American Paint Horse Association's Guide to

Coat Color Genetics

Contents

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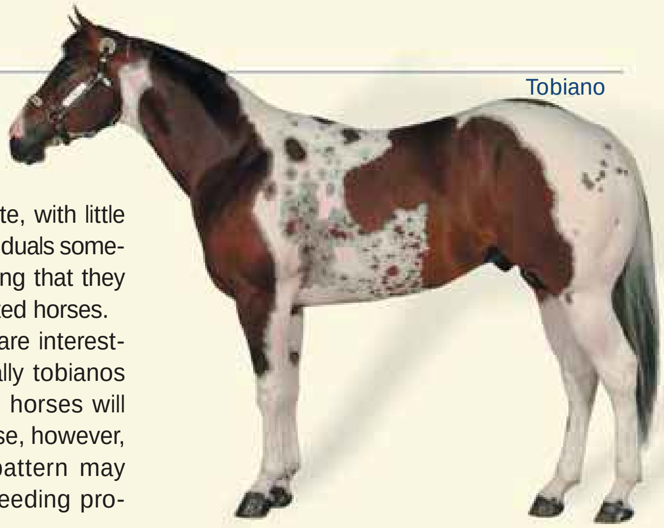
The Genetic Equation of Paint Horses

Paint Horses are unique from most other breeds because of their spotted coat patterns. Their base coats are the same colors as those of other breeds, but superimposed over these colors are a variety of white spotting patterns. The three patterns recognized by APHA are tobiano, overo and tovero.

The ability to recognize these patterns and understand the genetics behind them is essential for Paint Horse breeders. Being knowledgeable about coat patterns helps breeders and owners accurately describe their horses. Understanding the genetics that produce these patterns helps breeders increase the proportion of spotted horses in their foal crops.

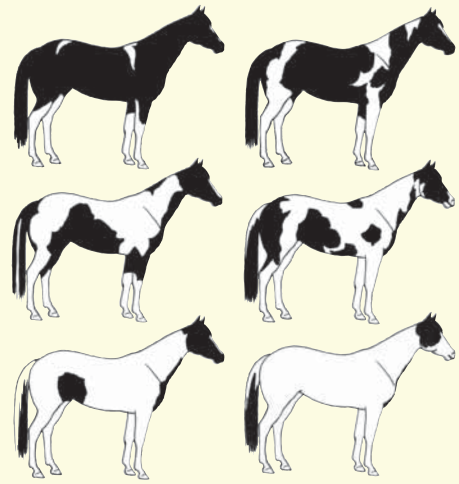
Following are descriptions of the major Paint Horse spotting patterns.

Tobiano



Tobiano

Typical Tobiano Patterns



The first major pattern is tobiano (pronounced: tow be yah´ no). The name tobiano is itself unusual and has an interesting history. In Argentina, it is the habit to name unusual colors after horses or people who connect the color to a specific event or individual. In the case of the tobiano horse, that event was the rescue of Buenos Aires by Brazilian General Tobias during a military action that took place in the 1800s. Many of the troops with Tobias were mounted on tobiano spotted horses from Brazil.

This color pattern had occurred only rarely in Argentina before this event (and was lumped in with all the other spotting patterns as overo), but became firmly associated with Tobias and his troops afterwards, ending up taking his distinctive name.

The tobiano pattern occurs in many breeds worldwide. It is common in pony breeds, some draft breeds and even occurs in some of the warmblood breeds. In some breeds, tobiano spotting disqualifies a horse for inclusion in the registry—this in spite of the fact that the trait may have been present in some of the foundation horses from which the breed sprang.

The characteristics of tobiano

A tobiano's feet and varying portions of its legs are usually white, the head usually has no more white than normally found on a non-spotted horse, and the spots usually cross the topline somewhere between the ears and tail.

Tobiano spots are typically crisply delineated from the colored areas and have a vertical arrangement. A tobiano's eyes are usually dark.

These horses can vary from quite dark, with only small amounts of white, to quite white, with little remaining color. The darker individuals sometimes have so little white spotting that they may be confused with nonspotted horses.

Minimally spotted tobianos are interesting because they are essentially tobianos that did not get spots. These horses will produce just like a spotted horse, however, and that is the reason the pattern may "mysteriously" appear in a breeding program for solid horses.

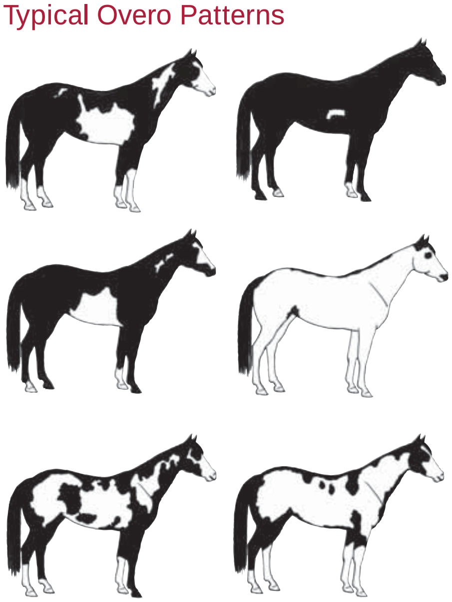
A clue to identifying these "nonspotted tobianos" is that they tend to have a large amount of white on the lower legs but little white on the head. This combination is otherwise rare because it is usually the case that non-spotted horses with a great deal of white on the head have a large amount of white on the feet, and vice versa.

In the middle portion of the range of tobiano spotting there is no problem telling tobianos from other Paint patterns. They are quite distinctive. At the whitest extreme, many tobianos are all white except for a colored head. This pattern is sometimes called "Moroccan," although the connection to the country of Morocco or its horses is tenuous at best.

Other details of the tobiano pattern include the fact that on many of these horses, the border between the white and colored areas consists of pigmented skin overlaid by white hairs. The result is usually a bluish cast to the border, almost like a halo or a shadow. Another peculiarity of some tobianos is the presence of "ink spots" in the white patches. These spots are small and generally round in shape.

Overo

Typical Overo Patterns



The second generally accepted type of spotting is overo (pronounced: oh vair´ oh). Knowing the history behind the term overo may be helpful in understanding the somewhat confusing situation of having multiple patterns with one name.

Overo is a Spanish word, originally meaning "like an egg." In this case, it refers to speckling or spotting. Long ago, in South America, the term overo was used for all the various spotting patterns in horses: tobiano, overo (all three types) and also the blanket and leopard patterns typical of Appaloosas. In Argentina, the word overo is still used to describe all the different spotting patterns other than tobiano.

In the United States, overo is usually used to mean "Paint, but not tobiano." This has resulted in the lumping together of three different spotting patterns under one name, and the result can be confusion in breeding programs.

The term overo covers three genetically distinct patterns: frame overo, sabino and splashed white.

Frame Overo

The name "frame" refers to the usual appearance, which is of white patches centered in the body and neck, and framed by colored areas around them.

The usual frame pattern has a horizontal arrangement and does not cross the topline, as does tobiano. The overo's head is usually quite extensively marked with white and the eyes are commonly blue.

The feet and legs of frame overos are usually dark, although white feet and minor

Frame Overo

white leg marks are as common on frame overos as they are on nonspotted horses. The white areas on frame overos are usually crisply and cleanly delineated from the colored areas, although some have a halo or shadow of pigmented skin under white hair directly at the boundary.

The frame overo pattern occurs in a limited range of horse breeds. It seems to appear only in breeds that have Spanish ancestry, including the Paint Horse.

The genetics of frame overo has only recently been documented. Frame overo behaves as a dominant gene. It is common to mate frame overo horses to nonspotted horses, and about half of the resulting foals are spotted.

On many occasions, though, there are records of frame overos being produced by two nonspotted parents. This is typical of a recessive gene, and it is not logical to have both a recessive and a dominant control over the same pattern.

Some of these horses are genetically frame overo, but have failed to get a body spot. They are essentially very dark frame overos—so dark that the spots are all gone from the body. They still have the gene, however, and can still produce frame overo-spotted offspring.

At the whiter extreme, frame overo is the pattern most closely associated with Overo Lethal White Syndrome (see page 16).

Recent characterization of the gene responsible for lethal white foal syndrome has confirmed that foals with two doses of the lethal white gene are white and die soon after birth from gut innervation abnormalities. Horses with only one dose survive.

This documentation is important for Paint Horse breeders. With DNA tests now available to identify the lethal white gene, it is possible to test breeding horses. Those with the gene can be mated to horses without it, resulting in foals that are about half carriers and half-non-carrier foals, but avoiding completely the production of lethal whites.

Sabino Overo

In literal Spanish, sabino (pronounced: sah bee´ no) means pale or speckled. In Europe, and increasingly in the United States, sabino is used to describe a unique and interesting pattern of white spotting in horses.

Sabino horses usually have four white feet and white legs. The white usually extends up the legs in ragged patches, and then extends onto the horse's body from the belly. The head is usually fairly white and the eyes are commonly blue.

Many sabino horses have partially blue, partially brown eyes. Flecks, patches and roan areas are common on sabinos, in contrast to the frame overos, which are usually more crisply marked.

Sabino occurs in a large number of breeds worldwide, including Paints, Thoroughbreds and Clydesdales. The pattern is commonly the cause of spotted foals that appear in breeds that frown on them, such as the British pony breeds and the Quarter Horse.

The sabino pattern is also a great imitator, and some of these horses are nearly perfect mimics of tobiano or frame overo. When the sabino pattern is minimally expressed, the horse usually has four white socks and a blaze. Usually there is some betrayal of the fact that these are not the usual white marks on horses, due to some ragged edge or long, narrow extension up the leg.

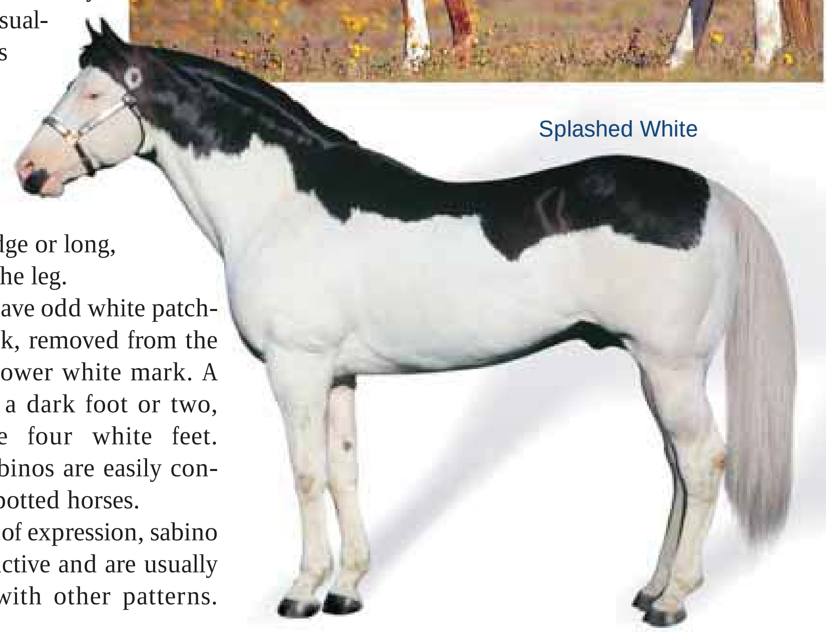
Some sabinos also have odd white patches on the knee or hock, removed from the main portion of the lower white mark. A few sabinos do have a dark foot or two, although most have four white feet. Minimally marked sabinos are easily confused with truly nonspotted horses.

In the middle range of expression, sabino horses are fairly distinctive and are usually difficult to confuse with other patterns. Most have white extending from the belly and have roan and flecked areas in addition to white areas. However, a few will be nearly entirely roan without patches of white. These could be confused with true roan horses, although the facial and leg white usually gives these away, and they do not have dark heads typical of true roans.

Another extreme is the sabino that is patched, but not roaned. Sabino horses can easily be confused with frame overos, especially if they have one or two dark feet. Most patched sabinos have smaller, more ragged patches than is typical of frame overos. In some cases, it is impossible to distinguish between horses that are truly sabinos and the frame overos that also happen to have white markings on their feet in addition to the frame overo pattern.

The whitest of the sabinos are nearly or entirely white. Some retain color only on the ears and others are white all over. One of the whiter ranges of expression includes color on the ears, chest and tail base. These are the Medicine Hat Paints that were prized

Sabino



Splashed White

by the Native American tribes of the Great Plains. Most sabinos that are largely white are very speckled and roaned, and some can be confused with Appaloosas.

Some sabinos are quite white and survive, which points to this being entirely different from the overo that results in lethal white foals when homozygous. Sabino, by itself, is not associated with lethal white foals.

Splashed White Overo

Splashed white is the least common of the spotting patterns, although it is increasing in frequency as breeders use more splashed white horses in their breeding programs.

The pattern usually makes the horse look as though it has been dipped in white paint. The legs are usually white, as are the bottom portions of the body. The head is also usually white and the eyes are frequently blue.

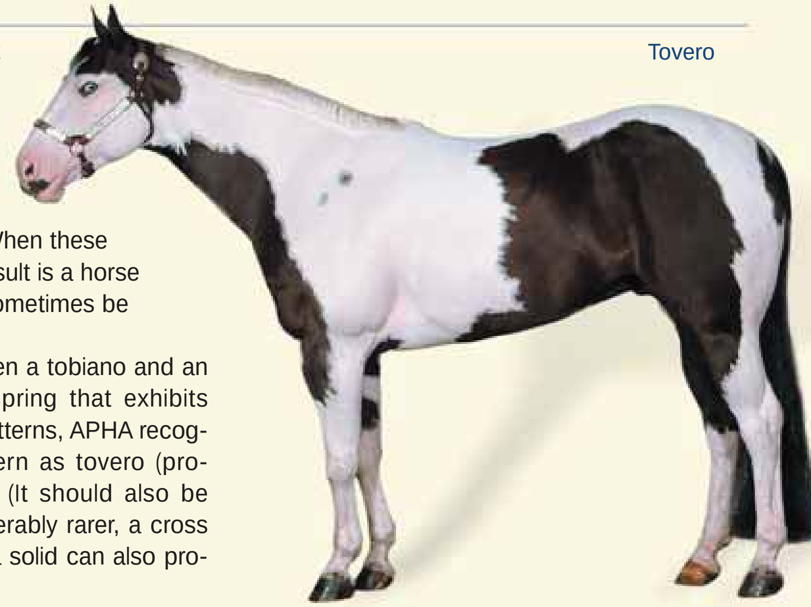
The edges of the white are typically crisp and clean, with no roaning. Some splashed whites have dark toplines, but on some the white crosses the topline.

Recent genetic evidence suggests that the splashed white pattern is caused by a dominant gene, because splashed white foals have resulted from splashed white to non-splashed white matings.

Some people have observed that many splashed white horses are deaf. This is not much of a problem if the trainer realizes the limitations of the horse in question and modifies the training program to meet the horse's special needs. Many of these horses go on to lead normal and productive lives.

Because no homozygous splashed white horses have ever been documented, researchers suspect that this is another gene that cannot exist in homozygous form. If this is true, the loss of hearing probably occurs early in gestation rather than at term. Because of this, the best strategy for producing splashed white horses is to mate them to horses without the splashed white pattern.

Tovero


Tovero

While each of the Paint patterns—tobiano, frame overo, sabino and splashed white—can mark a horse on its own, many horses sport combinations of these. When these patterns combine, the result is a horse with a pattern that can sometimes be difficult to classify.

When a mating between a tobiano and an overo produces an offspring that exhibits characteristics of both patterns, APHA recognizes the resulting pattern as tovero (pronounced: tow vair′ oh). (It should also be noted that, while considerably rarer, a cross between a tobiano and a solid can also produce a tovero.)

In this instance, the combined patterns pick up the white from each of their individual components. They are then genetically mixed to create a combination pattern on the horse's coat. For instance, a horse with a frame overo sire might inherit a white framed area on each of its sides. If the horse had a tobiano dam, it might inherit a white, blanket-like pattern that covers its entire back. The result might look something like the tovero shown on this page, which is mostly white.

Many of the combinations are called tovero because most are tobiano plus one of the other patterns.

Although the word tovero has been a part of APHA's vocabulary from the onset of the registry, it remains to this day somewhat of an ambiguous term.

Just as there are extremes within the tobiano and overo coat patterns—from mostly dark to mostly white—so are there extremes within the tovero pattern.

At one end of the spectrum—the mostly dark one—are those toveros that closely resemble tobianos except for their face markings, which show an overo influence. At the opposite end—the mostly white one—are those toveros whose only dark pigmentation might appear around the ears, eyes or chestnuts.

In between those two extremes is the horse that can be termed the "typical" tovero, distinguished by the four basic coat characteristics shown below. Typical toveros have:

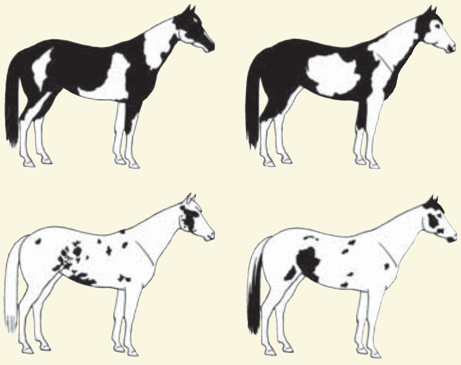
1. Dark pigmentation around the ears, which may expand to cover the forehead and/or eyes.
2. One or both eyes blue.
3. Dark pigmentation around the mouth, which may extend up the sides of the face and form spots.
4. Chest spot(s) varying in size. These may also extend up the neck.
5. Flank spot(s) varying in size. These are often accompanied by smaller spots that extend forward across the barrel and up over the loin.
6. Spots, varying in size, at the base of the tail.

Identifying the tovero pattern is not an easy task. During the Association's early years, some toveros were mistakenly classified as tobianos or overos. In defense of the people who misclassified those animals, two points must be made. First of all, during the registry's infancy, the pattern was much rarer than it is now. There simply weren't enough toveros being registered to establish a workable profile of what their physical characteristics were.

Second, it had not yet been firmly established how these horses would breed—what patterns they would produce that would prove or disprove their classification.

More than 40 years of Association growth has alleviated both of these conditions, and the APHA Registration Department now has the situation well in hand.

Typical Tovero Patterns



Understanding genes, simple dominance and the Punnett Square

Before you begin breeding for color, there are a few basic genetic concepts you should understand. Though genetics can seem daunting at first, by understanding genes and simple dominance, and knowing how to use the Punnett Square, any horse owner can plan their color breeding program with confidence.

Genes

Genes are the basic units of inheritance. Genes are linked to form a chromosome similar to the way pearls are threaded together to make a strand. Each particular species has a specific number of chromosomes (64 for the horse), and each chromosome has a duplicate mate.

Each gene on the chromosome has a mate, or allele, in exactly the same place, or loci, on each of the chromosome's matched pair. Basically, each pair of genes codes for a specific job. A pair of genes can control something as obvious as whether or not a cow will have horns, or it may be as subtle as coding for a specific portion of a bimolecular molecule, or controlling the function of other genes.

During the cell division in which one cell divides into either two egg or two sperm cells, only one member of each chromosome pair goes into each new cell. This provides every sperm and egg with only one copy of each gene. Upon fertilization, every chromosome, and therefore every gene, is reunited with its corresponding mate to create a unique individual.

In coat color genetics, one of the goals is to identify the possible genes in the parents and predict the probability of coat colors in their offspring. To help keep track of the genes whose function is thought to have been identified, geneticists assign a letter of the alphabet to the pair.

Understanding Simple Dominance

Gene interactions can be complex and confusing. Fortunately, some genes adhere to a relationship based upon simple dominance. Within this framework, there are two basic expressions of the same gene—one dominant, one recessive. The recessive form of the gene is submissive to the dominant form. The recessive gene is expressed only when both copies of the gene are in the recessive form.

Capital letters usually indicate dominant genes. Lowercase letters indicate recessive genes. This system is complicated by the use of superscripts. For example, the dominant form of the gene creating palomino is CC^{cr}. The recessive is referred to as C.

Regardless of the letters used, each individual obtains one copy of the gene from each parent. In the system of simple dominance, this pairing occurs in one of three ways:

Homozygous dominant—In this instance, both alleles are in the dominant form, as indicated by a capital letter, for example, AA. The color determination is under the control of the dominant gene, and all offspring created from this individual can only receive a copy of the dominant gene.

Homozygous recessive—Here, both copies of the allele are in the recessive form, for example, aa. The color determination is under the control of the recessive gene, and in many cases this means there is no expression.

For example, the recessive form of the gene for roan (Rn+), palomino (C), gray (g), tobiano (to) and dun (Dn^{nd}) allow the body coat to be expressed by the dominant gene.

Foals with a homozygous recessive parent will receive one copy of this parent's recessive gene.

Heterozygous—One member of the pair is dominant, while the other is recessive, for example, Aa. The dominant form is in control of the expression. Offspring have a 50-50 chance of inheriting either the dominant or the recessive gene.

Using the Punnett Square

A Punnett Square is a simple way to predict the possible genetic combinations from the mating of two individuals. To use this tool, first draw a square. Across the top, list the gene combination of the stallion. Down the left side, list the gene combination of the mare. Then, bring one value from each parent into the corresponding box within the square.

Stallion (aa) Mated to Mare (Aa)

		Stallion	
		a	a
Mare	A	Aa	Aa
	a	aa	aa

Each box represents a 25 percent chance of a specific gene combination. In the example above, foals from this cross have a 50 percent chance of getting the Aa combination and a 50 percent chance of getting the aa combination.

Breeding the Tobiano Paint

The tobiano pattern is under the control of the dominant gene TO. The most common genotype for the tobiano is the heterozygous TOto. Fifty percent of the foals produced from a heterozygous tobiano should have the tobiano pattern.

Fortunately, the homozygous tobiano TOTO exists. Having two copies of the tobiano gene does not increase the amount of white on the horse, but individuals carrying this rare genotype can often be identified by small dark hairs scattered in clusters in the white areas of the coat. Not all homozygous tobianos have these "ink spots" or "paw prints," nor do these markings occur only in homozygous horses. However, there is a strong association between this pattern and the TOTO individual.

Homozygous tobianos are beneficial to breeding programs due to their ability to produce tobiano offspring. Statistically, every foal produced from the mating should receive one copy of the dominant tobiano gene TO, thus creating a tobiano.

Occasionally, a homozygous tobiano mating produces a solid-looking horse. This horse carries the tobiano gene but has only limited white markings. These horses are often referred to as minimal-white tobianos.

For these horses, the tendency of the tobiano to have a dark head and white legs holds true. The head may be completely dark or have very little white on it. However, the legs will show the specific characteristics.

According to the late Dr. Ann Bowling in her book *Horse Genetics*, minimal-white tobianos have dark spots or streaks in the white markings extending up from the coronet. Also, the white extending over the hocks ends as a horizontal line.

As of this time, there has not been a case of a minimal-white tobiano that has failed to have white leg markings.

Even though these horses are registered by APHA as solid Paints, they are, in fact, tobianos and do pass on the dominant tobiano gene 50 percent of the time.

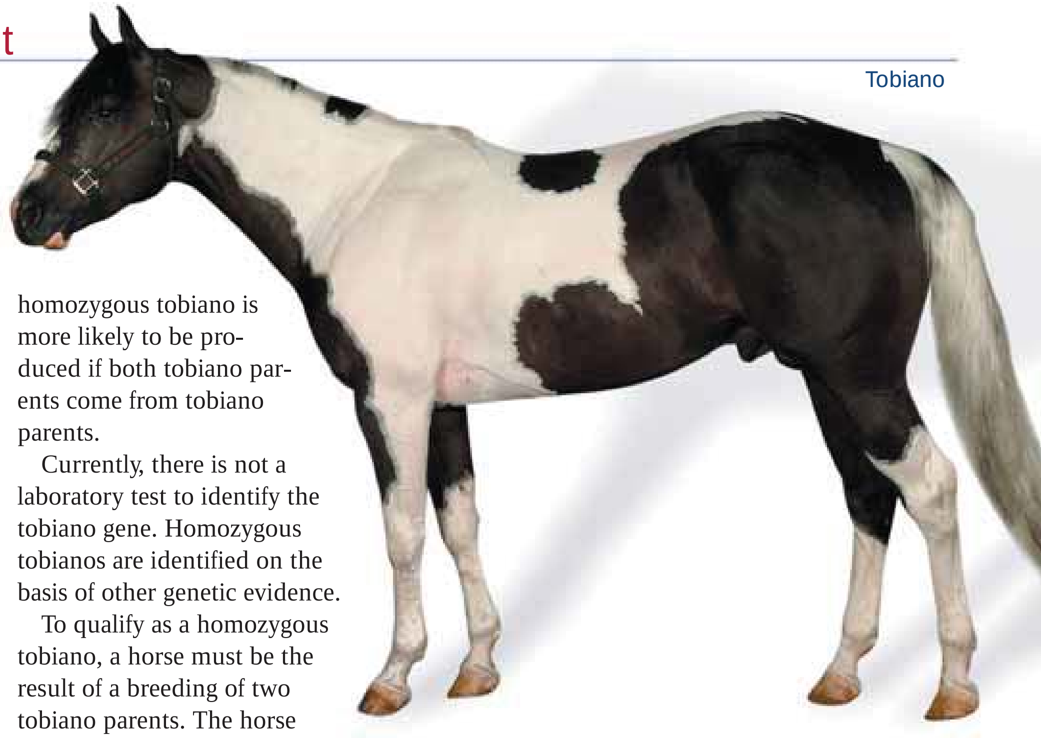
Homozygous tobianos result from the mating of two tobiano parents. According to the predictions of the Punnett Square, one out of every four foals produced by two heterozygous tobiano parents should be a homozygous tobiano.

Some Paint Horse breeders disagree with the Punnett Square projections, maintaining that the TOTO gene combination is harder to obtain. They also believe that a homozygous tobiano is more likely to be produced if both tobiano parents come from tobiano parents.

Currently, there is not a laboratory test to identify the tobiano gene. Homozygous tobianos are identified on the basis of other genetic evidence.

To qualify as a homozygous tobiano, a horse must be the result of a breeding of two tobiano parents. The horse should have a characteristic tobiano pattern, including ink spots, and a pedigree and breeding record that indicates homozygosity for the tobiano pattern.

According to the Punnett Square, a homozgyous tobiano stallion mated to a heterozygous tobiano mare should produce 50 percent homozygous foals and 50 percent heterozygous foals. No offspring should be solid.



Tobiano

Homozygous Stallion (TOTO) Mated to Heterozygous Mare (TOto)

		Stallion TO	TO
Mare	TO	TOTO homozygous	TOTO homozygous
	to	TOto heterozygous	TOto heterozygous

Determining Tobiano Homozygosity

Breeding a homozygous tobiano should produce all tobiano foals, with the exception of a rare minimal-white. A horse that produces five tobianos out of five solid mates is thought to have a 97 percent chance of being homozygous. Seven tobianos from seven solid partners increases the odds to 99 percent. Ten tobiano offspring from 10 solid mates increases the odds to 99.9 percent.

In addition, genetic marker analysis is used to try to identify homozygous tobianos. This analysis is similar to playing the game Clue. Certain facts are given, and then by the process of elimination one tries to determine which parent or parents supplied the tobiano gene. Remember, the horse must have been produced from the mating of two tobianos. Tovero parents do qualify.

The tobiano gene is linked to a gene unit comprised of the E gene (see page 12), the Rn gene (see page 17), and two other genes, ALB and GC, that code for blood proteins. These four genes lie so close together on the same chromosome that they are usually passed on as a unit to the next generation, making their presence an important clue to determining a tobiano's homozygosity.

This fact creates the opportunity to trace movement of the tobiano gene.

The ALB blood protein comes in two forms—A or B—while F and S are the symbols given to the two forms of the GC gene. A major clue to determining tobiano homozygosity is that 90 percent of the time, the tobiano gene is associated with the B form of the AL gene and S form of the GC gene.

The blood test that is currently used in the search for the homozygous tobiano determines which form of the AL and GC genes a particular horse has.

And don't forget that the expression of the E provides a color trace for the tobiano gene, as well. This means that the tobiano gene lies close to the gene that determines whether the base color of the horse is red or black—e or E, respectively. The goal is to determine which form of the E gene is linked to the TO.

(The roan gene, which is in the E Rn ALB GC unit, appears to commonly exist in the recessive form Rn+. It is extremely rare to find a roan tobiano.)

Breeding the Overo Paint

Little is known about the genetics that create overo patterns. It is commonly accepted that overo patterns are under the influence of one or more dominant genes. It appears that each of the patterns may be the result of a dominant gene, but it is also possible that there is only one gene and that gene modifiers change the pattern.

There is also some evidence that the genes that produce leg and facial markings may influence the amount of white on an overo. This appears to be true for the sabino and splashed white patterns.

The frame overo, like the tobiano, is thought to be less sensitive to these genes.

Time and research will eventually answer these questions. For now, here is what the three overo patterns seem to have in common.

All the overo patterns have a large range of expression. At one end, they appear mostly white. At the other end, a minimal-white overo may be hard to distinguish from a solid horse.

These minimal-white overos may be the reason that so many breeders think that overo appears at random from solid horses. It may also be the reasoning behind the belief that it is easier to get an overo by breeding an overo to a solid that has an overo parent. These overo breeding stocks may be minimal-white overos.

The development of a test to determine the presence of the overo gene(s) will go a long way toward sorting out this confusion.

The possibility of there being a homozygous overo does not look good. It is thought that the homozygous overo is plagued by the lethal white syndrome. Lethal white foals die shortly after birth due to lack of proper development of their digestive systems.

There have been cases of lethal white syndrome occurring from the mating of an overo to a solid. Because of this, the question becomes: Were these solid horses minimal-white overos carrying an overo gene and therefore producing a homozygous overo foal, or is there some other gene action associated with the overo that occasionally produces foals with the lethal white syndrome?

To confuse the matter further, each overo pattern has the ability to produce nearly white normal foals. This is not to say that these foals may not be plagued by some of the other problems associated with mostly white horses. There is some evidence that deafness may occur more often in nearly white horses. And with age, the pink skin around the eyes of a white horse quite often develops cancer.

In spite of the similar action of the hypothesized overo genes, each type of overo has a characteristic pattern.

Breeding the Frame Overo

Frame overos range from being nearly totally white to the minimal-white individual. The minimal-white frame overo characteristically has a lot of white on its face and a solid body with minimal white leg markings.

Regardless of the expression of the frame overo pattern, these horses produce overo foals 50 percent of the time. It has been hypothesized that the frame overo is under the control of a single gene, which is designated Fr.

Frame overos are known to produce lethal white foals. It is not known at this time whether this condition is created by a homozygous frame overo—FrFr—but the condition is highly correlated with large amounts of white on the foal.

Defining Minimal-White Frame Overo

- A great deal of white on the face.
- Solid bodies.
- Normal solid horse, minimal leg markings.

These horses may be registered as Solid Paint-Bred, but in reality they are overos and will produce overos 50 percent of the time.

Frame Overo

Breeding the Splashed White Overo

According to Dr. Bowling's work, the splashed white pattern is under the control of a dominant gene identified by the letters Spl. At this point, there has not been a documented mating of two splashed white overos creating a homozygous individual.

Defining Minimal Splashed-White Overo

- A great deal of white on the face.
- Solid bodies, perhaps with a small white spot on the belly.
- White leg markings.

These horses may be registered as Solid Paint-Bred, but in reality they are overos and will produce overos 50 percent of the time.

Splashed White Overo

Breeding the Sabino Overo

The color pattern referred to as sabino encompasses a wide range of patterns. It is possible that more than one pattern has been included in this category, but at the moment we are going to assume that this is the varied expression of a single gene. This gene has been designated as the dominant Sb gene.

Lethal whites have occurred from the mating of two sabinos, but viable white foals have also been documented. As with all the overo genes, the wide variation in pattern leads to a lack of predictability.

The sabino pattern is confusing genetically. In many, or most, families, it appears to be transmitted as a polygenic trait rather than as a single gene. Many horses appear to transmit it roughly in the percentage that they are themselves white. That is, a sabino Medicine Hat is likely to produce a higher percentage of spotted foals (or at least foals registerable as spotted) than is a minimally marked sabino.

Breeding for the sabino pattern has a few interesting quirks. In many breeds it is desirable to have flashy white marks, but not body spots. This includes the Clydesdale, Shire, Welsh Pony, Arabian and even the Quarter Horse (for some breeders).

Clydesdale breeders especially like the white marks, but most prefer a bay body color. The general rule that many Clydesdale breeders use is to mate horses with four white feet (and usually roany bodies, resulting from the sabino pattern) to horses with one dark foot. This tends to result in the mating of horses with too much sabino expression to those with too little expression. On average, the resulting foals come out with fairly minimal expression. In the Clydesdale, this means few body spots and relatively few roans, which pleases most breeders and buyers of this breed. They still do get the occasional Medicine Hat, though.

Some horses that lack body spots, but that have the high white socks that creep up toward the body, are indeed sabinos and can be useful in Paint breeding programs. The sabino pattern is a great pretender, but is also responsible for some very attractively marked horses.

The sabino pattern is probably the most common "cropout" from the Quarter Horse and Thoroughbred breeds. In many cases, an investigation of the cropout's parents reveals horses with extensive white markings. In reality, these parents are probably minimally marked sabinos, which occasionally produce foals with more sabino expression than themselves.

A few cropouts, including nearly white ones, have very dark parents, or even parents with no white marks. These parents are clearly not sabinos, and demonstrate that there may be mechanisms that can mask the expression of the sabino pattern.

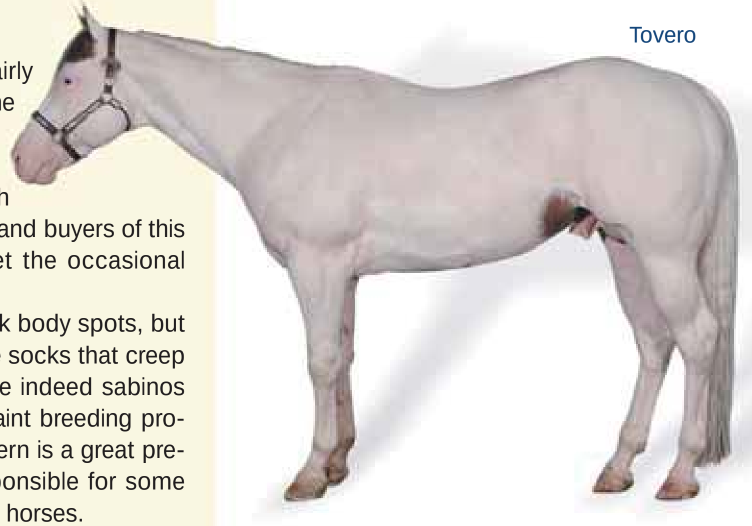
If the sabino pattern is merely an extension of "normal white marks," then this means that an occasional solid-colored horse (with no white marks) may be able to mask both white marks and the sabino pattern. The practical consequence of this is that such horses make poor choices for an outcross breeding program because they can decrease the percentage of spotted foals.

Sabino Overo

Defining Minimal-White Sabino Overo

- A great deal of white on the face.
- Possible small roaned areas on the body, often expressed as a narrow white strip up a leg or down the throat.
- Normal solid horse, minimal leg markings. These horses may be registered as Solid Paint-Bred, but in reality they are overos and will produce overos 50 percent of the time.

Tovero



Breeding the Tovero

The most interesting thing about Paint genes is that all four seem to be capable of combining with each other. The pattern created through the action of the tobiano gene and any overo gene is referred to as tovero. This name does not indicate which overo gene is present—just that the overo and tobiano genes are being expressed in the same individual.

It is possible that many overo horses have more than one overo gene creating their color pattern. The Medicine Hat Paint has been documented as being produced by crossing frame overos on tobianos, sabinos on frame overos and sabinos on tobianos.

From a color breeder's point of view, intriguing statistics are derived from horses carrying more than one copy of a Paint gene. Ignoring the homozygous tobiano that produces tobiano foals 99.9 percent of the time, a horse carrying two separate Paint genes should produce a spotted offspring 75 percent of the time from solid mates. A horse having three independent Paint genes is thought to produce a Paint foal 87.5 percent of the time. For the horse carrying four Paint genes, the percentage of spotted foals from solid partners hits an amazing 94 percent.

So, if the theory is correct and each overo pattern is under the control of a separate gene, there is more than one way to increase the odds of producing a spotted foal.

A Paint with one color pattern gene bred to a Paint with two Paint color genes produces a spotted foal 87.5 percent of the time. If both Paint parents have two Paint color-pattern genes, the odds of producing a spotted foal are greater than 99 percent.

The problem is that multiple copies of Paint genes produce more white on horses, and some pairings may create lethal white foals.

Coat Colors

A good horse is a good horse, regardless of its color. Yet, color can be a major asset when a horse is for sale, and it can make a difference in the amount of attention a horse gets in the show ring.

In addition to sporting various patterns of white patches—expressed as tobiano, frame overo, sabino, splashed white or tovero—every Paint Horse also has a background color.

Coat patterns have many background colors, and controlling them genetically can be complicated. Anyone wishing to breed for specific background colors has an interesting challenge before them. The breeder must combine specific colors with specific Paint spotting patterns, which requires careful planning and a knowledge of genetics.

Some Paint breeders prefer darker background colors, such as bay, chestnut and black, over the lighter colors such as dun, palomino, grullo or buckskin. The reason for this preference is because the contrast between the white Paint patterns and the darker base colors shows up better than it does with the lighter colors.

This rule, though, is not absolute, and the light-colored duns, grullos, buckskins and palominos are popular among many breeders. Taste in color is an individual preference.

Perhaps it is because of this variety of preferences that coat color genetics is one of the few areas of equine genetics where scientists have been able to develop sophisticated theories about how specific genes determine the color of a horse's hair.

However, it is important to realize that much of the theory of coat color genetics is just that—theory. At this point in time, only the presence of four color genes can be confirmed in the laboratory: the tobiano gene, the recessive form of a gene that creates a red horse, the cream gene and the agouti (bay/black).

The action of the rest of the color genes is purely hypothetical. Because of this, theories may change as more tests become available to identify specific genes.

Identifying coat colors can also be confusing. There is a tremendous range of shades within a color, and different types of color without recognized names. There are also coat colors that appear to be identical but are under the influence of different genes.

Breed associations have also contributed to some of the confusion. Thoroughbreds registered by the Jockey Club are called roans if they have a red body with white hairs. According to their definitions, grays are dark horses that are graying. Technically, whenever the gray gene is present, the horse is gray regardless of basic coat color. Horses of any color (with the exception of true white) can gray.

The American Quarter Horse Association, trying to keep up with the current coat color theory, has changed the description of a "buckskin." In the past, a buckskin was any canvas-colored horse with black points. It could have zebra markings and a line-back and still be a buckskin. Today, all line-backed horses with zebra markings are referred to as duns by AQHA, unless they are sorrel or chestnut duns. These are called red duns. Black duns are called grullos.

APHA's color criteria is the most descriptive of the three associations when it comes to roan, giving roan three basic colors: black (blue), bay and red. Starting in 2000, it became possible to register bay roans, while the term red roan designates sorrel/chestnut roans.

If all of this sounds confusing, take heart. It is possible to stack the deck in your favor when trying to produce a specific-colored offspring—if you understand the underlying genes that create the colors.

The Basic Rules of Coat Color Genetics

While it is true that the control of color is complicated, it is also true that the lighter colors are all dominant to the darker ones. This general rule is oversimplified, but it works in most cases.

Therefore, the light colors do not pop out—except rarely—as surprises. That is, you have to breed to a light color to get a foal of a light color. This fact has some consequences for Paint breeders.

If the breeder prefers the darker base colors, then it is important to always select the darker colors for their breeding programs. This is especially true if outcrosses are sought, because the lighter colors are fairly common in the Quarter Horse. They are present, but rare, in the Thoroughbred.

On the other hand, if the light base colors are desired, then it is important for the breeder to always include at least one light-colored parent in matings in order to boost the chances of producing a light-colored foal.

The downside of using two light-colored horses in a cross (specifically palominos and buckskins) is the occasional production of cream-colored horses—the cremello and perlino. These horses are nearly white, and it is difficult to see the contrast between any Paint spotting and the pale background color.

The line-backed dun colors only rarely can produce a cremello foal, making them safer to mate to other light colors because cream foals occur in such matings infrequently.

The darker colors, usually considered to include bay, chestnut and black, are easier for most breeding programs. These have a peculiar interaction in that chestnut (and sorrel) are recessive to bay and black, but act to cover them up. This means that it is impossible to tell just from looking whether a chestnut or sorrel horse has the genetic makeup to produce black or bay. Testing for the Agouti gene is helpful.

Reviewing the rules

To review, the basic rules for producing colors are:

- It usually takes at least one light-colored parent to produce a light-colored foal.
- Chestnut and sorrel, when mated to one another, can produce only more chestnuts and sorrels.
- Bay mated to bay, black or chestnut/sorrel can produce bay, chestnut, sorrel, and, rarely, black.
- Black mated to black produces black (or, rarely, chestnut or sorrel).
- Black mated to bay will usually produce a bay, fairly commonly produces chestnut or sorrel, and only rarely produces black.
- Black mated to chestnut will usually produce bay, but also chestnut or sorrel, and, rarely, black.

Color prediction is never 100 percent accurate. The best way to maximize the chance of a specific dark color is to test for the Agouti gene or to mate two parents of that color. Any other approach drastically decreases the probability of achieving the desired color in the foal.

Bay Horses

Bay is the second most common horse color. Controlled by the A gene, a bay horse has a reddish brown body with black points. The A gene creates these black points by limiting the placement of black on the horse's coat to the mane, tail, legs and ears.

The two genetic loci (locations) that control the color of the bay, black and sorrel horse are the Agouti (A) and Extension (E). The way these loci interact creates these three basic body colors.

Heterozygous Bay (AaEE) Mated to Chestnut (Aaee)

	Bay AE	aE
Chestnut Ae	AAeE bay	AaeE bay
ae	aAeE bay	aaeE black

Agouti controls the distribution of the red and black areas on horses that can form black pigment, i.e., blacks, bays, buckskins, etc.

The dominant A gene restricts black to the points, creating a bay. The recessive Agouti gene (a) does not restrict the black, resulting in an all-black horse. Therefore, foals with the genotype AA or Aa will be bay and those with the aa genotype will be black, providing they have the dominant Extension gene.

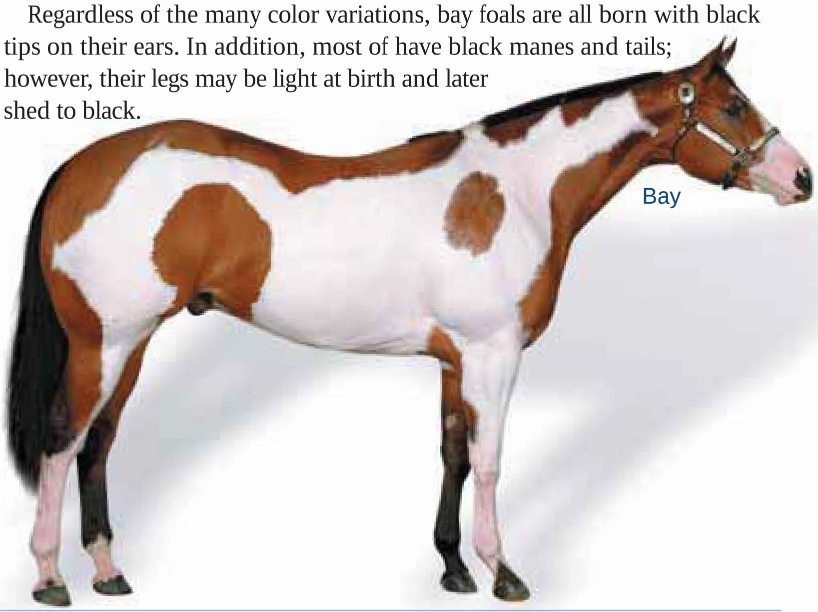
The Extension locus interacts with the Agouti to restrict or allow the expression of black, but unlike the bay gene, it is the recessive form of the Extension loci that does not allow the color. As a result, a foal inheriting two copies of the recessive black gene (ee) will be completely sorrel or chestnut, regardless of what type of Agouti alleles it carries.

In his book *Equine Color Genetics*, Dr. Philip Sponenberg describes the Agouti and Extension loci as switches. As a way to remember the effect each gene has on a horse's color, one can imagine that the Extension locus determines if the horse is "chestnut" or "not chestnut." If the horse is "not chestnut," then the Agouti locus acts as a switch to determine if the horse is "bay" or "black."

Understanding how the A and E genes work to create the bay color and affect the occurrence of sorrel and black will help you to better determine how other coat colors are created. However, there are still many subtle shades of the bay coat that cannot fully be explained by the action of the A and E genes.

Bays range in color from dark mahogany bays to blood bays to golden bays. These bay shades are thought to be under complex, multifactor genetic control. Even environment and nurture can cause a variation in coat color, with well-fed horses having a deeper, richer coat than those lacking in nutrition. Again, Sponenberg says these variations can be viewed as switches that trigger either a "dark," "middle" or "light" shade.

Regardless of the many color variations, bay foals are all born with black tips on their ears. In addition, most of have black manes and tails; however, their legs may be light at birth and later shed to black.



Bay

Black and Brown Horses

The black coat color is controlled by the E gene. It is the expression of the dominant E gene. The homozygous black horse (EE) has a very rich, black coat that is sometimes called jet black or coal black. Black horses have an entirely black coat and their color does not fade out over the flanks in the summer.

Though they are recognized by APHA as a separate color, brown horses are also genetically controlled by the E gene. Brown horses have black or nearly black coats with brown or reddish hairs on the muzzle or flanks.

Black is a popular color with many breeders, but it is fairly rare. The most reliable way to produce black horses is by mating two homozygous black horses. Breeding two heterozygous blacks is the second choice and breeding a black to any other color horse that carries a black gene is third. The reason for this is that the E gene is dominant over the e and the CC^{cr} genes that are present in palominos. Fortunately, breeders can have their black or brown horse tested for the recessive e gene so that they can determine if it is homozygous (EE) or heterozygous (Ee).

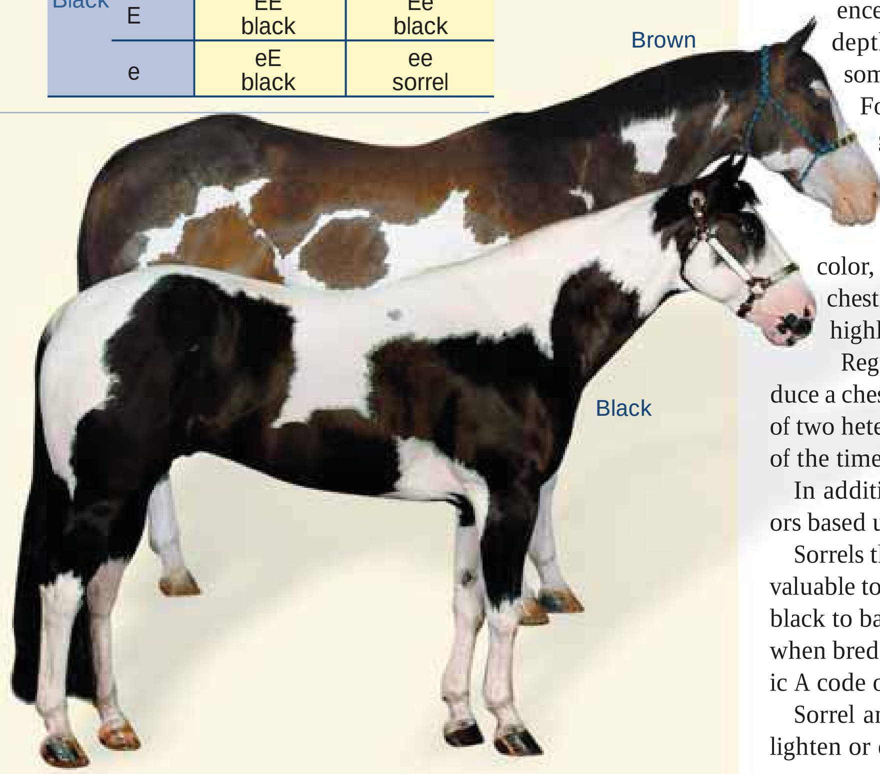
The problem with breeding black to sorrel is that many red horses carry the A gene, which turns the black coat to bay. According to statistics, a heterozygous black and a chestnut should produce a black foal 50 percent of the time.

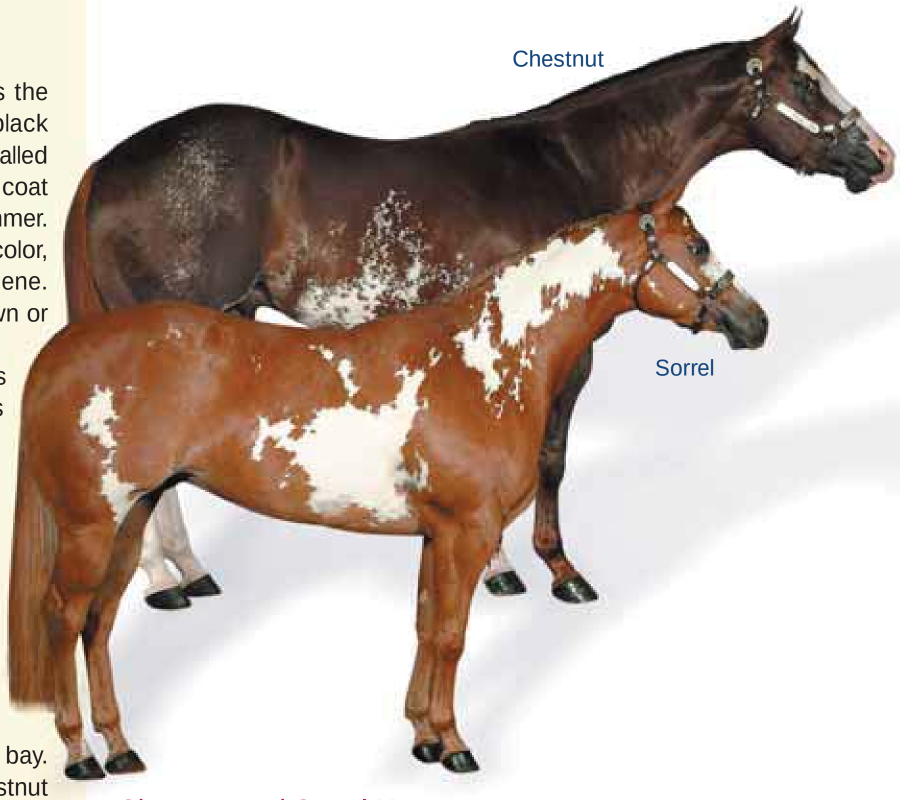
However, this is valid only if the chestnut horse (ee) does not carry the A gene. If the chestnut parent is heterozygous for this A gene, 50 percent of the blacks will become bays. If it is homozygous for this gene, 100 percent of the foals will be bay.

Black foals are usually born with a blue-gray hue to their coat and will typically shed to black as weanlings or yearlings.

Mating Two Heterozygous Black Parents (Ee)

		Black	
		E	e
Black	E	EE black	Ee black
	e	eE black	ee sorrel





Chestnut and Sorrel Horses

The chestnut horse and the sorrel horse are homozygous recessive ee individuals. Though there is no distinction between the two colors in the Jockey Club, most breed associations consider the chestnut and sorrel different.

Mating Heterozygous Black (Ee) Mated to Sorrel (ee)

		Black	
		E	e
Sorrel	e	eE black	ee sorrel
	e	eE black	ee sorrel

Both have a reddish body color with a reddish mane and tail, which can vary from dark to light to flaxen. The difference is in the depth of the body color. Chestnuts are a darker red that is sometimes close to black. Sorrels are a lighter or bright red. For the purpose of learning to utilize color genetics, this guide will use the terms interchangeably, because both colors are created by the homozygous recessive e.

Chestnut and sorrel come in many shades—from very light sorrel, which can appear close to a palomino color, to black chestnut. The best way to distinguish a black chestnut from a black or brown horse is by the copper-colored highlights on its legs.

Regardless of shade, two chestnut parents will always produce a chestnut foal, making it the easiest color to breed for. Mating of two heterozygous blacks (Ee) will produce chestnuts 25 percent of the time.

In addition, sorrel is a valuable color when trying to breed colors based upon the red color, like palomino, red roan and red dun.

Sorrels that have two copies of the recessive Agouti locus (aa) are valuable to breeders raising black horses because they will not turn black to bay. For the same reason, it will never produce a bay roan when bred to a blue roan. A test is available to determine the genetic A code of sorrel individuals.

Sorrel and chestnut foals are born with reddish coats that may lighten or darken when they shed.

Champagne and Cremello Genes

Scientists have identified three genes that create the coat colors palomino, buckskin and dun. Of these genes, the champagne and the dun (see page 13) gene, express themselves according to the rules of similar dominance. As a result, they dilute the horse's base color only when the dominant expression of the gene is present. Whether the horse has two copies of the dominant gene or only one, the coat color looks the same.

Palomino/Buckskin ($C^{cr}C$) Mated to Palomino/Buckskin ($C^{cr}C$)

		Palomino/ Buckskin C^{cr}	C
Palomino/ Buckskin	C^{cr}	$C^{cr}C^{cr}$ homozygous dilution (cremello/perlino)	$C^{cr}C$ dilution
	C	CC^{cr} dilution	CC no dilution

The Champagne Gene

The champagne (Ch) gene is not as commonly recognized as some other genes for coat colors. The dominant form of the champagne gene (Ch^{C}) gives horses an iridescent glow to their coats. Their eyes are amber and their skin is pumpkin-colored or a pinkish-gray. Researchers have identified the gene in the Tennessee Walking Horse, the Rocky Mountain Horse, the Quarter Horse and the Paint Horse.

In his book Equine Color Genetics, Sponenberg reports that the champagne gene dilutes a chestnut coat to golden with a flaxen mane and tail (golden champagne). Its action on black turns the coat to classic champagne, the bay coat becomes tan with a dilute mane and tail, known as amber champagne, while the action on brown becomes sable champagne.

A champagne-dilute foal is often born dark-colored and will lighten to champagne when it sheds for the first time. For this reason, it is likely that many champagne horses have been registered as palomino, buckskin and sorrel.

Owners of champagne horses who want their horse's color recognized can contact the International Champagne Horse Registry, which is the official registry for the color. To find out more, log on to their Web site at ichregistry.com.

The Cremello Gene

The cremello gene produces the palomino and buckskin color, but unlike the other dilution genes, it follows the rule of incomplete dominance. As a result, the gene can express itself in three ways, depending on the combination in which it occurs.

One copy of the dominant (C^{cr}) gene turns the horse's coat to either palomino or buckskin. Two copies of the C^{cr} gene dilute the coat to perlino or cremello.

The cremello gene is not expressed when it occurs in the homozygous recessive (CC) form. The same rule applies to the champagne and dun genes.

Cremello and Perlino Horses

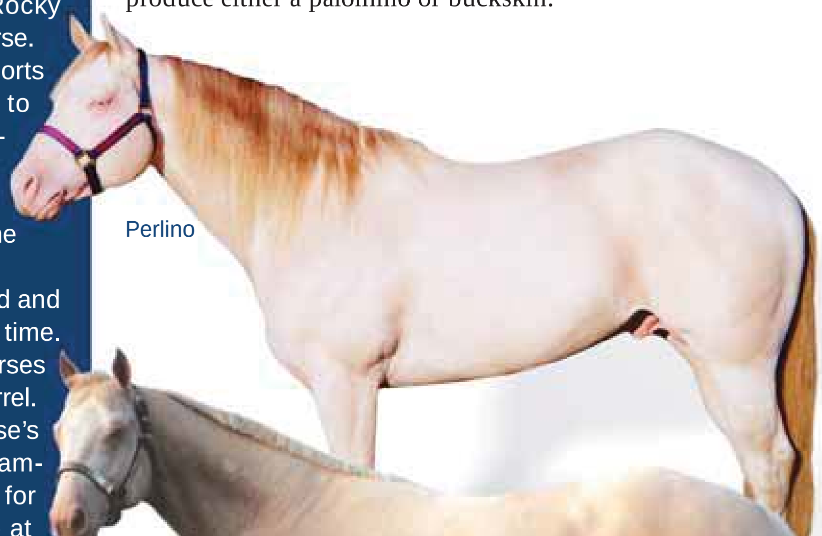
A horse that receives two copies ($C^{cr}C^{cr}$) of the cremello gene has a cream-colored coat with pink skin and blue eyes. When two pairs of C^{cr} occur in a horse with a chestnut base color, the resulting body coat color is called cremello. When two C^{cr} genes occur in a horse with a bay base color, it creates a color known as perlino.

As foals, a perlino and cremello look almost identical, both with pink skin, blue eyes and a washed-out coat color. White markings on the face and legs are barely visible next to the slightly yellow coat. Sometimes, these foals are mistakenly referred to as albinos.

Many breeders will not mate two palominos because of the chance of raising a cremello. Using the Punnett Square, you can determine that 25 percent of the foals from a palomino-to-palomino mating will receive two copies of the CC^{cr} gene.

Breeding palominos to buckskins, or buckskins to buckskins, results in a 25 percent chance of raising a perlino. The cremello gene creates both the buckskin and the palomino—the only difference is the base color upon which it is acting. Both palominos and buckskins result from the heterozygous ($C^{cr}C$) cremello gene combination. However, the buckskin's base coat color is bay, and the palomino's base coat color is sorrel or chestnut.

The benefit derived from cremello and perlino breeding stock is that Paint breeders can produce palominos and buckskins 100 percent of the time. A cremello bred to a sorrel will always produce a palomino and a perlino bred to a bay or sorrel will always produce either a palomino or buckskin.



Perlino

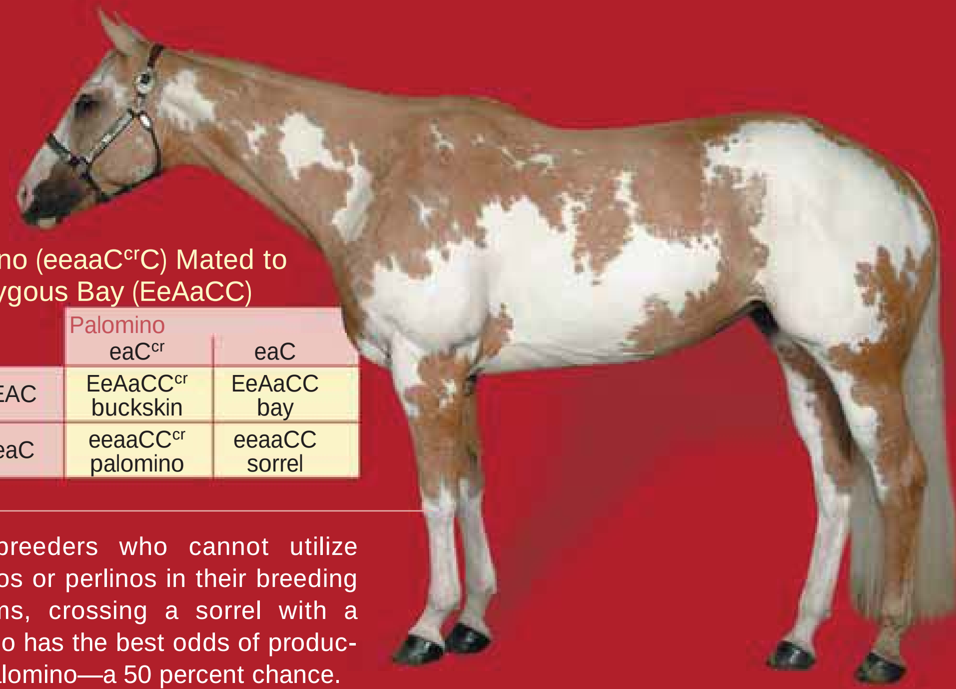
Cremello

Palomino Horses

The palomino horse is a chestnut horse (ee) with one C^{cr} gene. The Palomino Horse Breeders of America, a color breed registry for palominos, describes the color as that of a U.S. 14 karat gold coin, with variations from light to dark. However, the body coats can vary from a smoky gray to creamy yellow. Palominos may have manes the color of their bodies or they can be white, silver or mixed with sorrel. Their skin is usually gray, black, brown or mottled, without underlying pink skin or spots except on the face or legs.

A palomino foal's true color may not be evident at birth. Some will have yellowish bodies and white manes and tails, making them easy to identify. But some are born with a sorrel coloring. These foals tend to have an orange or pink tint to their coats, and their manes and tails may be slightly red. As weanlings or yearlings, these foals will shed their sorrel coat for their true palomino color.

Fortunately, a breeder in doubt has one sign on which they can rely. The color of the foal's eyelashes provides a good clue to the foal's eventual coat color. Palominos born with sorrel coats usually have light, golden eyelashes.



Palomino (eeaaC^{cr}C) Mated to Heterzygous Bay (EeAaCC)

		Palomino	
		eaC^{cr}	eaC
Bay	EAC	EeAaCC^{cr} buckskin	EeAaCC bay
	eaC	eeaaCC^{cr} palomino	eeaaCC sorrel

For breeders who cannot utilize cremellos or perlinos in their breeding programs, crossing a sorrel with a palomino has the best odds of producing a palomino—a 50 percent chance.

A palomino mated with a black horse may produce a palomino or a black foal, depending on which black gene combination it receives. The black gene (E) masks the expression of the C^{cr} gene. This is why a black horse crossed on a palomino is the third-best way to produce a black foal. Also, a heterozygous black (Ee) horse with a palomino parent can produce a palomino if it passes on a recessive e and a C^{cr}. If that horse's mate also has the recessive e gene, the resulting foal can receive an eeC^{cr}C combination, making it a palomino.

A variety of coat colors can result when breeding a palomino to a heterozygous bay. These foals have a 25 percent chance of becoming buckskin, palomino, bay or sorrel.

Of course, the Punnett Square only estimates gene action, because there are other factors that change breeding percentages. Its predictions work over a large population, but any horse can deviate.

Buckskin Horses

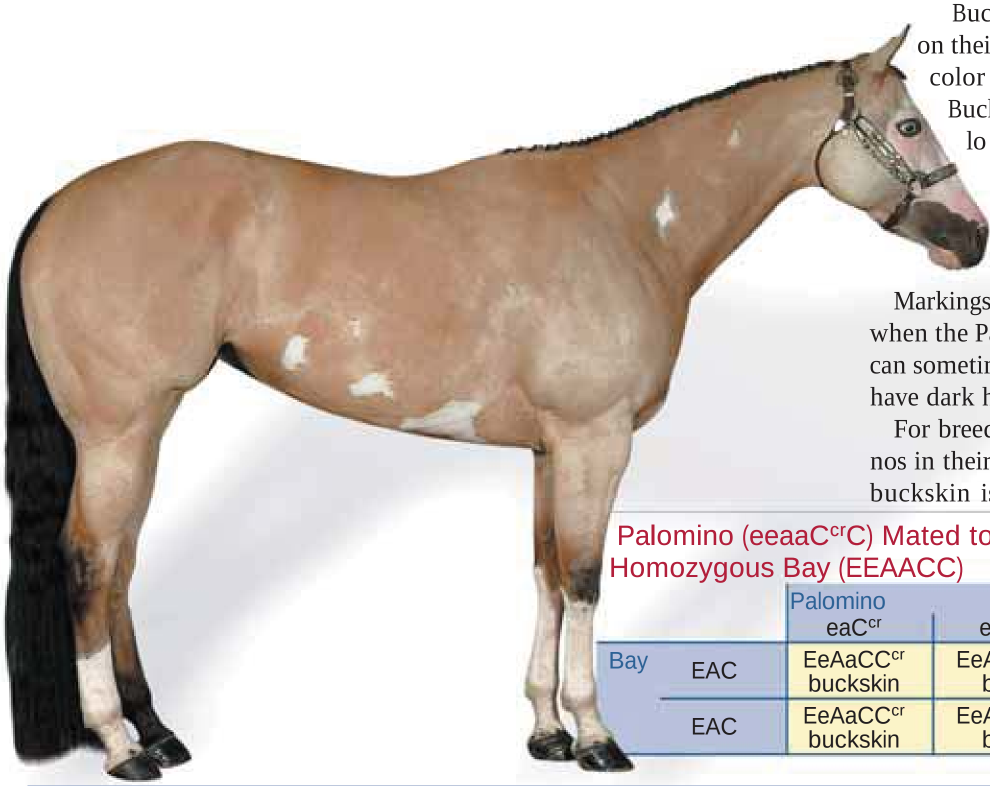
Buckskins are canvas-colored with black tips on their ears and black legs, like bays. Their body color ranges from purple to sand to cream. Buckskin is produced by the dominant cremello gene (C^{cr}) acting on a bay base color.

Buckskin foals are fairly easy to identify at birth. Born with light bodies and black ear tips, their legs may be dark but usually appear light and then shed to dark.

Markings can be tricky to detect on a buckskin Paint when the Paint gene colors the legs white. Hoof color can sometimes be helpful, as a buckskin Paint should have dark hooves.

For breeders who cannot utilize cremellos or perlinos in their breeding programs, crossing a bay with a buckskin is the second-best way of producing the color, with a 50 percent chance.

A 50 percent chance can also be obtained by breeding a palomino to a bay that is homozygous for the black gene and the bay gene (EEAA). This cross also produces 50 percent bays.



Palomino (eeaaC^{cr}C) Mated to Homozygous Bay (EEAACC)

		Palomino	
		eaC^{cr}	eaC
Bay	EAC	EeAaCC^{cr} buckskin	EeAaCC bay
	EAC	EeAaCC^{cr} buckskin	EeAaCC bay

Dun Horses

The coat color categorized as dun has one of the broadest ranges of colors and markings. For APHA purposes, horses with a dun coat are categorized as either dun or red dun.

Dun is the result of the dominant dun gene (Dn^{+}) working on a bay base coat. The effect is to lighten the body to a tan or golden yellow color. A red dun occurs when the Dn^{+} gene expresses itself on a chestnut or sorrel coat. Red duns have a light red, orangish or sometimes apricot coat color.

All duns, regardless of body color, have one thing in common—primitive markings. There are basically four types of primitive markings: zebra stripes, dorsal stripe (lineback), withers stripe and cobwebbing. Zebra stripes are bars on the side of the hocks and above or below the knees. A dorsal stripe is a dark stripe down the back. A withers stripe is a stripe across the withers, and cobwebbing is expressed by concentric darker rings on the forehead.

Not all duns express each of these traits, but some do. They can have any combination of these markings.

Researchers believe the dun gene lightens the body, leaving the horse's dark points unaffected and leaving the head darker than the body. The mane and tail are also often darker.

The lineback is the most common dun feature. The darker color of the lineback often continues into the mane and tail, where the gene action darkens the center of the hair and leaves the edges lighter.

Dark-colored horses such as black, bay and chestnut may have a back stripe without a lightened body color. Similarly, foals are sometimes born with a lineback that disappears when they shed. However, scientists believe these back stripes are not caused by the dun gene. These back stripes are referred to as "counter-shading".

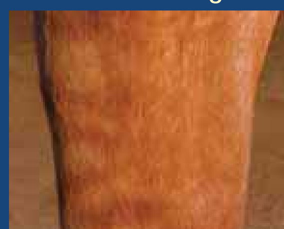
Dark edging on the ear is another common dun characteristic, but because this characteristic is common in other colors, it is probably not related to the dun gene (Dn^{+}).

Following the rules of similar dominance, the recessive dun gene (Dn^{nd}) does not affect the outcome of a horse's color. Scientists still do not know if the dun gene acts alone, or if there are other genes that work to create the many different dun characteristics.

Heterozygous Dun ($eeaaCCDn^{n+}Dn^{nd}$) Mated to Homozygous Bay ($EEAACCDn^{nd}Dn^{nd}$)

		Dun	
		$eaCDn^{+}$	$eaCDn^{nd}$
Bay	$EACDn^{nd}$	$EeAaCCDn^{nd}Dn^{+}$ dun	$EeAaCCDn^{nd}Dn^{nd}$ bay
	$EACDn^{nd}$	$EeAaCCDn^{nd}Dn^{+}$ dun	$EeAaCCDn^{nd}Dn^{nd}$ bay

Primitive Markings



Leg Barring: Horizontal stripes of varying widths appearing across the hocks, gaskins, forearms or knees.

Shoulder/Traverse Stripes: Neck and shoulder shadowing appearing as dark areas through the neck or withers.

Dorsal Stripe: Darker band of color running along the backbone from the withers to/into the base of the tail.

Grullo Horses

Grullo is one of the rarest expressions of the dun gene because it results from the action of the dun gene on a black base coat. It was once believed that grullos resulted from crossing palominos with black horses, but genetic research has since proved that theory incorrect.

The grullo coat varies from beige to bluish-gray to slate blue. They usually have dark or black heads and black points, mane and tail.

As the dun gene acts through similar dominance (see page 14), grullo is created by a single copy of the Dn+ gene. However, homozygous duns (Dn+Dn+) do exist and will pass on a dominant dun gene to each of their offspring, resulting in 100 percent duns and grullos.

Another interesting result of the dun gene occurs when a horse also carries the dominant form of the cremello (Ccr) gene, which creates cremellos, perlinos, palominos and buckskins. A black horse that receives the Dn+ gene and is also heterozygous for the cremello gene (CCcr) will result in a paler grullo. On a bay base coat, the primitive marks may remain but the body becomes more yellow, like a buckskin. On a sorrel coat, the primitive marks may be lost altogether and the body becomes the color of a palomino. For this reason, the colors of some horses may have been incorrectly registered, which could explain why breeders once believed a palomino could produce a grullo. In actuality, the palomino was a palomino-colored dun without the dorsal stripe.

Scientists believe that when CCcr x Dn+ occurs, the gene that has the most extreme expression of the base coat color is the one that is dominantly expressed. For instance, a chestnut coat would be lightened to palomino because palomino is a more extreme change than is red dun.

Heterozygous Black ($EeaaCCDn^{nd}Dn^{nd}$) Mated to Heterozygous Red Dun ($eeaaCCDn^{+}Dn^{nd}$)

		Black	
		$EaCDn^{nd}$	$eaCDn^{nd}$
Red Dun	$eaCDn^{+}$	$eEaaCCDn^{+}Dn^{nd}$ grullo	$eeaaCCDn^{+}Dn^{nd}$ red dun
	$eaCDn^{nd}$	$eEaaCCDn^{nd}Dn^{nd}$ black	$eeaaCCDn^{nd}Dn^{nd}$ sorrel

The Difference Between Roan, Gray and White

Three of the most easily confused colors are roan, gray and white. Though all result from white being added to the horse's base coat, each has a unique way in which it occurs.

The roan gene (RnRn) covers specific parts of the body with a light coating of white hairs that are evenly mixed within the base coat. The gray gene (G) begins as a light sprinkle of white over the entire coat. Each year, more white hairs are added to the coat until it is completely gray or white. The white gene (W) completely covers the body with an even, white coat before the foal is born.

By becoming familiar with the specific characteristics unique to each color, a breeder can reliably identify one from the other. Because these three genes add white to the basic coat color of the horse, the horse's other gene combinations of E, A, C^{cr}, Dn^{nd}, Ch, etc., still determine the color that is being covered by the coating of white.

Blue Roan ($EeRn^{+}Rn^{Rn}$) Mated to Sorrel ($eeRn^{+}Rn^{+}$)

		Blue Roan $E\ Rn^{+}$	eRn^{Rn}
Sorrel	eRn^{+}	$eERn^{+}Rn^{+}$ black	$eeRn^{+}Rn^{Rn}$ red roan
	eRn^{+}	$eERn^{+}Rn^{+}$ black	$eeRn^{+}Rn^{Rn}$ red roan

Roan

Roans are often confused with gray horses because both are characterized by having white in their hair coats. However, the difference between the action of the roan gene and the gray gene is evident once you understand the specific effect each has on a horse's coat.

The action of the RnRn gene places a certain amount of white hairs in the body coat. Sometimes, the roan pattern is uneven and is displayed in a paler fashion on areas such as the hindquarters, the heart girth, the barrel and the dock of the tail. Unlike the gray horse, a roan's head, mane, tail and lower legs usually remain solid or darker than the rest of its body.

A roan foal's color may be evident at birth, or may reveal itself after it sheds its foal coat. A roan horse does not grow more white hair as it ages. Instead, a roan coat may appear lighter in the spring and darker in the winter months.

The roan gene is dominant. It is believed to be linked to other genes that determine the horse's color, which complicates determining the inheritance of the gene because these linked genes are usually passed along as a unit. The roan gene is closely associated with the E gene, which determines a red or black base color, and the TO (tobiano) gene. Thus, roans have a higher percentage of offspring that are the same color as the roan parent.

For example, red roans, which have a sorrel base coat, bred to sorrels, produce 50 percent sorrels and 50 percent red roans. A blue roan, whose roan gene is linked to its dominant E (black) gene, is apt to produce a high percentage of black and bay roans. If a horse's roan gene is linked to the recessive e (sorrel) gene of a heterozygous (Ee) individual, the horse should produce only red roans when bred to sorrel mates.

Homozygous roans are extremely rare. Though it was once believed that the RnRnRnRn combination was lethal, the existence of a few homozygous roans disproves this theory.

It is important to keep in mind that the genetic codes controlling the roan gene are extremely complicated, so this is only a basic discussion of the coat color. Without a doubt, there is an exception to every rule and a hidden factor that cannot be seen on the surface.

Blue Roan

Blue roan is the common term for the RnRn gene acting on black. White hairs are dispersed over the body, giving a blue appearance to the horse. The head, legs, mane and tail are very dark.

Red Roan

The base coat of a red roan is sorrel or chestnut. Red roans have a uniform mixture of white with red hair on a large portion of the body, but are usually darker on the head and lower legs. The mane and tail may be red, flaxen or white.

Red roans with white legs and a blaze face are often referred to as strawberry roan, a term APHA does not officially recognize.

Horses with strawberry roan markings have shown a tendency toward producing excessive white by Quarter Horse standards. It may be possible to influence the occurrence of excessive white by carefully screening the mates for strawberry roans. Chestnut horses with stockings and blazes increase the chance that the white markings will spread. Solid-legged and solid-faced mates may help to keep the color to a minimum.

Researchers have also discussed the possibility that some of the strawberry roan markings are an expression of the sabino overo pattern gene.

Bay Roan

The bay roan, which has a bay base coat, is often called a red roan. APHA distinguishes between roans with bay base coats and those with sorrel or chestnut. The category of bay roan was added to the registration form, separating the two basic coat colors. Only sorrels and chestnuts with the roan gene are now registered as red roans.

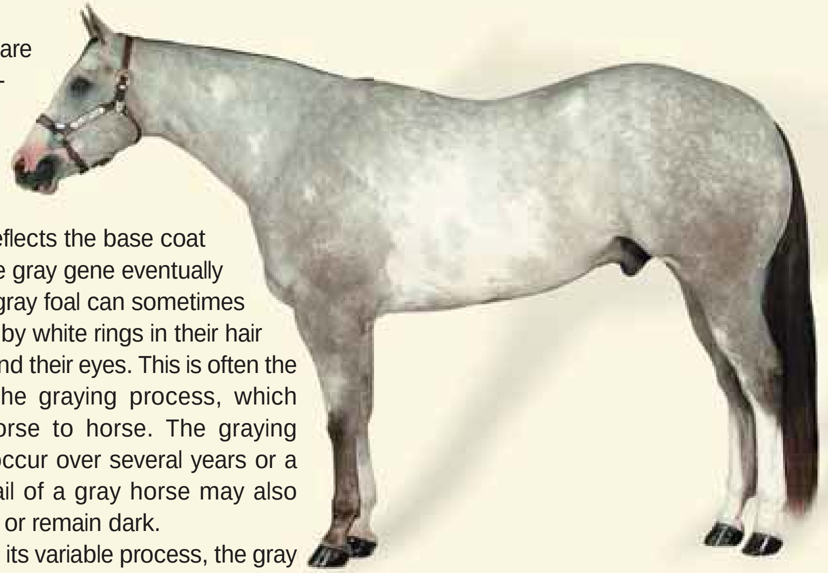
Gray Horses

With horse people and non-horse people alike, gray is one of the most popular coat colors. Perhaps this is because it seems to hide conformational faults and can make a plain head appear beautiful.

The irony is that gray is often an undesirable gene for breeders of white-patterned horses because the contrasting darker color gradually fades away. Because the gray (G) gene is dominant over all the genes discussed so far, it will eventually turn all other coat colors—dun, roan, bay, black, buckskin, champagne, dun, palomino, roan and sorrel—white.

However, the gray gene does not affect the white hair on the horse's body that is created by Paint Horse pattern genes, such as tobiano or overo, or white that occurs as a blaze, stocking or other marking. These white markings remain visible even as the gray horse becomes whiter-looking with age.

Because gray horses do become whiter with age, they are sometimes confused with the white horse. The difference is that a mature gray horse may appear white, but has dark eyes and dark skin. A white horse also has dark eyes but has pink skin.



Gray horses are born with a colored coat such as black, bay, sorrel, dun, etc. Their foal coat typically reflects the base coat color, which the gray gene eventually turns white. A gray foal can sometimes be determined by white rings in their hair coats and around their eyes. This is often the beginning of the graying process, which varies from horse to horse. The graying process may occur over several years or a lifetime. The tail of a gray horse may also become whiter or remain dark.

In addition to its variable process, the gray gene creates many shades and patterns, including primitive markings, dapples (round, shaded spots) and "fleabitten" coats (flecks of color dispersed throughout the body). It is still unknown which genes control the shades and patterns of grays and the speed of the graying process. Therefore, the idea that a homozygous gray (GG) will turn white faster than a heterozygous gray (Gg) is unproven.

What is known is that homozygous grays do exist and they produce gray offspring 100 percent of the time. Heterozygous grays produce gray foals 50 percent of the time.

Unfortunately, both homozygous and heterozygous grays are prone to melanomas (skin tumors). These tumors commonly occur beneath a gray horse's tail and around its ears. Fortunately, though they can be unsightly and disfiguring, only about 5 percent of these melanomas are malignant.

White Horses

In most breeds, including Paint Horses, true white horses are rare. Keeping this in mind, it may seem unusual to learn that the white gene (W) is dominant over all other coat colors, including gray. This means that any foal receiving one dominant white gene will be white.

White foals are born white and have dark eyes and pink skin, which eventually distinguish them from a gray horse. If they have a Paint Horse coat pattern, it is not identifiable because the markings blend in with their hair coat, unlike perlinos and cremellos, which have visible patterns and blue eyes.

APHA has included the white color on its registration form for some time. ApHC and the Jockey Club also list white as a registerable color, but it is extremely rare in both breeds.

Even though the white gene is known to be dominant, it is still somewhat of a mystery to scientists because two dark-colored parents have been known to produce a white foal. To explain this, researchers have concluded that a dark-colored parent carrying the recessive white gene (w) can pass a copy of this gene to their offspring. Once inherited by the unborn foal, the recessive white gene may mutate to the dominant form, creating a white foal. The white foals that resulted from these matings went on to breed as if they carried the W gene. This may suggest that the white allele has a high spontaneous mutation rate.

According to the Punnett Square, a white horse mated with a dark-colored horse will produce a white foal 50 percent of the time. Mating two white horses results in 50 percent white foals and 25 percent dark foals. (Before a white horse produces offspring, it is impossible to know what color of dark foals it will produce unless you have extensive knowledge of the horse's color pedigree.) The other 25 percent of the foals produced from a white-to-white mating are lethal. These homozygous white foals (WW) are usually resorbed during gestation.

However, these homozygous white foals are not genetically like foals that have Overo Lethal White Syndrome, which results from an overo-to-overo mating.

Distinguishing Differenced Between White and Cremello/Perlino Horses

	White (W)	Cremello/Perlino (CR^{CR})
birth color	white	cream to white
eye color	dark	blue
skin color	pink	pink
visibility of white markings	not visible	visible
genetic base coat	any genetic combination	sorrel or chestnut for cremello, bay for perlino
color production potential	produces 50% white horses regardless of mate's color	produces 100% palomino or buckskins, depending on genotype of mate

Overo Lethal White Syndrome

A Lethal White is a foal of overo lineage, born all white or mostly white. The foal may seem normal at birth, but usually begins showing signs of colic within 12 hours because of a non-functioning colon. Because the syndrome is always fatal, lethal white foals are often euthanized.

This condition, referred to as Overo Lethal White Syndrome (OLWS), is always fatal, and results in both emotional and economic loss to breeders.

Occurrence of Lethal White Syndrome

The body of all living things is made of protein, minerals and water. The proteins comprise a large proportion of the body's structure, and also regulate body functions by acting as hormones and enzymes.

The building blocks of proteins are amino acids, and the function of the protein is dependent on the order of the amino acids. The order of the amino acids is determined by DNA, which codes for the composition of the body, its growth and function.

The code for inherited conditions such as OLWS is in the DNA, and therefore its composition must be determined before it can be known how it causes disease.

Similar to how a protein is made of amino acids, DNA is made of bases. These bases are arranged in triplets that code for the amino acids.

When the base pairs change (through mutation) and cause an amino acid substitution, the function of the protein coded is altered. The alteration of protein function causes genetic traits, including disease.

Causative genes are responsible for similar conditions in other species, so research to determine the order, or sequence, of base pairs and the resulting amino acids for two "candidate genes" is crucial to understanding OLWS.

Finding the Lethal Allele

Based on studies by the University of Minnesota's Equine Genetics Group and Portland University, it has been concluded that OLWS foals have two lethal alleles (L/L); their parents have one normal and one lethal allele (N/L), and solid-colored horses of other breeds have two copies of the normal allele (N/N).

This is strong evidence that the gene mutation detected is responsible for OLWS. To date, researchers have tested almost 1,000 horses, and the results are consistent.

Proving the Lethal Theory

It appears that all overo horses are not the same, at least for this gene. Overos can carry either (N/N) or (N/L). Researchers have not found a living adult horse that has two copies of the lethal sequence (L/L), and they have tested several all-white Paints.

The geneticists have found carrier horses in overos, tobianos, toveros, Solids, crop-out Quarter Horses and Pintos. The discovery of the Lethal allele in Pintos is important in limiting the spread of this mutation, because many Pinto breeders are unfamiliar with OLWS and the gene is now making its way into other breeds that are crossing onto Pintos for color production.

By taking the lead in the investigation of OLWS, APHA has provided valuable information to all breeders.

Genetics in Overo Lethal White Syndrome

In the past few years, Lethal White Syndrome has been heavily examined from a genetic standpoint. In 1997, APHA approved a grant to the

Lethal Whites—Fact Versus Fiction

According to researchers at the University of Minnesota, there are three issues that may account for the fact that we do not see 25 percent of all overo-to-overo crosses producing lethal whites:

1. Not all lethal white foals survive to birth. Some are resorbed or aborted by the mare.
2. Not all lethal white foals that are born are reported.
3. Not all patterns that are currently classified as overo, such as sabino or splashed white, are lethal when homozygous.

In addition, many myths cloud the truth regarding lethal white syndrome. Below, the University of Minnesota Equine Genetics Group dispels nine of the most common myths.

1. Myth: All overo horses are carriers of the lethal allele.
   Fact: There are many overos that do not carry the lethal allele.

2. Myth: Twenty-five percent of foals from two overo parents will be lethal whites.
   Fact: Because there are overos that do not carry the allele, the incidence of lethal white syndrome is less than 25 percent in overo-to-overo matings.

3. Myth: Registered tobianos, Solids or Paint crosses cannot carry the lethal allele.
   Fact: There are tobianos that have overo bloodlines, and these horses can be carriers of the lethal allele. Solids and Paint crosses can carry the lethal allele.

4. Myth: Totally white Paints are not carriers of the lethal allele.
   Fact: These white horses are often carriers of the lethal allele.

5. Myth: All totally white foals born to two overo parents are lethal whites.
   Fact: There are totally white Paints that are not affected by the lethal white syndrome.

6. Myth: Mares cannot produce lethal foals in consecutive years.
   Fact: The genetic makeup of one foal does not affect subsequent births.

7. Myth: Only one parent determines if a foal will be a lethal white.
   Fact: Both the sire and the dam contribute a copy of the lethal allele.

8. Myth: Crop-out Quarter Horses cannot carry the lethal allele.
   Fact: A small number of crop-outs have been tested and found to be carriers of the lethal allele.

9. Myth: You can reliably tell the carrier status of a Paint by their color pattern.
   Fact: This is false.

University of Minnesota to support a research study aimed at locating the gene responsible for OLWS and developing a test to determine the disease.

Led by Dr. James Mickelson, Dr. Stephanie Valberg and Dr. Elizabeth Santschi, the research has now identified the gene that is associated with OLWS and is likely responsible for the condition.

Researchers are still working to more completely describe the inheritance of overo and, more than ever, it is clear that overo horses are at risk of carrying the OLWS gene.

Fortunately, horse breeders can now test their stock for the presence of this gene and use this information to assist in making mating decisions. This test allows breeders to positively identify horses that are carriers of the gene and to find new pedigree sources for their color breeding programs.

Testing for Lethal White

The diagnostic test for the overo gene uses a process known as ASPCR (allele specific Polymerase Chain Reaction). The test can be performed from either blood or hair samples with roots (hair preferred). The test identifies a specific mutation site in the DNA sequence that has been shown to be associated with Lethal White overo foals. Researchers know of no other mutations that are associated with Lethal White overo horses. However, owners requesting the diagnostic test should be certain to understand that there is the rare possibility that two NN horses could have a Lethal White foal, due to the sire and dam having in common a mutation at a site other than the one detected by this test.

Performing the Test

The test for the lethal form of the gene associated with OLWS is available from two universities.

All tests require hair samples be pulled from the mane or tail with the roots intact. The number of hairs required ranges from 15-30. Hair samples can be sent in a regular envelope. All samples must be clearly identified with the horses' registered name, number and other required information. A copy of the registration papers should be enclosed with the sample whenever possible.

Test results will be mailed to the owner or veterinarian, whomever is specified on the form. Results will not be given by phone.

Arrangements for testing can be made through APHA. Contact Field Services for forms and instructions.

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Walker, Dawn, "Lethal Whites: A Light at the End of the Tunnel," *Paint Horse Journal* Volume 31, No. 2 (February 1997): 114-119.

If you would like to learn more about equine color genetics, some suggested readings are:

Equine Color Genetics by Dr. D. Phillip Sponenberg. Published by Iowa State University Press in 1996. To order a copy, call (800) 862-6657.

Horse Genetics by Dr. Ann T. Bowling. Published by Oxford University Press in 1996. To order a copy, call (800) 445-9714.

COLOR DESCRIPTIONS

BLACK

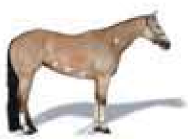
Entire coat, including muzzle, flanks and legs, are black; color may fade when exposed to the sun; could have rusty tinge during certain times of the year; early foals may be an overall mousy gray, then shed to black.

BROWN

Body color brown or black, with light areas at muzzle, eyes, flank and inside upper legs; mane and tail usually black.

BAY

Body color reddish brown, with variations ranging from dark blood bay to light bay and usually distinguished by black mane and tail, ear tips, lower legs.



BUCKSKIN

Body color yellowish or gold, mane and tail black; black on lower legs; lacks primitive markings.

BLUE ROAN

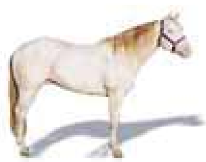
The overall intermingling of white hairs with a black body color; head, lower legs, mane and tail are usually solid or darker; does not get progressively whiter with age.

BAY ROAN

The overall intermingling of white hairs with bay body color; head, lower legs, mane and tail are usually solid or darker; does not get progressively whiter with age.

GRAY

Dominant over all other color genes; born any color with white hair progressively turning the coat whiter as the horse ages; dark skin; normally grays first around eyes and behind ears.



PERLINO

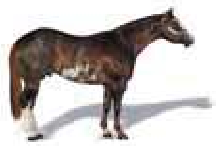
Double dilute of bay/brown resulting in body color of cream or off-white; lower legs, mane and tail light rust or chocolate shade; skin is pinkish or grey; eyes are blue or amber; the coat has enough yellow hue to allow white markings to be visible.

GRULLO

A form of dun with body color smoky or mouse-colored (not a mixture of black and white hairs, but each hair mouse-colored; mane and tail black; has black primitive markings.

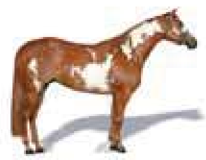
DUN

Diluted body color of yellowish or gold; mane and tail are black or brown; has black or brown primitive markings.



CHESTNUT

Body color dark red or brownish red; range from very light to liver chestnut; liver chestnut can be distinguished from black or brown only by the bronze or copper highlights on the legs; mane and tail usually dark red or brownish red, but may be flaxen.



SORREL

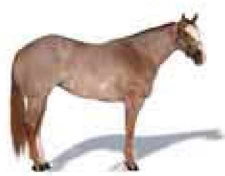
Body color reddish or copper-red; mane and tail usually same color as body, but may be flaxen or very dark brown.

PALOMINO

Diluted body color varying from rich gold to pale yellow; mane and tail generally pale or off-white but may be same color as body (with nonblack points).

CREMELLO

Double dilute of chestnut/sorrel resulting in body color, mane and tail of cream or off-white with pale, pinkish skin; the coat has enough yellow hue to allow white markings to be visible; eyes are blue or amber.



RED ROAN

The overall intermingling of white hairs with chestnut/ sorrel body color; head, lower legs, mane and tail are usually sorrel or dark red; does not get progressively whiter with age.

RED DUN

A form of dun with body color yellowish or flesh-colored; mane and tail are red or reddish; has red or reddish primitive markings.

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