The Genetics of Coat Color in the Cesky Terrier

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SUMMARY

The last 10 years has seen tremendous progress in the understanding of the molecular basis of the genetics of dog coat color. Of the approximately fourteen genetic markers that have been hypothesized for determining coat color, roughly one half of them (the most important half) have been identified, located on the chromosome, and characterized, and commercially available tests can be performed on individual dogs to identify these specific markers. Tests performed on three Cesky Terriers helps support theoretical understanding of the Cesky color options from a genetic standpoint.

The Cesky Terrier Genetic History

Cesky Terriers are unique in the dog world. This breed was established from three dogs, not three breeds of dogs, but *three specific dogs*. Mr. Frank Horak, a Czechoslovakian geneticist and hunter, began his experiment to found an improved upland game dog in 1949 by using one Scottish terrier bitch, Scotch Rose and two Sealyham Terrier Dogs, Buganier Urquelle and Jason's Amorous Artilleryman (isn't this a great name for one of our founder dogs?). Amorous Artilleryman was the son of Buganeir Urquelle. Scotch Rose was bred to Buganier Urquelle once and then back to her son Balda. Amorous Artilleryman was then bred to one of the Balda/Scotch Rose progeny, Diana Lovu Zdar. A brother and sister from this Amorous/Diana litter were mated and the breed was launched. Figure 1 shows three of these founding dogs.

In 1984 and 1985 after 35 years- of Cesky breeding, Mr. Horak bred a Sealyham bitch, Andra Z Rastamoru twice to Vanek Lovu Zdar, a light-pigmentation Cesky dog, with the goal of improving the fertility of the breed. However, studies show that the genetic contribution of Andra in the typical modern Cesky is less than 0-4%, so the three founder dogs are still the most significant contributors. There are also the inevitable stories of out-breedings done with poodles, dachshunds, other Sealys and Scotties, etc. Many of these are likely true and serve to add to the fun and mystery of the investigation. However, it is fair to say that more than 95% of the genetic composition of the average modern Cesky was inherited from the original 3 founder dogs, one Scotty and a Sealyham father and son.

An analysis of a database of Cesky Terriers carefully assembled by Diana Grant (Grancek Kennels) shows that most modern Ceskys are about 25 generations removed from the initial Scotch Rose/ Buganier Urquelle cross. It is important to understand that this reference to "generations" refers to generations of dogs that were actually bred. Many litters had no dogs that were bred and are not in the pedigree chain between modern dogs and the three founding dogs and are not included in this generation count. The first 6 generations were tightly inbred between the three founders and their progeny with very few dogs actually being bred as Mr. Horak was selecting dogs to match his mental image of the perfect hunting dog. At about generation 6, the available, breed-able dogs were so limited that one dog, Cedro Bohemicus, was used almost exclusively as the sire for future Ceskys. A modern Cesky Terrier has about 80% of their genetic code *identical* with Cedro. Cedro's grandson Echo Lovu Zdar and great grandson, Ben Prasek are by far the most popular sires of the breed.

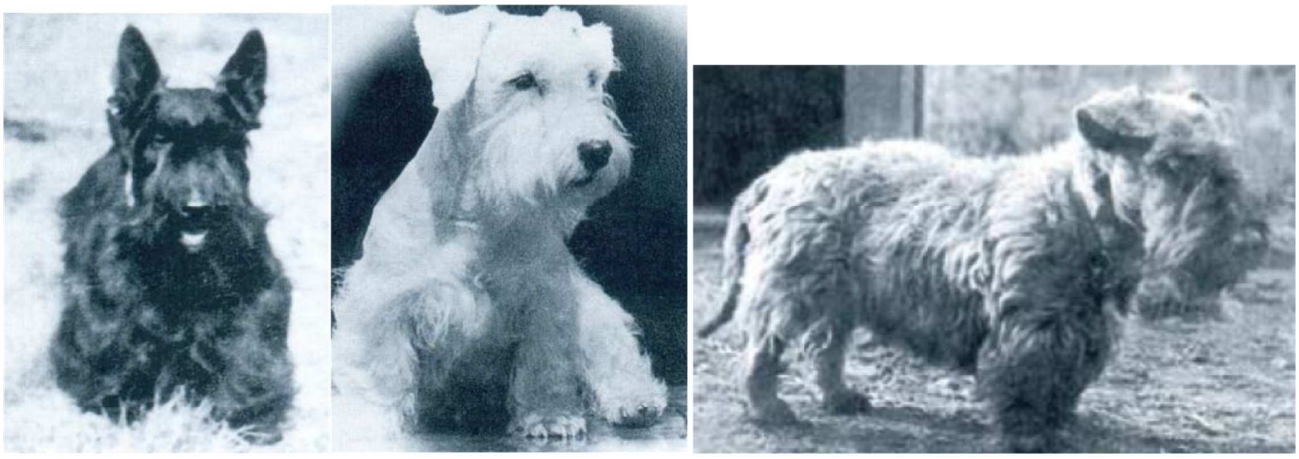

Figure 1: From left to right: Scotch Rose, the founding Scottie, Buganier Urquelle, the first of the founding Sealyham and Balda Lovu Zdar, the result of this first mating and the first Cesky dog. Balda was bred back to Scotch Rose to produce Diana Lovu Zdar, the founder Cesky bitch, who was then bred to Buganier's son, Amorous Artileryman. All subsequent breedings were Cesky to Cesky. Pictures from Hana Petrusova's book on Cesky Terriers.

This understanding of the founder dogs and the genetic bottleneck at approximately generations 6-9 are important in the Cesky pigmentation discussion. For example, we know that modern Scotties come in three colors, black, tan, and sable. This does not necessarily mean that the Cesky genome carries these three colors from the Scotty heritage. If Scotch Rose herself did not carry the genetic "palette" to create these three colors, then the Cesky does not carry them unless there are similar genes in the Sealyhams. Remember, it's just one Scotty, not all Scotties. The same goes for Sealyham Terriers, although we are talking about three "legal" Sealyhams. And even these limited genetic options were significantly reduced during the aggressive selection process of generations 1-6 as well as the Cedro Bohemicus bottleneck. The average modern Cesky Terrier has less than 35% of the genetic variability that Mr. Horak started with in the three founding dogs. The technical word for this lack of genetic variability is homozygosity. The goal of Cesky breeders is to scrupulously maintain as much remaining heterozygosity (genetic variability) as possible.

The Cesky Color

The pictures below show three Cesky Terriers that had DNA color testing performed (Paw Print Genetics, Spokane Washington), and the results are summarized in Table1. Otto (is a 3.5 year old dog, Rosie a 15mo old bitch, and Attila is a 6 mo. old dog. Attila is still a fairly dark puppy but is greying quickly. Notice the white marking on his chest. Rosie had a similar marker as a puppy. By the way, Otto is CH Grancek Otakar Malsville (Dk Ch Oneva Eduard Malsville x Ulhava del Monte de Haya Grancek), Rosie is Grancek Rozmaryna (Janski Ceskasson Blue Moon x Balzalka del Monte de Haya Grancek), and Attila is Attila del Caviano (Excalibur del Caviano x Idole du champ d'eole)

Three Color Tested Cesky Terriers.

Rosie

Otto

Attila

Table 1: Results from DNA testing for Color Markers

Test	Attila	Otto	Rosie	Expression
A Locus (Agouti)	a^t/a^t	a^t/a^t	a^t/a^t	Tricolor, black and tan (unless switched off by the K locus)
B Locus (Brown)	B/B	B/b	B/B	Black coat, nose and foot pads (B/b carries brown). b/b would produce brown coat, nose, and foot pads.
D Locus (Dilute)	D/D	D/D	D/D	Non dilute. d/d would produce dilute (pale) color at birth
E Locus (Black)	E/E	E/E	E/E	Black. e/e hands over pigmentation control to the A locus.
E^m Locus (Melanistic Mask)	E^m/E^m	E^m/E^m	E^m/e	Melanistic facial mask (E^m/e mask carrier but E^m still dominant)
K Locus (Red/Black switching)	K^B/k^y	K^B/k^y	K^B/k^y	No agouti expression allowed; "A" locus switched off.
S Locus (White Spotting, Parti, or Piebald)	S/S	S/S	S/S	No white marker. s^p is piebald and s^w is all white.

Much of the early work on canine color was done by Dr. Clarence Little (The Inheritance of Coat Color in Dogs, 1957). Since coat color is observable, it is a useful mechanism for the study of inherited traits. The letters assigned to the color genes are from Dr. Little, but work since around 2005 has been assigning molecular identifiers to these genes and actually locating them on the canine DNA. Dogs share most of these genes with other mammals (called gene conservation). There are two genes that determine coat pigmentation in all dogs (all mammals for that matter): The A (or Agouti) and the E (or Extension) locus. The A locus controls phaeomelanin, or red/tan pigmentation, and the E locus controls eumelanin, or black (or in some cases dark brown) pigmentation.

The canine color genotype also contains a K locus that acts like a switch between the two. This K locus is unique to the canine genome and has just recently been identified. It is the fairly complicated combination of these three loci that makes Cesky terriers a shade of black instead of a shade of tan/red. The markers shown above in all three dogs are really the key to Cesky pigmentation: (a^t/a^t, E/E, and K^B/k^y) and are very likely shared by almost all Ceskys. If the K locus had a different set of switching alleles, Cesky

terriers would be black and tan (similar to Welsh or Airedale terriers) with the color controlled by the A (a^t/a^t) locus. There are a few other options of the combination that could produce the Cesky pigmentation, but until these are found in a Cesky, I'll avoid the complication.

But then there is an added complexity of the time phased color characteristic. The vast majority of Cesky terriers are born black and turn grey during the first few years of their life. This is due to a *hypothesized* G marker that has yet to be located on the chromosomes, but it undoubtedly exists in some form. Some Ceskys stay dark instead of greying, so it seems logical that not all Ceskys have this greying G marker and there definitely is a time element involved since this lightening takes place in some dogs in months and some in years. We will understand this more thoroughly when the G locus has been isolated. But it is this greying of the Cesky along with the amount and timing of greying which provides the interesting variation in shading of Ceskys.

It is still unclear what causes the very pale Cesky terriers. I thought it might be the D (Dilute) locus for which there is a test. This locus produces the pale genotype in several of the breeds (Dobermans and bull terriers for example); these are the dogs that are born pale or "blue." However, Rosie, who is quite pale at 1 year, tested negative for the D marker. It is actually fortunate that the D marker is not in play, since there are some fairly serious skin problems associated with this gene. There are a number of other hypothetical genes that seem to be necessary to explain the full range of canine pigmentation, and it is likely one or more of these of these that cause the pale Cesky. Research will continue to isolate and locate these markers, and the genetic combinations that produce the range of Cesky pigmentation will come into better focus. There are a number of other canine pigmentation markers that have been located that are not relevant to Cesky terriers (such as Merle, Harlequin, Grizzle) that I will not discuss, although I did test Otto for Grizzle (negative).

Some Ceskys also have some white on them. White is tricky!!! The standard allows up to 20% but most have much less. Even though the standard allows 20% white, most Cesky breeders do not like any more than small white markings on their dogs and aggressively select away from white. White markings on dogs are created by the absence of any pigmentation in the hair. This is typically caused by three or more mutations in the S (technically the MITF) locus than can cause white spotting or even all-white. Sealyham's have a white (piebald) mutation (s^p) while the Westie has the all-white mutation (s^w). This MITF gene controls the flow of pigmentation to the hair follicles during the fetal formation, and by birth the die is cast. The most recent research suggests that this white marker is most likely expressed as a continuum of white options rather than discrete points (more analog than digital for you engineers).

White patches can also be caused by other impediments to the pigment flow to the hair which can be the result of a wide variety of genes, not necessarily pigment related, or simply chance from environmental factors; for example lack of sufficient gestation time for puppies. Both Rosie and Attila had (have) white markers as puppies, but their DNA shows S/S (no white) at the white locus. It is possible that all Ceskys with white markers will test S/S at the S (or white) locus, so we're still looking for an explanation. We do know that Horak and other early (and present) Cesky breeders select very strongly away from white, and this selection process has undoubtedly influenced the color genome.

The tan that shows up on many Cesky puppies that usually gradually fades with age is likely due to the early expression of the A (Agouti) allele before it is blocked by the K/E combination or due to an imperfect blocking process. It is important to recognize that these tan markings are different from the brown Cesky that results from a mutation on at the B locus.

The elusive brown Cesky is the result of mutations at the B locus that results in dark (or chocolate) brown instead of black. There are actually three "b" mutations. This is a recessive gene, so it takes two b alleles (any combination of the three mutations) to result in a brown dog. Mr. Horak reported a brown Cesky in one of his early litters, but there were no progeny. The most recent brown Cesky that has been reported is from the del Monte de Haya kennel of Hana Petrusova that can likely be traced back to the Andra Z Rastamoru outcross. Otto is a brown allele carrier, and although Rosie's brother is a brown carrier, Rosie is not. There are a number Ceskys that have been identified as b carriers, so it is likely that some brown Ceskys will be bred in the future, now that DNA tests can identify carriers.

The melanistic mask is a marker (Em) that expresses itself as a dark face and sometimes tail and feet. Only one allele at this locus is required for the mask expression. The dark mask will of course only express itself in dogs that lighten with age, and it is likely that certain dilution genes could wipe the dark mask away. And of course this will not show in dark Ceskys.

The surprising part of the DNA results on these three dogs is that they were almost identical in their genotype but are quite different in their phenotype (appearance). If you look at the test results in the table without looking at the pictures you would assume that Otto, Attila, and Rosie would have very similar pigmentation. I think it is likely there are other unidentified genetic markers at work to produce Rosie's very light pigmentation. Since the Em allele is dominant, all three dogs should have a dark mask, so where are the dark masks of Rosie and Attila? Rosie shows some slight evidence of the melanistic mask with the dark ears and dark tail, but the unknown gene(s) causing the very light pigmentation is (are) likely washing the dark mask away. You do have to wonder if the melanistic mask marker might be the reason the tan facial furnishings are still very pronounced at 15 months and have not faded. Attila also has this Em marker and his face already shows signs of greying and does not seem inclined to stay dark. The explanation of the difference in appearance in these three dogs with almost identical pigmentation test results will only become clear when additional markers are identified and tests are available for them.

Most of these interesting color genetic markers seem to have come from the Sealyham side of the blanket. I've seen recent Sealyham color DNA tests and they are quite similar to the ones in Table 1 except for the S/S. As a matter of fact there were several pups in the one litter I saw that had the b/b marker (brown). Scotch Rose's contribution seems to have been to remove the white from the cross, probably by eliminating the s^w and/or s^p (piebald) marker. Mr. Horak did fairly drastically select for desired traits for the first 10 generations or so, and you do have to wonder how many white dogs he discarded to eliminate the "mostly white" marker. Based on these results I would hypothesize that much of the white we see on Ceskys is not the result of mutations at the S locus as expected, but rather other more complicated physical or genetic constraints on pigment migration prior to birth. This will likely take some time to sort out.

For those of you who have further interest in canine pigmentation I recommend C. B. Kaelin and G. S. Barsh, "Molecular Genetics of Colour, Texture and Length in the Dog," in *The Genetics of the Dog*, ed, 2012 (you can find it online), or the webpage Genetics of Coat Color and Type in Dogs which can be found at this address: http://homepage.usask.ca/~schmutz/dogcolors.html. This very readible webpage is the creation of Dr. Sheila Schmutz, one of the primary researchers in the DNA of canine pigmentation.