

COLOUR IN BULL TERRIERS – Part 1 – Expression of Colour

Coat colour is of major interest in Bull Terriers as the breed was originally defined by the colour white. James Hinks of Manchester, England specifically bred an all-white dog which he called the Bull Terrier (distinct from the many so-called Bull-and-Terrier dogs of the time). This dog was very popular from its emergence in 1862 and resulted in the founding of the Bull Terrier Club in England in 1887, which was dedicated to the development of the White Bull Terrier. The coloured Bull-and-Terrier type dogs in England only emerged in a registered breed nearly 50 years later with the registration of the Staffordshire Bull Terrier in 1935.

Despite this, coloured Bull Terriers did exist which resembled the White Bull Terriers more than their broad-headed Staffordshire Bull Terrier precursors. Some White Bull Terrier enthusiasts were interested in the Coloured Bull Terrier and were trying to breed a coloured dog able to compete in the show ring with White Bull Terriers. One of these was Thomas W. Hogarth, a Scottish veterinarian, Bull Terrier breeder and judge. Hogarth recorded the colours of offspring resulting from 340 different matings in his books – “The Coloured and Colour Breeding” (1932) and “The Bull Terrier Notebook” (1936). This data formed the basis of a scientific paper “Coat Color Inheritance in Bull Terriers” by Briggs and Kaliss for the “Journal of Heredity” in 1942. Unfortunately, some of Hogarth’s data was not reliable – newborn puppies are not always easy to classify by colour as their coat colour changes over the first few days. In 1933 Richard Glyn published “The Seven Sources of Colour in Bull Terriers” in which he proposed that only seven individuals were crossed with White Bull Terriers between 1910 and 1925 resulting in the modern Coloureds. He reiterated this idea in his 1950 book “Bull Terriers and How to Breed Them”. In 1957 a genetics textbook “The Inheritance of Coat Color in Dogs” by Clarence Little provided some enlightenment on dog coat colour genetics and is today still considered to be the authoritative work on the subject. “The New Complete Bull Terrier” by Ernest Eberhard contains a chapter called “Breeding for Color” by Miss Montague Johnstone of Romany Kennels, most famous for breeding Coloured Bull Terriers able to compete with, and win against, White Bull Terriers in the show ring. Interestingly, Miss Montague Johnstone’s article, first written in 1954, still provides clear, concise advice for the modern breeder of Coloured Bull Terriers. Mrs Winkie Mackay-Smith in her book “From James to Jim” describes Bull Terrier colours in terms of layers of colour, first a base coat of red, then the options of a brindle layer, a black layer and finally a white layer to create the different colour possibilities. This explanation without genetic details works very well in explaining the colours we see in the breed. Dr David Harris, in his book “Full Circle – A History of the Colored Bull Terrier”, is more scientific, doing a sterling job of summarising the known genetics of dog coat colour at the time (published in 1990) and applying it to the Bull Terrier. In this, he provides the first explanation of Bull Terrier-specific coat colour genetics since Briggs and Kaliss, fifty years before. In 2007 a team of geneticists led by Prof. Gregory Barsh at Stanford School of Medicine discovered the K-Series locus. This was the first major change in dog coat colour genetics since Little’s work in 1957. The purpose of this article is to apply these new ideas specifically to the Bull Terrier.

An overview of basic genetics is needed before considering the specifics of colour in the Bull Terrier. All members of the *Canis* genus, including jackals, wolves and domestic dogs of all breeds (*Canis familiaris*) have 78 chromosomes (compared to 46 chromosomes in humans). Half of these chromosomes (39) are inherited from the sire (the male parent) and half (the other 39) from the dam (the female parent). The chromosomes contain the genetic material through which the characteristics of dogs are inherited from their parents. The position on the chromosome where genetic material for a particular trait is found is called a locus (plural loci). The genetic material determines the characteristics or traits of the individual and is called a gene or, in the plural, genes. The different possible expressions for a characteristic or trait are called alleles. Alleles occur in pairs – one on the locus of the chromosome from the sire and one on the same corresponding locus of the chromosome from the dam. When two different alleles are present at the same loci, it is called heterozygous and when two of the same alleles are present at the same loci, it is called homozygous. In a heterozygous case, a dominance relationship between the alleles determines the expression of the trait. Dominance can be complete in the case where the dominant allele

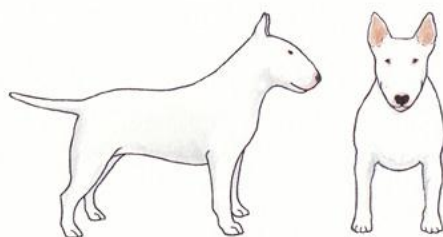
hides any effect of the recessive allele. Dominance can be incomplete where the effect of the alleles is a combination of the dominant and the recessive. Although alleles occur in pairs, more than two alleles (consider them as genetic options) may exist for particular loci and then different combinations of dominance may exist. Alleles are identified using a letter of the alphabet, an uppercase letter indicates a dominant allele while a lowercase letter indicates a recessive allele. Superscripts are used to distinguish between alleles when there are more possibilities. For example, in humans blue eyes are represented as *bb* to indicate a homozygous recessive case. Brown eyes may be indicated as *BB* (also homozygous but dominant) or *Bb* (heterozygous where the brown allele is dominant over the blue allele). A complication in gene inheritance is that while genes code for the structures of particular proteins (in this case those proteins involved in the production and distribution of pigments), genes can also code for when and where other genes are turned “up” or “down” or “on” or “off”. Little is understood of this modifier behaviour and it is the subject of ongoing research. When considering the genetics of an individual, there are two ways of describing the traits of that individual – either using genotype or phenotype. Genotype is the actual genetic code that an individual possesses in its chromosomes – this we cannot see directly. Phenotype is the manifestation of that genetic code – what we can actually see. The dominance relationships between alleles determine how genotype translates into phenotype.

Colour inheritance in dogs is complicated as there are 14 different loci (positions on the chromosomes containing genetic material) that are believed to determine the colour patterns of a dog's coat. Of these 14 loci, only 4 are important in determining coat colour in Bull Terriers. This is because not all the colour options exhibited by other dog breeds are possible in Bull Terriers. When a breed is registered, the gene pool is restricted as no dogs other than those registered will breed with one another. Raymond and Lorna Coppinger in their 2004 book “Dogs – A New Understanding of Canine Origin, Behaviour and Evolution” say that if when registering a breed and effectively closing the stud book with 500 unrelated founding males, inbreeding will start by the tenth generation – that could be just fifteen years later. For a breed such as the Bull Terrier that is almost 150 years old, this would effectively mean inbreeding has taken place for over 100 years. While this raises concerns over breed-specific illnesses, it also means that some alleles or gene options have been lost. If only one allele for a particular locus is present in the gene pool then all individuals of this breed will share the same trait. This applies in varying degrees to all breeds of dogs. To use a human example, consider a group of people isolated from the rest of the population, all of whom have blue eyes (which is homozygous recessive – all member have the genotype *bb*). If this group breed only amongst themselves, all babies born will have blue eyes. Any eye colour other than blue would have been lost from this population.

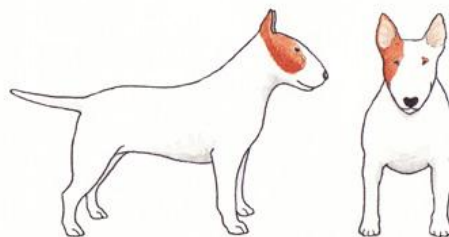
There are a limited number of coat colours in Bull Terriers. Here is a descriptive list of these colours:

1) **White** –

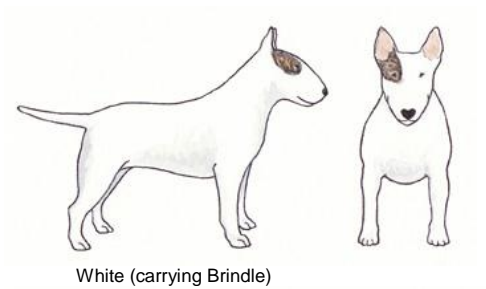
These appear all white but they may have patches of the colours described below, most likely on the head near the ears and eyes. They are, however, not really white as all white Bull Terriers carry colour and pass on colour to their offspring even though that colour may not be visible. The white expression is a ‘mask’ hiding the true genetic colour of the dog.



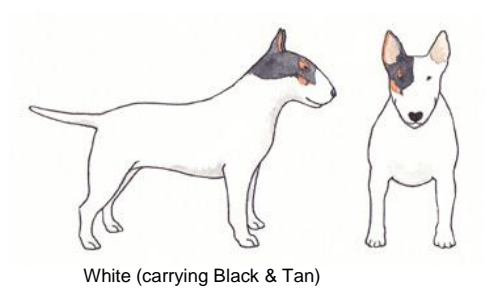
White (no visible colour)



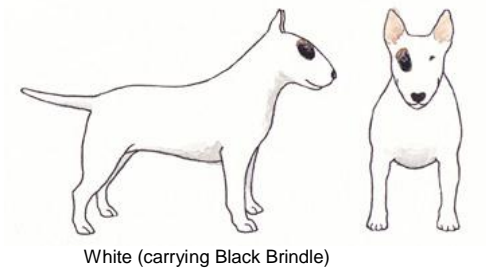
White (carrying Red)



White (carrying Brindle)



White (carrying Black & Tan)



White (carrying Black Brindle)

2) Red –

This colour ranges from tan through to deep, dark, rich, rust red.

There are different varieties –

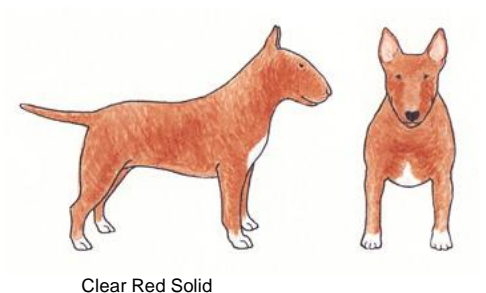
Red Solid – red with hardly any white markings – it might have a small white blaze on the nose, patch on the chest and white on the toes

Red & White – red with strong white markings on the nose, collar, chest, underbelly, lower legs and feet and tail tip

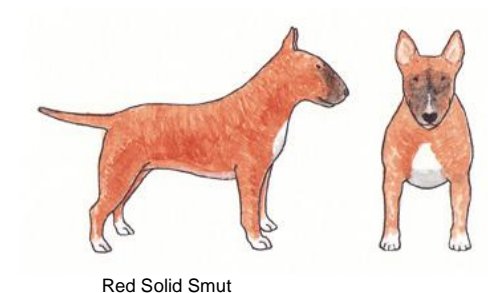
Red Smut – red with a dark mask on the face and tip of the tail

Clear Red – red with no dark mask on the face or tail

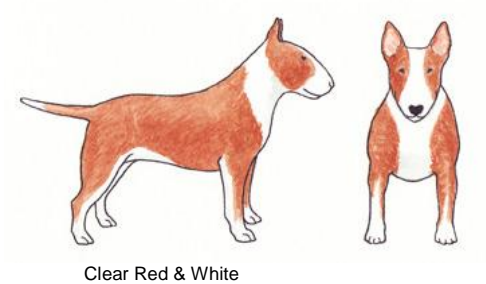
This results in four different combinations –



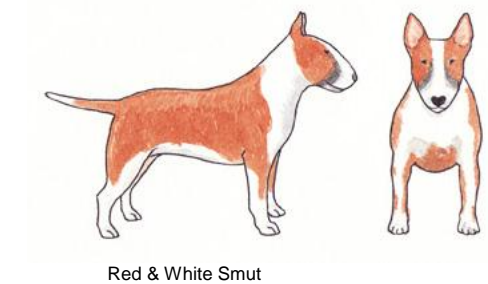
Clear Red Solid



Red Solid Smut



Clear Red & White



Red & White Smut

3) Fawn –

This colour is a very pale version of tan or red (it may be almost cream-coloured) and is believed by geneticists to be just a paler version of Red. Rufous polygenes are multigenetic modifiers which enhance warm colour but when these are inactive, as in the case of the fawn colour, the expression which results is a rarer and less favoured 'cold' colour.

There are similar varieties to Red –

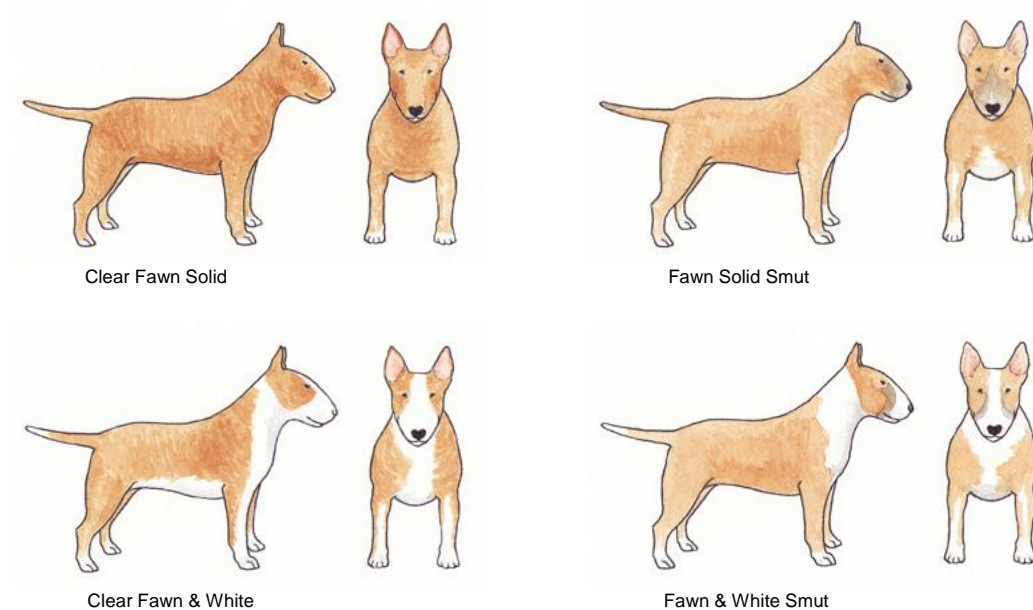
Fawn Solid – fawn with hardly any white markings – it might have a small white blaze on the nose, patch on the chest and white on the toes

Fawn & White – fawn with strong white markings on the nose, collar, chest, underbelly, lower legs and feet and tail tip

Fawn Smut – fawn with a dark mask on the face and tip of the tail

Clear Fawn – fawn with no dark mask on the face or tail

This also results in four combinations –



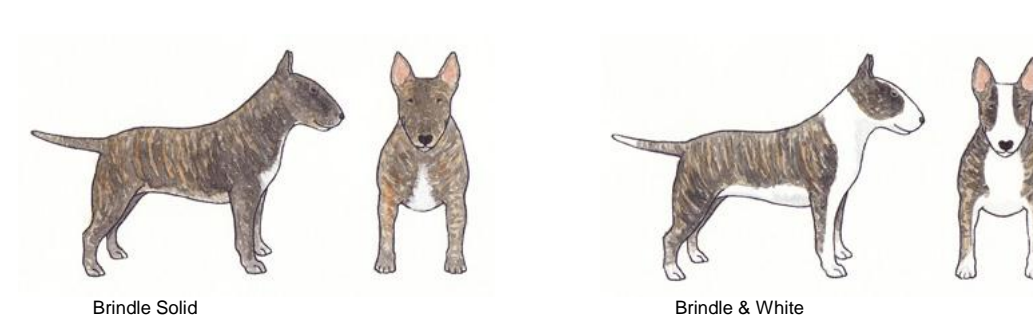
4) Brindle –

This is a pattern of fine black lines superimposed on a variable red or fawn base colour producing a wide range of colours – gold brindle, silver brindle, red brindle and from light to dark brindle.

There are two varieties –

Brindle Solid – brindle with hardly any white markings – it might have a small white blaze on the nose, patch on the chest and white on the toes

Brindle & White – brindle with strong white markings on the nose, collar, chest, underbelly, lower legs and feet and tail tip



5) Black & Tan/Tricolour –

This pattern is black with tan markings on the eyebrows, cheeks, chest, lower legs and bottom. If minimal white is present, it is called a **Black & Tan Solid** but if there is black and tan colouring with white markings on the face, collar, chest, underbelly, feet and tail, then it is called **Tricolour**.



Black & Tan Solid



Tricolour

6) Black Brindle –

This pattern is black with brindled markings on the eyebrows, cheeks, chest, lower legs and bottom. The brindle colour can be very variable. If minimal white is present, it is called a **Black Brindle Solid** but if there is black and brindle colouring with white markings on the face, collar, chest, underbelly, feet and tail, then it is called **Black Brindle & White**.



Black Brindle Solid



Black Brindle & White

Let us now consider the 14 loci and the different alleles which determine the colour genotype options and compare the Bull Terrier to other dog breeds. All mammals have two forms of melanin in their coats. Eumelanin is a dark form (black/brown) and phaeomelanin varies from light cream through yellow, tan and red to a deep mahogany colour. The 14 loci act on the pathways that produce these two major pigments or on the distribution of these pigments in the coat. The combined effect of these loci is the colour of the dog. Of these 14 loci, ten of them are identical in all Bull Terriers and therefore cause no variation in Bull Terriers. Let's evaluate these ones first.

The B-Series Locus – Black/Brown Pigment Series

The gene at this locus, known as TYRP1, is responsible for black or brown pigment at any location but is particularly visible in the nose and around the eyes and mouth. There are *B* and several *b* alleles. A *bb* genotype is responsible for liver-coloured or even pink-coloured noses. All Bull Terriers have the *BB* genotype and phenotype of the black pigment so this locus causes no variation in Bull Terriers.

The C-Series Locus – Colour Depth or Albino Series

This dilution gene causes albinism in many mammals but not in dogs. Most dogs are believed to be *CC* for full colour expression but a *c^{ch}* allele when homozygous, *c^{ch} c^{ch}*, causes chinchilla in

some breeds or silvering of colour as seen in liver-coloured dogs. All Bull Terriers are believed to have the *CC* genotype and full colour expression phenotype.

The D-Series Locus – Pigment Density Series

This *MLPH* gene is associated with dilute colour and causes black coats to show gray or blue and brown coats to show pale brown in the double recessive genotype *dd*. This is not expressed in Bull Terriers. All Bull Terriers are believed to have the *DD* genotype and normal pigment density.

The G-Series Locus – Progressive Greying Pattern

This gene is responsible for the replacement of coloured hairs with uncoloured hairs as the dog ages. This loss of pigment may begin in puppyhood, progress and cease once adulthood is reached or continue throughout the dog's lifetime. It is not fully understood and this gene may or may not cause the greying around the muzzle when the dog is very old. Bull Terriers are believed to have the genotype *gg* i.e. no progressive greying pattern. However more research is needed into this gene as many Tricolour Bull Terriers seem to show this phenomenon in their phenotype.

The P-Series Locus – Pigment Dilution

Not much is known about this gene which is believed to dilute both melanins: eumelanin and phaeomelanin. It causes pink eyes in some mammals. It is occasionally seen in Pekinese dogs. Bull Terriers are believed to be *PP* or not diluted.

The I-Series Locus – Intensity Dilution

This little-known gene appears to be responsible for the dilution of the phaeomelanin pigment only. All Bull Terriers are believed to be *II* i.e. intense colour with no dilution.

The M-Series Locus – Merle Pattern

This is another dilution gene known as *SILV* and is responsible for the merle and double merle coat patterns seen in some breeds. The pattern is caused by the *M* allele and although dominant, it seems to have a comparatively high probability of mutating back to the *m* allele of no merle pattern. This locus has absolutely no effect in Bull Terriers as all are believed to be *mm* – no merle pattern.

The H-Series Locus – Harlequin Pattern

Harlequin is a pattern of ragged black patches on a white background often seen in Great Danes but does not occur in Bull Terriers at all. The *H* allele is only expressed if the *M* allele causing the merle pattern is also present. Bull Terriers are thus *hh* at these loci.

The T-Series Locus – Ticking Pattern

Ticking is shown by coloured hairs appearing in the areas left white by the *S-Series Locus*. The alleles are *T* for ticking and *t* for no ticking. Ticks are a fault as laid out in the Standard of the Bull Terrier so this phenotype has been selectively bred out. All Bull Terriers should have the *tt* genotype with no ticking. Of course mutation of the gene from *t* to *T* could, and does, cause ticking to appear.

The R-Series Locus – Roan Pattern

Roan is a pattern consisting of intermingled pigmented and unpigmented hairs often occurring in dogs also showing ticking. Future research may reveal that it is a variation of ticking rather than a separate pattern. At present, Bull Terriers are believed to be *rr* i.e. no roan pattern.

The next four Series are the ones which influence coat colour variation in Bull Terriers.

The A-Series Locus – Dark Pigment Pattern or Agouti Series

There are actually five alleles possible in the A-Series loci. This is known as the Agouti gene and its expression is affected by both the K-Series and the E-Series loci. We will consider only the options available in the Bull Terrier breed, which are the two alleles A^y and a^t . A^y is completely dominant over a^t – this means that this a^t pattern will only be visible as a double recessive, $a^t a^t$. (The capital letter A was reallocated to the A^y allele when the A^s allele, which was considered the most dominant in this series, was moved to the K-Series where it became K^B .)

The genetic options for Bull Terriers are:

Genotype	Phenotype	Comment
$A^y A^y$	Tan/Sable colour	Either of these are carried by Fawn and Red Coloured Bull Terriers.
$A^y a^t$	Slightly darker Tan/Sable colour	
$a^t a^t$	Tan Point/Black & Tan Pattern	This is carried by Black & Tan, Tricolour and Black Brindle Coloured Bull Terriers.

Basically there are two base coat options for a Bull Terrier: the red/fawn colour or a black pattern over the red/fawn colour where the red/fawn colour is visible as marks on the eyebrows and cheeks and edging the black on the chest and lower legs and on the bottom under the tail.

The K-Series Locus – Brindling Pattern

This locus was only discovered in 2007 by the Genetics team under Prof. Greg Barsh at Stanford University. Before this, the characteristics of this locus were attributed to the A-Series locus and the E-Series locus. There are three alleles – K^B , k^{br} and k^y where K^B is dominant to k^{br} and k^y while k^{br} is dominant only to k^y . As the K^B allele for a fully black coat is not present in the Bull Terrier population, the only alleles affecting Bull Terriers are k^{br} and k^y .

This results in the following genetic possibilities:

Genotype	Phenotype	Comment
$k^{br} k^{br}$	A-Series colour with brindling pattern on the tan/sable	Either of these are carried by Brindle and Black Brindle Coloured Bull Terriers.
$k^{br} k^y$	A-Series colour with brindling pattern on the tan/ sable	
$k^y k^y$	A-Series colour with no brindling pattern at all	This is carried by Red, Fawn, Tricolour or Black & Tan Coloured Bull Terriers.

As the k^{br} allele is dominant, if a Bull Terrier has this allele, it will display the brindle pattern and can pass on the brindle pattern. A dog not showing brindle, has no brindle to pass on to its offspring. The only exception is in a White Bull Terrier carrying the k^{br} allele, which can pass on brindle but doesn't display it due to the white mask.

The E-Series Locus – Pigment Extension

The MC1R gene present at this locus is responsible for the melanistic mask being present or absent in Bull Terriers. The mask causes darker colour on the muzzle extending mainly up towards the eyes and sometimes visible on the top of the back and tail. Until 2007 it was believed that this locus controlled the brindle pattern as well as the dark mask which is known as smut marking. It was believed that a dog could either be brindle or smut but not both. With the separation of these loci, Brindle dogs (in fact any colour) can also have smut markings even if they are not visible due to the dark overall colour. This locus has three alleles which are *E*, *E^m* and *e*. The *E* allele causes normal colour extension with the colour defined by the A-Locus Series. The *E^m* allele causes a dark mask on the face over the colour defined by the A-Locus Series. The *e* alleles in its homozygous state (*ee*) overrides any A-Locus Series expression and produces a phenotype of solid yellow as seen in breeds such as the Labrador Retriever. It is believed that the *e* allele is not present in Bull Terriers.

This results in the following options for Bull Terriers:

Genotype	Phenotype	Comment
<i>EE</i>	Solid colour as defined by A-Locus Series – no dark mask	
<i>EE^m</i> <i>E^mE^m</i>	Colour as defined by A-Locus Series but with a dark mask	The dark mask can often be obscured by white face markings caused by the S-Series

This gene is a difficult one to consider as the dark mask is only really properly visible in Red Solids (and Fawn Solids) causing Red Smut (and Fawn Smut). In Red & White and Fawn & White dogs (and even in Brindle & White), the mask is covered by the white facial patches and can only be visible as black lip markings or black tear marks. In Brindle and Black & Tan colours, the dark mask is not seen unless in the case of Brindle, the Brindle colour is very pale. The back facial mask may be much more common than it appears to be.

The S-Series Locus – White Spotting Pattern

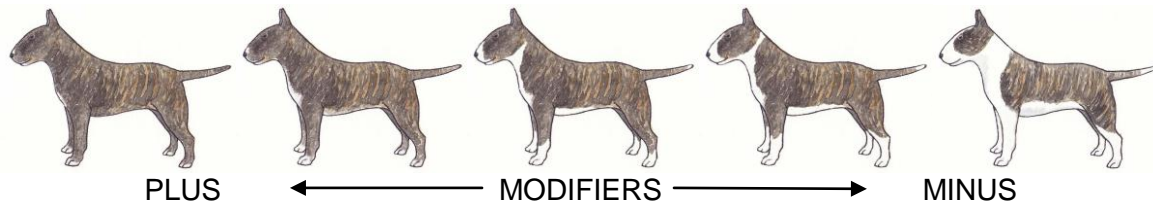
This is a very interesting locus affecting the distribution pattern of coloured or of white areas on the body surface. There are 4 established alleles –

- *S* for solid colour – refers to self-coloured – or solid colour with little or no white
- *sⁱ* for irish spotting – variable white on the face, chest, underbody, lower legs and feet and tail tip
- *s^p* for piebald – more than half white, it appears to have large coloured spots on a white background.
- *s^w* for extreme white – completely white, it may have some colour markings but these are confined to the head

Each of these alleles causes a certain amount of coloured and white areas and these fluctuate around an average colour distribution for each allele which the main gene tries to produce. Unfortunately this is a particularly complicated locus due to the effect of genetic modifiers. Modifiers are genetic factors independent of the main gene that act on the expression of the main gene. In this particular case, there are modifiers called 'plus' modifiers which cause more pigment in the phenotype than is expected for the genotype and there are modifiers called 'minus' modifiers which cause less pigment in the phenotype than expected for the genotype. This results in it being almost impossible to discern genotype from phenotype except in the case of the extreme white dog which would be *s^ws^w*. Even in this case, minus modifiers cause the dog to be completely white whereas plus modifiers cause coloured patches on the head. While it was believed that the *s^p* piebald allele was not found in Bull Terriers any more, recent increases in the occurrence of white markings high on the hind legs and on the backs of coloured Bull Terriers suggests that it is

present. Even a single copy of this genetic allele arising from spontaneous mutation could cause significant white markings in conjunction with the influence of the minus modifiers.

The following diagram is an adaptation of a similar diagram for colouration in the Basenji in Clarence Little's 1957 book "The Inheritance of Coat Color in Dogs" showing how individuals with the same genotype – in this case $s^i s^i$ – can have such variable phenotypes due to the actions of modifiers.



This means that there is huge overlap in phenotype between different genotypes. Although the above dogs all have the genotype $s^i s^i$, those towards the left would look the same as dogs with the genotypes SS , Ss^i and those dogs towards the right would look the same as dogs having the genotypes Ss^w and $s^i s^w$. Thus the genotypes SS , Ss^i , $s^i s^i$, Ss^w and $s^i s^w$ are indistinguishable from each other due to the action of the plus and minus modifiers. When looking at Bull Terriers, there are clearly three colour patterns as far as white markings are concerned: all white (with patches of colour on the head in some cases), strong white markings on the nose, chest, collar, neck, underbelly, lower legs and tail tip and minimal white markings (most likely on the toes, chest or nose). To simplify any genetic analysis we can assign the following genotypes to these phenotypes:





Genotype	Phenotype	Comment
$s^i s^i$	Little or no white confined to the blaze, chest and toes	This is the case in the so-called Solid Bull Terrier
$s^i s^w$	White blaze, chest, collar, underbelly, lower legs and feet and tail tip, white may only cross the back of the body at the neck	This is the case in the Coloured & White Bull Terrier
$s^w s^w$	All white – may have some colour markings confined to the head	This is the case in the so-called White Bull Terrier

We may be excluding the S allele and the SS , Ss^i and Ss^w genotypes but as they are indistinguishable from $s^i s^i$ and $s^i s^w$ genotypes when expressed, this has little effect on our genetic analyses. Rather it is the significant influences of the plus and minus modifiers on *all* of the alleles of this S -series gene and their possible genotypes that cause confusion between Solid-Coloured and Coloured & White Bull Terriers. Sometimes a genetically Solid-Coloured dog can have quite significant white on the chest – it proves it is genetically Solid-Coloured by an inability to produce White puppies. Alternatively, a dog with hardly any White marking can unexpectedly produce a White puppy thereby demonstrating that genetically it is actually Coloured & White.



The $s^w s^w$ genotype is the one that James Hinks was originally breeding for in the 1800s. The effect of this genotype is a white mask over a Coloured Bull Terrier. All White Bull Terriers still have colour genetically and can pass these colours on to their offspring. As all White Bull Terriers have this double recessive, when bred with each other they will always only produce White puppies. It is interesting that when this white marking is on the muzzle for example in the case of a Coloured & White Bull Terrier, it can hide the smut markings caused by the E -Series Locus. Sometimes just a portion of the smut mask is visible forming a black lip marking or tear marks on the sides of a white blaze.

Putting these four loci together there are a variety of genotype options which would describe the phenotypes observed in Bull Terriers.

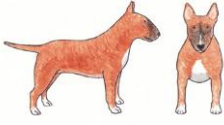
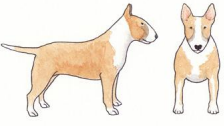
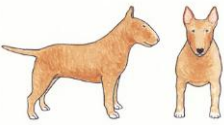

WHITE BULL TERRIERS

Phenotype	Option	Genotype	Comment
White carrying Red/Fawn 	1 2	$A^Y A^Y k^Y k^Y s^w s^w$ $A^Y a^t k^Y k^Y s^w s^w$	No E-Series locus has been included as the effects are not visible in White Bull Terriers.
White carrying Brindle 	1 2 3 4	$A^Y A^Y k^{br} k^{br} s^w s^w$ $A^Y A^Y k^Y k^Y s^w s^w$ $A^Y a^t k^{br} k^{br} s^w s^w$ $A^Y a^t k^{br} k^Y s^w s^w$	
White carrying Black & Tan 	1	$a^t a^t k^Y k^Y s^w s^w$	
White carrying Black Brindle 	1 2	$a^t a^t k^{br} k^{br} s^w s^w$ $a^t a^t k^{br} k^Y s^w s^w$	



BLACK & TAN/ TRICOLOUR BULL TERRIERS

Phenotype	Option	Genotype	Comment
Black & Tan Solid 	1	$a^t a^t k^Y k^Y s^j s^j$	Again, the E-Series locus has been omitted because it cannot be determined from the phenotype.
Tricolour 	1	$a^t a^t k^Y k^Y s^j s^w$	



RED BULL TERRIERS

Phenotype	Option	Genotype	Comment
Red/Fawn Solid Smut 	1	$A^y A^y k^y k^y E^m E^m s^i s^i$	The E-Series locus effects are most visible on Red Coloured dogs. For this reason, this part of the genotype has been included here to distinguish between Red Smuts and Clear Reds. If the E-Series locus was not considered, then these 12 genetic options would decrease to 6.
	2	$A^y A^y k^y k^y EE^m s^i s^i$	
	3	$A^y a^t k^y k^y E^m E^m s^i s^i$	
	4	$A^y a^t k^y k^y EE^m s^i s^i$	
Red/Fawn & White Smut 	1	$A^y A^y k^y k^y E^m E^m s^i s^w$	
	2	$A^y A^y k^y k^y EE^m s^i s^w$	
	3	$A^y a^t k^y k^y E^m E^m s^i s^w$	
	4	$A^y a^t k^y k^y EE^m s^i s^w$	
Red/Fawn Solid Clear 	1	$A^y A^y k^y k^y EE s^i s^i$	
	2	$A^y a^t k^y k^y EE s^i s^i$	
Red/Fawn & White Clear 	1	$A^y A^y k^y k^y EE s^i s^w$	
	2	$A^y a^t k^y k^y EE s^i s^w$	

BRINDLE BULL TERRIERS

Phenotype	Option	Genotype	Comment
Brindle Solid 	1	$A^y A^y k^{br} k^{br} s^i s^i$	Because it is so difficult to distinguish between a Brindle dog with a mask and one without a mask, the E-Series locus has not been included to simplify the task of predicting colour probabilities in litters.
	2	$A^y A^y k^{br} k^y s^i s^i$	
	3	$A^y a^t k^{br} k^{br} s^i s^i$	
	4	$A^y a^t k^{br} k^y s^i s^i$	
Brindle & White 	1	$A^y A^y k^{br} k^{br} s^i s^w$	
	2	$A^y A^y k^{br} k^y s^i s^w$	
	3	$A^y a^t k^{br} k^{br} s^i s^w$	
	4	$A^y a^t k^{br} k^y s^i s^w$	

BLACK BRINDLE BULL TERRIERS

Phenotype	Option	Genotype	Comment
Black Brindle Solid 	1 2	$a^t a^t k^{br} k^{br} s^j s^j$ $a^t a^t k^{br} k^y s^j s^j$	Again, the E-Series locus has been omitted because it cannot be determined from the phenotype.
Black Brindle & White 	1 2	$a^t a^t k^{br} k^{br} s^j s^w$ $a^t a^t k^{br} k^y s^j s^w$	

In conclusion, initiatives like the Canine Genome Project, are resulting in major advances in our understanding of dog genetics. Work with many different breeds of dog is simplifying the ability to identify the genotypes of individuals and to use this information to predict the probability of particular inherited characteristics in dog litters. Dog breeders can obviously use this information in planning their breeding programmes (specifically in mate selection). Litter outcomes can also be used to verify genotypes of parent dogs.

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REFERENCES

- Barsh, G. 2007. How The Dog Got Its Spots. *Nature Genetics*: 39(11):1304-1306.
- Bowling, S. A. Color Genetics in Animals. <http://bowlingsite.mcf.com/Genetics/Genetics.html>
- Briggs, L. C. and Kaliss, N. 1942. Coat Color Inheritance in Bull Terriers. *Journal of Heredity*: 33: 223–228.
- Burford, A. G. The Genetics of Breed Color in the American Pit Bull Terrier. *American Dog Breeders Assoc. Publication*.
- Candille, S.I., Kaelin, C.B., Cattanaach, B.M., Yu, Bin, Thompson, D.A., Nix, M.A., Kerns, J.A., Schmutz, S.M., Millhauser, G.L., and Barsh, G.S. 2007. A^β-Defensin Mutation Causes Black Coat Color in Domestic Dogs. *Science*: 318(5855): 1418–1423.
- Coppinger, R. and Coppinger, L. 2001. *Dogs – A New Understanding of Canine Origin, Behaviour and Evolution*. Scribner, N.Y.
- Eberhard, E. 1971. *The New Complete Bull Terrier*. Howell Book House, New York.
- Glyn, R. H. 1950. *Bull Terriers and How to Breed Them*. Hall Publisher, Oxford.
- Harris, D. O. 1990. *Full Circle – A History of the Colored Bull Terrier*. D. O. Harris, USA.
- Hogarth, T.W. 1932. *The Coloured and Colour Breeding*. Walker, Galashiels.
- Hogarth, T.W. 1936. *The Bull Terrier Notebook*. Walker, Galashiels.
- Kerns, J.A., Cargill, E. J., Clark, L. A., Candille, S. I., Berryere, T. G., Olivier, M., Lust, G., Todhunter, R. J., Schmutz, S. M., Murphy, K. E. and Barsh, G. S. 2007. Linkage and Segregation Analysis of Black and Brindle Coat Color in Domestic Dogs. *Journal of Genetics*: 176: 1679-1689.
- Little, C.C. 1957. *The Inheritance of Coat Color in Dogs*. Comstock, Ithaca, N.Y.
- Mackay-Smith, W. E. 1980. *From James to Jim: The Next Ten Years, 1969-1978*. KNA Press.
- Ostrander, E. A. and Wayne, R.K. 2005. The Canine Genome. *Genome Research*: 15: 1706-1716.
- Schmutz, S. M. and Berryere, T.G. 2007. Genes affecting coat colour and pattern in domestic dogs: a review. *Animal Genetics*: 38(6): 539-549.
- Schmutz, S.M., Berryere, T. G., Ellinwood, N. M., Kerns, J. A. and Barsh, G. S. 2003. MC1R Studies in Dogs with Melanistic Mask or Brindle Patterns. *Journal of Heredity*: 94(1): 69–73.