The Genetics of Breed Color In The American Pit Bull Terrier
by Amy Greenwood Burford B.S.

One of my responsibilities as a member of the staff of the American Dog Breeders Association is to be the 'color expert'. I believe that my many years of experience in the breed, as well as the opportunity to have grown up in a true 'American Pit Bull Terrier' family. has given me the exposure that it requires to know the descriptive terms to describe the many diverse colors in our breed. The color description that is placed on your ADBA registration papers does not in any way attempt to depict the genetic makeup (genotype) of the individual dog. Instead it is a description of the dogs actual color that you see (phenotype). This color description is used for identification only and in many cases does not predict what color combinations the individual dog will produce in its offspring.

Over the course of the last few months, I have received a surprising number of questions concerning color and the genetic inheritance of color. Questions such as: 1. The blue color in the APBT in the past was very rare. How are so many kennels now producing blues in such numbers? 2. It is possible to produce a puppy with a black nose, when both parents have red noses? 3. Where does the chocolate coloring come from? 4. How did I produce a brindle from a line that has never had brindle dogs? In my review of the genetics of color in the American Pit Bull Terrier, I will review a few of the principals of genetic inheritance in general and look at the research that has been done in the field of color genetics in our breed in an attempt to give our readers a better understanding of color genetic as well as provide answers to the above questions.

GENETIC PRINCIPALS

Each offspring inherits one half of their genetic make-up from their sire and one half from their dam. All members of the genus canis, to which all dog breeds belong have 78 chromosomes. They appear in pairs and consist of chains of DNA material. Small sections of these DNA chains make up genes, the genetic code for the production of certain proteins in the individual dog. The genetic material for particular traits in the dog are located in certain regions on the chromosomes called loci (plural) or locus (singular). The different assortment of genes that are possible are a particular locus are called alleles. In many different breeds, through selective breeding, only one allele is found at a particular loci, leading to all members of the breed having the same trait. This is why purebred dogs will breed true, for those characteristics that distinguish one breed from another. Alleles exhibit a dominance relationship when paired with a different allele. When the alleles are different at the same loci, they are said to be heterozygous. When the alleles are alike at the same loci, they are said to be homozygous. Dependent upon how many different alleles are possible there are multiple combinations of dominance. The term epistatic (above), means more dominant and hypostatic (below) means less dominant. Geneticists use an upper case letter: example (A), to signal a dominant allele, and a lower case letter: example (a) to denote a recessive allele.

The study of color genetic within a breed can be complex, as there are nine different locations (loci) on the chromosomes that effect the final color that you see in your dog. At each loci are two or more alleles, or gene choices, that interact according to their dominance-recessive relationships. At loci that have more than two alleles, the relative dominance in the series have been listed in order of their dominance.

Genetic research into the genotypes of coat color has not been done with UKC or ADBA

registered APBT. The reason is this: throughout the history of our breed, dogs have not been bred for color. All colors were considered equal. An individual dog was selected as breeding stock based upon a multitude of factors, none of them being color. The canine genetic research into the genotype of color has been done solely in AKC registered breeds. One of the breeds that has been studied is the American Staffordshire Terrier. As a matter of review, it is important to understand that every dog accepted into the AKC registry as an American Staffordshire Terrier was also registered with the UKC or ADBA as an American Pit Bull Terrier. The year was 1936, and the popularity of the Our Gang Comedy and show's mascot, Petey, prompted the AKC to open their stud book to the breed as long as the breed name could be changed to the American Staffordshire Terrier. No other breed has been crossed into the AKC American Staffordshire Terrier lines, so we are justified in examining the results of this research and applying it to our ADBA registered dogs. The researched results of the color genotypes possible in our breed, at the nine loci responsible for the determination of color are presented below:
As/Ay/at, B/b, C, D/d, E/Ebr/e, g, m, S/si/sp/sw, t

Locus A Series: Dark Pigment Pattern
This locus has six different alleles possible in the canine population. Only three are present in the APBT breed.
(As) dominant Black
(Ay) dominant Yellow
(at) bicolored pattern (tan 'Doberman like' markings on a solid coat)
The A alleles are pattern factors that control the amount and area distribution of dark and light pigment. They act within the hair follicle to switch pigment synthesis between light and dark. It is important to remember that alleles at this locus interact with Locus E alleles.
(As) - DOMINANT BLACK: This allele produces uniform coverage of dark pigment over the entire body. Its action is expressed in all dogs with black or brown coats. The (As) allele is almost completely dominant over others in the A series. The black color ranges from pure black to a black with a brownish cast (seal). Geneticists are uncertain if the allele is incapable to produce pure black without additional help from another locus, or if the brown cast indicates a heterozygous allele.
(Ay) - DOMINANT YELLOW: The (Ay) allele restricts dark pigment, producing yellow colors. When homozygous, the coat can be clear gold, but often has black tipped hairs, especially on the head and down the back.
(at) - BLACK AND TAN PATTERN (BICOLORED): The typical tan points are above each eye, on each cheek, on the lips and lower jaw, extending under the throat, two spots on the chest, below the tail, and on the feet to the pasterns and hocks, extending up the inner sides of the legs. These tan points can occur on black or seal, blue, chocolate or red solid colored dogs. A great deal of variation can occur with these tan points, even within the depth of the pigment. In some dogs the tan points are not always marked and the color contrast is not always distinct.

Locus B Series - Black/Brown Pigment
(B) black pigment
(b) brown pigment
This locus contains only two alleles, the dominant (B) producing black skin and nose pigment and the (b) recessive allele, producing brown pigment. In dogs that are red or buckskin, the Locus (B) alleles are expressed in skin color, most visible around the eyes and nose. The black

nose indicates the genotype is (BB) or (Bb), both which would be expressed as black nose because of the dominance of the (B) allele. A light brown or red nose is (bb), or homozygous recessive. Being homozygous recessive, both parents must contribute one recessive (b) gene to the offspring to produce the red nose. When breeding two dogs with the (bb) genotype, the only resulting combination in the pups would be (bb) or red nose.

Locus C: Pigment depth
The Locus C series controls the production of pigment throughout the coat. In dogs, the expression of the Locus C alleles is based on observation rather than experimental studies. The American Staffordshire Terrier breed is felt to have only the dominant (C) allele at this locus. The C allele allows the full expression of color, of dark and light pigments. The allele (cch) or Chinchilla Dilution, found in other breeds at this locus, causes the light pigments to be diluted out in various degrees. This would account for the varying shades found in many littermates depending on their homozygous or heterozygous pairing. The chinchilla dilution allele (cch) does not affect the dark pigment, thus allowing for the white dog with black skin pigment and black nose. Other researchers (Robinson) feel that other modifier polygenes are responsible for this phenotype.

CC	full color
Ccch	medium shade
cchcch	pale shade

Locus D pair: Pigment density

(D)	intense pigment density
(d)	dilute pigment density

The locus D pair modifies the density of the pigment. The dominant (D) gives full density in both the heterozygous (Dd) or the homozygous (DD) combination. The homozygous recessive (dd) alleles dilute the color. When the dogs basic color is produced by dark pigment, genotype (Bbdd) or (BBdd) yields the color known as blue. The black coat is modified as well as the skin pigment to a gray or blue pigment around the eyes, pads and nose. When the dogs basic color is produced by a light pigment the genotype bbdd (dilute brown pigment) produces a fawn with a silvery cast known in our breed as a fawn/bluies. The skin pigment around the eyes is flesh colored as well as a red or brown colored nose.

Locus E Series: Extension

(Em)	black mask
(Ebr)	brindle
(E)	extension of dark pigment
(f)	restriction of dark pigment

The Locus E alleles affect the extension of dark pigment, and all of the alleles at this locus interact with those of locus A.
(Em) - BLACK MASK: This allele is dominant to all others in the series and is expressed as a black mask on dogs that are not solid black. One researcher, Robinson, considers the evidence that the black mask belongs in the E series as unconvincing and assigns it to a different series.
(Ebr) - BRINDLE PATTERN: The brindle allele produces the brindle pattern with stripes or bars of dark pigment on a background of light pigment. In dogs with the dominant (As) allele, which produces a solid coat of dark pigment (brown or black), the (Ebr) allele is masked because

there is no light pigment on which it can act. It is dominant over the extension (E) allele. In our breed, interactions with alleles at the B and D loci produce a rich variety of brindle colors:

Ay-B-D-Ebr- black brindle
Ay-B-ddEbr- blue brindle
Ay-bbD-Ebr- brown or chocolate brindle
Ay-bbddEbr- fawn brindle

(The (-) as the second allele at the locus pair denotes an allele that is uncertain because of the dominant nature of the first allele. It could be homozygous or heterozygous with any of the other alleles.)

(E) - EXTENSION: The E allele produces normal extension or expression of dark pigment. It interacts with Locus A alleles to produce a variety of effects:

As-E- black/brown
Ay-E- red or buckskin with or without black ticked hairs (on head and back) referred to as sable in other breeds

(ee) - RESTRICTION: The homozygous (ee) alleles restricts the expression of dark pigment, producing the yellow shades by light pigment. It does allow the expression of dark pigment on the nose, lips and eye rims. It is recessive to all other alleles in the E series. Homozygous (ee) alleles interferes with the expression of most Locus A alleles.

As-ee buckskin
Ay-ee light tan

Locus G pair: Progressive Graying

(g) uniform color throughout life

Research concludes that the AST breed are homozygous (gg) with dogs retaining their coloring throughout their lifetime. The G dominant allele present in other breeds produces a silvering or graying of the coat over time and the recessive (g) allele, giving a uniform color throughout the dogs lifetime.

Locus M Pair: Merle Pattern

(m) uniform pigment

Research has shown that our breed has only the recessive (m) allele at this locus. The homozygous recessive (mm) produces a uniform pigment in the breed. The (M) dominant allele produces the merle or dapple pattern. The dominant (M) allele has been identified in Collies, Shetland sheepdogs, Australian Shepherds, Cardigan Welsh Corgis, Great Danes, Louisiana Catalhoula, Spotted Leopard Dogs and Dachshunds.

Locus T Pair: Ticking

(t) no ticking

Research has shown that our breed has only the recessive allele (t) at this locus which in the homozygous recessive (tt) allows no ticking. The dark ticking that we see in our breed is determined on the Locus A series by the dominant (As) allele, not on the Locus T Pair. In some breeds this is known as a sable. In the APBT, traditionally this coloring is called black or brown ticked. There are modifier polygenes that control the location and extent of the black ticking in the breed. The dominant (T) allele at this locus causes the tiny flecks of pigmented hair in otherwise non pigmented (or white) areas. The T allele is typical in breeds such as the English setter and many of the hound breeds.

Locus S Series: White Pattern
The alleles of the Locus S series produce the white markings that are often seen in our breed. Researchers identify four alleles at this locus:

S	solid color
si	Irish spotting
sp	piebald spotting
sw	extreme piebald spotting

The above sequence reflects the decreasing areas of pigmented hairs. There is some question about the relative dominance of and interaction between the alleles in their heterozygous forms because the expression is complicated by modifier polygenes which affect all of the alleles. Our breed, which research shows carries all four of the alleles, show all ranges of white markings from solid colors to all white.

(S)- SOLID COLOR: The homozygous (S) alleles produce a solid colored coat. The modifiers will, on occasion, produce a small amount of white markings on the throat, chest, toes, abdomen and belly.

(si) - IRISH SPOTTING PATTERN: This allele produces a pattern of white on the muzzle, forehead, chest, belly, feet and tail tip. The varying size of the white area is affected by the plus and minus modifiers. Breeds thought to be homozygous for this are the Boston Terrier, Basenjis and Collies.

(sp) - PIEBALD SPOTTING PATTERN: This allele produces a widely varying areas of white. In the homozygous (spsp) genotype you would see a white dog with dark patches.

(sw) - EXTREME PIEBALD SPOTTING PATTERN: This allele further decreases the pigmented area and, depending on the plus or minus modifiers, the pattern can range from solid white to white with spots on the ears, around the eyes, and in the tail area.

GENOTYPE SUMMARY in the American Staffordshire Terrier:

Black	As-D-E-
Blue	As-ddE-
Black & Tan	atatD-E-
Red	AyD-E-
Fawn	AyddE-
Brindle	Ay-D-Ebr-
Blue Brindle	Ay-B-ddEbr-

CONCLUSION:
Question # 1: **In times past, the blue color was considered as rare in the breed. How are kennels now producing blue dogs in such great numbers?**
The D Locus pair is the loci that modifies the dark Pigment pattern to blue with the homozygous recessive (dd) alleles. Because kennels are selecting blue individuals which are homozygous recessive (dd) the only allele that a blue parent can give to their offspring is the recessive (b) allele. Breeding two blues together doubles up the recessive trait to (dd) which

modifies the dominant (As) allele to blue. If a resulting offspring happens to get the (Ay) allele from one of its parents, then the (dd) will modify this color to a fawn/bluies. If breeders are breeding dogs for the blue color, since the gene is homozygous recessive, 100% of their offspring will be (dd) and depending on the (As) or (Ay) allele on the Locus A series will have blue or fawn/bluies pups.

Question # 2: It is possible to produce a puppy with a black nose from two parents, both with red noses?
The red nose in our breed is produced from the Locus B pair with the homozygous recessive (bb) genotype in combination with the (Ay-) genotype. Mating two dogs with the genotype (bb) the result would be 100% of the pups having red noses (bb). If a pup with a black nose was produced in one of my litters where both parents had red noses, then DNA testing with parentage verification would be necessary to determine the actual sire to the black nose pup. New alleles can be produced through mutation, but proof of parentage would have to be determined using DNA to rule out a duel sired litter.

Question # 3: Where does the chocolate color come from?
The chocolate color comes from the Locus B pair with the homozyous recessive (bb) in combination with the (As) allele. The dilution gene (dd) will also modify this dark chocolate to a light or almost milk chocolate. In most cases, the nose color is also light brown or as we say 'chocolate/red nose'.

Question # 4: How did I produce a brindle from a line that has never had brindle dogs?
The Locus E Series (Ebr) allele causes the brindle color pattern when this dominant allele is present in combination with the (Ay) allele. The (Ebr) allele is dominant except in dogs with the (As) allele. In the case of the (As), the (Ebr) allele does not have a light pigment to work on, the brindle will remain hidden. In tracing a brindle dogs bloodline, somewhere in the generations you should see a brindle dog since the (Ebr) allele is dominant. Again, if this was my litter, I would ask for parentage verification using DNA to rule out a dual sired litter.

In conclusion, I would like to advise breeders to look beyond a dog color in determining quality in terms of breeding stock. Selection should be made looking to breed type, temperament, structural soundness and overall health in that order. If the colors of the pups that result from your breeding 'Just doesn't make sense', invest in parentage verification using DNA testing. The cost is cheap, and the peace of mind is great.

Want to learn more? Contact the ADBA for a list of references.