By
Sherry E. Wallis

Original article published in *Akita Dog*, the newsletter of the Akita Club of America, 1997

A Discussion of White Spotting In the Coat Color of Dogs

Probably more dog breeds have white markings than don't, but the allowable amount of white and its placement have a great variety among them even though the mode of inheritance seems to be the same from breed to breed and has been well researched. To understand how it is inherited doesn't require a course in genetics 101, thank heavens, or we'd all be snoozing by the end of this page! That's the good news.

The bad news is that it's a complicated subject. I have to assume that anyone reading this has some basic grasp of genetics. I'm **not** a geneticist. The courses I took in genetics in college are as applicable to the modern day developments as a course in Model-T repair would be to a modern mechanic. Yes, the thing still has an engine and wheels, but today's car is just a wee bit more complicated.

The Internet has a number of informative sites can help you, and I've provided links to some on the page where you downloaded this article. Check these even if you are familiar with genetics, because new discoveries are being made daily.

The Mechanics of Color

A dog's hair color comes from granules of pigment deposited into the individual hair., granules produced by cells called melanocytes.[1] Present at the base of the hair shaft, these pigment producing factories are responsible for all color, and when they do not function for some reason the hair has no color. It is white. While this can be a function of age, it can be caused by the dogs genetic makeup, injury, or even birth order.

The melanin itself comes in two colors in dogs: black and red/brown. The shape, distribution, quantity, and color of the melanin in each hair create the vast variety of colors we see in dogs. Some breeds, like Akitas, have many colors within the breed's gene pool; whereas others, such as Rottweilers or Belgian Sheepdogs, have only one.

Coat Color

When talking about coat color within a breed, specialized descriptors give a good picture to those who are familiar with appearances within that breed. When someone says they have a "sable" collie, everyone who's seen Lassie knows this is the familiar golden color we associate with the breed. Further, they "know" that the dog has some kind of white markings. Although they also use the term sable, it is applied to an altogether different color in German Shepherd Dogs. A sable German Shepherd is an agouti or wolf-colored dog, and they almost never have any white markings. What is white on the collie is filled in with tan on the Shepherd.

Will the real sable please stand up!

A standardized terminology about color would make discussion much easier, since descriptors aren't consistent from breed to breed. I'll try to define any terms I recognize as ambiguous.

To make matters more complicated, when we describe a breed's color, we usually refer to the predominant color of the dog. The three dogs below are all referred to as reds, yet they are quite different in color, and, in fact, their colors come from different genetic pathways. Further, the term fails to account for any of the additional colors on the dog. White and black are present on both the Akitas, and rust on the Doberman.

Will the real red please stand up?

Marking Patterns

These additional colors make up what are called markings, and nomenclature is anything but standardized. To make things even more confusing, marking patterns are often referred to as colors. The Akita standard says that the breed comes in many colors including pintos and brindles, but both of these are marking patterns. Both pintos and brindles can come in all sorts of colors, including red, silver, and fawn.

Have you ever looked at the optical illusion drawings, where you have to say which figure is in the foreground and which is in the background? Some people see the image one way, and some another. Markings can have the same quality. Because white stands out, we often speak of its position rather than that of the color. We might say, "White extends up the leg." In fact, that's not what happens at all!

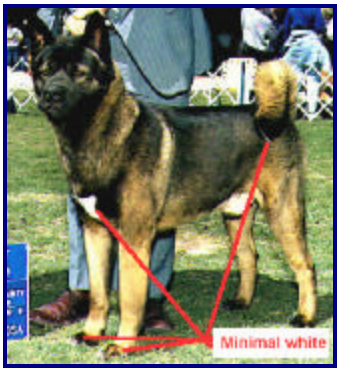
At the beginning of embryonic development, the melanocytes of the neural crest appear. These help form pigmented structures in the body. They spread out from the base of the brainstem, moving outward and down, and wherever they go, pigment is produced in the hair shaft. If their progress is stopped, through either a mechanical or genetic means, past that point, the hair will have no pigment. It will be white.

While determining exactly what coat color we're looking at can be confusing, white markings are obvious, a characteristic making them easy to study. Experimental breedings to identify modes of inheritance were being done long before modern genetics began explaining what was happening.

So, please keep several points in mind as you read this discussion. First, comments on the behavior of the marking pattern are directed to a continuum of dogs rather than one individual. In other words, “white progresses up the leg” really means that as the amount of white increases from one dog to the other, this is how it appears. Second, saying that white is a color or that it moves is a convenience of discussion. In fact, white is the absence of color and its distribution is the result of the extension or inhibition of color. Third, many of the illustrative photos in this discussion have been "painted" by a computer program. These are obvious because the texture is different and are intended for your reference, not as a demonstration of computer technique. An interesting side issue is whether the same dog with different marking patterns appears to have different body proportions--but that's another subject!

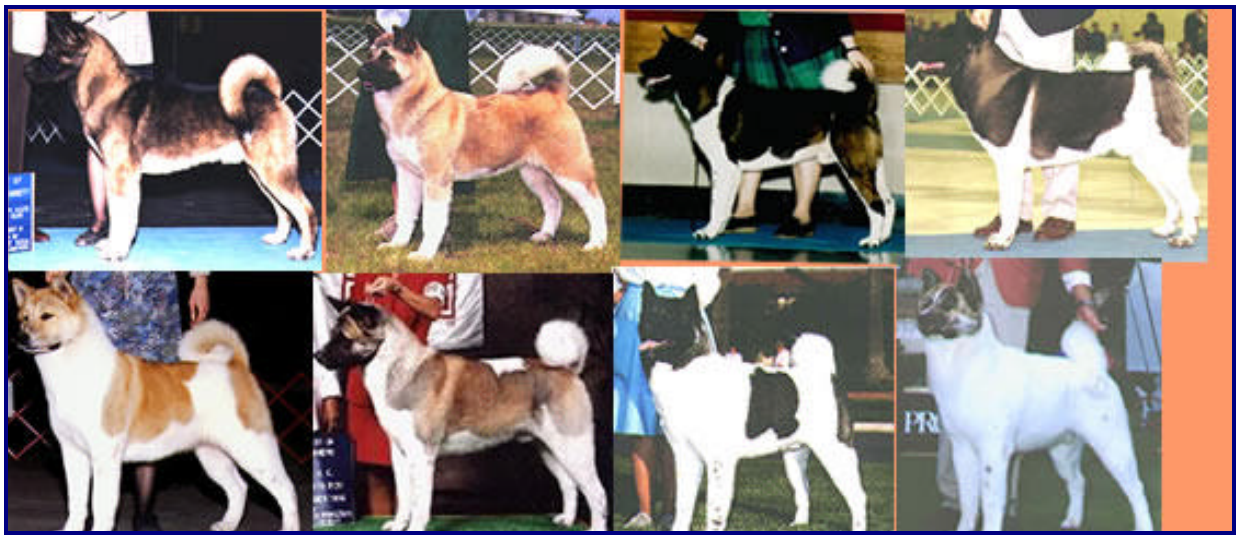
White Markings

As you look at white markings patterns, you'll the white progresses in a regular pattern from one dog to the next. It begins with a few hairs on the chest, belly, and extremities, even if it's just a few hairs. From this minimal amount, white extends upwards and around, except that chest markings may move under the belly, up the chest, or both.



If the dog has only a little white as does the one on the right, it will be on the breastbone, front and rear toes, and/or the tip of the tail. Add a little more (actually you are subtracting color, but that's a technical point), and it is above the paws, sometimes higher on the front than the back; a bigger spot on the chest that tends to move up the neck; and moving towards the base of the tail with more white on the underside than the top.

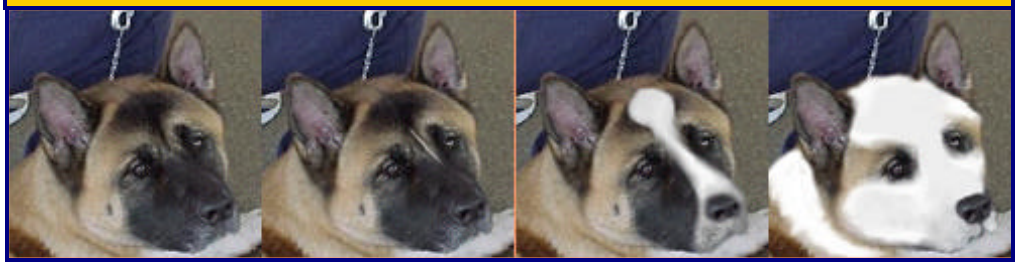
As the white increases further, it divides the dog into thirds, leaving color island on the head, body, and rump. White moves up the chest and around the neck forming a collar, up the sides from the belly forming a saddle, and up the loin area from the rear legs and belly, separating the rump which may end with a white tail.



Head Markings

White markings also have a regular progression on the head (shown below). The minimal is a very thin, white line that runs from the upper third of the muzzle, up the stop between the eyes to the start of the furrow. This blaze may be only a few hairs wide as you see on the first dog on the left. As it begins to widen, it also runs further up the head. Nosebands are commonly seen with moderate blazes. Minimal blazes begin at the front of the muzzle upward to the eyes, but large ones may also run to the back of the mouth, what I think of as a raccoon mask. Depending on the dog's genotype, they may or may not be symmetrical, so the blaze may veer to one side above the eye and/or the dog might have only half a nose band (right photo above). I should mention that the pictured dog also has a black mask over the red ground color. The mask is independent of the white markings.

The same dog with increasing amounts of white on the head.



Body Markings

On the extremities and the front of the body, again, white progresses in a regular fashion beginning with a few white hairs on the chest and toes. The latter move up the foot and then the leg while the former spreads outwards from the prosternum area.

As you can see from the photos below, white on the chest, neck, and legs is loosely correlated so that eventually, it runs together. The youngster in the center is a good illustration of a pattern that is just shy of this. From the sixth dog on, white on chest has merged with that of the leg. On the seventh, it has begun to move upwards on the neck. The last dog is an extreme white piebald, where only the head and a few body spots are colored.

White progresses up and out on the extremities, chest, and tail.

Imagine the white collar of the fifth dog moving up and meeting a wider facial blaze. This type of marking will progress to dividing the head roughly into halves. Eventually, the result will be an all- or almost all- white dog that is actually an all-over spot.

This is not the only or even the most common genetic pathway to a white dog, but it does ex-

ist. Because of the way color is deposited into the hair shaft during embryonic development, some color patches almost always remain on this type of "white" dog. These are most often seen at the base of the ears, in a spot on either side of the mid back, and at the base of the tail, just atop the croup.

Genetics of White Spotting

By convention, the gene that controls white markings is referred to as the spotting gene and the series of alleles available are denoted by the letter S with a superscript that refers to the specific allele. In order of dominance, these then are:[2]

- **S**—No spotting, solid colored dog
- **S^I**—Irish spotting
- **S^P**—Pinto
- **S^W**—Extreme White Piebald[2]

The amount of white on dogs with the same alleles in the Spotting series can vary. A dog homozygous for S^I (genotype, S^IS^I) may well have less white than a dog with the same alleles in this gene because the gene is affected by genes in other location. It may also be affected by environmental and developmental factors. Modifiers in other locations that extend or restrict the amount of color on the dog have long been theorized but not identified.

Three breeds with merling

Genes in the M (Merle) series and the C (Chinchilla) series also can produce a white dog (See, the article on noses on this website). The dominant allele of the M or Merle Series produces its own white and interacts with the S series alleles, so that white markings in merles not as predictable and can seem quite random.

Most Great Pyrenees dogs of today are marked like the dog on the left. Many are even whiter and most have much less color than the group above attending a show in the early 1900s.

The color of these two dogs is produced in part by recessives in the C series. The father is pure for white, and some fading is apparent in the son who appears to be heterozygous for white. His lightened color indicates that the allele for white isn't completely recessive to that for red.

The C series genes cause fading of both types of melanin. Just as the S series can produce a white dog that is one big spot, the C series can produce one whose color has faded totally. Because the S and C series genes are in different locations, they can both affect color on the dog.

How white dogs most commonly occur genetically varies from breed to breed. The white of Great Pyrenees, for instance, is clearly from the S series as you can see from the above

photos, where tweedy color remains on the ears.

White Akitas and German Shepherd Dogs, however, are most commonly from fading. Wherever the coat color would be strong on these dogs, some light buff or biscuit color can be seen, especially when the dogs are wet. Usually, this is about the base and rims of the ears and along the back, especially pronounced when the dog has a dorsal stripe (strip of darker color running along the spine) or a saddle marking (like a German Shepherd's) that would have been black rather than red.

One distinction between white resulting from the C series versus that from the S is that in the latter, the white is usually the same shade of white all over the dog; whereas, C series whites have shadings so in the same dog you may see buff, light strawberry , ivory, cream, and/or champagne. The restriction of color by the S series gene is usually more complete, although this does not always hold true. I've noticed that my red Akitas often have more yellow in their white markings than do those of other coat colors.

Arctic or sub-Artic Spitz breeds also have a special adaptation to their environment. The tips of the hairs are open like straws, so that sunlight can pass through the hair shaft to the skin. A tiny area at tip of the hair is unpigmented and also clear, so that it glistens as if it were tipped with cellophane. Samoyed coats are like this, and while it is most common on white hair, I've seen it in the colored body coat of Akitas.

Akita—SS

The Solid (SS)

A dog that is homozygous (both alleles in the gene pair are the same) for solid color has very little or no white on his body. This is the most dominant pattern in the S series and is the only allele available for some breeds, like the Labrador Retriever. A few white hairs on the chest or a few on the feet might be present in an SS dog but those are due factors other than the S series genes.

I've never seen an Akita without white hairs somewhere, but I've been told they exist. I suspect their presence is to outside the often-postulated outside modifiers. These may act on all white to make it extend further, so that an SS Akita might have considerably more white than an SS Rottweiler, Belgians, German Shepherd, Doberman, or Rottweiler to name a few.

Corgis and Malamutes are among breeds that maintain correct Irish spotting by restricting the amount and location of white markings

Irish Spotted (S^IS^I)

The next most dominant pattern is named for research subjects, Irish rats. Irish spotting, as the allele is called, is denoted as S^I. This common pattern has symmetrical markings with regular margins, appearing on some or all of the head, neck, legs, belly, tail, and chest. Breed standards that prohibit white on the body or restrict the amount of white on the dog represent an attempt to maintain a gene pool that is either S^IS^I or SS^I (SS will also occur),

The "eagle" design on this bitch's chest is frequently found with Irish spotting.

On Irish spotted dogs markings do not extend into the body except perhaps at the bottom of the belly. Collars are more common in some breeds than others, but they are restricted to the neck above the withers. Examples of Irish spotted dogs are Boxers, Alaskan

Malamutes, and Springer Spaniels. A homozygous Irish-spotted dog bred to another homozygous Irish-spotted dog will produce Irish-spotted offspring of the genotype $S^{I}S^{I}$. Modifiers will also affect how much white appears on the dog, so that one dog may have white socks and a star on his chest while another may have white to the elbows and a white bib along with a collar, a noseband and blaze.

Two Pinto Akitas

Pinto ($S^{p}S^{p}$)

The line between a pinto and an Irish-spotted dog isn't always clear. Modifiers may cause excessive white on a dog that is pure for Irish spotting and may cause less white on a dog pure for pinto. Typical of the homozygous pinto ($S^{p}S^{p}$) are:

- White traveling into the body coat.
- Irregular, jagged margin
- Asymmetry.

Typical pinto

Note that the color is independent of spotting. The dog can be black, silver, gray, fawn, red, etc. It can even be affected by another marking pattern, as you can see here with this brindle pinto.

The color progression tends in pintos tends to divide the body into thirds with white crossing the neck and then moving up the neck and down the back as well as moving up the loin. This strip may be quite broad on the side and tends to narrow over the back. It may extend up only one side, and legs may have differing amounts of color. Most have collars and some incursion of white into the color on the loin. Classic pinto markings divide the color up into patches, although the impression is always of a colored dog with a lot of white.

Pintos with modifiers that restrict color may have bandit-mask head markings, a collar that extends up to the head and down the midline of the back and body color broken into patches. Those with modifiers that extend color may have an almost-blanketed back (above right). Still, white incursion occurs into the body, although it may be minimal. Pinto marking patterns display great variety than Irish Spotting. The Akita standard defines pintos as having evenly placed head markings and color over a third of the body, a pretty accurate description of the minimum amount of white on a pinto as well as the typical placement of spots.

Piebald Akitas are often referred to as "*hooded*" because in this breed, color on the head is quite persistent.

Pinto is recessive to S and S^{I}; however, a homozygous pinto bred to a homozygous pinto ($S^{p}S^{p}$ x $S^{p}S^{p}$) will only produce offspring of the $S^{p}S^{p}$ genotype. Granted, different modifiers that might be inherited can result in a range of patterns, but they will be clearly identifiable as pintos. The two dogs pictured on the left are distantly related to my own Akitas yet I still get this marking pattern consistently. Compare them to the black one on the above right or those on page 3, and you can see that it is reliably inherited from one generation to the next.

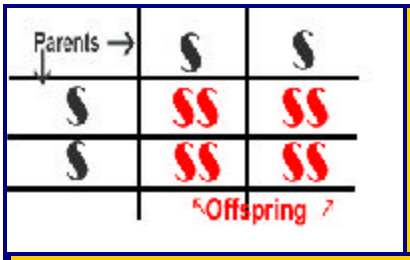
The same dog with different markings. From the far left: Solid (SS), Irish Spotted ($S^{I}S^{I}$), Pinto ($S^{P}S^{P}$), and Extreme White (Piebald) ($S^{W}S^{W}$). This dog should be assumed to have few if any modifiers to the spotting gene.

Extreme White Piebald ($S^{w}S^{w}$)

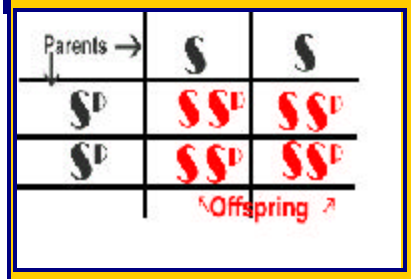
The last of the alleles in the spotting series is the extreme white, which is referred to in this document as piebald. This allele, designated as S^{w}, severely restricts the amount of color migrating from the neural crest to the extremities and may eliminate it altogether. The pattern is quite common in many spaniels and hounds and occurs often in what are referred to as parti-colored dogs, such as the Chin and Papillon[3].

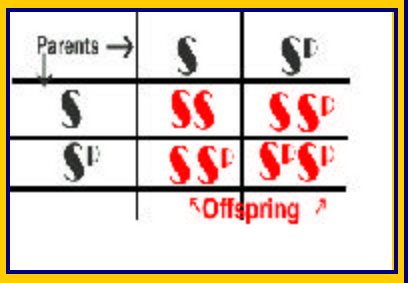
Color tends to remain around the eyes and ears, on either side of the spine at the middle of the back and at the base of the tail. Both the White Bull Terrier and the Great Pyrenees are examples of dogs that are homozygous for this allele or $S^{w}S^{w}$

The piebald gives the impression of being a white dog with colored markings; whereas, the impression of a pinto is of a colored dog with white. When you breed a piebald to a piebald, you get Piebald, which are SWSW. Taken through enough generations, some dogs resulting from



This chart shows what you might expect from the breeding of two dogs of identical genotype. Each of the offspring receives one allele from the mother and one from the father. In this case, since the only allele available is S, the offspring all have the same SS genotype as the parents. This would be the case in a breeding of two Labrador Retrievers, for instance





In these two examples, the possibilities increase. On the left is the crossing of two homozygous dogs, one pure for Solid and the other pure for Pinto. Since only one allele is available from each parent, all the offspring have the same genotype in this series, although the influence of other genes as well as environmental factors may mean they do not look exactly alike. They are all heterozygous with a dominant gene for Spotting and a recessive one for Pinto. This scenario produces 100% heterozygosity.

When heterozygous dogs are crossed, the genes sort back out, so that 25% of the offspring are SS, homozygous or pure for Solid; 25% are homozygous or pure for Pinto, and 50% are homozygous Solid and Pinto.

As you can see, once allelic variation is possible, the likelihood is that heterozygous dogs will outnumber homozygous ones. Once more than two alleles are available, however, heterozygous dogs won't have the same genotype.

pure piebald breedings will be white. Again the presence of modifiers may allow more or less color on the dog.

THE HETEROZYGOUS SPOTTING PATTERNS

Obviously, when multiple alleles of a gene are present in a breed, unless a preference for one allele over others exists, heterozygous dogs (those where the alleles of the gene pair are not identical) will outnumber the homozygous ones.

You can see this by looking at the possibilities with the square demonstrated on the previous page. The top and side slots have one of the two alleles each parent can contribute. Combining these allows you to easily see the genotype possibilities for the offspring.

Although the S series has a dominance hierarchy, none of the S series alleles is completely dominant over any of the recessives. Heterozygous dogs show some blending of characteristics. In breeds where allelic variation is limited, where perhaps the only common alleles are for solid or Irish Spotted, the appearance of puppies is somewhat predictable. For instance, a Solid bred to an Irish-spotted dog will produce a dog with white but usually less than on the IS parent.



The left and center dogs are SS^{I}. The difference in the amount of white and its distribution can be due to many factors, including white modifiers. Both have less white on them than the Irish Spotted dog on the right.

As the number of available alleles increases, the predictability decreases because different genotypes can produce similar markings.

The experimental breedings of beagles done by Dr. Leon Whitney a veterinarian at Angell Memorial Animal Hospital in New York, demonstrated quite clearly that when multiple alleles of the S series are present in a gene pool, predicting genotype from the dog's appearance isn't always possible.



While factors outside the action of the S gene influence the amount of white that appears within the same allelic pattern, they generally do not affect its placement. As a result, the SSI dog with modifiers that inhibit the extension of color might end up with as much white as one homozygous for Irish spotting that has modifiers that extend the amount of color.

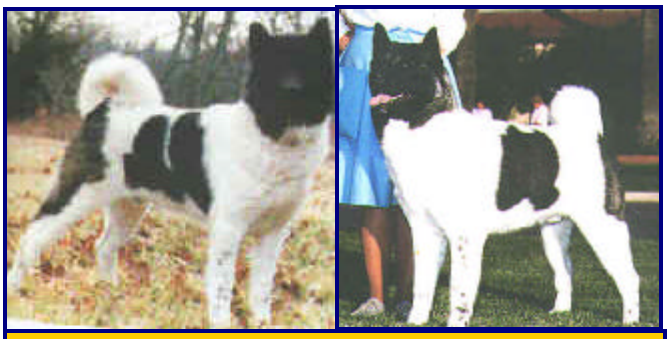
When you introduce more than two alleles, none of which are completely dominant over the others, identifying the genotype from the appearance becomes more difficult still. The three dogs above have patterns typical of Irish spotting. The only way to be sure of the genotype is by

looking at puppies from a number of breedings. The one most likely to be a true S^IS^I is the one on the left because her markings have not only symmetry but also smooth margins. White on the legs of the center dog is uneven and jagged. She could well be SS^P. The amount of white and broken color (uneven margins where the color and white meet) strongly hints at the presence of an S^P allele in the third dog (right). You can't see it in the photo, but on the other side, he had a white splotch on his hip. Still, he is more solid than patched, and his tail and legs are symmetrical and even, which speak to the presence of S^I.

Breeds that have only Irish spotting will often penalize the incursions of white into the body that is present in the third dog. This is an empirical recognition of the blending quality of these alleles, and is present in their standards to prevent the appearance of pintos. Likewise, breed standard for dogs that should be solid will either not allow white at all or will severely restrict it to less than appears on any of the dogs on this page.

The wild card in the bunch is the Piebald allele The heterozygote for S^IS^W may well appear to be pure for pinto. Some of the clues that the phenotype (what the dog looks like) and genotype (what he actually carries genetically) are not the same are:

- an uneven distribution of patches
- marked asymmetry (head and/or body markings)
- less than a third of the body colored
- Presence of white haws and a white third eyelid.



To see why this dog is S^W, you need to look at both sides. Although he might have color over 1/3 of his body, it is most certainly not evenly placed. The other allele could be either S^I or S^P.

Likewise, the S^PS^W dog will have more white than a pinto normally has and may also have an even greater asymmetrical distribution of color on the body. Modifiers that extend color, however, may make this genotype indistinguishable from a dog pure for pinto. They can do the same thing in the case of the SS^W.

SPOTS OR NOT

Selecting for a particular genotype in a breed is relatively easy if the S^W allele isn't present (and you're not dealing with merles). As a rule of thumb, when the Piebald allele isn't a possibility, white markings of the puppies will fall somewhere in between that of the parents.

The Piebald allele, however, can produce puppies with much more white than either parent. If you want to, the quickest way to correct the color loss produced by this allele is to select a breeding partner that is clearly SS. Most of the offspring from this type of breeding will fall into the continuum from Irish spotting to pinto. Even if Piebald result from this type of breeding, they are more likely to have a greater expanse of color than the Piebald parent.

Likewise you can achieve more white by choosing a dog with alleles from the less-colored recessives. While using a Piebald might seem the fastest way to obtain more flash, you must consider the trade-off. When you introduce the alleles for Piebald even though the immediate offspring will fall somewhere in between, you will eventually see Piebald back in subsequent generations. In some breeds, its influence is irrelevant, but in others, where white is restricted,

The black male here is a son of the dog on the previous page. He and the red female are parents of the four in a row below. The three on the left are examples of blending; they have more white that their mother and less than their father, whose sire is the dog pictured from two vantage points

When you compare the far left dog with is sister in the adjacent photo, you can see the difference in the regularity of their markings. His have jagged edges and hers are very smooth. White extends into the body color of the brother. If you extend the white of the diamond on his back and the line coming up his loin, you can see he got a good start on a marking pattern very like his paternal grandsire (pictured on the previous page). This dog might well be SS^W in genotype, and so may his cousin pictured below right.

She is another generation removed from the sire and grandsire, but you can see the S^w allele is still present and influencing her markings. The pattern is very similar to her great grandsire's, Keeping more color on one side than the other. Her sister is all white on one side of her body and completely colored on the other , and their brother is very similar to his cousin, the dog above far left. He has the same spot on the back but slightly more white on one side and virtually identical markings on the other.

you'll want to think long and hard about introducing this allele into your breeding program.

More white will come from breeding to either an Irish spotted or a pinto, but the results will certainly not be so dramatic as with the Piebald. Further, if the Irish Spotted appearance actually comes from the SS^W, you can actually reduce the amount of white on the progeny because some of them will be SS with little or no white at all. If the partner is pure for S^I, however, you will end up with puppies more white than the one parent but less than the other.

Absent the piebald gene, you will never get more color by breeding dogs without it together. That is SS dogs just produce SS progeny. In pintos and Irish Spots, you may get variation in the patterns but the amount of white will be fairly consistent with that of the parents.

You will not get a pinto by breeding two dogs homozygous for Irish Spotting (S^IS^I) nor will you get the "tuxedo" markings of the Irish spotted dog from breeding pure pintos (S^PS^P). So, if you have a litter of pintos out of a Solid and an Irish Spotted Dog, you probably are using an Irish Spotted dog whose genotype is actually SS^W.

Likewise, pintos of the S^IS^W or SS^W genotype bred together will result in a litter with Irish spot, pintos, and Piebald. Remember that genetic predictions are based on large sample sizes, so you may not see this in a single litter although it will happen more often than not.

Obviously, since I breed Akitas, most of my examples are these dogs, and certainly this discussion is slanted towards their breeding dynamics, but the S series gene behaves similarly in all breeds. In common with many hounds, Akitas have all alleles in this series available in their gene pool, but even in breeds with limited possibilities, knowing something about how these genes affect white markings and how they interact should help you breed to obtain what you want. Also, please remember that white in the coat is influenced by other genetic pathways, like the Merle gene, so if you have these in your breed, you will have to take them into consideration.

I hope this helps you understand a little more about how the spotting genes affect color and how they are inherited. If you have observations, photos, or questions, please feel free to contact me.

Notes

[1]Actually, pigment in the hair is also affected by the presence or absence of enzymes. This can result in color being absent, altered, or faded. The actions of the S series genes are thought to occur from early cell-disablement during embryonic development; whereas, enzyme effects can and do occur in later stages of development. White markings on a puppy don't really change much in terms of distribution or size, although what may seem like a huge blaze on a puppy can be nothing more than a few white hairs on a large adult.

[2]Genetic notation assigns a letter to denote specific genes and superscripts to identify the various alleles. Like colors in dog breeds, though, sometimes these notations don't agree. The most dominant allele is usually identified with a capital letter. Recessive alleles are noted by the capital and a superscript. The ones used here are commonly accepted, except that S^{ew} is sometimes referred to as S^{sp}.

[3]This allele has long been referred to as an "extreme white" or "extreme white piebald." Actually pinto and piebald are synonyms, but for the sake of convenience and to save a lot of extra typing, I use the term piebald to refer to this marking pattern.

[4]Talk about confusing. Parti-colored means "two" colors according to the dictionary. However, all parti-colored breeds have a ground color, like red or black and white, which isn't really a color. The second color of the "parti" is white, which isn't really a color. Further, many of these breeds also have a "tri-colored" variation, which is a black with tan points. When the definition of the color states, "parti-colored," it's easy to see that someone might consider the tri-color improper, but this, alas, is not at all the case. The tan or rust is actually a marking, just like the white and isn't considered as part of the base or ground color. Further, breeds like German Shepherds and Dobermans are never considered to be "parti-colored" despite having just two colors.