INHERITANCE OF COAT COLOR AND COAT PATTERN IN THE DOMESTIC CAT

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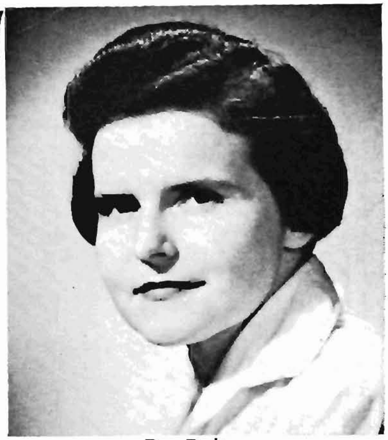
Perhaps the most interesting aspect of genetics as applied to cats is the inheritance of coat color and pattern. Certainly a basic knowledge of genetic color control is of practical importance to the breeder. Therefore, a summary of present knowledge in this sphere, no matter how brief, can be useful as a foundation for further study.



Dr. Peltz

Melanin

Color in hair and skin is produced by melanin under genetic control. The material itself is the black, brown, and reddish products of tyrosine. Melanin granules are formed in special cells called melanocytes, which in the embyro are located in the neural crest. They migrate to the skin and hair bulbs. These cells contain tyrosinase which converts tyrosine to melanin. The speed with which they migrate to a predetermined site and the rate of maturation of the individual melanocyte determines the pattern of pigmentation. The physiologically young and active melanocyte produces pigment rapidly. As it matures, the rate of melanin production slows. Therefore, genetically determined time and location of these special cells regulates where and how much pigment will be set down.

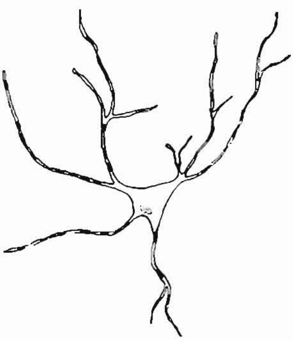


FIGURE 1

There are two forms of melanin granules; those which are perceived as Black-brown and those which appear reddish in color. The former are called eumelanins, and the latter are termed phaeomelanins. How the color appears is determined mechanically because under genetic control melanin granules may be of one type or the other. The granule size and shape as well as their location and arrangement may be changed to result in differences in color.

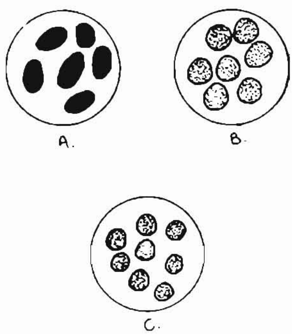


FIGURE 2

NOTE: See explanation of illustrations (done by the author) at end of article. Dr. Peltz, physician, practices in Decatur, Ga.

Coat Color and Pattern

Color inheritance in the cat is sex linked, and all cats, no matter how they appear, are genetically black or red or black and red. In addition one must remember that agouti ticking is a basic characteristic of animal fur. To begin, therefore, the color and pattern of cat's coat is determined by:

1. the presence or absence of melanin.
2. the type melanin present.
3. the presence or absence of agouti ticking.

1.) Agouti Ticking

The appearance of ticking is caused by bands of different colors on individual hairs. A pair of autosomal (non-sex) chromosomes determine the presence of agouti ticking. If agouti ticking is present, it represents a genetically controlled pattern. If such ticking is absent, the coat is black. In other words, the alternative to agouti ticking is black.

If the cat is genetically black or red, or ticked or non-ticked, or black and red, how then do other colors and patterns occur? In the discussion on melanin it was pointed out that mechanical changes in the granule could occur. The distribution of granules can also be changed. When such alternations occur, the basic pigment appears as a different color. These changes, too, are controlled genetically. Another series of genes determines the level of intensity of the basic hue.

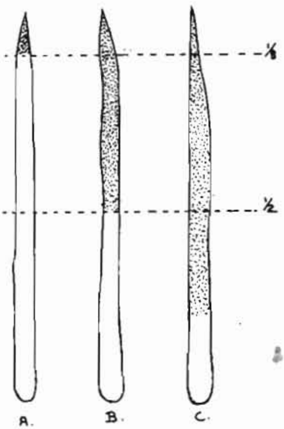


FIGURE 3

2.) Black

The solid black coat is the alternative to the presence of agouti ticking, and is recessive to it. The pigment is eumelanin, and it is restricted either to single hair or to entire coat. The genetic symbol for black is (aa) which indicates its recessiveness to (A) or agouti. There is no set standard of gene symbols for the cat; and it is possible to find black symbolized as (B); or (E^D) or (D^d) for dominant black.

3.) Blue

The distribution of eumelanin granules can be changed by the presence of a recessive gene known as the maltese diluter and which is symbolized as (d). Maltese dilution thus changes black to blue by causing a different arrangement of granules. If black is symbolized as (aa), then blue is represented as aadd.

4.) Red

The solid red coat is determined by the presence of nondiluted phaeomelanin and the absence of agouti ticking. The symbol for red is (R) or (Y), and the red coat is aarr.

5.) Cream

The cream coat is the dilute of red; and the change in color is brought about by the maltese diluter. The symbol is aaRRdd.

6.) Black and Red

The combination of the two colors results in a pattern known as tortoiseshell. The true tortoiseshell is black, red and cream, and how this pattern is achieved is related to the speed of migration of the melanocytes, the length of their physiologic activity and the activity of the X chromosomes of the female.

The tortoiseshell cat is the ultimate example of how sex-linked color operates in the cat. Since the female has two (X) chromosomes she has two sites for color. Obviously the (XY) male has only one. If we use the following diagrams to show how color is carried on the X chromosome it will be easier to understand. In addition, let us represent red as (R) and black as (B) for these examples.

First the results of a breeding between a red male and a black female can be shown as follows:

	Dam		Sire	
	Black Female	x	Red Male	
	(X^BX^B)		(X^RY)	
Gametes	(X^B)	(X^B)	(X^R)	(Y)
Offspring	(X^BX^R)		(X^BY)	
	Tortoiseshell female		Black male	

Reverse the situation and breed a black male to a red female:

	Dam		Sire	
	Red Female	x	Black Male	
	(X^RX^R)		(X^BY)	
Gametes	(X^R)	(X^R)	(X^B)	(Y)
Offspring	(X^RX^B)		(X^RY)	
	Tortoiseshell female		Red Male	

It becomes apparent that when black and solid red cats are mated the female kittens are tortoiseshell because of incomplete dominance between black and red. It is also apparent that the resulting male kittens are the color of their dam.

The pattern of juxtaposition of large patches of color is determined in the embryo at the time of migration of the melanocytes from the neural crest. Another factor which plays an important part in pattern predetermination is the activity of the X chromosome. Dr. Mary Lyon has hypothesized that either one or the other of the X chromosomes of the female becomes relatively inactive.

The decision as to which X chromosome becomes almost totally inactive occurs early in the embryonic life, and the decision remains unchanged. The Lyon hypothesis is partly based on physical differences observed in X chromosomes. Since color is carried on these chromosomes in the cat Dr. Lyon's theory should be of great interest to the breeder. For it is impossible to tell which X chromosome, the paternal or maternal X contribution, is to become inactive. Therefore, the tortoishell pattern is set in the embryo by the dosage influence of one of the X chromosomes together with the rate of pigment production and the speed of migration of the melanocytes.

Breeders and geneticists have been intrigued by the occasional appearance of the tortoiseshell male. The tortoiseshell male has a sex chromosome makeup of XXY rather than the normal XY.

7.) Blue-Cream

Just as black was diluted to blue and red to cream by the maltese dilution system, tortoiseshell black and red are diluted to blue and cream.

Tabby Patterns

The tabby coat pattern is due to a combination of agouti ticking interspersed between areas of solid black coat. Ticking is produced by alternating bands of intense and dilute grey and yellow.

Tabby striping is considered to be the basic coat pattern in cats, and the ghost pattern of tabby striping is almost universally seen in the young self coated specimen as well as in other cats with pattern restriction. In 1907 Pocock described a thickening of the skin in those areas covered by black striping and blotching. The skin in those areas not covered by black were not as thick. It has been theorized that the difference in skin thickness is responsible for tabby "ghost patterns" in non-tabby cats. In addition hair length seems to either influence or be influenced by the unrestricted black areas. There is a tendency for the hair to be shorter when it is black and nonticked.

Tabby patterns are of three main types with restrictions of black striping, blotching and spotting to specific areas.

1.) Lined Tabby Coat (t^l)

This particular tabby pattern is characterized by the narrowness of the black lines. The black stripes are narrow and closer together than in any of the other typical patterns.

2.) Mackerel Tabby Coat (t^+)

In contrast to the lined tabby, the black stripes in the mackerel coat are wider and farther apart. The black vertebral streak is also wider and continuous to the tail without interruption.

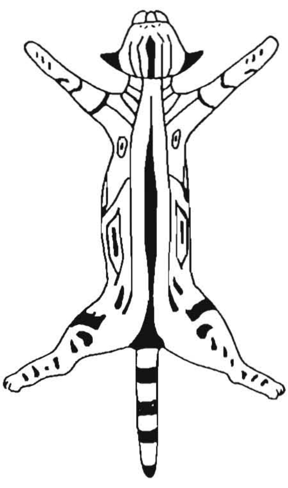


FIGURE 4

3.) Blotched Tabby Coat (t^b)

Distinct from the other two basic tabby patterns is the blotched coat which is characterized by whorls of black in addition to striping. The vertebral black stripe is separated from the whorls by two wider bands of black which run parallel to the central black line.

Tabby patterns are caused genetically by a combination of the effects of the autosomal genes producing agouti ticking plus sex-linked black under the influence of one of the three (or possibly more) tabby alleles, together with one or more genes causing modification of the striping patterns. It has been assumed that the allele (t^+) producing the mackerel pattern is most dominant in the series.

The members of the tabby allele series produce their effect and thereby cause pattern formation by regulating the migration of melanocytes. As the melanocyte matures, it loses its biochemical activity. And since more active melanin granule production occurs in the early life of the melanocytes, it follows that those cells migrating more rapidly into areas specified by one of the tabby alleles will produce more intense pigment.

Bearing in mind all of the above genetic controls of pattern and ticking it is possible to concentrate on the variations of the sex-linked color.

1.) Silver Tabby

One of the alleles of the albino series, the silver allele, has the effect of reducing the level of yellow and red pigment in agouti ticking, and in so doing produces a silver effect in those areas of ticking.

2.) Brown Tabby

The brown tabby is endowed with eumelanin on its sex chromosomes. The alteration of black to brown is caused by a reduction in the rate of melanin production in specific areas. Again, it is the tabby alleles which cause the change on rate of speed of pigment formation. Melanin granules are changed to a round form for the color brown to become apparent.

3.) Blue Tabby

A change in the arrangement of the ovoid eumelanin granules through the influence of the maltese diluter causes the appearance of blue color. Therefore, such a change in the presence of agouti ticking and sex-linked black produces the blue tabby.

4.) Red Tabby

The interaction of phaeomelanin, agouti ticking and a pair of the tabby alleles produces the red tabby coat. Addition of maltese dilution produces the cream tabby coat.

Abyssinian

An ultimate refinement of agouti ticking and the tabby pattern is seen in the Abyssinian cat. The genetic background of this cat is not specifically determined although it is probable that the lined tabby pattern has been refined through selective breeding to produce this group of cats. The ruddiness of the coat indicates the presence of phaeomelanin. In the Abyssinian, as in the other forms of tabby, the shredding effect on the melanin granules produces the pattern. One exception to sex-linked color inheritance is the sorrell Abyssinian. The lined tabby alleles in the presence of agouti ticking persist, but there is dilution of the normal black bands to brown, and the reddish bands are very slightly reduced in color intensity. These cats have appeared in breeding between standard Abyssinians. In such instances it would appear that a recessive autosomal gene has brought about the color dilution.

There have been other breedings between standard Abyssinians and Tortoiseshell and Reds which have resulted in hybrid sorrell colored cats of typical Abyssinian ticking. These cats, of course, when bred will behave as any sex-linked red cat.

Albino Alleles

Solid color can be altered by a group of alleles which not only control the intensity of hue but which also restrict the level of pigmentation to specific areas. The albino alleles produce a reduction of phaeomelanin intensity more rapidly than they affect eumelanin. In addition, a thermo-sensitive enzyme system present in the Burmese and Siamese cats alters pigment intensity levels.

1.) The Silver Allele

In order of dominance the silver allele is reported by Keeler and Cobb to be recessive to full color. That there is more than one silver allele is a definite possibility. The silver allele (c^{ch}) acts to reduce red or yellow and because of such action an interesting newer group of cats have been bred. These are the Cameos which result from crosses between silver and red.

The degree of tipping on each hair is increased when the silver allele occurs in the absence of agouti genes. The combination of silver plus eumelanin in the absence of agouti genes causes the smoke phenotype. The shaded silver represents another variety of cat in which the degree of black (or in the case of the Cameo group, red) tipping is extended to a greater degree than in the chinchilla and to a lesser degree than in the smoke patterns.

In other words, there are three degrees of tipping of individual hairs. If the silver allele is present with black pigment, the least amount of shading occurs. If the degree of tipping is increased, the shaded pattern occurs; and if agouti ticking is absent, the degree of tipping is extended almost to the base of each outer hair to produce the smoke pattern.

When silver and phaeomelanin combine, the same pattern effect occurs; the only difference is in the pigment. The Shell Cameo is comparable to the Chinchilla pattern; the Shaded Cameo is comparable to the Shaded Silver and the Red Smoke is comparable to the Black Smoke.

The effect of silver is far reaching in producing unusual colors. The Cameo color patterns (red and silver) if combined again with silver will result in shaded Tortoiseshell coats.

2.) Burmese Allele

Black is altered to brown under the influence of the Burmese allele. There is a certain degree of thermosensitivity caused by this allele which is most apparent in the kitten stage. The Burmese kitten has deeper pigmentation on the face, ears and the lower third of the extremities which is lost in the mature cat. The Burmese allele is dominant to the Siamese allele and recessive to silver.

3.) The Siamese Allele

The Siamese allele is the next most recessive in the albino series, and it ranks only above the albino allele, itself. The existence of a thermosensitive enzyme system is most apparent in this group of cats;

the degree of lability of the system being readily apparent. Specific enzyme activity is required for color production and full intensity. When the enzyme is affected, color intensity can be restricted. The system becomes inoperative in the Siamese in temperatures over 101 degrees. Pigmentation is most intense in those areas of the body which are cooler, i.e., the face, tail, and lower extremities. Restriction of the level of intensity of the same color occurs in warmer parts of the body. Hence, the Siamese pattern of points is produced by this defect. The dark black-brown color referred to as seal is sex-linked eumelanin restricted in its distribution by a defective enzyme system and influenced by the presence of autosomal browning genes. The level of pigmentation is determined by the Siamese allele. There is a question as to whether seal black is dominant black in the Siamese.

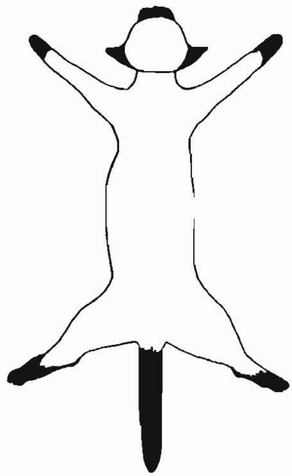


FIGURE 5

Seal Point

It has been stated that the Siamese allele by itself causes eumelanin to dilute to brown color. This dilution effect plus the inability of the enzyme system to function properly produces the typical Seal Point Siamese color and pattern.

Blue Point

Addition of the maltese diluter to the already diluted Siamese Seal color produces the Blue Point color and pattern. This blue color is produced in the same manner as in other cats. There is a change in the arrangement of melanin granules. It has been suggested that the Siamese allele is not responsible for the dilution of seal black and brown, but that a pair of autosomal browning genes is responsible for the various degrees of dilution in the Siamese colors.

Chocolate Point

Further dilution of seal black results in chocolate color. The brown mutation is recessive, and its existence has been reported by Ullman and Hargreaves.

Lilac and Frost

Although the terms Lilac and Frost are often used synonymously, there are minor differences between the two coats which suggest different genotypes. It has been postulated that if blue is diluted in the absence of browning genes then the color is Frost; if only one browning gene is present and blue is diluted, the color is Lilac.

Albino Allele

Albinism is a recessive condition, and it is represented as the most recessive member of the albino allele genes. The condition results from a biochemical block in the formation of melanin granules. Melanocytes are in adequate numbers, but their ability to function physiologically is lost. There is a histiologic difference in the ablino hair follicle. In addition to the usual cells, there are large clear cells present. The eyes of the Albino cat are perceived as reddish pink and on occasion as very pale blue. There is no pigment in the iris of the eye; and the colors noted are merely the reflection of light off the walls of blood vessels in the eye.

White Coats

The hair follicles of white coats differ from those found in the Albino in that there are not large clear cells. In addition, cats with white coats have pigmented irises. Therefore, the capacity to produce melanin is present and active.

White coats are produced by the effects of dominant white, recessive white and piebald spotting. Disagreement exists as to which genes are responsible for the blue-eyed white coated cat. It has been suggested that blue eyes occur as a result of dominant white together with piebald. The blue eyes would result when piebald spotting is in the region of the eyes. The copper-eyed white is due to recessive white genes while the odd-eyed white combines recessive white and piebald spotting.

It is important to emphasize that the genetics of the white coat is unsettled.

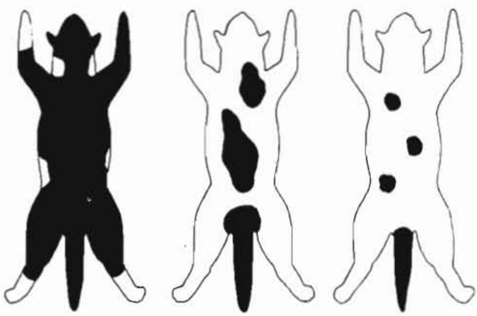


FIGURE 6

One point of interest is the association of deafness and blue eyes. Certainly not all blue-eyed whites are deaf. Embryologically melanocytes and cranial nerve ganglia are derived from the neural crest. If the genes for white spotting interfere with the migration of melanocytes from the neural crest, then it is possible for those genes to cause defects in the formation of the certain structures in the auditory apparatus. In other species white spotting genes produce anatomic defects in addition to spotting. It is beyond the scope of this paper to discuss deafness and other defects in relation to color genetics. The reader, therefore, is referred to the paper by Wolff and the review by Billingham and Silvers in the list of literature.

Since there are many genes responsible for white spotting and since these genes can be influenced by other modifying genes; it is difficult to say that a cat is homozygous for any particular pair. However, homozygosity for any pair(s) of white spotting genes would produce a cat with a solid white coat because the cat would be one entire white spot. How is one to distinguish such a white cat from the cat which is genotypically (WW) ? The white coat observed in a cat with pigmented eyes may be the result of genes acting at the W locus or the S locus or both. The extreme $s^w s^w$ (white spotting) cat is for all practical purposes difficult to distinguish from the genotype WW.

Brown Coat

The solid brown coat is due to a brown mutation which was noted first in the Siamese. Ullman and Hargreaves transferred the gene for brown to a cat without a defective enzyme system and thus produced a solid brown coat.

FIGURE 7

The transfer involved a series of breeding between Chocolate Point Siamese and solid colored domestic short hairs. Breedings between the Chocolate Point and the Russian blues were also accomplished. The cat resulting from these crosses is the Havana Brown.

Dilution of the brown coat produces lavender. The brown coat is symbolized as aabb, and the lavender coat is aabbdd.

Summary

Because of a growing interest in genetics most breeders are aware of sex-linked color inheritance in cats. The purpose of this brief review has been to stress other factors which are involved. Sex-linked color transmission is only one segment of a complex living process, and coat color and patterns are not merely the results of adding the action of genes to other genes. The total equation must be considered.

FIGURE 8

Therefore, final coat color involves:

1. Melanin, in relation to
    a.) level of biochemical activity.
    b.) rate of production.
    c.) mechanical changes in granule shape, size and distribution.
2. Time, in relation to
    a.) migratory speed of melanocytes.
    b.) the total efficiency of genes.
3. Dosage effect of X chromosomes.
4. Modification of sex-linked color by non sex-linked genes.

SYMBOLS

Sex-linked black	= X^B	Albino alleles		Autosomal brown	= b
Sex-linked red	= X^R	smoke	= c^{sm}	Maltese dilution	= d
Agouti	= A	shaded	= c^{sh}	Dominant white	= W
Non-agouti	= aa	silver	= c^{ch}	Recessive white	= w
Tabby alleles		full color	= C+	Spotting	= s^1, s^2, s^3, etc.
lined tabby	= t^l	Burmese	= c^b		
mackerel tabby	= t+	Siamese	= c^s		
blotched tabby	= t^b	Albino	= c		

LIST OF ILLUSTRATIONS

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