

INHERITANCE OF COAT-COLOR IN CATS

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TWO PLATES

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I. INTRODUCTION: THE COLOR FACTORS OF DOMESTIC CATS

In a series of experiments begun at the University of Pennsylvania in the autumn of 1914 and extending up to the present time, the inheritance of coat-color in cats has been investigated. Although the number of litters obtained has not been large, it has been found possible to determine several points in regard to the mechanism of heredity by means of critical crosses. This has been largely due to the fact that the characters studied segregate for the most part cleanly from each other so that it has been easy to classify the animals.

My thanks are due to Dr. McClung and to Dr. Colton for the kindly interest which they have taken in the work and to the

University of Pennsylvania for the expense of the experiments. I also wish to thank the Zoological Society of Philadelphia for the opportunity of crossing my cats with the Caffre cat.

Before presenting the data and discussing the inheritance of the various characters in detail it may be well to name and to define briefly the factorial differences involved.

The ticking or agouti series contains at least two and probably more different factors. Black, non-agouti, or uniformity, *a*, is a recessive allelomorph to agouti, *A*. An extreme amount of ticking is frequently observed, and this represents, in all probability, a third allelomorph in the series. Results are not conclusive, but are consistent with such a hypothesis. This extreme ticking may tentatively be called *A'*.

The banding or tabby series contains at least two and probably three different allelomorphs. They may be called lined, *B'*, striped, *B*, and blotched, *b*. The allelomorphism of these is again merely tentatively assumed, but I believe there is good reason to consider them as a triple allelomorphic series. The agouti and the banding factors will be discussed fully later in this paper. It may merely be stated here that all cats are either lined, striped, or blotched and that there are no intergrades. The character of the banding is, however, easily recognized only in the presence of ticking. In the black or non-agouti series banding exists as 'ghost patterns' recognizable usually but not always in the fur of kittens, and only occasionally distinguishable in full-grown cats.

Intense pigmentation, *M*, is a simple dominant over dilute or maltese, *m*.

White, *W*, is a simple dominant over color, *w*.

Yellow, *Y*, is allelomorphic with black, *y*. This locus is sex-linked and shows the male to be digametic. The heterozygous female is *usually* yellow-spotted or tortoiseshell, but may range in color to solid black or solid yellow.

White-spotting is very irregular and probably depends upon many factors. It will not be considered in detail in the present paper. It appears to segregate independently of the factors above mentioned.

Albinism, as we have it in the rodents, is apparently unknown in cats. It is possible that Siamese dilution represents an approach toward this condition.

Variations in the tone of coloration are extensive, but apparently not clearly segregating. Silvers represent a reduction of yellow pigment and also of black. Smokes are very dark silvers. The lighter bands of tabbies are straw- or cream-colored, varying to white in silver tabbies and brown in brown tabbies. Occasionally the brown varies to a rusty red. Silver creams are yellow cats in which the yellow pigment is reduced to a minimum so that the hair sometimes appears almost white. According to fanciers, silver tabbies bred together occasionally throw brown tabbies.

II. PRESENTATION AND DISCUSSION OF DATA

A. *Maltese dilution*

Maltese dilution appears to be a simple Mendelian recessive. It apparently exists in combination with all other factorial differences, but I have not as yet seen its representative in the lined or narrow type of banding. It is always sharply distinguishable from black, but shows considerable variation in its own intensity. It is to be compared to slaty-blue in the mouse, the rabbit, and the dog. No corresponding color is known in the rat or in the guinea-pig. Cream or dull yellow is its corresponding color in the yellow series; blue and cream, in the tortoiseshell.

Five litters from dilute by dilute gave sixteen dilutes—eight males and eight females.

Six litters from intense by intense gave twenty-four intense—sixteen males and eight females.

Five litters from intense males by dilute females gave five intense males, nine intense females, and one dilute male.

Eight litters from dilute males by intense females gave nine intense males, three intense females, nine dilute males, and eleven dilute females.

These data show merely that maltese dilution is not sex-linked.

B. White and white-spotting

White-spotting in cats is exceedingly irregular in amount and distribution, but tends to appear more commonly on the under parts. There appears to be no regularity in dominance and probably many factors are involved. The degree of white-spotting in the parents tends to appear again in the offspring, although wide segregation occurs. I have usually selected cats with relatively small amount of white and have obtained kittens of the same general character.

Solid white appears to be a complete dominant over color whether the color is self or spotted with white. It is possible that it may be allelomorphic with one or more of the white-spotting factors, but my data are not conclusive on this point. Castle ('16) regards it as possibly an extreme form of white-spotting.

A cream male (8)¹ with slight amount of white crossed to a blue-eyed deaf white female (7) sired (6) three pure white kittens; one male and two females. The kittens had normal hearing and developed yellow eyes. The male had a slight smutti-ness of the hairs on top of the head which appeared when he was two weeks old and then shortly disappeared. The females never developed any pigment in the hair. The same pair of cats mated again and produced two solid white kittens which were not reared.

The cream male (8) was later mated (32) to a yellow-eyed white with normal hearing (22). Two whites, a male and a female, were produced, as well as two females that were entirely self color, a blue and cream and a cream. I was unable to detect any white hairs on these two pigmented kittens. It would appear, then, that the white mother carried factors which dominated the slight white marking of the father, and thus produced totally self-colored kittens.

¹ Individual numbers have been inserted after mention of any animal that is referred to more than once in this paper. Matings have been numbered similarly. It will thus be possible for the reader to check up the genetic composition of any animal by its progenies from various matings.

Dr. Little reports a mating (43) of a yellow-eyed white male by a cream and white female. A single yellow-eyed white female was produced.

A mating (35) of a blue-eyed white Angora male (16) by a yellow-eyed short-haired white female produced three solid whites and a black that was self-colored except for very small white spots between the legs. A mating (36) of the same male by a maltese female produced a solid white and a near self black.

Besides these I have three records of blue-eyed white females which produced both colored and white offspring. The male parents were unknown. One produced a solid white yellow-eyed female and a solid black male. One produced in two litters six solid white and three almost entirely black. The third produced a solid white and an intense striped tabby with belly, nose, breast, and feet white.

Davenport ('05) reports a mating of a black Manx male by a blue-eyed, deaf, white female, which produced two whites, one black, one tiger, and one maltese.

The interesting correlation of blue eyes and deafness with white coat is not yet satisfactorily explained. Dominance of eye color seems very irregular. I am informed by breeders of white cats that yellow-eyed by yellow-eyed may produce blue-eyed, and also that blue by blue may produce yellow. Odd-eyed cats also frequently appear in these crosses.

Przibram ('08) reports experiments with odd-eyed white Angora cats. Results were very irregular. The cats bred true to whiteness. As regards correlation of deafness and blue eyes, he says,

Von Interesse ist es, dass, soweit eine Prüfung des Gehörs unternommen werden konnte, die blau-blauen erwachsenen Katzen alle völlig taub waren, was ja mit früheren Beobachtungen von Darwin und Rawitz übereinstimmt; die asymmetrischen Augenfarben scheinen dem ganz entsprechend mit einer halbseitigen, die Seite des blauen Auges betreffenden Taubheit betroffen zu sein. Die Correlation zwischen blauen Augen und Taubheit bleibt also auch bei der asymmetrischen Vererbung bestehen. Dabei bleibt die Correlation zwischen 'blauen Augen' der Katzen und 'Taubheit' auch für die Körperhälfte bestehen.

Dr. C. C. Little showed me a black and white cat with odd eyes. The hair surrounding the blue eye was white, while that about the yellow eye was black. Blue eyes in pigmented cats are rare, except of course in the case of the Siamese.

I would suggest, therefore, as a working hypothesis that the incidence of white-spotting in connection with the dominant white factor produces the blue eye, or in other words a 'white spot' about the eye of a white cat makes the eye blue, while a 'pigmented spot' about the eye of a solid white cat makes the eye yellow. It may be also that a 'white spot' in the ear of a white cat makes it deaf. This would explain why it is so difficult to get blue-eyed white cats with normal hearing as it would be difficult to localize the 'white spot' upon the eye and to keep it away from the ear. This may also explain why odd-eyed cats are frequently defective in hearing only on the side having the blue eye, as noted by Przibram. It would not be a difficult matter to test this hypothesis.

C. Solid yellow and yellow-spotting

The tortoiseshell cat has been the subject of much interest and discussion in genetic literature dealing with sex-correlated phenomena.

Doncaster ('05) considered the problem and tried to explain the peculiarities of inheritance by variations in dominance. Little ('12) suggested the hypothesis of a single sex-linked pair of allelomorphs with the male digametic. He used the term 'sex-limited character,' which has since been restricted to simple Mendelian heredity in which sex reverses the dominance of the allelomorphs. Doncaster ('12) accepted Little's suggestion as in general satisfactory, but pointed out that occasionally black females are produced from matings of black female by yellow male. According to Little's hypothesis, the females should always be tortoiseshell from the reciprocals of black by yellow and the males should be like the mother, disregarding of course dilution, tabby, etc. Doncaster suggests an occasional break in sex-linkage to explain these anomalous blacks, as also the

occurrence of the rare tortoiseshell male. In 1913 he gave a further discussion of the subject and an excellent summary of data collected from fancy breeders. In 1914 he suggested non-disjunction of the sex-chromosomes in oögenesis to explain the matroclinous black females. These explanations are all more or less unsatisfactory for one reason or another, as admitted by Doncaster and by Little.

I have pointed out (1915) that the hypothesis of simple sex-linkage first suggested by Little may be sufficient to account for the conditions if it be considered that the heterozygotes, which must be females, vary from black through various degrees of yellow-spotting to solid yellow. In the male, presumably, conditions are much more stable, as it is impossible to have a heterozygote. Thus I have suggested that a gametically yellow male ($YX -$) may become tortoiseshell by extreme selection of black extension factors, while a gametically black male ($yX -$) may become tortoiseshell by an extreme selection of yellow extension factors. The possibility is of course not excluded that there may be a single factor or particular combination of factors that produces yellow-spotting in the male.

Ibsen ('16) has suggested close coupling of two pairs of sex-linked allelomorphs, and attempts to explain anomalies by crossing-over. This does not account for all the results, however, as he himself points out.

The data concerning the tortoiseshell problem which I have gained from my experiments are as follows:

A long-haired cream male (8) ($a.b.m.Y$)² was crossed (12) with an intense striped tabby (25) ($A'.B.M.y$). There resulted one maltese ($a.B.m.y$) and two intense striped tabby ($A'.B.M.y$) males and one blue and cream ($a.B.m.Yy$) female.

The same male was crossed twice (9 and 30) to a black (20) ($a.B.M.y$). There resulted three black ($a.B.M.y$) and two maltese ($a.B.m.y$) males and two orange and black ($a.B.M.Yy$) and three blue and cream ($a.B.m.Yy$) females.

² The genetic formula includes only factors known to be present. The duplex condition is not expressed except in the case of the sex-linked pair $Y-y$ in which dominance is variable.

The same male was crossed (33) to an intense striped tabby (3) (A.B.M.y). There resulted one intense striped tabby (A.B.M.y) male and one blue and cream (a.b.m.Yy) female.

The same male was crossed (13) to a maltese (17) (a.b.m.y). There resulted one maltese (a.b.m.y) male and two blue and cream (a.b.m.Yy) females. These blue and cream females are of interest as they are almost anomalous blacks. They were mentioned by me in a previous paper (1915, p. 519). They are almost entirely dilute blacks except for a very restricted amount of white on the under parts. One has a very small amount of cream bordering the white at a few points, and a small cream spot on the back. The other is entirely without cream except for a few cream hairs on one leg and at the tip of the tail. These kittens then represent a very close approximation to the anomalous black.

A short-haired cream male (24) (A'.b.m.Y) was crossed twice (34 and 49) with an intense striped tabby (3) (A.B.M.y). There resulted five males—three maltese (2 a.B.m.y and 1 a.b.m.y), one black (a.B.M.y), and one intense striped tabby (A'.B.M.y); and four females—two blue and cream (a.b.m.Yy), one orange and blotched (A.b.M.Yy), and one blue and cream striped (A'.B.m.Yy).

Summarizing matings of 'yellow' male (YX -) by 'black' female (yX yX), we have seven matings giving fifteen 'black' males (yX -) and thirteen 'tortoiseshell' females (YX yX).

Crosses of yellow male by tortoiseshell female are as follows:

A cross (37) of an orange striped male (B.M.Y) by a blue and cream female (26) (a.b.m.Yy) produced two orange-striped females (B.M.Y).

A short-haired cream male (24) (A'.b.m.Y) was crossed (44) with an orange and black female (28) (a.M.Yy). There resulted one cream (m.Y) male and three females—two cream (m.YY) and one blue and cream (a.m.Yy).

The same male was crossed (45) with another orange and black female (30) (B.M.Yy). There resulted three males—one black (a.M.y), one blotched maltese (A'.b.m.y), and one cream (B.m.Y).

The same male was crossed (47) with a blotched blue and cream (13) (A.b.m.Yy). There resulted two males—one maltese (a.b.m.y) and one cream (b.m.Y); and three blotched blue and cream (A.b.m.Yy) females.

Summarizing crosses of 'yellow' males (YX -) by 'tortoiseshell' females (YX yX), we have four matings giving three 'black' males (yX -), three 'yellow' males (YX -), four 'yellow' females (YX YX), and four 'tortoiseshell' females (YX yX).

The long-haired cream male (8) (a.b.m.Y) mentioned above was crossed (32) to a yellow-eyed white cat (22). There were produced one white male, one white female, one cream female (B.m.YY), and one blue and cream female (a.B.m.Yy). Since a cream kitten as well as a blue and cream was produced, it is probable that the yellow-eyed white was gametically a tortoiseshell.

Dr. C. C. Little has very kindly supplied me with data in regard to an anomalous cream female (23) which breeds like a tortoiseshell. This female he has given to me along with three of its offspring. She has, while in my possession, produced four kittens by her cream son. They are two cream females, one cream male, and one maltese male. The maltese male would of course not be expected from a mating of two yellows. The under parts of the anomalous female are white. The upper parts are entirely cream and show the blotched pattern very plainly. No trace of black pigment can be found, although I have examined samples of the hair from various parts of the body under the microscope.

The following gives in detail the offspring from this anomalous cream female. The unexpected progeny are recorded in italics.

When crossed with (42) a dilute blotched male (A.b.m.y), she produced two males—one *blotched maltese* (A.b.m.y) and one *maltese* (a.m.y); and one blotched blue and cream female (A.b.m.Yy).

When crossed with (39 and 40) an intense striped male (A.B.M.y), she produced in two litters two males—one orange

(M.Y) and one cream (24) (A'.b.m.Y); and two females—one *black* (a.M.yy) and one orange and black (a.M.Yy).

When crossed with (41, 46, and 50) her cream son (24) (A'.b.m.Y) she produced in three litters three males—one *blotched maltese* (A.b.m.y), one *maltese* (a.b.m.y), and one cream (m.Y); and two cream females (m.YY).

When crossed with (38) an orange-striped male (B.M.Y), she produced one *black male* (a.M.y) and three females—two striped orange (B.M.YY) and one *striped orange and black* (a.B.M.Yy).

Summarizing the matings of this cream and white female, we find that when bred to 'black' males (yX -) she produced *two 'black' males* (yX -), two 'yellow' males (YX -), two tortoiseshell' females (YX yX), and one *black female* (yX yX).

When bred to 'yellow' males (YX -), she produced *three 'black' males* (yX -), one 'yellow' male (YX -), four 'yellow' females (YX YX), and one *tortoiseshell female* (YX yX).

Of these matings Dr. Little says: "The dilute yellow and white female is interesting because she forms gametes carrying black and breeds exactly like a dilute *tortoiseshell* and *white* animal, although there is no trace of black pigment anywhere on her." She is then an anomalous yellow. Dr. Little further states: "Dilute yellow, like the same color in mice, does not depend upon the depth of color, but is essentially a *dull* yellow ranging anywhere from intense pigmentation to dilute cream color." It is of course relatively not as intense as the orange. It is possible that this variation in cream color is due to the same factors which produce the variations towards silver in tabbies and others.

Yellow-spotting in cats may be compared essentially to the same condition in guinea-pigs. In the latter there is great range of variability as in the former. In cats, however, one of the allelomorphic pairs determining black or yellow extension is much more potent than the others and is sex-linked. The heterozygous female (YX yX) represents a much more unstable condition as regards spotting than either of the homozygous females or than either of the haploid males, for in the heterozygote the factors yellow, Y, and black, y, are balanced against each other.

The sterility of the tortoiseshell tom has frequently been remarked upon. Cutler and Doncaster ('15) discuss this question and show drawings of sections of the testis of a sterile cat of this sort. Normal reproductive cells are altogether lacking. In summarizing the data on sterility of male tortoiseshells, they find that one was certainly fertile, two completely sterile, one almost if not quite sterile, and two doubtful. It appears, then, that sterility may be highly correlated with yellow-spotting in the male.

The black-yellow allelomorphic pair in cats is of particular interest, as it is the only case of sex-linkage known in mammals, other than the sex-linked defects of man.

D. Siamese dilution

Bateson ('13) says of the Siamese cats: "These animals, which breed perfectly true, were introduced from Siam, where they have been kept for an indefinite period as pets of the royal household. Like the Himalayan rabbit, Siamese cats are born almost white, but the fur becomes a curious fawn with darker chocolate points on the ears and extremities." Crosses of Siamese by other cats are cited by Weir ('89). Quoting from a Mr. Young, he says (p. 76), "They invariably showed the Siamese cross in the ground color." But Lady Dorothy Nevill says, "None showed any trace of the Siamese, being all tabby."

Two pregnant females of common cats brought into the laboratory produced kittens of a peculiar ashy color with darker extremities. The kittens resembled very closely adult Siamese cats.

One of the pregnant females, a maltese (5) (a.m.) produced (15) two females which were ashy, with nose, ears, feet, and tail slightly darker, and two females and two males which were ashy with black extremities. A record taken fifty days after birth showed that the lighter kittens had become maltese, while the kittens with black extremities had become steel colored or almost black. They later became completely black. Ghost patterns were seen on four of the kittens, but unfortunately a critical

examination was not made of the other two. Ghost blotched was very much accentuated by the ashiness, but ghost striped did not appear especially so. It is probable for this reason that the two doubtful ones were ghost striped. Of the other four the maltese was ghost striped, and the three steels were ghost blotched.

The other pregnant female (2) was a black and white (a.M). She produced (4) four kittens—two black females upon which no record of ghost pattern was made, an ashy female with black extremities, and an ashy male with dark but not black extremities. Sixty-six days after birth the ashy female had developed into a steel black which clearly showed ghost-blotched pattern, and eighty days after birth the ashy male was maltese with ghost-blotched pattern very evident.

Unfortunately, the inheritance of this peculiar ashy color could not be followed out at the time the kittens were on hand. I am, therefore, unable to say whether it represents the heterozygote for Siamese dilution.

E. Banding and ticking

a. Statement of factorial differences and description of characters. Ticking or agouti in cats, as in rodents, is characterized by yellow bands on the hairs. It increases with age so that kittens are relatively less ticked than cats. I have tentatively considered the agouti factors as a series of triple allelomorphs— A' , much ticked, A , little ticked, and a , non-ticked, with dominance of A' over A and a , and of A over a .

The banding factors, I have also represented as triple allelomorphs— B' , lined, B , striped, and b , blotched. These factors affect the formation of yellow pigment, in a yellow cat (A or $a.B.M.Y$) forming bands of straw color alternating with orange. In a tortoiseshell tabby cat ($A.B.M.Yy$) the orange bands in the 'yellow spots' are continuous with the black bands in the 'black spots,' while the straw-colored bands are continuous through both regions. In a tortoiseshell ($a.B.M.Yy$) alternate banding of straw and orange shows clearly in the 'yellow spots,' while the

'black spots' are uniform black. The same condition obtains in the case of maltese dilution, but the contrast in the bands is not as obvious and there is general reduction in the amount of yellow pigment.

Uniformity or lack of banding in yellow cats is apparently due, as has been pointed out to me by Dr. Sewall Wright, to some other condition than the lack of the agouti factor. As regards the existence of such cats, Mrs. Leslie Williams ('08) writes: "The self-orange Persian is more of an ideal than a reality, for it is actually a red tabby without the tabby markings, and at present it is a case of 'more or less,' the upshot being that the least marked cat in the class takes the prize."

Silvering is a general reduction in the amount of yellow pigment. The straw bands of tabbies then become white. Figure A shows a silver-striped tabby skin. Black stripes alternate with white. In the skin shown in figure B, on the other hand, there is a considerable amount of yellow pigment. A striped tabby (9) brought into the laboratory pregnant had lighter bands of a decidedly reddish color. This apparently represents the opposite extreme of variation from silvering. Intense black stripes alternated with rusty red. She gave birth (22) to three male kittens—one striped with black and red; one blotched with black and red, and one striped with black and straw color. Here, then, is an indication that the extreme reddish tone is hereditary.

For an understanding of banding we may first consider figure B. The skin shown here is from a striped tabby male (7.2) forty-two days old. It may be seen that the bands run longitudinally along the back and are most easily seen near the mid-dorsal line posteriorly. On the sides the bands are transverse and tend to be broken into spots. We may think of this condition as having been produced by longitudinal and transverse waves of pigment-forming metabolic activity. The longitudinal waves form transverse bands. The areas of greatest activity form orange bands in yellow cats, while in tabbies these bands are black. The areas of less activity form, of course, the lighter bands. The transverse waves appear to originate at the mid-dorsal line. They form longitudinal bands on the back. As

they pass outward and down the sides, the areas of greater activity tend to thicken the transverse bands. In the areas of less activity the transverse bands are often evanescent. It thus appears that black or orange spots, in tabbies or yellows, respectively, are produced in the regions of greatest metabolic activity.

The ticking and the banding factors *appear* to act in the same regions, and thus the ticking reveals the straw-colored rather than the orange bands. Agouti is, however, in all probability uniform over the body surface in cats as in rodents. This matter will be discussed in detail after the presentation of data.

The skin shown in figure B had a high degree of ticking, and thus shows the longitudinal bands clearly. The cat shown in figure A is less ticked and the increased amount of black pigment on the back obscures the longitudinal bands. Figure D shows a very dark-striped tabby. While the bands on the sides are clearly seen, the longitudinal bands are obliterated by the black pigment. The cats shown in figures B and D are from the same litter and represent extreme segregation of ticking.

As has been said, ticking increases in cats as in rodents with maturity. The same kitten may, therefore, show different degrees of it at different ages. It is thus necessary to consider age in making comparisons with respect to this character. Ticking always segregates sharply from black. Various degrees of ticking ranging from that shown in figure B to that shown in figure D, however, occur. I have classified the extremes tentatively as A' and A, but their allelomorphism with a is uncertain. There may be intermediate allelomorphs or the variations may be due to modifiers.

The blotched pattern is shown in figures F and H. Figure F is from a kitten extremely ticked at birth. Such a kitten develops into a cat that has yellow in all of its hairs. The black bands of the kitten become ticked in the adult. The lighter bands become entirely straw-colored. We have in this extreme ticking an approach toward the sooty yellow, as in the mouse.

The skin shown in figure H is from a kitten one week old. Nevertheless, it is much darker than that shown in figure F. Such a kitten develops into a dark-blotched adult. The ticking

increases with age until the cat appears much like the kitten shown in figure F.

For a discussion of the blotched pattern in comparison with the striped, the degree of ticking shown in figure F is most favorable. The bands shown here are broad and consequently not as numerous as in the striped. A median dark longitudinal band down the back is cut just behind the shoulders by dark and light transverse bands. The alternation of dark and light bands is not as obvious in the blotched pattern as in the striped, since the bands are relatively wide and the longitudinal and transverse bands interfere with each other. The tendency of the bands to become broken into spots or blotches may be explained in the blotched, as in the striped, by a conflict of longitudinal and transverse waves.

The lined or narrow-banded pattern is rarely seen in cats in this country. The bands are extremely narrow and frequent and are best seen when the hair is very short and the ticking is of just the proper degree. Figure C shows a rather dark-lined cat (28.3) forty-five days old. The narrow banding shows clearly about the edge of the skin and to some extent on the sides. Such a cat becomes somewhat lighter when it grows older. It is very dark when young and appears black and tan like figure G, which is from a lined kitten (19.3) one week old. Narrow bands are seen in the tan areas of the latter and the back and sides show narrow bands when the skin is turned in certain relations to the line of vision. These narrow bands are really a 'ghost pattern' comparable to the 'ghost patterns' of striped and blotched seen in fully black cats. They may be seen in the fur running transversely down the sides. On the skin they may be seen running in the same way and also longitudinally down the back. They are much narrower and more numerous than the bands of striped cats. Lined cats occur in Africa and to some extent in Europe. They are known as African, Caffre, or Abyssinian cats.

In black and maltese kittens 'ghost patterns' are seen clearly in the skin and are not difficult to recognize in the fur. As the kittens become older the ghost patterns sometimes show more clearly in the fur for a time, although they disappear from the

skin. In adult cats ghost patterns are occasionally seen. I have been able to classify all black or maltese kittens as either striped or blotched. A lined cat lacking agouti has not yet been obtained, but this I am hoping to do in time by the proper crosses.

Figure E is from the skin of a lined kitten at birth. It is an extremely ticked example and would probably have grown to a sooty yellow adult. The back is black, but well scattered with ticked hairs, thus differing from the skin shown in figure G. The transverse bands are shown about the edge of the skin at the sides and about the tail. The longitudinal bands are suggested by two ticked spots at the back of the neck. Just posterior to these spots are two parallel ticked lines. On the body near the tail may also be seen longitudinal bands.

Fundamentally, then, the lined, the striped, and the blotched patterns are comparable, differing only in the width of the bands.

A pair of lined cats is owned by the Zoological Society of Philadelphia. The male is dark while the female is much lighter. A comparison of the degree of ticking of the two may be of interest. The back of the male is black, the sides very dark showing narrow ticked bands. The back of the female is dark but ticked and grades into sooty yellow on the sides, showing no dark banding. The banding on the head and breast of the male is for the most part black, while in the female it is brown shading to sooty. In the male the back and end of the tail are black, while ticked rings are seen only toward the base. In the female the entire tail is ringed with sooty yellow. In both animals the feet are sooty yellow, the soles black. In the male the black bands of the sides extend down the legs to the feet, while in the female the sooty yellow of the feet extends well up on the legs.

b. Experimental data. When bred together (19) the lined cats produced four kittens—a dark-lined male, the skin of which is shown in figure G; a dark-blotched male, the skin of which is shown in figure H; a dark-blotched female, and a light-lined male (21). The last-mentioned animal has been raised and is now in the possession of Dr. Charles Penrose, of Philadelphia. It has been examined by the writer, who finds that at the age

of two years and three months it is in color almost the exact counterpart of its mother. It has, therefore, received from its mother the factor A' while its three sibs have received the factor A for which the mother is presumably heterozygous, unless indeed she is carrying non-agouti, a . The cross may be expressed: $AAB'b \times A'AB'b = 1 AAB'? + 1 A'AB'? + 2 AAbb$. Whether or not the two lined offspring are homozygous for B' or carry b is unknown.

The dark-ticked lined male was bred to a very much ticked blotched female (14). This female had been brought in pregnant and had produced (11) two blacks showing ghost striped, one blotched, and two striped. One of the striped had a *very high* degree of ticking. The skins of the others were not saved and no determination of the exact amount of ticking was made at the time. When bred to the dark-ticked lined male this female produced four kittens—one lined and three blotched. The lined is shown in figure E and one of the blotched in figure F. The other two blotched were similar in amount of ticking to that shown in figure F. This female may then be considered as of formula $A'abb$. The cross to the lined male, $AAB'b$, gave 1 $A'AB'b$ and 3 $A'Abb$. Larger numbers would probably have shown some dark-ticked kittens.

The same male was bred to the black and white female (2) mentioned under the discussion of Siamese dilution. She had produced (4) by an unknown male two ghost blotched kittens—a black and a maltese—and two blacks in regard to which no ghost pattern was recorded. When bred to the lined male she produced (29) four kittens—three lined and one blotched. All the skins were kept and all were very dark. The mating may therefore be represented: $\sigma AAB'b \times \varphi aabb = 3 AaB'b + 1 Aabb$.

The lined male was also bred to a black female (10) which showed indistinct stripes in her fur. She had produced (23) from an unknown male four black males, all showing stripes as ghost pattern. When bred to the lined male she produced (28) one lined and two striped kittens. The lined is shown in figure C and one of the striped in figure A. The other striped was

about the grade of ticking as that shown in figure A. If my hypothesis of the allelomorphism of the agouti factors is correct, these striped kittens must represent a light variation in the dark agouti. In the case of these kittens the light color may be due to silvering, as there is practically no yellow in the fur of either of the striped, although the lined shows a fair amount. The cross may be represented: ♂ $AAB'b \times \text{♀ } aaBB = 1 AaB'B + 2 AaBb$.

A highly ticked blotched male (11) was crossed (14) with a black female (15). Four highly ticked blotched kittens similar to figure F resulted. The cross may be represented: ♂ $A'A'bb \times \text{♀ } aabb = 4 A'abb$. The same male was later crossed (25) with a maltese striped female (4). Three intense striped and two intense blotched resulted. Unfortunately, the grade of the ticking was not determined.

A very dark striped female (3) was crossed (16) to a very dark blotched male (6). Six kittens were produced—two blotched, three striped, and one black showing stripes as ghost pattern. The blotched and two of the striped were dark. The other striped was slightly lighter. It was not, however, as light as those that are grouped as much-ticked. It shows clearly, nevertheless, that ticked cats may produce offspring apparently more ticked than themselves. The cross may be represented: ♂ $Aabb \times \text{♀ } AaBb = 3 AA \text{ or } AaBb + 2 AA \text{ or } Aabb + 1 aaBb$.

The same dark-striped female (3) was crossed (33) with a long-haired cream male (8) which appeared from other crosses to be homozygous for blotched and for non-agouti. The two kittens were a blue and cream female showing blotched as ghost pattern and a dark-striped male. The latter has grown up and shows exactly the same dark coat-color as his mother. The cross may therefore be represented: ♂ $(aa.bb.mm.Y-) \times \text{♀ } (Aa.Bb.-Mm.yy) = 1 \text{ ♂ } (Aa.Bb.Mm.y-) + 1 \text{ ♀ } (aa.bb.mm.Yy)$.

The dark-striped female (3) was mated twice (34 and 49) with a short-haired cream blotched male (24) and produced nine kittens as follows: Males, 1 a.B.M.y., 2 a.B.m.y., 1 A'.B.M.y., 1 a.b.m.y. Females, 1 A'.B.m.Yy., 2 a.b.m.Yy., 1 A.b.M.Yy.

The light-ticked kittens probably inherited the factor A' from their yellow father. That the male carries the factor A' is shown by the fact that when crossed (45) with a black and orange (30) there were produced three males—a black and white in which there was so much white that it was impossible to determine the ghost pattern, a cream, showing stripes, and a blotched maltese in which the ticking stood out extremely clearly. The latter is being raised and differs decidedly in amount of ticking from many other blotched maltese cats in my possession.

The long-haired cream male (8) was crossed twice (9 and 30) with a black female (20). Ten kittens were produced, all of them showing stripes as ghost pattern. The female is therefore $aaBB$. The cross may be expressed: $\sigma aabb \times \varphi aaBB = 10 aaBb$.

The same male (8) was crossed (12) to a much ticked striped female (25). Of the four kittens produced two were non-ticked and showed stripes as ghost pattern and two were much ticked and striped. The cross may therefore be expressed: $\sigma aabb \times \varphi A'aBB = 2 aaBb + 2 A'aBb$.

The same male was crossed (13) to a maltese female (17). Three dilute kittens resulted, all with blotched ghost pattern. $\sigma aabb \times \varphi aabb = 3 aabb$.

It is clear, then, that the cream male (8) does not carry the ticking factor, for when crossed with two non-ticked females it has sired thirteen non-ticked kittens. It also probably is homozygous for blotched, although it does not show the pattern, for when crossed to a maltese female it sired three blotched kittens.

It thus appears that the long-haired cream (8) does not carry agouti and does not show the blotched pattern, while the short-haired cream (24) carries strong agouti, A' , and shows the pattern. Whether the agouti factor tends to bring out the pattern more strongly in a cream may yet be an open question. I am inclined to think that the pattern is obscured to some extent in long-haired cats by the length of hair.

An orange-striped male was crossed (37) to a blue and cream female (26) that showed ghost blotched pattern. Two orange-striped females resulted. The cross may be expressed: $\sigma (BB.Y-) \times \varphi (bb.Yy) = 2 (Bb.YY)$.

c. *The number of loci involved.* The facts thus far collected, then, are consistent with the assumption of two loci, one for the banding factors and one for the ticking factors. Since, however, all variations from very light to very dark ticking occur and since dark-ticked cats heterozygous for black may produce kittens of somewhat lighter grade than themselves, it is probable that factors at other loci recombine to modify the ticking. Tests are now being made which, it is believed, will determine definitely whether light ticking and dark ticking are both allelomorphic with the same factor for black; that is, whether they form a triple allelomorphic series.

The three types of banding, lined, striped, and blotched, are each entirely distinct. No intergrades have been observed. The natural assumption is to suppose that they form a triple allelomorphic series, B' , B , and b , as I have tentatively assumed. But if two loci are involved the conditions might be expressed as follows: A lined cat might be $LLBB$, $LLBb$, $LLbb$, $LlBB$, $LlBb$, or $Llbb$. A striped cat might be $llBB$ or $llBb$. A blotched cat would then be the double recessive, $llbb$. This scheme apparently fits the genetic data thus far collected. Striped and blotched would act as a pair of simple allelomorphs, B and b . The crosses involving the lined cats would be expressed by supposing that they are both of formula $Llbb$. Bred together they produced lined, $LLbb$ or $Llbb$, and blotched, $llbb$. Crossed with blotched, either black or ticked, $llbb$, they give lined, $Llbb$, and blotched, $llbb$. Crossed with homozygous striped, $llBB$, they give lined, $LlBb$, and striped $llBb$.

The same crosses for testing the agouti factors will also test the allelomorphism of the banding factors. Other combinations that are being made with lined should give yellow and maltese lined.

d. *Physiology of color-production.* Reference should now be made to Wright's ('17) papers on color inheritance in mammals. Wright classifies color factors according to their effects on either one of two enzymes. Enzyme 1 is the basic enzyme for color production which, acting alone on chromogen, produces yellow. Enzyme 2 is supplementary to enzyme 1. It has no effect alone

either on chromogen or on yellow pigment. Combined with enzyme 1 it oxidizes chromogen to sepiä.

The agouti factors are considered as determining an inhibitor of enzyme 2. "Factor *A* determines the production of an inhibitor with the same subtraction effect on enzyme 2 everywhere." This inhibitor acts in waves along the individual hairs. The regions of greatest concentration determine the yellow bands, while those of less concentration are black.

In yellow cats it is seen that banding occurs over the surface of the body, straw-color alternating with orange. Banding, therefore, affects enzyme 1. In black cats the bands are almost indiscernible. There is, then, enough of enzymes 1 and 2 generally distributed to produce a uniform black. In the presence of the agouti factor, however, yellow bands appear in the individual hairs. These bands are much wider in the areas corresponding to the straw-colored bands of yellow cats. In fact, the black may be here entirely obliterated. The hairs in the areas corresponding to the orange bands of yellow cats are much darker and may be without apparent ticking. It therefore appears that the banding factors affect enzyme 2, for if enzyme 2 were uniformly distributed as in rodents, the agouti factor should cause a uniform ticking over the body surface, not an alternation of dark and light bands.

The banding factors may be thought of, then, as determining waves of general metabolic activity affecting both enzyme 1 and enzyme 2. In the black cat the regions corresponding to the orange bands in the yellow cat would be a dense black, a sort of black dominant to agouti, comparable to Punnett's ('12 and '15) dominant black in rabbits, while the regions corresponding to the straw-colored bands would be comparable to ordinary black in being recessive to agouti.

For helpful criticism and discussion of these matters I am much indebted to Dr. Wright, whose papers I have already mentioned.

III. THE ORIGIN OF COLOR VARIETIES OF THE CAT

It is generally assumed that the domestic cat is polyphyletic in origin. Darwin considered this to be the case. Keller ('02) discusses the matter and agrees with Darwin on this point. Elliot ('83) believes that the cat is descended from a number of wild species and supposes that it has crossed at various times with small wild cats in different countries. He attempts to trace the well-known color variations as well as variations in form to such hybridizing.

Rope ('81) and Pocock ('07) both recognize the characters blotched and striped and believe that all cats, whatever their color, fall in one or the other of these two classes. Pocock states:

It is needless to say more in support of the contention that if a decided difference in the 'pattern' of Domestic Cats exists, it must be regarded as furnishing a surer basis for their classification than the length of hair, the tint of the coat, or the stunting of the tail. It may also be claimed with assurance that the pattern supplies a more important clue to the ancestry of the Domestic Cat than the features just mentioned. . . . Frequently at all events the so-called 'blotched' pattern can be detected in certain lights even in 'Whites' and 'Blacks.'

Pocock also recognized the lined variation, called by him Abyssinian.

Cats of the so-called 'Abyssinian' breed may be descended, for anything I know to the contrary, from specimens of *F. ocreata* directly exported from Abyssinia. They are certainly not unlike some self-coloured examples of that species. On the other hand, it would, I imagine, be difficult to separate them from fulvescent 'Ticked' Cats, which appear to me to be nothing but examples of the torquata-type in which the pattern is broken up and evanescent.

The torquata type is what I have called striped. Pocock discusses the synonymy of wildcats and of the domestic cat. The whole matter appears to be much confused.³

³ The wildcat of Europe is usually called *Felis catus* L., but inasmuch as Linnaeus' description agrees with the blotched pattern while the European wildcat is striped, it is considered by Pocock and others that Linnaeus was referring to the domestic cat. *Felis sylvestris* Schreber is therefore chosen as the name for the European wildcat. Of the striped form Pocock says: "To feral or do-

Dr. A. Nehring ('87) believed that the cat has a dual origin, being descended from a domestic Chinese cat and from the Egyptian cat, *Felis maniculata*. The origin of the striped pattern is easily traced to the European wildcat or to the African wildcat. Of the blotched type Richard Lydekker (*Encyclopaedia Britannica*) says:

It may be suggested that the blotched tabby type represents Dr. Nehring's presumed Chinese element in the cat's parentage, and that the missing wild stock may be one of the numerous phases of the leopard-cat (*F. bengalensis*), in some of which an incipient spiral arrangement of the markings may be noticed on the shoulder.

The attempt is made by many authors to trace all variations in morphology and color to some wild ancestor. To do so appears to me unnecessary, as all such variations might occur under domestication. The strictly domestic color variations in the cat may be considered maltese, white, white-spotting, yellow, and Siamese dilution. Such variations, if they occur in nature, appear to be blotted out, as they are certainly not characteristic of any wild species. They occur in numerous domestic animals and may be said to be variations by which domestic species 'mimic' each other.⁴

mesticated examples of this cat have been given many names, of which *torquata* is the best known and *angorensis* or *striata* possibly the oldest. . . . It closely resembles in pattern two existing species, namely, the so-called Egyptian cat (*F. ocreata*) and the European wildcat (*F. sylvestris*)."

Pocock thinks that the blotched or *catus* type is derived from some extinct, probably Pleistocene cat of western Europe.

Pocock uses the term *torquata* for striped and *catus* for blotched, which is just the reverse of many other authors.

There is, further, a so-called *Felis torquata* of India that is considered by some to be related to the spotted desert cat (*F. ornata*).

Inasmuch as I have wished to name genetic factors rather than species of cats, I have discarded the Latin names and have adopted the English words blotched and striped, in regard to which there can be no confusion.

⁴ By the use of the term 'mimic' I wish merely to denote what in my estimation underlies many at least of the phenomena which biologists have attempted to explain by the mimicry hypothesis. There are only a limited number of ways in which an organism may vary. Thus a mammalian coat may vary in dilution and distribution of the pigments black, brown, and yellow. No other pigments can be developed.

Numerous cases of resemblance, moreover, are in all probability due to homologous factorial differences, even in widely separated species. Metz ('16)

On the other hand, variations in the ticking factors and in the banding or pattern factors occur both in wild and in domestic mammals. Such variations in the domestic cat produce color patterns closely similar to numerous wild species. Variations from red to silver occur in wild cats. The tiger has a high degree of red with a moderate amount of ticking. Thus the pattern is very well marked. In the lion and the puma as well as in the jungle cat and others, the red is reduced to yellow while the ticking is very intense. Hence the pattern appears only in young animals and is obliterated by the increase of ticking incident with maturity. Other cats like the ounce or snow-leopard and Pallas' cat represent an extreme reduction of yellow pigment comparable with silvering in domestic tabbies. Loss of agouti producing black varieties of leopards and others are well known. Small species of African and Asiatic cats vary so in color that much confusion has resulted in taxonomy. All of this diversity may apparently be reduced to variations in ticking, in banding, and in the red-silver series. Spots, I believe, are produced by crossing of longitudinal and transverse waves of pigment-forming metabolic activity. In these respects the domestic cat tends to 'mimic' its wild relatives, but whether the variations have originated by crossing or by mutation is an open question.

IV. THE SUMMARY

The inheritance of color variations in the domestic cat has been investigated at the Zoological Laboratory of the University of Pennsylvania.

Maltese dilution segregates distinctly from intense color and is probably recessive.

Solid white is a simple and complete dominant over color. White-spotting is very irregular in inheritance. There is partial correlation between dominant white, blue eyes, and deafness.

has shown that mutations have occurred in *Drosophila virilis* (species B) producing characters similar to mutant characters in *D. ampelophila*. Such variations are inherited according to a similar mechanism and show comparable linkage relationships. I am of the opinion that resemblances in the colors and patterns of different mammals are often due to such genetic homology.

It is suggested that irregularities in inheritance of blue eyes and deafness may be explained by correlation with white-spotting.

Yellow is determined by a sex-linked factorial difference from other colors. The heterozygous female is usually yellow-spotted or tortoiseshell, but ranges to solid black or tabby and to solid yellow. It is suggested that yellow-spotting in the male depends upon extreme selection or segregation of other factors.

Kittens resembling adult Siamese cats have been produced from common cats.

Banding cleanly segregates in three different widths. It is probable that the factorial differences involved act as triple allelomorphs.

Much-ticking, little-ticking, and black probably constitute a triple allelomorphic series. Intergrades occur between much-ticking and little-ticking.

Ticking follows banding in its distribution.

Black-spotting in wild Felidae and in domestic tabbies is explained by crossing of transverse and longitudinal bands.

Color varieties are classified as those that 'mimic' other domestic animals, and those that 'mimic' wild species.

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PLATES

PLATE 1

EXPLANATION OF FIGURES

A. Skin of silver-striped tabby, probably little-ticked, but with reduction of pigment due to silvering.

B. Skin of much-ticked striped tabby. The longitudinal bands are obvious as well as the tendency of the transverse bands to become broken into spots.

C. Skin of little-ticked lined cat.

A and C are from sibs from cross of dark-ticked lined by black.

D. Skin of little-ticked striped cat.

B and D are from sibs.

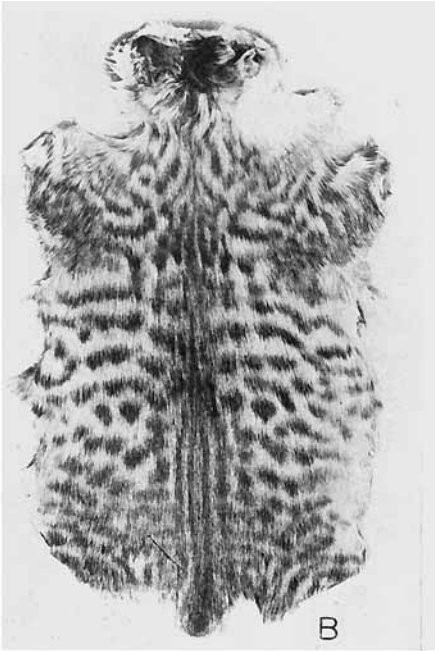
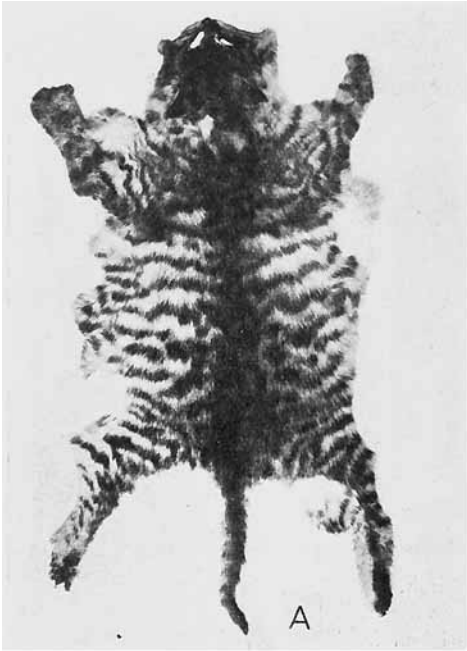


PLATE 2

EXPLANATION OF FIGURES

E. Skin of much-ticked lined kitten at birth.

F. Skin of much-ticked blotched kitten at birth.

E and F are from sibs from cross of little-ticked lined by much-ticked blotched.

G. Skin of little-ticked lined kitten one week old.

H. Skin of little-ticked blotched kitten one week old.

G and H are from sibs from cross of little-ticked lined by much-ticked lined.

The animals, the skins of which are shown in figures A, C, E, F, G, and H, had the same male parent, a little-ticked lined or Caffre cat owned by the Zoological Society of Philadelphia.

