The Genetics of Color In Labradors

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Seeing that two of the dogs I brought in for CERF exams were black Labs, the vet's assistant started telling me about her yellow Lab bitch. She was planning to breed her bitch--had bred her before to a yellow stud, and was planning this time to use a chocolate belonging to the same owner. We talked at length, and finally I asked her if she knew that the breeding she planned (chocolate x yellow) would almost certainly produce black puppies. "Why yes," she answered, "I got six black and six yellow last time."

In this article I shall try to explain the inheritance of the black, yellow and chocolate colors in Labradors. I will show how to use information from pedigrees and previous breedings to predict pup colors, and make clear why a chocolate x yellow breeding is expected to produce black pups, but black from a yellow x yellow breeding indicates a misbreeding. I have drawn upon the discussion of color genetics in Malcolm Willis's *Genetics of the Dog* **[1]**, although the information is also published elsewhere.

The inheritance effects we see are a consequence of sexual reproduction, which involves the "mixing and matching" of genetic material from sire and dam to produce offspring, which are genetically diverse. This genetic material is stored and passed on in the form of **DNA** (deoxyribonucleic acid), which is an enormously long molecule made up of a sequence of "bases," or smaller molecules, linked together. DNA is actually made up of two linked strands wound around each other to form a double helix, with each base on one strand linked to a base on the other strand. These base pairs are the elements (like letters of the alphabet), which make up the genetic code.

A sequence of base pairs, which codes for a particular trait, is called a **gene**. We think of a gene as the basic unit of inheritance, although sometimes changes (mutations) can occur in the sequence of base pairs that makes up a gene. Genes are strung one after another along the DNA molecule. The DNA of a dog exists in 78 different pieces called chromosomes (humans have 46). A close look at the chromosomes shows that they occur as pairs, one member of each of the 39 pairs being supplied by the sire and the other coming from the dam. While the two chromosomes in a pair are not identical, they are the same length and contain genes for all of the same traits in the same order.

This means that each dog has two versions of every gene, one inherited from its sire and one from its dam. They may be identical, or they may be different **alleles** of the gene. For example, a dog may have inherited the allele that codes for black coat (**B**) from its sire, and the allele that codes for chocolate (**b**) from its dam. It is useful to have a name for the portion of a chromosome that alternative alleles, like those for black and chocolate, can occupy. We call it a **locus** (Latin for "place"), and so we can refer to the B locus as that part of the genetic code, which determines black vs. chocolate. (It is possible for more than two alleles to be associated with the same locus, but there are only two at each locus discussed here.) Yellow is determined at a different locus--more on that later.

The most straightforward type of gene expression is simple dominant expression, where one allele is said to be dominant and the other is called recessive. The dominant allele, if present, determines the trait. Since every dog has two copies of each gene, one from the sire and one from the dam, every dog has combination, or **genotype**, **BB**, the genotype **Bb**, or the genotype **bb**. In the case of black vs. chocolate coat color, **B** (black) is dominant. The **B** allele is needed for the dog to be able to form black pigment. If it is absent, the dog will have no black on it anywhere: its coat will be brown (unless yellow--more on that later), its eyes are apt to be yellow or gold, and its nose and the rims of its eyes, as well as its lips, will be pigmented brown. If the dominant **B** allele is present, the dog will be able to form black pigment and its eye rims and nose will be black, as will its coat if it doesn't happen to be yellow.

The **B** allele is present for both **BB** and **Bb** genotypes, so both of these will be able to form black pigment. The **b** allele has no detectable effect in the **Bb** dog. This is characteristic of a recessive gene. In the **bb** dog, **B** is absent, no black pigment will be formed, and the dog will have brown nose and eye rims and a chocolate coat (again if it is not yellow). Interestingly, the breed standard for Labradors calls for "hazel" or brown eyes in a chocolate; the chocolate Labs brought to us for training have generally had light eyes--usually yellow or gold.

If the genotypes of parents are known, the genotypes likely for a litter of pups, along with the probability of each, can be predicted. Either of the sire's genes for a given locus can combine with either of the dam's genes for a given locus. Constructing a **Punnett Square** helps keep track of the possible combinations. A Punnett Square has a row for each allele the sire could possibly contribute, and a column for each allele the dam could contribute. Each entry in the square table is the result of combining the sire's allele for that row with the dam's allele for that column, and each possibility is equally likely. For example, if a black stud which was known to have sired chocolate puppies (genotype **Bb**) was bred to a chocolate bitch (**bb**), the Punnett Square would look like this:

Punnett Square for Bb sire bred to chocolate (bb) dam			
*		Dam can contribute	
		b	**b**
Sire can contribute	**B**	Bb	Bb
	b	bb	bb

Two of the four possibilities (50%) are **Bb**, which is black, due to the presence of one **B** allele. The other two are **bb**, chocolate, because of the absence of the **B** allele. Thus we could predict that this breeding would give half black, half chocolate pups. Keep in mind that in real life, the makeup of a litter often does not exactly match our predictions; we expect 50% males and 50% females, but a litter might well contain three males and eight females.

We can also reason backward from the colors in a litter to learn about the genotypes of the parents. If the sire in the previous example was bred to a black bitch from black parents and the litter included at least one chocolate puppy, we would know the bitch was **Bb**. Since a chocolate puppy (**bb**) must receive a **b** allele from each parent, the bitch carries the **b** allele, and since she is black, she must also carry **B**. The Punnett Square in this case would be

Punnett Square for Bb sire bred to Bb dam			
*		Dam can contribute	
		B	**b**
Sire can contribute	**B**	BB	Bb
	b	Bb	bb

If all puppies were black, we might suspect that the bitch was **BB**, but we wouldn't know for sure. Since the probable number of chocolate pups would be 25% of the litter but probabilities are often violated in a litter of pups, the absence of chocolates would not prove that the dam was **BB**. If no chocolate pups were produced in two or three breedings, we might feel pretty certain.

Yellow is determined at a different locus, the E locus, and is completely independent of the alleles present at the B locus. Yellow color is sometimes described as a modification of the hair (it does not affect eye or nose pigment) and occurs only when two recessive **e** alleles are present--genotype **ee**. The presence of a single dominant **E** (genotypes **EE** and **Ee**) will ensure a non-yellow coat, which may be black or chocolate depending upon the genes present at the B locus.

As with chocolate, the recessive yellow color (**ee**) can only occur when an **e** allele is received from each parent, so the presence of a yellow pup in a litter is an indication that both parents carry **e**. A breeding of two yellows is **ee** x **ee**, and any way you look at it; the only combination possible in the puppies is **ee**, also yellow. Hence the conclusion that black puppies from yellow x yellow indicate misbreeding.

The occurrence of black, chocolate, and yellow in Labradors is completely accounted for by specifying the alleles present at the B and E loci, making its color inheritance among the simplest in dogs. Other genes, which I have not seen fully characterized, determine how light or dark the yellow or chocolate colors may be. In a black dog, these modifiers are present but invisible.
White markings on the chest and toes are considered to be due to additive (polygenic) effects, called plus and minus modifiers. The recessive genes for "white spotting" which occur in many breeds are believed to be absent in Labradors**[2]**. Dogs which inherit many minus modifiers are likely to have white on their chests and/or feet, while dogs with many plus modifiers will be solid colored with no white.

Equipped with an understanding of the inheritance of **B**,**b**,**E**, and **e** alleles, we can try to determine the color genotypes of dogs using pedigree and progeny information, and we can make predictions about the colors of puppies produced in certain breedings. If a dog is chocolate, we know it is **bbE-**, where the dash indicates it may have either an **e** allele or a second **E**. If it has a yellow parent it must have received an **e** from that parent, and is **bbEe**. If it has produced yellow pups, it must have the capability to give them the **e** allele, and again must be **bbEe**. If it has been bred several times to yellows and produced no yellow pups, it is probably **bbEE**. If neither parent is yellow, but at least one is known to carry yellow, and the dog has never been bred to a dog that throws yellow, it is impossible to know whether it has the **e** allele and hence carries yellow.

A yellow with a black nose and dark eyes must be **B-ee**. If it has a chocolate parent or is known to have thrown chocolate pups, the "hidden" allele must be **b**. Yellows with brown noses and eye rims and yellow eyes also occur, although this color is disfavored under the breed standard. The genotype is **bbee:** these dogs are both yellow and chocolate. A breeding to a black (**B-E-**) is expected to produce black pups, but since the light-eyed yellow has neither the **B** nor **E** alleles needed for a black dog, it is incorrect to say that it "carries" black.

If we know the genotypes of both sire and dam, we can construct a Punnett Square which accounts for both B and E loci, and predict the proportions of all colors in a litter. Consider a breeding of a sire and dam, both of which are black but known to throw both yellow and chocolate. Such a sire was advertised a couple of years ago as producing an "abnormally large" proportion of colored pups when bred to bitches carrying the correct gene. Being black, sire and dam must both be **B-E-**; having produced yellow and chocolate pups, each must also have the **b** and e alleles, so in each case the genotype is **BbEe**. A **BbEe** parent can contribute the four combinations of alleles **BE**, **bE**, **Be**, and **be** to various pups.

Punnett Square for BbEe sire bred to BbEe dam					
*		**Dam can contribute**			
		BE	**bE**	**Be**	**be**
Sire can contribute	**BE**	BBEE	BbEE	BBEe	BbEe
	bE	BbEE	bbEE	BbEe	bbEe
	Be	BBEe	BbEe	BBee	Bbee
	be	BbEe	bbEe	Bbee	bbee

All combinations are assumed to be equally likely, so if probability were followed exactly, we would get

BBEE	1 pup in sixteen	or	6.25%	black
BbEE	2 pups in sixteen	or	12.50%	black
BBEe	2 pups in sixteen	or	12.50%	black
BbEe	4 pups in sixteen	or	25.00%	black
bbEE	1 pup in sixteen	or	6.25%	chocolate
bbEe	2 pups in sixteen	or	12.50%	chocolate
BBee	1 pup in sixteen	or	6.25%	yellow
Bbee	2 pups in sixteen	or	12.50%	yellow
bbee	1 pup in sixteen	or	6.25%	yellow with brown nose and light eyes.

To summarize, out of sixteen pups we expect nine black, three chocolate, and four yellow, one of which has a brown nose and light eyes. The "normal" expectation is seven colored pups out of sixteen, or nearly half.

We can also predict the result of the yellow x chocolate cross mentioned in the introduction. Let's arbitrarily assume the yellow does not carry chocolate and thus has the genotype **BBee**. Let's assume that the chocolate does carry one e allele and is capable of throwing yellow: **bbEe**. The Punnett Square is simplified by the fact that the dam can only supply one combination of alleles, **Be**, and the sire can contribute two, **bE** and **be**.

Punnett Square for bbEe sire bred to BBee dam			
*		**Dam can contribute**	
		Be	**Be**
Sire can contribute	**bE**	BbEe	BbEe
	be	Bbee	Bbee

Half of the puppies are **BbEe** (black) and half are **Bbee** (yellow). With different assumptions about the "hidden" alleles, we might have found 25% black with yellow, chocolate, and light-eyed yellows present, or we might have obtained an all-black litter. In any case, some black puppies are expected, as mentioned in the introduction.

To summarize, the black, yellow, and chocolate colors in Labs are determined by the genes at the **B** and **E** loci (pl. of locus). At least one copy of the **B** allele is needed for dogs to form black pigment, and **BB** and **Bb** dogs will be black or yellow with black noses. Dogs having the **bb** genotype are chocolate or yellow with brown noses, and must inherit a b allele from each parent. Dogs having the **ee** genotype have yellow coats (and must inherit an e allele from each parent). A single copy of the dominant **E** (genotypes **EE** and **Ee**) is sufficient to make the coat non-yellow: either black or chocolate depending what is present at the **B** locus.

I hope this explanation of Labrador color inheritance as understood by geneticists helps clear up the confusion involved in breeding for color and predicting what colors will occur in a planned litter. Perhaps misbreedings, like the one mentioned in the introduction, can be identified before the pups are registered. Remember though, that the numbers of each color in a litter, like the male-female ratio, seldom exactly match the theoretical probabilities--so don't count your puppies before they're whelped.

Notes

1. Willis, Malcolm B., *Genetics of the Dog*, New York: Howell Book House (1989).
2. Willis (1989) 71-73, 93-94.