

# COLOUR INHERITANCE IN CATS, WITH SPECIAL REFERENCE TO THE COLOURS BLACK, YELLOW AND TORTOISE-SHELL.

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## I. INTRODUCTORY.

This paper has two objects: (1) the critical examination of experimental data on, and of current hypotheses concerning the inheritance of black, yellow, and tortoise-shell coat colours in cats; (2) the suggestion of possible explanations for the occurrence of (a) unexpected colour classes in ordinary crosses between blacks, yellows, and tortoise-shells, and of (b) both sterile and fertile tortoise-shell males which appear extremely rarely.

The fact that the work of all investigators of this subject has left the two points above mentioned not satisfactorily accounted for justifies an attempt to explain the observed experimental results, even though at this time no additional breeding data are offered for consideration.

## II. THE FACTS REQUIRING EXPLANATION.

The critical and apparently contradictory facts which have been brought out by breeding experiments with cats, and which must be satisfactorily accounted for and explained, are briefly as follows:

(1) *In crosses between yellow males and black females, where the expectation on the basis of complete sex-linkage is black males and tortoise-shell females, black females are sometimes produced.* (Doncaster, 1913.)

(2) *In crosses between yellow males and tortoise-shell females, where yellow males, black males, yellow females and tortoise-shell females are the only classes expected on the basis of complete sex-linkage, black females are sometimes produced.* (Doncaster, 1913.)

(3) *In crosses between two yellow cats, although only yellow young are expected, two aberrant results have been noted.*

(a) A mating of this type has produced tortoise-shell females besides yellows of both sexes. (Doncaster, 1913.)

(b) A mating of this type has produced tortoise-shell females and black males besides yellows of both sexes. (Whiting, 1918.)

(4) There is no record of two black cats crossed together having given yellow or tortoise-shell young.

(5) *Tortoise-shell males are produced much more rarely than any of the aberrant classes recorded under headings 1, 2, and 3 above.* (Doncaster, 1913; Wright, 1918.)

(6) *Such tortoise-shell males are usually sterile.* (Cutler and Doncaster, 1915.)

(7) *If they are not sterile they apparently do not give tortoise-shell sons, but breed as yellows.* (Doncaster, 1913.)

In considering these facts, investigators have usually tried to explain all of them by a single hypothesis. (Doncaster, 1913; Whiting, 1918.) This has proved to be difficult and unsatisfactory. (Ibsen, 1916; Wright 1918.)

It is believed that the experimental evidence favours the existence of two genetically independent agents at work in the production of these aberrances, for

(a) The appearance of the unexpected individuals noted under headings 1, 2, and 3 above, is relatively frequent, and produces regular results involving neither sterility nor the formation of new colour types.

(b) On the other hand, the occurrence of tortoise-shell males is *very infrequent*, not regular, and is in a majority of cases intimately connected with sterility.

Such being the case, an effort will be made to explain the appearance of the unexpected individuals noted under headings 1, 2, and 3 by one hypothesis and the occurrence of tortoise-shell males by a different one.

### III. THE RELATION BETWEEN YELLOW AND BLACK.

One of the first points to be established is the nature of the genetic relation between yellow coat colour and black coat colour.

In this connection Ibsen, 1916, and Wright, 1918, believe black or extension of black pigment to the coat, to be epistatic to yellow or the restriction of black pigment from the coat. Doncaster, 1913, and

Whiting, 1918, consider the two coat colours allelomorphic, the heterozygote being commonly tortoise-shell.

The terminology used by them is as follows:

*Ibsen*, 1916: Black  $B$  is dominant to orange  $b$  which is borne in the  $X$  chromosome. Under ordinary conditions the factor for orange  $b$  is closely linked to  $T$ , a factor for tortoise-shell which acts only in the presence of  $B$ -black. The female is  $XX$ , the male  $X\theta$  in formula.

*Wright*, 1918: Black is due to the action of a factor  $A$ , while tortoise-shell is produced by heterozygosis of an "extension" factor  $E$ . Tortoise-shell females are thus  $Ee$ , yellow males  $e-$ , and black males  $E-$ , in formula. The factor  $E$  is borne in the  $X$  chromosome. The female is  $XX$ , the male  $X\theta$  in formula.

*Doncaster*, 1913 considers that yellow and black are allelomorphic, and expresses yellow by  $Y$ , and black by  $B$ . Where both are present, a  $YB$  or tortoise-shell animal is produced. The female is  $XX$ , and the male  $X\theta$  in formula.

*Whiting*, 1918 also considers yellow  $Y$  to be allelomorphic with black  $y$ , and supposes  $Y$  to be borne in the  $X$  chromosome. The female is homozygous, the male heterozygous for  $X$ .

In 1912 I employed much the same terminology as that of Doncaster, but in view of the production of blacks and tortoise-shells by two yellows and the failure of blacks when crossed *inter se* to produce anything except blacks, it is probable that the relationship between these two colours may be more accurately expressed in somewhat the following manner:  $B$  a factor for the production of black pigment which is found in all  $X$  gametes.  $Y$  a factor for the restriction of black pigment from the coat allelomorphic to  $y$ , a factor for the extension of black pigment to the coat. One "dose" of  $Y$  is normally completely epistatic to one "dose" of  $B$ , thus producing yellow individuals; but two "doses" of  $B$  to one of  $Y$  produces a tortoise-shell. The factor  $Y$  and its allelomorph  $y$  are also borne in the  $X$  chromosome. Thus:

$YBX$	$YBX$	Yellow female
$YBX$	$\theta$	Yellow male
$yBX$	$yBX$	Black female
$yBX$	$\theta$	Black male
$YBX$	$yBX$	Tortoise-shell female

This type of relationship will become clear as the crosses are taken up in detail, and is further made use of in explaining the occurrence of tortoise-shell males.

IV. AN ATTEMPT TO EXPLAIN THE APPEARANCE OF UNEXPECTED INDIVIDUALS OF NORMAL COLOUR TYPES. (Headings 1, 2, and 3, Section II, above.)

It is tacitly assumed by all investigators that at some time or times in the past, there must have been a genetic change, ridding certain gametes of the epistatic colour factor, whether it be the  $Y$  of Whiting, the  $E$  of Wright, or the  $T$  of Ibsen. Had this not been the case neither the hypostatic form nor the tortoise-shell heterozygote could have appeared.

We may, then, for the sake of argument accept the set of symbols given above, and assume that the change from  $Y$  to  $y$  must have occurred. There is no experimental evidence to show how recently or how frequently this change may have taken place, but if we assume that it is still taking place in a portion of the gametes of certain individuals—which seems entirely probable—all the results obtained under headings 1, 2, and 3, may be accounted for. Such a change from an epistatic to a hypostatic condition would be directly comparable to the appearance of the recessive pink-eyed mutation in a stock of dilute brown mice recorded by the writer in 1916.

Animals in whose gametes this mutative process was occurring *de novo* would show no trace of it in their own somatic characteristics, but would, upon breeding, give results in agreement with the actual aberrant classes obtained.

We should thus expect that an occasional yellow female would form gametes  $yBX$  in addition to those containing  $YBX$  which she normally produces. Similarly, certain yellow males would be found which showed by their progeny that they were forming among their  $X$  gametes some which were of the constitution  $yBX$  instead of the normal  $YBX$  type.

Yellow males of this unusual kind would, when crossed with black females, give among their progeny a certain number of black females, in number depending upon the frequency with which the unusual  $yBX$  sperm was formed. This fact would explain the aberrances listed above under Section II, Heading 1.

Similarly, such unusual yellow males would, when mated to normal tortoise-shell females, give rise to a certain number of black females in addition to the other classes normally expected. This would cover category two of exceptions mentioned above (Section II).

Finally, a yellow forming  $yBX$  gametes, when crossed with a normal yellow or with one of its own type, would give rise to unexpected black

or tortoise-shell young, the proportion depending upon whether the yellow male or the female or both were concerned in the formation of the  $yBX$  gametes.

Thus if the male was alone concerned, tortoise-shell females, but *no black males* would be likely to appear among the progeny. This appears to be the case in the mating recorded by Doncaster (1913) in which two yellows gave among their progeny three blue females with a cream coloured patch (tortoise-shells). If, on the other hand, the female parent was the unusual mutative individual, *black males* would occur in addition to tortoise-shell females and yellows of both sexes. This condition was realised in the case of female dilute yellow # 23 (formerly owned by me) whose breeding record is reported by Whiting, 1918. An explanation of this sort would account for the aberrances noted under Section II, Heading 3, above.

From the number of tortoise-shell and black young obtained in the two cases referred to, and from the numerical relation of the black females under headings 1 and 2 (Section II) to the expected colour classes (Doncaster, 1913), it seems probable that yellow animals forming  $yBY$  gametes do so in approximately 50% of the gametes they form, as would a normal heterozygote.

In addition to yellow animals, certain tortoise-shell females might theoretically be expected to show the same phenomenon. Such animals would form an excess of, or possibly exclusively,  $yBX$  gametes, and, in so far as they did so, would breed as blacks. Such an occurrence would, however, give rise to no unexpected classes of young in crosses, but might result in the *absence* of some of those normally expected from certain matings. Quite naturally this fact might, in a small number of progeny, escape notice.

*There is no evidence to show that the appearance of any of the classes above referred to is in any way connected with a break in sex-linkage or with the occurrence of tortoise-shell males, and we may therefore, until such evidence is presented, fairly consider them as independently produced.*

#### V. CRITICISM OF EXISTING HYPOTHESES TO EXPLAIN THE APPEARANCE OF UNEXPECTED INDIVIDUALS OF NORMAL COLOUR TYPES. (Headings 1, 2, and 3, Section II, above.)

Attempts to explain the appearance of the aberrant colour classes referred to, have involved either (a) the breaking of sex-linkage with "crossing over" in the male, or (b) the occurrence of a series of modifying

factors determining the relative degree of black and yellow pigmentation. They may be separately considered as follows:

(a) Doncaster's hypothesis of a break in sex-linkage: this hypothesis, which in a modified form is a basis for Ibsen's later explanation of the appearance of unusual colour types, involves, if it is to explain the exceptional black females, the existence of "crossing over" in the male between the  $X$  and the  $\theta$  chromosomes. Such crossing over has not, in so far as I am aware, been demonstrated in any forms in which the male is  $X\theta$  in formula as in cats. It further would suppose that, as tortoise-shell males were formed by the same process, they would be expected to occur with as great frequency as the exceptional black females. It further leaves entirely unexplained the appearance of blacks or tortoise-shells from a cross between yellow animals. These objections seem to be of sufficient weight to throw the chances against Doncaster's or Ibsen's hypotheses.

(b) Whiting's hypothesis of modifying factors which at one end of the series would serve to make tortoise-shell animals yellow, and at the other end of the series make them black, remains as a possibility though seriously invalidated by certain points as follows:

(1) There should be records of black females (genotypically tortoise-shell) which if crossed with other blacks should give yellow males and tortoise-shell females, or if crossed with yellow males should give unexpected yellow females. Neither of these results has been recorded.

(2) Doncaster, 1913, reports that the three tortoise-shell females produced from a single cross between two yellows were "blue with a cream patch" thus showing that they were near the *black* end of Whiting's modifier series. Inasmuch as under his hypothesis one of their parents must have been at the opposite or yellow end of the series, it is difficult to explain how and why many of its progeny should show the condition characterising nearly the other end of a graded series.

(3) The occurrence of these young in a single mating makes it seem likely that the particular animal was forming ordinary  $yBX$  gametes in a considerable number.

(4) The tortoise-shell young produced by dilute yellow female # 23 already referred to, before she was sent to Dr Whiting, were normal tortoise-shell in colour; if anything, more nearly on the *black* end of the graded series, than on the yellow. This case serves to support that

reported by Doncaster, and tends to show that the yellow animal *transmitted to its progeny no peculiar set of modifiers*.

VI. AN ATTEMPT TO EXPLAIN THE OCCURRENCE OF (a) STERILE, AND  
(b) FERTILE TORTOISE-SHELL MALES.

(a) *The production of sterile tortoise-shell males.*

It is agreed by all those who have reported on breeding experiments with cats that the female appears to be homozygous, the male heterozygous, for sex. The former is therefore  $XX$ , the latter  $X\theta$  in formula. This places cats in the same category with *Drosophila*, and this in turn means that one may rightfully turn, and in fact *should* turn, to the magnificent work of Morgan and his associates in any attempt at explaining a peculiar result which shows exceptional conditions of sex-linkage.

If one considers the phenomena of non-disjunction of the  $X$  chromosome in *Drosophila*, reported by Bridges in 1913, and later (1916 *a* and *b*) further established by him after an extensive series of breeding experiments, one cannot fail to be impressed by the similarity between the results of that process in *Drosophila*, and the observed experimental facts in cats.

For example, non-disjunction is neither frequent in its occurrence nor is it clear enough in its hereditary behaviour to give striking numerical results in as slow breeding an animal as a cat, unless it were watched for deliberately. In *Drosophila* it gives rise to two very significant exceptions to the normal sex-linked inheritance. First, it produces animals *apparently males, which are sterile*, and second, *mosaic forms* are apt to arise in non-disjunctive stocks. If one considers that the majority of tortoise-shell cats *which are apparently males are sterile*, and second that they are also a *mosaic* form in a sex where commonly none is found, the comparison becomes interesting and extremely suggestive.

We may now consider what the probable results of non-disjunction would be, did this phenomenon exist in cats.

The characteristic of primary non-disjunction is that in oogenesis the two  $X$  chromosomes go together into a single egg, leaving another egg without even the normal single  $X$ . This may be shown as follows:

Non-disjunctive female  $XX$   
forms gametes  $XX$  and -

If now the eggs of such a female are fertilized by sperm of a normal male we have four possible types of zygotes.

Eggs	Sperm	Zygote	
XX	X	XXX	Dies
-	X	X-	"Near male" always sterile
XX	$\theta$	XX $\theta$	Female with peculiar gametic condition
-	$\theta$	$\theta$ -	Dies

Bridges has demonstrated that the XXX and  $\theta$ - forms die, and that the X- form although appearing like a male is always sterile. If now we imagine a cross to be made between a tortoise-shell female cat showing non-disjunction and a normal yellow male, we should have the following condition:

Non-disjunctional Tortoise-shell female	YBXyBX	Normal Yellow male YBX $\theta$
Forming gametes	YBXyBX and -	Forming gametes YBX and $\theta$
Zygotes	(a) YBXyBXYBX Dies	
	(b) YBXyBX $\theta$ Tortoise-shell with peculiar gametic conditions	
	(c) YBX- "Near male" always sterile	
	(d) - $\theta$ Dies	

If now one assumes that absence of the  $\theta$  chromosome allows the "near male" class (c) to develop into a tortoise-shell, disturbing the normal relation of yellow to black to produce a somatic mosaic, we could account for the appearance at rare intervals of tortoise-shell "near males" which were not fertile. It seems not unlikely that the absence of the  $\theta$  chromosome might well upset the somatic relationships of certain of the characters whose factors are carried by the X chromosome. This would account for the appearance of a tortoise-shell "male" from a mating of yellow male  $\times$  tortoise-shell female. (Doncaster, 1913.)

Another mating which, according to Doncaster, has produced a tortoise-shell male is that of yellow male by black female. Here, if the black female showed non-disjunction, the following condition would be found:

Black non-disjunctional female	yBXyBX	Normal yellow male YBX $\theta$
Forming gametes	yBXyBX and -	Forming gametes YBX and $\theta$
Zygotes	(a) yBX yBX YBX Dies	
	(b) yBX yBX $\theta$ Black female with peculiar gametic conditions	
	(c) - YBX Tortoise-shell? "near male" always sterile (as in previous mating)	
	(d) - $\theta$ Dies	

The third type of mating reported by Doncaster as having produced a tortoise-shell male is that of black male with tortoise-shell female. Here everyone is in difficulty. If, as Doncaster suggests, the occasional crossing over of Y, the factor for yellow, to a  $\theta$  gamete is responsible for



the production of a tortoise-shell male, nothing that could happen in either the gametes of the black male or of the tortoise-shell female would produce a tortoise-shell male. On Whiting's hypothesis we should have to suppose that the tortoise-shell female, although she herself showed no marked modifiers (or she would have been black), transmits unusually heavy modifiers to her sons. These gametes would in turn have to be met by an equally heavy set of modifiers from the black male, or a yellow would result.

Further than this, by Whiting's hypothesis the yellow male is  $YX\theta$  in constitution, and this makes the source of the black that he must produce somatically under the influence of modifiers in order to become a tortoise-shell, uncertain. This condition is, of course, not impossible but is highly improbable. Finally, the phenomenon of non-disjunction meets with distinct difficulties. Unless the black male forms gametes with neither the  $X$  nor  $\theta$  chromosomes present it would be hard to see how the tortoise-shell male could be produced by this mating. Formation of sperm without  $X$  or  $\theta$  would not be likely. Yet the possibility exists and may therefore be considered. What seems to me altogether more likely is that the breeder's records on which Doncaster based his observation were in this case uncertain or incorrect, a circumstance quite possible in cats even with the best possible intentions.

(b) *The production of fertile tortoise-shell males.*

We have seen that peculiar tortoise-shell females of formula  $YBXyBX\theta$  may possibly be produced by primary non-disjunction. If now one of these females is crossed with a black or a yellow male peculiar yellow males of the constitution  $YBX\theta\theta$  would be formed as follows:

	Non-disjunctional Tortoise-shell female $YBXyBX\theta$	crossed with	Yellow male $YBX\theta$
Forming gametes	$YBXyBX, YBX\theta,$ $YBX, \theta, yBX\theta$ and $yBX$	Forming gametes	$YBX$ and $\theta$
Zygotes	(a) $YBXyBXYBX$	Dies	
	(b) $YBX\theta YBX$	Peculiar yellow female	
	(c) $YBXYBX$	Yellow female	
	(d) $\theta YBX$	Yellow male	
	(e) $YBXyBX\theta$	Peculiar tortoise-shell female	
	(f) $YBX \theta\theta$	Peculiar yellow male	
	(g) $YBX \theta$	Yellow male	
	(h) $\theta\theta$	Dies	
	(i) $yBX\theta YBX$	Peculiar tortoise-shell female	
	(j) $yBX\theta\theta$	Peculiar black male	
	(k) $yBXYBX$	Tortoise-shell female	
	(l) $yBX \theta$	Black male	

If now such a peculiar yellow,  $YBX\theta\theta$ , is mated with any female showing primary non-disjunction—an animal which might well prove to be a fertile tortoise-shell male would be produced. Thus :

Non-disjunctional Black female $yBXyBX$	crossed with	Non-disjunctional Yellow male $YBX\theta\theta$
Forming gametes $yBXyBX$ and —	Forming gametes	$YBX\theta$ , $YBX$ , $\theta$ and $\theta\theta$
(a) $yBXyBX$	$YBX\theta$	Dies
(b) $yBXyBX$	$YBX$	Dies
(c) $yBXyBX$	$\theta$	Peculiar black female
(d) $yBXyBX$	$\theta\theta$	Peculiar black female?
(e) — $YBX\theta$		“Tortoise-shell male” fertile?
(f) — $YBX$		“Tortoise-shell ‘near male’ sterile”?
(g) — $\theta$		Dies
(h) — $\theta\theta$		Dies

Here the assumption is made that an animal formed from the combination of gametes,  $YBX\theta$  and —, may be somatically a tortoise-shell, and that the  $\theta$  chromosome which is brought into the zygote by an  $X$ -bearing gamete does not in all cases exert its full influence until gametogenesis. The  $YBX\theta$ -male would then be supposed to develop somatically just as does the  $YBX$ -animal, but upon gametogenesis the  $\theta$  chromosome of the  $YBX\theta$ -male is able to prevent the sterility which exists in its absence. This seems quite possible, for it appears that in *Drosophila* the  $\theta$  chromosome is not needed for the development of the normal male somatic characters, but that it is necessary, however, for successful gametogenesis in the male.

A fertile tortoise-shell male would, when he formed gametes, behave exactly like a normal yellow male. That is to say, although he was himself the product of a combination of  $X\theta$  and — gametes, he would in gametogenesis form only  $X$  and  $\theta$  gametes, just as would a normal male. This has been the breeding behaviour of the one recorded certainly fertile tortoise-shell male (see Doncaster, 1913) which acted in crosses with tortoise-shell females apparently exactly as a yellow male would have done.

It will be seen that the above hypothesis, although somewhat complicated, is nevertheless in accordance with experimental facts and accounts for sterile and fertile types of tortoise-shell males; it explains their infrequency of appearance, and possibly their failure to transmit their own colour pattern to their descendants; it is supported by the work of Bridges with *Drosophila*—the most completely investigated form showing a similar type of sex-linkage; it is further capable of experimental tests.

VII. CRITICISMS OF EXISTING HYPOTHESES TO EXPLAIN THE OCCURRENCE OF TORTOISE-SHELL MALES.

(1) Doncaster's hypothesis, as already pointed out, requires "crossing over" in the male between  $X$  and  $\theta$  chromosomes—a condition not shown to exist in gametogenesis of any  $X\theta$  male form. It further fails to account for (a) the comparative infrequency of tortoise-shell males as compared with aberrant black females, (b) the sterility of the majority of tortoise-shell males, and (c) their peculiar behaviour in breeding.

(2) Ibsen's hypothesis does away with the need of crossing over in the male, but fails, as does Doncaster's hypothesis, to meet or explain points (a), (b), or (c) stated above.

(3) Whiting's hypothesis of modifiers would not be able to give a tortoise-shell male which according to his formula would be  $XY\theta$  without adding a factor for black to the formula given by him to be carried in the  $X$  gamete. It further would suppose that by selection (which undoubtedly has occurred) it would be possible to transmit the necessary modifiers to a considerable number of his male progeny, thus forming tortoise-shell males—and this, though great efforts have been made, has proved impossible. Whiting's hypothesis, like those of Doncaster and of Ibsen, takes no account of the sterility of the majority of tortoise-shell males.

(4) Wright's hypothesis is that tortoise-shell males are really  $XX$  individuals in which the abnormality lies not in the colour but in the sex. He likens them to certain sex intergrades already described in some forms by other investigators. This hypothesis meets trouble when a fertile tortoise-shell male is encountered. It also is contrary to the evidence obtained by Bridges who shows that in *Drosophila*  $XX$  forms are females, even though they contain other abnormalities of chromosome distribution.

VIII. SUMMARY AND CONCLUSIONS.

(1) The genetic constitution of the normal colour varieties of cats as regards yellow and black pigmentation appears to be as follows:  $B$  = a factor producing black pigmentation,  $Y$  = a factor which restricts black from the coat,  $y$  = a factor allelomorphic to  $Y$  and hypostatic to it, allowing black pigment to extend to the coat.

$YBX$	$YBX$	Yellow female
$YBX$	$\theta$	Yellow male
$yBX$	$yBX$	Black female
$yBX$	$\theta$	Black male
$YBX$	$yBX$	Tortoise-shell female

(2) The unexpected but normally pigmented individuals appearing in certain matings (Headings 1, 2, and 3, Section II) can be accounted for by supposing that  $Y$  becomes  $y$  in a certain proportion of the gametes of exceptional individuals.

(3) Sterile tortoise-shell males may possibly be "near males" formed as a result of non-disjunction of the  $X$  chromosome and therefore  $YBX-$  in constitution.

(4) Fertile tortoise-shell males may also be the product of non-disjunction (secondary) and would be zygotes formed from the fusion of gametes  $YBX\theta$  and  $-$ . These males in gametogenesis would behave as ordinary yellows.

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