

RABBIT GENETICS

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Review Article

The C locus: rabbit genetics for full color development, chinchilla, seal, sable, pointed black and red-eyed full white

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Abstract. The scientific literature is scarce in information of classical genetics on coat color inheritance in rabbit. However, several websites for hobbyists contain very useful and correct information about this issue. Unfortunately, such sources, although very nice structured and well documented, are not always accepted by the editors, reviewers or evaluators as credible references in manuscripts and research project proposals. Therefore, a scientific synthesis in a review paper using this atypical scientific information (websites, blogs and electronic guides for hobbyists) is quite necessary prior to any further research of genetic improvement in rabbit. The paper is a review on rabbit genetics for full color, chinchilla, seal, sable, pointed black and red-eyed full white in rabbits.

Key Words: rabbit genetics, *Oryctolagus cuniculus*, C-family, albino, chinchilla, full color.

Introduction. Classical genetics is very important for animal production at the small scale farming level in subfields such as: poultry, cuniculture, ornamental fish farming, laboratory animal production etc (Mag-Muresan & Pop 2004; Mag & Bud 2006; Petrescu-Mag 2007; Pricop 2009; Pricop & Pricop 2011; Bud et al 2011; Petrescu-Mag et al 2013).

Coat color development in *Oryctolagus cuniculus* depends on genes located at several loci on rabbit's chromosomes. These genes act together to produce quite a variety of different colors and patterns. It is already well known that the most important loci involved in color expression in the rabbit are *A*, *B*, *C*, *D*, *E*, *En*, *Du*, *Si*, *V*, and *W*. There are also other genes acting as color modifiers, controlling the intensity of certain colors or patterns. These modifiers are not single genes, but multiple ones that pool their effects (Cieslak et al 2011).

We can classify the color genes (*lato sensu*) in two groups. First, the color pattern genes (determining which pattern will be expressed: agouti, tan, or no pattern). All of the other genes are the color genes (*sensu stricto*). These genes determine the placement and intensity of the color pigments on the hair (DebMark Rabbit Education Resource).

Notation System. There are two classical notation systems available worldwide for the genetics of coat color. The notation system presented above is an English one, definitely different from that used by Botha et al (2011), which is a German system of gene notation. In US, Canada and Australia the most frequent system is the English system while in Europe (except UK) the German system is predominant. In the near future, a newer system of gene notation will be implemented due to the latest results in the field of molecular biology (Fontanesi et al 2006).

Colors and Patterns of Rabbits in the Wild. Rabbits in the wild have a brownish fur color called agouti (Searle 1990). This wild type fur is made up of three to five bands of color at different levels: the hair closest to its skin is gray, the gray is followed by yellow, and on the tips of the fur is black. These wild type animals have white fur on their bellies. The agouti pattern is found also in some domestic rabbit breeds today: Gray Giant (see

Figure 1), Viennese Gray etc. The rabbit breeders call this color chestnut. There are several variations of this agouti pattern in domestic rabbits. Such variations are induced by the other color genes and modifiers working together (DebMark Rabbit Education Resource).

Two Pigments, a Lot of Colors. A rabbit has only two possible pigments that can be expressed in its fur: one is yellow and the other is dark brown. The absence of both yellow and dark brown pigments results in completely white animals (see Figs 8-9) (Searle 1990). Because of the absence of pigments in the skin the white fur is most often associated with red, ruby or pink eyes. All of the colors possible in rabbit fur are simply combinations of these two pigments or lack thereof. The expression can appear on the same or different hairs, in certain patterns, and at different intensities. As a general rule, rabbits that have short hair, such as Rex breeds, have more intense color expression. Animals that have longer hair, such as Angora varieties, have diluted color expression. This dilution is due to the fact, given the same genetic background, the number of pigment granules in the hair is the same. In short hair, the melanic granules are packed more closely together, making a more intense color. In longer hair the melanic granules are spread further apart from each other, giving a pastel color (DebMark Rabbit Education Resource; see more in Huffmon G. M.).

The C Locus: Rabbit Genetics for Full Color Development, Chinchilla, Seal, Sable, Pointed Black and Red-Eyed Full White. Although there are many color genes involved in the coat color expression, the C-family of genes is called the "color genes". The alleles placed at C locus control where and how much color will be expressed rather than which color will be expressed (Stroupe 2004-2008). Beginning with the most dominant and ending with the least, the color alleles are *C*, which is the full color allele, *c^{chd}*, which is the chinchilla allele, *c^{chl}*, which is the sable allele, *c^h* which is the Himalayan allele, and *c*, which is the albinism determining allele (Petrescu-Mag et al 2013).

Full Color Development. The dominant color gene is the "full color" allele represented in the English gene nomenclature by the capital letter *C*. There are many full color breeds all over the world (see pictures in Figs 1-2): chestnut, black, black tortoiseshell, blue, orange, and lilac. Genotypically, a full color rabbit may be either: *C-C*, *C-c^{chd}*, *C-c^{chl}*, *C-c^h*, or *C-c*. In full color rabbits, the color is not restricted to a certain part of the body, but it spread over the surface of the entire animal (Stroupe 2004-2008).

Chinchilla. The next allele according to dominance is chinchilla, which is represented by *c^{chd}* (*chd* = chinchilla-dark). The chinchilla gene will be expressed if paired with any gene except the full color *C* gene (Oroian et al - unpublished data). Genotypically, chinchilla rabbits can be either *c^{chd}-c^{chl}*, *c^{chd}-c^h*, *c^{chd}-c*, or *c^{chd}-c^{chd}*. When the chinchilla gene is expressed in rabbits, there is white or pearl fur where the full color rabbit has more yellow in the fur. The *c^{chd}* gene causes the yellow pigment to be reduced (see pictures in Figure 3). For example, an orange rabbit differs from an ermine only in that the orange is a full color rabbit and the ermine expresses the chinchilla gene. Once the yellow pigment is eliminated from the orange, only the pearl remains (Stroupe 2004-2008).

Sable. The next allele is the sable gene represented by *c^{chl}*, which stands for "chinchilla-light". Phenotypically, the sable gene removes yellow pigment from hair shafts and removes some of the darker pigments, giving a rabbit a shaded look. Genotypically, sable rabbits are either *c^{chl}-c^h* or *c^{chl}-c*. Smoke pearl and sable point rabbits are two examples of animals with the *c^{chl}* as the dominant color allele (see Figure 4). There is a peculiar expression of *c^{chl}* in sable rabbits due to its incomplete dominance. Two copies of the sable allele (*c^{chl}-c^{chl}*) produce a dark sepia color (called "seal") resulting in an almost black animal (see Figure 5) (Stroupe 2004-2008).

On What Extent Chinchilla are Pure Breeds? The principle of pure breed conservation is totally against crossbreeding of animals from different breeds for show. Such a champion, claimed "purebred animal", will segregate sooner or later. However, experts believe that the best chinchilla colors are produced with either an albino or Himalayan gene paired with the chinchilla gene (Stroupe 2004-2008). The sable allele, in

combination with chinchilla-dark, tends to muddy the color due to co-dominance, and therefore this combination is unwanted (Oroian et al - unpublished data).



Figure 1. The full color development in Gray Giant rabbit breed (Photo: Miklos Botha).



Figure 2. The full color development in Black Giant rabbit breed (Photo: Miklos Botha).



Figure 3. The chinchilla (c^{hd}) color in the Cluj Rabbit breed (Photo: Miklos Botha); breed created and described by Botha et al (2013) as the second Romanian breed in history.



Figure 4. Examples of Chinchilla light (heterozygous for c^{chl}): Smoke pearl (left) and Sable point (right) (http://www.oocities.org/falls_acre_rabbits/mr-colors.html).



Figure 5. Example of Chinchilla light (homozygous for c^{chl}): Seal rabbit (http://www.oocities.org/falls_acre_rabbits/mr-colors.html).

The Himalayan Gene. The history of the Himalaya trait is quite controversial among zoologists and rabbit breeders. There are many opinions about the origin of this phenotype but no solid scientific evidence exists so far. Today, many domesticated rabbit breeds are acromelanistic: Himalaya (called also Russian), Californian, Transylvanian Giant, Debrecen White (see Petrescu-Mag et al 2011-2012; European Association of Poultry Pigeon and Rabbit Breeders 2010), and all these breeds descend from

Himalayans. The recessive Himalayan allele c^h in homozygous form (c^h-c^h), or heterozygous form (c^h-c), converts tyrosinase into a thermolabile form, with greater production of melanin in colder body parts (Searle 1990) (see Figs 6-7). This biochemical process leads to a specific color expression: although eyes are pink, ruby or red and coat is white, the nose, ears, feet and tail are black, brown, grey or blue, function of other genes involved.

The Red-Eyed White. There are tens of breeds of Red-eyed white rabbits. All color is erased from the fur and eyes (Searle 1990). Like in the case of Himalayans, the eyes are pink, ruby or red (see Figs 8-9). Red-eyed whites are albino rabbits and are not genetically related to blue-eyed whites (Viennese Whites) at all (Stroupe 2004-2008).

Albinism (derives from Latin *albus* = white) also called achromatosis, achromia, or achromasia, is considered a congenital disorder characterized by the complete (typical albino) or partial (mosaic animals) absence of melanin in the skin, hair, other skin productions and eyes due to absence or dysfunction of tyrosinase, a copper-containing enzyme involved in the production of black pigment. Albinism results from inheritance of two recessive gene alleles from the parents and is known to affect all vertebrates, including humans (Cieslak et al 2011). In the wild, animals with albinism lack their protective camouflage and are unable to conceal themselves from their predators or prey; the survival rate of animals with albinism in the wild is usually quite low (Hiler 1983; Dobosz et al 2008). However the novelty of albino animals has occasionally led to their protection by groups such as the Albino Squirrel Preservation Society. Intentionally bred albinistic strains of some animal species are commonly used as model organisms in biomedical study and experimentation, although some researchers have argued that they are not always the best choice (Creel 1980). Examples include the BALB/c mouse and Wistar and Sprague Dawley rat strains, while albino rabbits were historically used for Draize toxicity testing (Draize et al 1944). The yellow mutation in fruit flies is their version of albinism (wikipedia.org).



Figure 6. The Himalaya phenotype in Californian Rabbit breed (Photo: Miklos Botha).



Figure 7. The Himalaya phenotype in Transylvanian Giant Rabbit breed (Photo: Mircea Rosca www.MirceaRosca.com); first Romanian breed in history.



Figure 8. The red-eyed white/albino phenotype; New Zealand White (Photo: M. Botha).



Figure 9. The red-eyed white/albino phenotype; White Giant breed (Photo: M. Botha).

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