

COAT COLOR IN THE TOLLER:

Breed history and current genetics.

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(February 2007)

INTRODUCTION: This article has been written to offer breeders of the Nova Scotia Duck Tolling Retriever a "hands-on" approach to coat color genetics and to acquaint readers with the more recent advances in coat color research, especially as they apply to the Toller. We are not "there" yet: we don't have all the answers today, but we are now on the road to answering completely and accurately all these old and persistent questions of how coat color is inherited. Breeders should keep abreast of current research so that they can breed knowledgeably. This article will start with needed terminology and then quickly move into a discussion of the various color genes, outlining known facts and recent advances. Some notes on the tradition and history of color in the Toller and a few comments on the relevance of color to a breeding program are offered in conclusion.

The Basics:

Let's begin with a bit of basic terminology. We must first define a few terms just to put them in place and get them out of the way. **A LOCUS** is simply the location of a gene; the place it lives on a particular chromosome-its street address if you will. **LOCI** is the plural. An **ALLELE** is one particular form of a gene at any given locus. Essentially you have a wild type allele (the "standard" gene), and any variation is then defined as a mutation. A mutation can be an improvement in some way, a simple variation, or can sometimes be detrimental, but is not necessarily so. Some mutations are "dominant" and many mutations (and more typically in purebred dogs) are "recessive." A dominant allele will change the dog's color when the dog has just one copy while a recessive allele requires two copies to change the dog's color. Some alleles are somewhere in between and are called "incomplete dominants" or "co-dominants." This means that the trait is seen with just one copy but that it is more pronounced if you have two copies. Some genes have a specific effect all on their own, but many are altered by the affects of genes at other locations. A phenotype, (or what you see) is the result of their combined action (and various non-heritable conditions as well).

Mutations for pigment produce the variations in coat color that we see, as well as some defects in dogs. Genes named under the old "Little" system typically were identified by what sort of effect the mutation had. The M Locus, for example, was named for the "merle" gene, as here was a dominant mutation that caused a solid coat to appear patched or dappled. The C Locus was named for the "chinchilla" gene, which is a recessive mutation that washes out a rich gold coat to a pale cream color. Under the new system, now emerging, genes are being named in an even more cryptic manner, but the newer names are more accurate and reflect new molecular data. So we shall all have to get used to them. The old Extension or "E" locus, for example, is now referred to as MC1R. This sounds rather fearsome to most of us already a bit bemused by the "E locus," but is simply "gene speak" for the actual gene (the melanocortin receptor 1) that has been found to cause the effects we associate with the E Locus. So this is a step forward really, and when you see these sorts of names that means the actual gene has been found and the action of the gene is known. Knowing this might make it easier to try to remember the new names. This is real progress, as it represents the first time we have real knowledge of the genes involved, and each discovery is quickly producing a DNA test to identify the dogs that carry that mutation. That translates into breeder power, as you will then be able to select the dog you want at the direct, genetic level.

One more quick note on nomenclature: pigment in dogs comes in two basic forms. **Eumelanin** is the dark pigment that is black, brown (i.e. chocolate) and blue by our breeder terminology. The other pigment is **phaeomelanin** and this is the bright pigment that produces red, yellow, and cream colors in canine coats. Each type of pigment is affected by different genes. Some genes function to affect the intensity of the pigment and so change jet black eumelanin of the hair coat to the warm brown tone called "chocolate" in breeds like the Labrador Retriever, and causes the nose on Tollers to change from black to a brown that is referred to as "self." Other genes are "pattern" genes and alter the distribution (not the color) of the pigment; like sable, which gives you a darker overlay (the eumelanin) over a brighter coat (the phaeomelanin). When you have more than one mutation, you can get more than one effect on the same dog. For example, you can have a normal sable Toller with either a black overlay and a black nose or a brown sable Toller with a brown or "self" nose. In the latter case both the brown pigment mutation and the sable pattern mutation are acting to produce the final effect. Note also that "white" genes are actually genes which disable the body's ability to make pigment, as areas of white actually LACK pigment (i.e. white is not a "third" form of melanin). All white genes in the Toller are actually spotting genes.

Melanocytes are the pigment producing cells of the body. The coat color genes can be divided into two groups; those that control the development, differentiation and distribution of melanocytes and those that directly affect pigment synthesis. The mature melanocytes are located at the base of the hair follicles where they synthesize pigment and release it into the hair shaft. Absence of the melanocytes leads to white spotting. As you can imagine there are lots of different genes that can mess up the melanocytes being in the right place. There is a separate set of genes whose protein products are important for proper deposition of pigment into the hair follicle. If the pigment is not evenly distributed along the hair shaft then it changes the color of the dog's coat. Dilute coat color is caused by pigment clumping in the hair shaft.

When thinking of a gene, try to not think of the dog you **see** so much (i.e. try to forget the phenotype for a moment), and start to think about the **biology** of the thing-what the gene does to make the color or pattern we see. For each gene there is a specific molecular action taking place. Thinking this way (rather than thinking "there is no buff in my pedigree!") will help you understand not only the new information on coat color, but help you learn about genetics and how disease and inherited traits in general actually occur. Each functioning gene is preserved DNA code that results in the formation of a protein. Proteins literally build bodies. Mutations alter the protein formed, so the changes you see are a result of the gene acting differently due to the alterations that occurred to it on a (sub)-molecular level. Isolating this change is the first step to identifying and controlling the gene in question. Traits that are "genetic" (that is heritable) are ultimately under our control given the right tools, so defining a trait as heritable is less dooming an individual to its fate than offering us all a hopeful message that we are going to be able to select just what we want in our dogs. That's another change we need to make in our mentality about genes: knowing a trait is inherited is **GOOD** news, even if the trait is a disease or unwanted color! So be glad a trait is inherited, as that means we can ultimately choose to have it or not have it in our dogs.

Variations in hair color can arise from either differences in pigment synthesis, or in the deposition of pigment. Hair shafts can contain black, brown, gray, red, yellow, or colorless pigment granules, where the color of the granule is dependent on the kind and amount of pigment inside it. Each hair shaft can contain greater or lesser amounts of granules, thus producing variation in shade and intensity of color. The color and amount of granules can vary between hairs and along the length of the hair shaft in a single hair.

AGOUTI LOCUS: Most all Tollers are homozygous for the sable agouti allele called **ay**. The Bannasch Laboratory tested 16 Tollers and found that they were all homozygous for the agouti allele sable. Anecdote suggests that there are some tan-point (**at**)Tollers (think Doberman markings), so this recessive allele may well exist in this breed. Tan-point puppies are the result of a mating with two tan-point carriers. In Tollers, in order to see the tan points the dogs must also have a specific allele at MC1R- more in the next section!

The agouti series works by modifying the amount of black versus yellow hair in the coat. One extreme is an all black dog and the other extreme is an all yellow dog. In between these two extremes are the sable color, black and tan and the normal allele which gives a strong banded pattern like you see in wolves.

a^y = Dominant allele that restricts dark pigment distribution; produces fawn/sable.

a^w = agouti "wild-type" allele: gives wolf-grey coloration. Also called a^g.

a^t = tan point allele: gives bicolored animal; dark body with tan points.

Red (mahogany dark red to bright red to even

EXTENSION LOCUS: Clear red animals, or "gun dog reds," are recessive for an allele at MC1R called **e**. These animals are unable to express dark (eumelanin) pigment in their hair coat, but can still show it in their skin (including eyes, as well as lips & noses). So, clear red Tollers can have black (or brown) noses and eye rims, but never appear shaded even though they are all also technically "sables" in the sense they are a^y agouti homozygotes. The genetic term for this is called **epistasis** and basically it means that the action of one gene can mask the action of the other. If no dark pigment is produced then you can't see if it is distributed into banded hair or tan points. It takes at least a single dominant <E> for any of the A locus genes to express. So Tollers that are shaded reds, puppies that had masking or sabling when young, these dogs have at least

Here is an example of a sable pup with light eyes and brown nose pigment. These pups also usually fade to a nice rich red.



pale yellow) animals with any black hairs in their coats (even if only as puppies!) are a^y genetic sables. This "color"--which varies wildly in shade given its optics--has many names in dog breeds, but is traditionally called sable from the black overlay on a red coat. If the animal is a <bb> recessive "brown" dog, this is going to be less obvious than with one with black hairs, but shading of any kind along the spine especially suggest the dog is a a^y sable. Sables tend to lighten as they age: many pups look "muddy" at birth but are a bright clear color by adulthood typically, so bright reds that are genetic sables could easily be confused as adults with the "clear red" described next. The distinction between a sable and a clear red Toller would only be noticed at a young age.

one dominant <E> gene at the extension locus. Labrador yellows, Irish Setters, and all Golden Retrievers are typically <ee> "recessive" reds. As Tollers apparently have both reds present in the breed, and both reds can interact with the "3rd" dog "red"--which is actually the B recessive brown described below--it's important to recognize all these reds **do not** come from exactly the same genetics, even if they look a lot alike. So, with so many "reds", the situation in this breed is likely subtle as to variation and requires a careful eye.

The MC1R gene has two known alleles that are now well defined:

E = allows for self colored dog; i.e. the actions of alleles of the Agouti locus can be seen.

e = restricts pigment to red/yellow (no dark

pigment can form).

The shade of red/yellow here is in large part a result of variation unrelated to the MC1R gene's main action, as ee clear red dogs, like aY homozygous shaded red dogs can come in a variety of shades. MC1R red dogs are typically born paler so their puppy coat is lighter than their ultimate adult color. This is a distinction to the shaded or agouti red, where the puppy is darker

than the adult, because the coat typically "clears" as that dog matures. Also, it's commonly observed that the paler shades of clear"red" (which can be very pale yellow or even cream) cannot produce the darkest shades of clear red, i.e. dark red or dark golden puppies do not ever come from pale blond parents in Breeds like Golden Retrievers and Labradors. So assumably some other pigment gene is acting here.

Clear or "Gun-dog" Red Tollers from pups to adult



Clear red pup with brown pigment



Clear red pup with black pigment



In the adult Toller there is very little difference between the coat color of this clear-red dog and that of the adult sable. Notice how the coat has now darkened from the lighter coloring shown in his puppy picture. This is a young dog and his coat may darken even further as he ages.

According to what we know of the history of the Toller, the initial focus in the creation of this breed was in creating a red dog, something resembling the coloring of a fox. In order to achieve this, red from a variety of different canine sources was used. This has given Tollers mutations in three different red causing genes. Since most Tollers tend to either darken or lighten toward a similar tone of red as adults, no matter which color they looked like as pups, Toller breeders generally don't distinguish between clear red or sable red when defining the colors of their pups on registration paperwork. The AKC choices for Tollers when defining the color of Toller puppies are "Red", "Golden-Red", "Fawn" and "Buff". "Red" is the default color on

the paperwork, but really, genetically what differentiates a "red" from a "golden-red" from a "fawn"? Sometimes, it's nothing, just shades of a clear-red dog, but sometimes it's a sabling gene hidden in that rich red coat. There really is nothing in the registration paperwork color choices which clearly indicates whether the dog is a sable or clear red. In the adult Toller this is a subtle difference, but for those who want to know what colors they are mixing into the "paint" of their puppies there are genetic tests available that can give breeders an exact picture of the color genetics he or she is dealing with. Color genetics testing is available through companies like Healthgene and Vetgen for a reasonable price.

Now that we've discussed the many ways red can be expressed genetically in the coat of a Toller, it's time to take a look at buffs, white markings and nose color.

BROWN LOCUS: Brown is the recessive gene that has been romantically called "chocolate" in some breeds and is also called "red", "liver", or "brown" in various other breeds. The dominant allele here produces a black dog, the recessive results in a brown dog. Actually it turns out there are at least three different recessive brown mutations here but they all cause the same coat color change. This gene is formally called **Tyrosinase Related Protein 1**, or **TYRP1** for short, and is found on canine chromosome 11. Again, this sort of "alphabet soup" name means that the gene and its action are known.

Tollers can have black or brown noses, so both the dominant here and at least one of the brown recessive alleles exists in our breed. In Tollers the nose color is described as self or black. Most of the "self-colored noses are probably recessive

brown. Even the black can be confusing since it can fade.

B = Dominant allele that allows for a fully pigmented (black) dog.

b = Recessive that permits the expression of brown (chocolate, liver, red) dilution..

Brown dogs (brown nosed dogs) are, quite literally, bleached in pigment at the molecular level (eumelanin is unprotected from hydrogen peroxide). This diluter gene works particularly on eumelanin (black) pigment; phaeomelanin (red) pigment is not affected. So in clear red Tollers this gene just affects the nose, eye rims and lips. However in sable Tollers that are not homozygous for clear red, the sabling will be brown rather than black.

Those blasted buffs

The two buff puppies in the litter can be easily distinguished from their littermates.



This three month old buff pup has very light eyes and his skin and fur appears to be bleached or faded.

DILUTION LOCUS: This is the gene that results in the blue Doberman and the blue Dane and probably causes buff in Tollers. The dominant allele here allows for full expression of color in the coat and the recessive produces a diluted color. Thus, a buff Toller is the product of two Tollers that carry the recessive dilute color gene allele. The color is present at birth (i.e. it's not a graying gene, where the dog "fades" as he matures). Dilute dogs have lighter colored noses and lighter eyes than their normal littermates. The change in color is caused by a change in the distribution of the pigment within the hair. Dilute dogs have clumps of pigment rather than a smooth even coating. Dilute is not related to pattern, so any dog of any color,

including the shaded (sable) Toller, can "show" dilute.

D = allows for black pigment to form.
d = produces blue/slate/gray dilution.

This gene affects skin and coat color simultaneously. Buff Tollers appear to be dilute in that they have lighter eyes and noses and lighter hair color than their littermates. Some breeders have reported a dilute puppy that grows up to appear normal. Since there is a test available for dilute, it would be interesting to test dilute Tollers to see if the ones that darken have the same mutation as the ones that stay light colored. Again, testing for color genetics is available through Healthgene or Vetgen for a reasonable price.

Adult Buff Tollers



Here is that same pup as an adult. While his eyes are no longer a bright blue, notice how light they still are. Also notice his fur. It's almost as if he has been given a silvery overlay.



When pictured alongside of a non-dilute Toller, a Toller Buff appears to be faded or bleached.

The troubles with white: too much, too little, or just right

SPOTTING LOCUS:

This is the traditional location of recessive white spotting patterns present in many dog breeds, including Tollers. There may actually be two or more loci involved in recessive white spotting, however tradition has placed the alleles together at the S locus. There are four alleles and incomplete dominance postulated to explain the variations seen in dogs. The truth may in fact be more or less complicated. It is an active area of research because of the association of white spotting with deafness in dogs, mice and people.

This series goes from solid to white. There can be heterozygotes: intermediate hybrids in pattern with one more dominant and one more recessive gene that produce an intermediate phenotype that is deceptive as to breeding capacity, plus there is always some range for each gene in question. The most likely alleles present in the Toller are shown below

S = allows for self-colored dog: no more than 10% body white confined to the toes and chest even when full expression of white is present.

sⁱ = "Irish pattern": produces an extension of white from 10% to 30% in a symmetrical pattern involving some or all of the following areas: feet/lower legs/belly/chest/tail tip/collar/muzzle and blaze. Recessive to S, this locus demonstrates incomplete dominance, so intermediate types appear in heterozygotes.

The problem for Tollers is the breed standard dis-

qualifies dogs with a white collar or other "excessive" white markings, and these can be part of the expression of "true-breeding" "Irish" dogs, ie. Irish homozygote. So, while the SS homozyte is going to always produce a dog nearly solid, and the S/sⁱ heterozygote ("Irish hybrid") will likely always produce a dog within the standard, in it's full range, the Irish allele can produce too much white on a Toller to meet the standard.

Note that nose color is NOT inherited separately from coat color, and in fact it is a well established principle of coat color genetics that nose color largely INFORMS as to coat color. Nose/skin color is a huge clue as to what coat color genes a dog has inherited. That said, again, inheritance is not monolithic and so not every aspect of every physical feature is purely and directly inherited after all. So as to skin color, especially with brown dilute dogs, the shade of the nose/eyerims can vary from bitter chocolate a fleshy tone, never mind some changes in nose color (again, especially with dilute colors) are seasonal, medical or what-have-you. Nose/eye rim color (that is SKIN color) in dilutes tends to appear a bit lighter than coat color; it can be the same, but is never darker. Eye color with diluter genes is also affected (lighter than black pigmented equivalent littermates, for example). So called "modifiers" are irrelevant and beg the case anyway (i.e a "modifier" is a separate gene with it's own function and interdependence in genes is anyway commonplace, so this term as absolutely no real meaning and was therefore discarded from even relevant lay discussions in the past decade). Eye color is affected by coat color genes, but also has its own dynamic.

CONCLUSIONS:

As Toller owners and breeders we usually don't think of our dogs as being anything other than red or occasionally buff. We are all aware of the fact that there is more than one way to reach that beautiful red we see in our adult dogs. Many of us have kept a watchful eye on our sable pups waiting for the dark masks and tails to fade into a beautiful rich red. But, as you can now see, there is a little more to this business of being red than meets the eye. Our little red dogs seemed so simple, but in fact their red coat color comes from 3 different red genes. What this gives us are four genetically distinct colors: clear red with a brown nose, clear red with a black nose, sable red with a brown nose and brown overlay and sable red with a black nose and a black overlay.

Given the health concerns we have for our breed, color receives little attention when it comes to genetics, mostly because, to us, these guys are just little red dogs. Given the fact that the history of our breed contains a number of different breeds including herding breeds and sporting breeds, it makes sense that we reached our current state of red by adding a number of different types of red into the mix. We are used to thinking about whether our dogs have black or brown noses and some of us might even have preferences. With new color genetic testing available for other breeds it would probably be easy to put together a test kit for Tollers where those who have preferences as to sable-red vs. clear-red, and/or brown noses, vs. black wouldn't have to experiment or guess in their breeding programs. Breeders could also test for dilutions like D to avoid producing buffs in litters where this might be a concern.

RESOURCES:

HEALTH GENE: Offers DNA-based technology including gene tests for coat color in dogs: blue, brown, both reds (agouti & extension). Website is:

<http://www.healthgene.com/>

GENMARK: Offers DNA-based technology including gene tests for coat color in dogs: merle (and soon harl) gene(s). Website is: http://www.genmarkag.com/canine_faqs.php/

Vetgen: Offers DNA-based technology including gene tests for coat color in dogs
www.vetgen.com

S. M. Schmutz, Ph.D. A current researcher on coat color in dogs who has worked extensively with coat color in the various breeds. She has a tutorial and informational website: GENETICS OF COAT COLOR IN DOGS:

<http://skyway.usask.ca/~schmutz/dogcolors.html>

JP Yousha. Author of various articles on health and color issues in dogs, research liaison for coat color research in the Great Dane. Former Chairman, Health and Welfare Committee & member of Color Research Committee, GDCA. Current member (new) Health & Research committee. Email: danehealth@gdca.org Phone (CT): 432-684-8940. Links page for color-related articles: <http://www.chromadane.com/chlinx.htm>.

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