Color Genes in the Poodle

by Dr. John Armstrong

Pigmentation in most mammals is primarily due to the presence of melanin, which is synthesized in specialized cells called melanocytes. Melanocytes come from a population of cells, called the neural crest, that is located on the dorsal mid-line of the early embryo. (Neural crest cells also contribute to a wide variety of other cell populations in the animal.)

There are two related types of melanin, dark melanin (black or brown) and light melanin (tan or reddish). In the hair, melanin is found in minute pigment granules. The genetics of coat color is largely concerned with the genes that affect the number, shape, arrangement or position of these granules, or the type of melanin they contain.

In poodles, the most common color is black. However, there is no black gene, but rather a number of genes that work together to produce black.

Specification and migration of the neural crest

The first event that could be altered is the correct specification of cells in the neural crest. If the subpopulation that would normally give rise to melanocytes never forms, the result would be an animal without pigmentation in the skin or hair. However, mutations affecting this process generally affect other neural crest derivatives and are lethal. To my knowledge, there are no known mutants of this type in the poodle.

There are also genes that affect the pathways of migration of the cells destined to form pigment. This can result unpigmented (white) areas. Two such genes have been described in dogs, *S* (spotting) and *M* (Merle). Mutant alleles of the Merle gene have not been reported in the poodle. The *S* alleles include:

- *S* ... self (complete pigmentation; dominant)
- s^i ... Irish spotting
- s^p ... piebald spotting
- s^w ... extreme white piebald

Dogs homozygous for Irish spotting have irregular white patches. The number and size of these patches is extremely variable. This is probably the allele that produces mismarks.

The piebald allele produces a fairly well defined pattern of dark and white areas. The traditional parti-colored black and white poodle, once common, and accepted for show, is likely s^ps^p. Now, inexplicably, only solid colored poodles are accepted for conformation showing.

The extreme white piebald allele is thought to be responsible for all-white animals in some breeds, but not in the poodle.

Synthesis of melanin (the *C* gene)

One thing almost universally agreed upon by geneticists is that true albinos, lacking all melanin-based pigments, result from a deficiency in the enzyme tyrosinase. Albinos are homozygous for the recessive mutant allele *c*. *CC* or *Cc* dogs have full color, as determined by the other genes carried. Albinos (*cc*) have no pigment in the nose, eyes, hair or skin - and are very rare.

In many mammals, there is a third allele, chinchilla (c^{ch}). In mice, this allele produces defective tyrosinase which cannot synthesize the normal amounts of melanin. For some reason, the melanin that is made is primarily the dark eumelanin. The degree to which the coat is lightened depends on the species. The eyes and nose generally remain dark.

In dogs, most authorities classify a chinchilla-like mutation as an allele in the C series, but I have seen no studies establishing that it directly affects the activity of tyrosinase. Chinchilla is said to have no noticeable effect on eumelanin, but reduces the color to cream in dogs that would otherwise be tan, apricot or yellow (golden). If this is correct, then a black or brown poodle should be unaffected, but a "chinchilla-apricot" ($c^{ch}c^{ch}ee$) would be cream. However, I can't help wondering whether the chinchilla allele may account for so-called "bad" blacks.

Genes affecting the relative proportion of the two melanins (*A* and *E*)

A dog carrying both an *A* (agouti) and an *E* (extension) allele will have the dark melanin (as both are dominant, only one copy of each is necessary), whereas a dog that is either *aa* or *ee* will have the lighter melanin. Generally, when all breeds are considered, *aa* more often produces yellowish-tan and *ee* the more reddish tones. Apricot poodles likely fall into the second group. Though Willis says that the a^t allele (black and tan bicolor) is found in the poodle, it is certainly rare, and would be a fault.

Genes affecting the structure of the pigment granule (*B* and *D*)

These genes do not affect the synthesis of melanin, but rather the structure and organization of the pigment granules.

The *B* gene (brown) determines whether the dark melanin-containing granules appear black (*BB* or *Bb*) or brown (*bb*). A true brown must have no black pigment anywhere including the eyes and nose.

The *D* (dilute) gene affects the apparent intensity of the pigmentation, but not through an actual reduction in the amount of melanin present. There are two alleles described in the literature, *D*, which is dominant and gives full color, and *d*, which leads to a clumping of the pigment granules in a homozygous (*dd*) animal. This leads to reduced light absorption.

In an otherwise black animal, the *d* allele is supposed to produce a "Maltese" blue (slate grey) animal, and possibly cafe-au-lait when acting on a brown. Confusion between the effects of this gene and that of the greying and silvering genes (see below) is common. The Maltese blues are said to be born blue. However, these seem to be much less common than the silver-blues, at least among the Standard poodles.

Unknown action: rufus (*R*), silver (*V*) and grey (*G*)

Red poodles are rare, generally appear in apricot lines, and appear to be the result of a separate gene. Willis, citing Robinson, talks about "rufus"genes, that are poorly characterized, but may act to darken an apricot or brown coat. As the poodle pedigrees for reds suggest only one such gene, I propose that it be called *F* (rufus; *R* is already used for roan). The recessive allele, *f*, produces red in an apricot (i.e. *eeff*), and may also affect brown, but is supposed to have no effect on black.

Most authorities describe a dominant allele (*G*) for graying; non-grey would be *gg.* Some also consider it to be the gene for silver, in which case it would have to be a partial dominant. Willis (1989), however, says that silvers are dilute greys (*ddG*); he does not indicate whether *ddGG* and *ddGg* would be the same. Searle (1968) says simply that "this dominant gene apparently leads to a progressive greying in coat-color throughout life and seems to be present in poodles."

My own study of standard poodle pedigrees is consistent with the interpretation that grey and silver are separate genes. To avoid confusion, lets call the silver allele *V*. It is given a capital letter because it is a partial dominant. In other words, if a poodle is alleles, *vv* would be black, *Vv* would be a dark blue-grey (but is commonly called blue, leading to confusion with blues caused by the dilution factor, *d*) and *VV* would be silver. Both blues and silvers are born black and "clear" during the first year, or sometimes even later. Consequently, many are registered as black and this is never changed in the official records. In addition, some are registered as grey. (However, knowledgeable breeders say they can recognize a silver shortly after birth.)

This gene also affects brown and apricot, as follows:

BBEEvv	black	...*Vv*	blue	...*VV*	silver
bbEEvv	brown	...*Vv*	silver-beige	...*VV*	champagne
BBeevv	apricot	...*Vv*	cream	...*VV*	white

The greying gene, in contrast, leads to a gradual accumulation of silver-grey hairs in the coat, generally beginning around 4-5 years of age, much as in humans. The dam of one of my own poodles (a black Mini) is two years younger than the sire, but looks older as she is turning grey and he is holding his color.

If you have managed to stick with me this far, you will likely have noticed that two different genotypes have been mentioned as possibilities for cream: *eeVv* and $c^{ch}c^{ch}ee$. Evidence for the first comes from crosses between silvers and apricots, which produce blues and creams. Lets take a look at this more closely:

Silver, *EeVV* x apricot, *eevv* => 1/2 blue, *EeVv*, and 1/2 cream, *eeVv*. (If the silver is not carrying the *e* allele, only blues will be obtained.)

However, creams are also obtained in crosses between two blacks, often at close to the expected 1/4 for a recessive trait, and with no other colors than black and cream appearing. These cannot be silvered apricots, as at least one of the parents would have to be blue, and both blue and apricot progeny would be expected in addition to black and cream.

In summary

A black poodle should be *A-B-C-D-E-F-ggS-vv*. Except for *V*, all these genes show normal dominance as far as we know. Writing the genotype as *A-*, for example, is to be interpreted as meaning that the second allele make no difference to the phenotype. The effects of the genes, singly, are as follows:

bb	brown
ch ch	"bad" blacks? (supposedly only affects light melanins)

c c	
dd	"Maltese blue" dilution (affects all colors)
ee	apricot
ff	intensifies red tones in apricot and brown
GG or *Gg*	progressive greying later in life (dominant)
s^i s^i	Irish spotting (mismark)
s^p s^p	piebald spotting (Parti-color; black & white)
VV or *vv*	silver or blue (partial dominant)

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