as determined by the Agouti and Extension loci. The effect on black is the only one I think I have seen, and the result was nearly black round dark spots on a dark grey background, with smaller round dark spots in a nearly white background on the face.

Another phenomenon that may be related to dilution is the tendency of some animal’s fleeces to weather and fade. In sheep these tendencies have been shown to have some genetic control. Some blacks, for example, fade to brown or off black, while others retain a good true black color. This fading is complicated, and some animals are basically born faded, with the darker color growing in after the birthcoat has emerged. These subtle changes may be telling us something about the underlying color genes present in the animal, but I have not seen any data to help unravel the mystery of these. Mating “non fading” to “non fading” is probably a very good way to increase “nonfading” animals, while mating “fading” to “fading” animals is probably warranted if the fading is desirable. In a mature fiber market both types would be useful, and so there is no inherent strength or weakness with either type.

White Spotting

White spotting has a specific connotation for color geneticists, and basically includes any regions of the coat (or even individual hairs) that have failed to obtain pigment, with the result being white hairs or patches. Multiple patterns of white spotting occur in most species, and alpacas appear to be no exception.

White spotting patterns have a consistent peculiarity in that each pattern can vary from very minimal to very extensive. In the middle range of expression the different patterns can usually be distinguished one from another. At the extensive end of the range they can

be confused with one another or with white alpacas. At the minimal end of the range they can be confused with solid colored alpacas that lack white spotting.

piebald spotting

Piebald spotting is one pattern of white spotting in alpacas. Piebald animals generally have color remaining around the eyes as eye patches, and usually white encircles the neck at some point. White is usually expressed ventrally and on the legs. The inheritance of piebald spotting is somewhat confusing. Many llama breeders insist that it is recessive, and it may well also be in alpacas. At the dark end of the range these animals could easily be confused with nonspotted animals, at the pale end with white animals. Piebald spotting can be superimposed over any background color, but is more obvious on the darker colors since the contrast is greater. This pattern is more common in llamas than in alpacas, but does occur in both and by itself is no indication of past crossbreeding.

tuxedo or caped spotting

The tuxedo (or “caped” as a translation from Spanish “capirote”) pattern can be confused with piebald spotting but appears to be a different pattern under separate genetic control. This pattern generally has white on the underline from the head to the rear. Most tuxedo animals have color remaining on the back of the neck, barrel, and back, and are white on the face, lower neck, legs and belly. This pattern can be superimposed over any background color, and is probably inherited as a dominant gene. This is superficially similar to the pallor of the head and neck on grey animals, but is a distinct pattern that can be combined with any base color.

roan or grey

The pattern that is called “grey” by most alpaca breeders is probably what a geneticist would rather call “roan”. In most species roan is an intermixture of white and colored hairs. Roan alpacas generally have white or nearly white heads, frequently have white legs, and the body coat is a combination of dilute (grey), dark, and intermixed hairs. The result is usually a reasonably uniformly grey fleece, although the animals betray their peculiar mixture of colored areas when freshly shorn. Dark roan animals may be confused with nonroans, and light roan animals may be confused with white animals. Roan is likely a dominant gene, although there is some evidence that the darkest ones do not behave the same as the medium and light ones. In addition, no greys appear to be homozygous. The proof for this would be a grey only producing grey and no nongrey offspring following mating to nongrey mates. In nearly every instance where greys have been mated sufficiently to nongreys, some nongreys have been produced, which demonstrates that the greys do not have two doses of the roan gene.

The nomenclature of roans is important to alpaca breeders, since grey fleeces are desirable. Roan on a black background yields silver greys (dark, medium, or light). Roan on a mahogany background or a dark bay background yields the browner sort of rose grey. Roan on a light bay or “red with black trim” background yields the redder version of rose grey. On a fawn background the roan can be difficult to appreciate, and is likely to be missed as contributing to the final color.

minimal white marks

What I call minimal white marks are reasonably common on the heads and legs of alpacas. These usually do not affect the fleeced portions of the animals, and so are usually overlooked as being important to color genetics. Frequently these are small enough to be inconsequential, and the genetics of these is probably complicated. Some,

though, are probably minimal expressions of piebald spotting and so might be important in making breeding decisions.

rare types of white spotting

I have seen a few patterns of white spotting that do not fit into any of the previous categories. One of these is a dark headed roan. These animals have roan (or grey) bodies, but dark heads and legs. If this pattern is behaving as it does in other species it is probably dominant.

A second pattern is probably best called speckled. I have only seen a pair of these animals. The dam was light red with distinctive white speckles along her bottomline and extending up along her sides. Her cria was more extensively white, and was indeed nearly all white with numerous scattered small to medium sized red spots throughout most of the coat. In the minimal and medium ranges of expression this variant would result in a very interesting fleece. While details of the inheritance are uncertain, the existence of a rare pattern in a mother-son pair suggests that it is dominant.

A very tantalizing pattern is present in Nance Sturm's herd, and the animal appear to be a shaded roan. This might be an Agouti phenomenon, but does appear to be a roan phenotype instead. The roaning is more developed ventrally, and the legs are attractively striped with dark regions on the fronts of the legs.

Genes Causing Patterns of White Spotting

pattern of white/locus allele symbol

Roan roan RnR

nonroan Rn+

Spotting spotted Ss

nonspotted S+

Tuxedo tuxedo Tutu

nonspotted Tu+

Dark Headed Roan ??

Speckled ??

White

White is a difficult fleece color (or lack of color) to understand because it is an endpoint that can be achieved through different means. White animals could be very dilute, or could be very white spotted, or could be both. The important concept here is that multiple mechanisms for whiteness might well exist in alpacas.

Most white alpacas produce white or pale offspring following mating to any other color, indicating that dominant mechanisms for whiteness are relatively common among alpacas. Some white alpacas consistently produce the color of their mates, indicating that such animals are recessive to all other variants. The problem is to distinguish these types of white visually, and of course that cannot be done.

As a type of white, the blue eyed white is controversial. Some of these animals are deaf. Most owners of these indicate that they function normally in alpaca society, and so this appears to not be a very debilitating condition. From the alpaca's viewpoint it may not matter much whether they can hear or not, although we tend to impute to it serious consequences from a human point of view. Obviously, if clicker training is your strategy then the deafness would be a problem for both the alpaca and you.

What little evidence I have seen points to at least one mechanism for producing blue eyed

white animals. At least some of these are the result of combining spotting (probably either the piebald or the tuxedo types) with roan. Whether this accounts for very many blue eyed whites I don't know, but it does account for some. This information can be useful, since blue eyed whites mated to dark, nonspotted mates will produce (in about equal proportions) solid colored, spotted, roan/grey, and blue eyed white.

The occurrence of blue eyed whites from a combination of spotted and roan patterns also implies that greys and spotted animals should not be mated together if the goal is to avoid blue eyed whites. Following the mating of a spotted and a grey animal the expectation is equal numbers of grey, spotted, solid, and blue eyed white offspring.

The issue of eye color is very complicated, and most blue eyed animals (like me) see and hear fairly normally. It is probably not possible to completely avoid all blue eyed animals, and multiple genetic mechanisms probably account for the different types of eye colors. Some of these are more common with some colors than others. A generally safe strategy in most instances is to mate blue eyed animals to dark animals with dark eyes. Animals with dark grey, dark blue, or eyes that are mixture of colors are probably not the same genetically as the blue-eyed whites and pose little threat to a breeding program aimed at avoiding these. Some of light eyes seem to be connected with certain colors (roan) and may pop up whenever such animals are bred. Most of these appear to hear fine.

Breeding for color

Strategies for breeding for specific colors are speculative at this point, but a few principles are probably safe. First, and hardly surprising, is that the best way to reproduce a color is to mate two of the desired color together. That is not always possible, though, and reproducing rare colors can be intriguing and frustrating.

Mating any color to a black animals is probably the quickest way to ascertain what is lurking behind lighter colored animals. This strategy is also probably sound for reproducing rarities like the dark and shaded mahogany animals. I would also use this strategy for rare patterns such as the harlequin/appaloosa and uniform charcoal greys. Eventually it will be interesting to see what these modifications do to other base colors, but numbers will have to increase first.

White animals are the greatest unknown, since it is certain that they are hiding some genetic machinery for color production under their whiteness. If white is desired, then clearly white to white matings are the best way to proceed. If colored offspring are desired, then white to dark (and probably bay or black are best here) are the matings most likely to disrupt the whiteness and reveal what is underneath.

This quick overview demonstrates that the inheritance of color is complicated. The results produced by alleles at each of the different loci act together, and the final combination of the actions of these yields the one result that we appreciate as the color of an alpaca. By taking the different components and analyzing them individually it is possible to appreciate the intricacies of how the final colors are produced. Understanding the significance of the components is also the basis for being able to manipulate these in breeding programs to produce the colors that are desired. It is important to remember that while color is important and fascinating in all of its intricacy, it is only one among many critical factors to consider in a well-thought breeding program to produce sound, colorful alpacas with great fleece characteristics.

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Last fall Cleve and Bev Fredericksen were kind enough to share data from their herd, and this helped immensely to target some interesting facts as reasonably well established, or as needing further work. Since then Andy Tillman has also tantalized me with a few results, and these have also shaped my thinking. Conversations with Nance Sturm and Ingrid Woods have also been helpful, as has Eric Hoffman.

Figures:

1. pale shaded fawn. stippled areas are pale fawn, white areas are cream.
2. shaded fawn. stippled areas are fawn, white areas are cream.
3. red with trim. hatched areas are red/brown, black areas are black.
4. bay. hatched areas are red/brown, black areas are black.
5. shaded mahogany. black areas are black, hatched areas are red/brown.
6. black. black areas are black.
7. piebald spotting, minimal expression. dark areas are colored, white areas are white. This animal would be classed as a whole-colored fleece, disrupting accurate identification for color genetics study.
8. piebald spotting, medium expression. dark areas are colored, white areas are white.
9. piebald spotting, maximum expression. This animal would be classed as white, but is really piebald spotted.
10. tuxedo spotting. medium expression. This pattern usually leaves color on the back.
11. roan. hatched areas are roan (grey), black areas are fully colored, white areas are white or very pale.
12. dark-headed roan. hatched areas are roan (grey), dark areas are colored.
13. speckled, dark expression. dark areas are colored, white areas are white.
14. speckled, light expression. dark areas are colored, white areas are white.

bio

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