Colors

By Laura Tanos, veterinarian and Lagotto breeder, Italy *

This article is not a detailed discussion of dog color genetics, but rather a practical summary to help understand color transmission in the Lagotto.

Lagotti are usually of the following colors: "Off-white unicolored, white with brown or orange spots, brown roan, brown (in different shades) with or without white, orange with or without white. Some subjects feature a brown or dark brown mask. These markings in different shades are normal."

Each coat type is the result of interactions between several properties: the color of colored hairs (brown or orange), the distribution of colored hairs (unicolored or spotted), the distribution of white parts, etc. These properties are dependent on each other and are subject to specific requirements which may or may not occur.

Each property is determined by a set of genetic codes, DNA segments called genes, and each gene can have several variants, called alleles.

Alleles can be dominant, referenced with uppercase letters, A, B etc. or recessive, marked with lowercase letters, a, b, etc. Some genes have only two alleles, but others may have as many as 3 or 4 alleles, forming a dominance order.

Genes (and their alleles) responsible for certain properties are always in pairs, two alleles, one inherited from the father, the other from the mother. When the alleles are equal, the dog is homozygous (AA - dominant homozygous, aa - recessive homozygous) with respect to that gene; otherwise, when they are different, the dog is heterozygous (Aa), always only from the point of view of that specific gene, as it can be homozygous for one gene and heterozygous for another

Each puppy inherits one allele (of each property) from its father and the other from its mother. The possible variations are:

♀ \ ♂	**E**	**E**
E	EE	EE
E	EE	EE

EE x EE = 100% EE

♀ \ ♂	**e**	**e**
e	ee	ee
e	ee	ee

ee x ee = 100% ee

♀ \ ♂	**E**	**E**
e	Ee	Ee
e	Ee	Ee

EE x ee = 100% Ee

♀ \ ♂	**E**	**e**
E	EE	Ee
E	EE	Ee

Ee x EE = 50 % EE + 50 % Ee

♀ \ ♂	**E**	**e**
e	Ee	ee
e	Ee	ee

Ee x ee = 50% Ee +50% ee

♀ \ ♂	**E**	**e**
E	EE	Ee
e	Ee	ee

Ee x Ee = 25% EE + 50% Ee + 25% ee

Pairs of alleles behave differently.

With simple dominance the dominant allele also manifests itself by being present alone, independent of the other allele in the pair, thus manifesting itself both in heterozygous (Ee) and homozygous (EE) form.

Example: Dogs with brown pigmentation are either of the genotype EE or Ee, in the case of a heterozygous pair type Ee, although brown in color, they will also have orange pigmentation. The recessive allele will always have to be present as a homozygous pair (ee) to express itself. Example: Orange colored dogs are always of the genotype ee.

Where there is incomplete dominance or co-dominance, a heterozygous dog (Rt-r) will show an intermediate phenotype between the dominant (Rt-Rt) and recessive (rr) homozygous phenotypes.

Example: Dogs with colored dots on their white parts have a homozygous dominant genotype (Rt-Rt). Dogs with pure white parts, without dots, have a recessive homozygous genotype (r-

r). Heterozygous dogs (Rt-r) are dotted, but far less, hence they possess an intermediate phenotype between the two.

Genes and their alleles do not have the same manifestation strength; some of them may be masked by other genes.

Example 1: a unicolor (dominant property on spotted dogs) can mask a roan (which is the same dominant property in the brown-white), because a unicolor doesn't leave white parts, hence it doesn't give the roan the possibility to manifest itself, which would have been visible only on these parts.

Example 2: orange (recessive property in brown) can mask blotches because the allele "e" in recessive homozygous form (ee) changes all pigments (brown and tan) to orange.

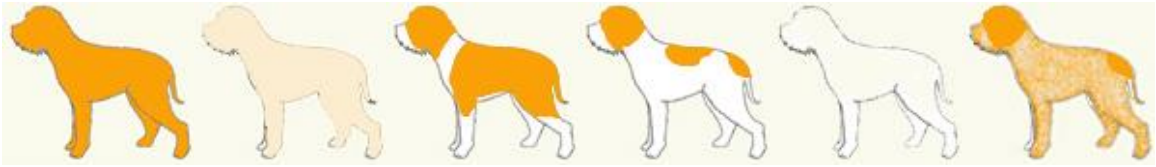
The result of the interaction of all these genes is what we see as the final color of the dog - unicolor or spotted, orange or brown, etc. - this is called a phenotype. On the other hand, what we don't see, but maybe want to know, is the genotype, the code that describes which 2 alleles of each gene are present in the dog, and can have a form like AABBCC..., AaBbCc..., aaBBCC..., etc. Heterozygous dogs for a given property have a phenotype corresponding to the dominant allele but are carriers of the recessive allele and therefore of the recessive genotype.

The colors of dogs are determined by a number of genes, but only those which are important for this breed are discussed here, and even these are presented only in a very simplified way, to facilitate understanding.

Color of pigmentation (brown or orange)

Pigmentation refers to the color of the dog's colored hair, the color of the nose, i.e. all non-white parts. With Lagotti, pigmentation can either be brown or orange. The color of the nose is always conclusive, as it shows the exact color of pigmentation.
These standard colors have brown pigmentation:
unicoloured brown, brown with white spots, roan brown, white with brown spots and tan.

These standard colors have orange pigmentation:
unicolored orange, orange with white spots, orange white and off-white



Genetically, there is also the roan-orange color, which is similar in color to the Italian hound. However, since all the orange spots become clear with age, in practice it is almost impossible to separate the roan-orange from the white-orange or unicolor orange: all these dogs are generally listed as orange, white-orange or possibly off-white. It is possible to see the roan-orange color at the age of 4-8 months, when the orange is still dark.

Brown or orange pigmentation is determined by the E gene, and these alleles are essential for the breed:

E - brown pigmentation
e - orange pigmentation

The E allele has a simple dominance that also manifests itself in a single dose, so all Lagotti with brown pigmentation (unicolored brown, fiery brown, brown with white, brown-white and roan brown) have an EE or Ee genotype. Lagotti with orange pigmentation (unicolored orange, orange-white, orange-white, or dirty-white) have an ee, recessive homozygous genotype.

To know if a brown pigmentation dog is an orange pigmentation carrier, we can either do genetic testing for the E-e gene or consider some rules:

- If a dog with brown pigmentation has one parent with orange pigmentation, it is definitely an orange pigmentation carrier.
- if a dog with brown pigmentation has ever had at least one puppy with orange pigmentation, regardless of its partner's color, it is certainly a carrier of orange pigmentation.
- if a dog with brown pigmentation, crossed in different combinations, consistently litters only brown-pigmented puppies, it is very likely that it is not a carrier of orange pigmentation.
- two dogs with orange pigmentation can never breed puppies with brown pigmentation.

Orange pigmentation nuances (at birth)

Orange dogs from birth begin to show a great variety of color nuances, from dark orange (called apricot in the poodle) to barely visible shades of orange, which in other breeds are called beige, cream, white, etc. In Lagotti, the lighter, almost white nuances, are usually called (and are referred to as) off-white.

All these hues are caused by genes not yet totally understood and there are several theories on which gene causes this dilution, but they all seem to agree on two aspects: the darker color is more dominant while the lighter is recessive, creating a palette of colors that show an order of dominance.

One theory explains this dilution with the C gene (chinchilla), with alleles:
C - no lightening of the orange pigment.
cch - chinchilla - partial dilution of orange pigment
ce - extreme dilution of orange,

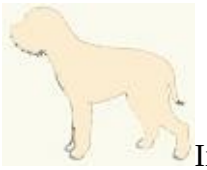
However, recent research has shown that C gene alleles are not found in dogs, thus there is another theory for the dilution of the orange pigment, which assumes the existence of gene I (intensity) with alleles:

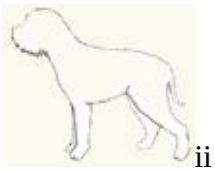
I - intense orange
i - diluted orange

and it is also assumed that these alleles show incomplete dominance, hence heterozygous dogs (Ii) would have an intermediate tinge.

Regardless of what gene is present in the dog, one thing is certain, orange tones occur in the Lagotti, and show dominance as described by both theories, which could be equally applied.

 II

 Ii

 ii

Dilution of all colors (with ageing)

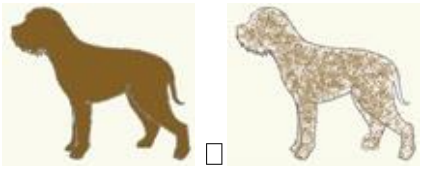
The G gene is responsible for the loss of pigment color intensity, both brown and orange. It has alleles:

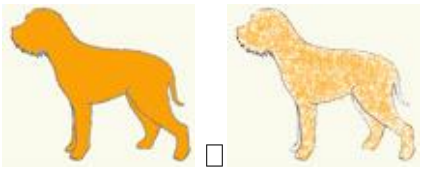
G - graying, with age, the coat gets progressively grayed by the appearance of white hairs mixed with pigmented hairs

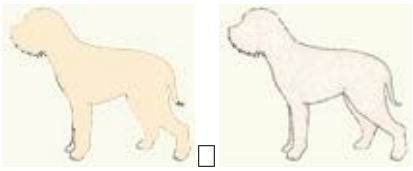
g - does not cause graying, dogs stays dark, as at birth

It shows a heritage of the incomplete dominance type. Gg heterozygous dogs lose color more slowly.

Almost all Lagotti, regardless of pigment color (brown or orange), become lighter with age; brown parts become gray-brown, orange parts a sort of cream, beige, barely visible. It is therefore very probable that a G gene is present in most Lagotti. However, some specimens have been observed, even if very rarely, which maintain a dark color even after a certain age, so we cannot exclude the presence of the allele "g" in the genetic patrimony of the breed.







Color distribution (unicolor-spotted)

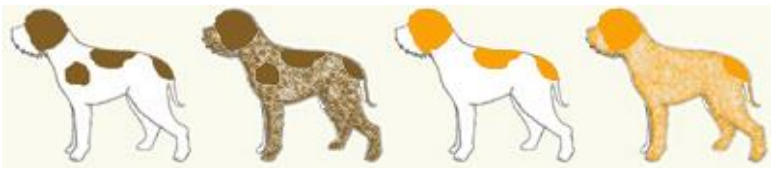
Going by the distribution of colored fur, there are unicolored and spotted dogs.

Unicolors are:

unicolor brown, unicolor orange, and off-white.

Spotted or patched are the colors:

brown-white, roan-brown and orange white (and also roan-orange)



The distribution of spots is controlled by the S gene, which has a series of alleles with several variants presenting an incomplete dominance between them, ranging from the unicolored dominant without any white spot to a more recessive predominantly white with a few small colored spots.

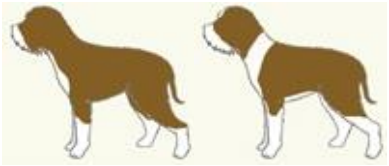
The S gene has the following alleles: (even if there are several alleles, only two of them are always present in each dog)

S - solid - unicolor: It is the most dominant, producing a completely pigmented coat with possible small white spots (no more than 10% of the total coat area), usually on the feet the tip of the tail or a white spot on the chest. These spots do not occur with homozygous (SS)

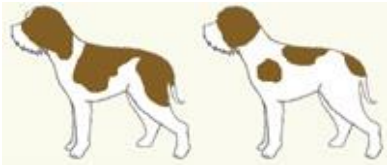
 genotype: SS

 genotype can be: Ssi, Ssp

si - irish spotting as known in English, results in the extension of the white from 10% to 30% of the coat area, usually on the feet, paws, belly, tip of the tail, chest, muzzle and collar. Through the action of modifiers, the white can be more or less extended, making it difficult to distinguish an "si" pattern from an "S" or, its opposite, from an "sp".

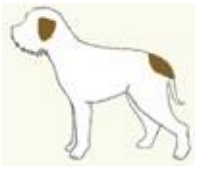
 the genotype can be: sisi, Ssi, sisp, Ssp

sp – piebald in English, the white covers more than 50% of the coat surface, distributed randomly. "S" is incomplete dominant of "sp". These two genes in pairs can produce coats which look phenotypically solid or Irish sized.

 the genotype can be: spsp, sisp, spsw, Ssw

sw - extreme white piebald in English, almost completely white, colored spots are found near the tail line, or on the ears, or near the eye. Homozygous species may suffer deafness,

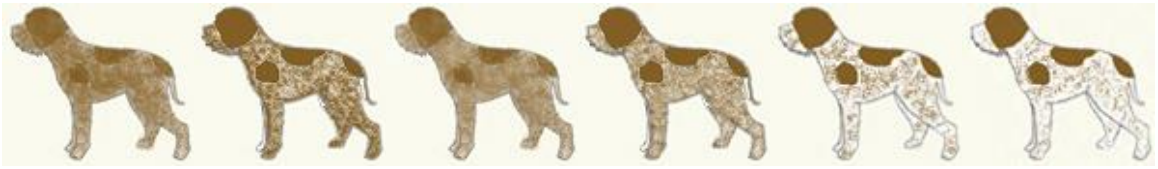
especially if the pigment is not present near the ears. It is incomplete recessive with respect to "S" or "si" and, in couple with one of these two alleles, produces seemingly piebald coats.

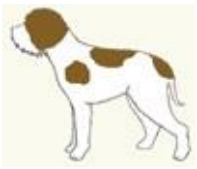
 the genotype is swsw

It should not be confused with off-white. An almost completely white Lagotto of genotype sw-sw will always have a pure snow-white base color, with a brown nose and at least some colored hairs, while off-white dogs have a cream shade, light beige, butter color, with an orange nose and a different genotype (see below).

We can generally conclude that the more colored the parents are, we should have more colored puppies. However, there are no precise rules for the inheritance of the sizes: we can get spotted litters from completely unicolored parents, and vice versa with rare occurrence of unicolored litters from spotted parents.

White base (pure white, spotted, roan)





Dogs with spots at birth have a white background color that after a few weeks can either remain pure white or change into different possible shades of roan, from dark roan, when the adult dog looks almost unicolored, to very light, where large spots are clearly visible on a barely colored background coat. There are several theories that try to describe the genes that cause the roan. More research still needs to be done to identify the exact genes, but the theories agree that the roan is dominant towards a pure white (base).

From experience with different litters of different roan and brown-white parents, the most likely explanation lies in describing these combinations with one gene and its three alleles in incomplete dominance.

R- roan, in the white parts of the white coat. Pigmented hairs appear over time; a uniformly dispersed mixture of colored and white hairs, without forming small unicolored spots.


RR

Rt – ticking in English, causes the reappearance of pigment on white areas in the form of dots or speckles on a white base. The spots are numerous in homozygous dogs. In some cases, when the coat is too grown, it can be confused with a roan. However, it is NOT genetically roan, but brown white. When sheared short, the colored spots become clearly visible on the white base.


RtRt

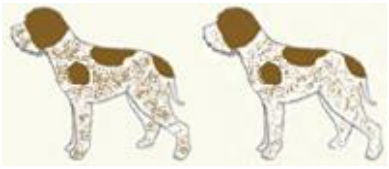
r - no roan expression - white areas remain pure white and are also free of spots or blotches.


rr

Assuming incomplete dominance, heterozygous dogs have different shades:


R-Rt - the white parts become a mixture of roan and spotted. Along the dog's coat length is a pale roan. When sheared, the spots can be observed especially on the legs and tail.

 R-r - is a mixture of less colored hair with more white hair - the dog is a light, silvery roan, both in long and sheared coat.

 Rt-r - few dots on a white base - especially visible when the dog is sheared short.

In theory, two brown-white dogs can never give birth to roan puppies of any shade. However, dogs with lots of spots (RtRt) are sometimes considered roan, even if in genotype they do NOT have the R (roan) allele only Rt (spots). It is, however, difficult to differentiate between the colors caused by these two alleles in phenotype.

Brown or orange unicolored dogs with no white parts can be of any genotype of the R gene. We don't see them because these alleles without the white parts can't reveal themselves.

There is also the color roan-orange, but it is very difficult to see. It can be observed especially when the same litter has orange-white puppies (patchy, white background, genotype r-r, Rt-r or Rt-Rt) and also roan-orange, (genotype R-R, R-Rt or R-r). The roan-orange puppies become more orange after a few weeks than their orange-white siblings. It should however be noted that almost always, the puppies with orange pigmentation, especially with the diluted orange pigment, when the colored hairs are barely visible, are generally all recognized as orange-white, without specifying whether they have orange hues in their white parts. Therefore, orange-white dogs (in general) can easily have roan genotype, and thus, with a brown-white partner, they can have roan-brown puppies.

Homozigous dogs for the roan (RR) become so dark that at an older age it is difficult to tell whether at birth they were unicolored or patched roan.

Tan (and sable)

The standard color is tan-brown. It is a recessive color and generally rare, though in certain bloodlines it occurs more often. The "at" allele is responsible for this color and is found within the series of alleles of the A gene, called agouti, which is responsible for the spread of the yellow pigment within the black pigment (in Lagotti, the black is modified to brown by the B gene, see below, but it is the same pigment).

Sable color (or 'zibellino' in Italian, but sable is more used) is not yet standard with the Lagotto breed; the standard refers to it as brown (in different shades). The gene is however present in the breed, and a lot of recognized 'brown' dogs are practically genetically sable.

There are two types of pigments, pheomelanin - red, fawn, yellow, cream pigment, known as orange in the Lagotto, and eumelanin - black, brown, grey pigment, known as brown in Lagotti.

Both the tan and sable are the result of 3 color genes, E, K and A.

E-series alleles are present (in order of dominance):

E - allows for the expression of genes K and A - brown pigmentation in Lagotti.

e - prevents the formation of eumelanin, and also the expression of the K and A genes. e/e Homozygous Lagotti have orange pigmentation, regardless of what alleles they have in the K and A genes; thus, all orange white, unicolored orange and roan-orange Lagotti are referred to as "orange".

If the dog is orange (white orange etc.) it has the genotype "ee", which changes all the pigmentations to orange, even those of the markings and shades of the sable. Therefore, the orange pigmentation of a dog cannot be seen if it is "tan" or "sable", for the "ee" genotype masks all the effects of the K and A genes. (concealed tan, concealed sable, eekkAtAt, eekkAyAy etc.).

<u>K series alleles are present (in order of dominance):</u>

K - prevents the formation of pheomelanin, hence also the expression of the A gene

k - allows the expression of the A gene - when present in a Lagotto with homozygous form k/k, we get to see both tangy and sable colors.

Therefore, to see the tan and sable colors of dogs, we must have the E gene in homozygous dominant EE or heterozygous Ee form, and the K gene in homozygous recessive kk form. When these two conditions are met, then the gene Ay or at is revealed:

A-series alleles are present (in order of dominance):

Ay - sable, light or dark: a mixture of hairs with eumelanin and pheomelanin pigments

Aw - leopard color (wild): individual hairs are colored in alternating strips of eumelanin and pheomelanin

At - tan

a - recessive black (brown with respect to Lagotti) - no pheomelanin present.
So, to have sable and tan Lagotti:

- the E gene must be in E/E or E/e form (if it is e/e then the Lagotto is "orange")
- the K gene must be in k/k form (if it is K/K or K/k the Lagotto has no orange pigment)

Where these two conditions are met, then you can see the effect of the A gene, which may be:

Ay/Ay - sable

Ay/At - sable

Ay/a - sable

At/At – tan 

At/a – tan 

With regards to the Aw allele - despite the fact that genetic testing has shown it to be present in the breed - I wouldn't want to write much, as it is present in such a small percentage that we have no information about it. To date, no dog with E/- k/k Aw/- genotype has been tested to see what a leopard colored Lagotto would look like in reality. Same goes for the allele "a" - recessive brown, which has never been tested in E/- k/k a/a form.

The Finnish laboratory MyDogDNA carries out a series of genetic tests involving colored genes. These statistics are then provided by them.

About 800 Lagotti have been tested with MyDogDNA Pass and MyDogDNA 2015. (The first panel failed to differentiate between the alleles "At" and "a", the second, after 2015 did).

Allele frequency:

Ay - 9 %.

At or at - 91%

After 2015, the new panel allowed for the differentiation of the alleles "At" and "a". Based on these tests, the frequency of the allele "a" is about 15% (from 91%). About 350 Lagotti were tested in the new panel.

The combinations present were:

Ay/Ay - about 1 %
Ay/At - 15.5%
Ay/a - 4%
At/At - 78%
At/a - 1.5 %
As stated earlier, in order to see these colors, it is necessary to have the E and K genes in the "right" setting, hence the percentage: sable-colored Lagotti about 1% and tan-colored about 2.5%.
There is an increase in "brown" dog breeds (genotype E/E or E/e) - with brown pigmentation. This includes all colors from unicolored brown, roan brown and white brown. On the other hand, there is a reduction in "orange" dogs (genotype "e/e" masking the "K" and "A" gene). This phenomenon also leads to more and more sable dogs.

It is very important to properly define what sable is and how the color is recognized in the pedigree, because if a sable dog is recognized as "orange" (orange white, unicolor orange, off-white, cream, tan, etc.) and then bred with a real "orange" it can result in puppies with brown pigmentation, which could never happen from two genuine oranges, and could pose great problems for breeders in questioning the reliability of that pedigree, etc.

Black.

There were no black Lagotti, not even among the eliminated defects. But we need to talk about the genetics of black to understand how it occurs.

The basic black pigmentation is modified to brown in the B gene, with alleles:
B - black pigmentation.
b - black modified to brown

The allele B is dominant and therefore the phenotype would manifest even if B would be present in single copy. This means that the allele B is NOT present in the breed. Lagotti of any color - including also the apparently white unicolored ones – always have a brown nose instead of black. There is never any black pigmentation anywhere in the body, so the genotype is always "bb", recessive homozygous, where you cannot "hide" the dominant B allele. From two Lagotto a black, black-white, black roan, not even white with the color of the black nose, or any variation of black, can never come out, because all these ones should have at least one B allele, on the contrary, if their parents are really Lagotti, genotype "bb", there is no possibility to appear a B allele. This is impossible, even though we know that in the past dogs of other breeds were randomly used in breeding, resulting in litters with black spots or black nose etc.; because as explained earlier, to have a dog with black pigmentation (genotype Bb or BB) one or both parents must have black pigmentation. This is not possible even among grandparents, or great-grandparents, etc. of any dog breed, as a dominant allele cannot "jump" even a generation without appearing. Hence, should you find a black pigment puppy (black,

white with black spots, roan black, or white with black truffle) in a litter of Lagotti parents, you can be sure that that puppy is definitely not from the desired father, (maybe the mother escaped and was co-opted by the neighbor's dog, etc.), a genetic test will certainly prove this.

* Translated from the Italian Lagotto Romagnolo Club