TRICOLOR INHERITANCE. III. TORTOISESHELL CATS[1]

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DONCASTER has published several papers dealing with the inheritance of color in cats, the first of which appeared in 1904. LITTLE (1912) and WHITING (1915) have also written on the same subject. Both DON-CASTER and LITTLE have established that the colors orange (yellow) and black are sex-linked. According to them the female is homozygous and the male heterozygous for sex. On their interpretation a female bearing the orange factor in one chromosome and the black factor in the other is a tortoiseshell, i.e., an animal spotted with black and orange. Black and orange are, accordingly, allelomorphs, but neither is dominant to the other. Orange females are represented by DONCASTER (1913) as *YX.YX;* orange males, *YX.bx;* black females, *BX.BX;* black males, *BX.bx;* and tortoiseshell females, *BX.YX.* LITTLE's method of representing the above color types is essentially the same as DONCASTER'S.

For the normally expected color types DONCASTER and LITTLE have the same interpretation, but they differ as to the origin of the unexpected classes (see table 1). LITTLE considers the rare tortoiseshell male a mutation, while DONCASTER thinks it may be due to crossing over in the male. The latter has presented his idea in the following manner:

Black female, *BX.BX* × *YX.bx,* yellow male
Gametes, *BX, BX*   *Yx,bX*

Black female, *bX.BX*   *Yx.BX,* tortoiseshell male
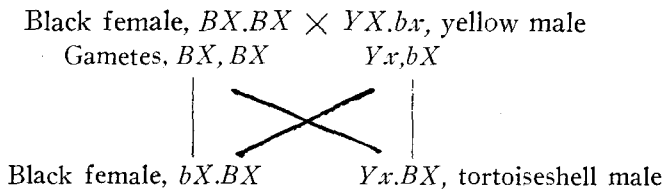
The above scheme would also account for the unexpected class of black females which occurs in the black female × yellow male mating.

DONCASTER admits that there are some difficulties connected with his interpretation. Among these are his *bX.BX* black females, which as he says should give, when mated to orange males, not only tortoiseshell females but also *YX.bX* orange females. He fails to point out that

TABLE 1
DONCASTER'S *cat data.*

Parents	Females			Males		
	Orange	Black	Tortoise-shell	Orange	Black	Tortoise-shell
1. Black ♀ × orange ♂		**13**	48		46	**1**
2. Orange ♀ × black ♂			16	20		
3. Tortoiseshell ♀ × orange ♂	47	**5**	43	54	38	**1**
4. Tortoiseshell ♀ × black ♂		12	21	35	29	**1**
5. Orange ♀ × orange ♂	40		**3**	48		

This table gives DONCASTER'S (1913) data. The offspring about which there was any doubt are not included. The numbers in heavy type represent the individuals of the normally unexpected classes.

they should in addition give *bX.bx* males. Since *b* means the absence of both black (*B*) and orange (*Y*) one would have to assume that these males are neither orange, black nor tortoiseshell. He also states that tortoiseshell or black females mated to tortoiseshell males do not get tortoiseshell male offspring as one would expect by his hypothesis. Another criticism of much greater weight than any of the foregoing is that he has crossing over of a sex-linked factor taking place in the male, which is assumed to be heterozygous for sex. This is contrary to all known facts, for in those cases even in which a *Y* chromosome is known to be present it has never been demonstrated that it carries any hereditary factors.[2]

WHITING'S (1915) explanation for the unexpected color types is entirely different from DONCASTER'S. He thinks that the black females in matings No. 1 and 3 (table 1) are in reality tortoiseshells which have had the black pigmentation extended to such a degree that little or no orange is visible. It is quite possible that some of the unexpected blacks were obtained in this manner. I have obtained a few "self" black guinea-pigs from tortoise × tortoise matings (IBSEN 1916), but it seems improbable that over 20 percent of the total female offspring in mating No. 1 should be accidental blacks, as would be necessarily the case on this hypothesis.

[2] JOHANNSEN (1913, pp. 609-612) believes DONCASTER is not justified in postulating sex chromosomes as bearers of the factors for black and orange. He therefore makes some modifications of DONCASTER'S interpretation in order that the factorial treatment may be more "purely Mendelian." Male cats are represented factorially as *Mm* and females as *mm,* and the factors for black and orange are assumed to be rather closely linked to *m.* Even with these modifications the hypothesis is essentially the same as DONCASTER'S and is open to practically the same objections.

WHITING also discusses the possibility of white spotting affecting the phenotypic appearance of an animal. In a tortoiseshell the white areas may fall, he suggests, on those spots which would otherwise have been orange and thus leave only the black pigmentation visible. Such an animal would be a black-and-white in appearance. This condition is well known in guinea-pigs. Unless, however, the amount of white spotting is relatively large with respect to the amount of yellow the chance of its all being covered, so as to produce a black-and-white, is very small (IBSEN 1916). According to BARTON (1908) a piebald (black-and-white) is usually white only on the face, breast and feet. If any of the blacks in mating No. 1, therefore, had been white even to this extent, it is probable that they would have been classified as piebalds rather than as blacks. Even though they were not so classified, it is still improbable that the usual small amount of white would have covered all of the yellow.

The rare tortoiseshell male, WHITING suggests, is "genetically a yellow with an extreme of black extension factors or a black with an extreme of yellow extension factors." This hypothesis lacks definiteness, and is practically impossible to prove or disprove.

From what has preceded it is evident that the hypotheses offered are far from perfect in that they either fail to explain adequately all the facts or are difficult to test experimentally.

I have been attracted to the problem of inheritance in the tortoiseshell cat because of its resemblance to the tortoise guinea-pigs with which I have been working. In guinea-pigs the self black condition is dominant to tortoise, but it is evident that this is not the case in cats. Tortoise in guinea-pigs is due to a definite single factor, while in cats DONCASTER and LITTLE assume it is due to the interaction of the black and orange factors. WHITING postulates extension factors governing the relative amounts of black and orange.

It seems possible to explain many of the apparent anomalies of color inheritance in cats by assuming that the tortoiseshell coat is due to one definite factor, which I have called T, and which can act only in the presence of black (B), causing the black to be restricted to spots and leaving orange areas between. Two other assumptions are necessary in order to explain all the facts; first that black (B) is dominant to orange (b), as in guinea-pigs, rats, dogs, etc., and second, that under ordinary conditions T (tortoiseshell) is closely linked to b (orange). These points can be brought more clearly to mind by an inspection of figure 1,

in which the factors are represented as being lineally placed on the sex chromosome. It will be noted that two sets of allelomorphs are assumed rather than one as was postulated by DONCASTER and LITTLE. It must also be kept in mind that since T acts only in the presence of B (black) it will have no visible effect on males carrying the b (orange) factor or on females homozygous for this factor.

So long as T and b remain on the same chromosome the hypothesis here presented is as efficient as DONCASTER's or LITTLE's in explaining the normally expected classes in the different matings. It is by means of the occasional crossing over of the factors that the attempt will be made to explain the unexpected classes.

At the outset it may be stated that the hypothesis accounts for the unexpected black females and all the tortoiseshell males, except the one
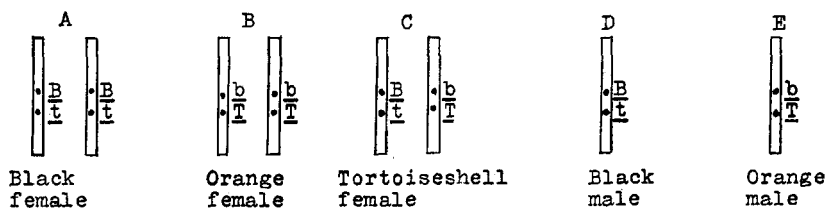

Figure 1. Diagrammatic representation of sex chromosomes bearing color factors showing normal condition in which T and b (orange) are postulated to be closely linked.

in mating No. 1, which, however, may be explained by a combination of WHITING's hypothesis and my own. The tortoiseshell females in mating No. 5 are explained on WHITING's hypothesis, which seems adequate in this particular case, as will be explained later.

I shall first take up the way in which tortoiseshell males may be produced. Since T and b are by hypothesis closely linked, we must assume that crossing over takes place only rarely, and it can occur only in the female. Its occurrence in a homozygous female (figure 1, A or B) would produce no effect in the offspring. The heterozygous female (figure 1, C) is a tortoiseshell and normally forms gametes Bt and bT. When crossing over takes place gametes BT and bt are produced. If this female were mated to an orange male, bT.—, the following classes would occur as a result of the crossing over:

$BT.bT$, tortoiseshell ♀,

$bt.bT$, orange ♀,

BT.—, *tortoiseshell* ♂,

bt.—, orange ♂.

This would account for the tortoiseshell male in mating No. 3. With a black male, $Bt.$—(figure 1, D), the offspring resulting from the crossing over are,

> $BT.Bt$, tortoiseshell ♀,
> $bt.Bt$, black ♀,
> $BT.$—, *tortoiseshell ♂*,
> $bt.$—, orange ♂,

thus accounting for the tortoiseshell male in mating No. 4. DONCASTER (1913) states that he knew of several tortoiseshell males besides those listed in table 1, all of which came from tortoiseshell females by unknown sires. It would therefore seem that tortoiseshell males, when they occur, come almost invariably from tortoiseshell females. This agrees with my hypothesis, according to which tortoiseshell males can be produced only by tortoiseshell mothers. The one recorded in mating No. 1 as having a black mother is an apparent exception. I have no explanation for this case, unless perhaps as already intimated the female was in reality a tortoiseshell, but with so little orange showing that she was recorded as a black.

In the paragraphs just preceding I have tried to indicate how tortoise-shell males are produced. I shall next show what kind of offspring are expected from them.

DONCASTER records the mating of a tortoiseshell male with a black female. The female was not kept in confinement after copulation was observed, and DONCASTER says there may be some doubt as to the paternity of the offspring. The only offspring recorded are a black male and tortoiseshell female, which are exactly what would be expected by hypothesis:

> Black ♀, Bt Bt
> Tortoiseshell ♂, BT —
>
> F_1 $\begin{cases} Bt.BT, \text{ tortoiseshell ♀} \\ Bt.\text{—, black ♂} \end{cases}$

When tortoiseshell females are mated to tortoiseshell males DON-CASTER states that the following four types of offspring are obtained: tortoiseshell females, *orange females,* orange males, and black males. On my hypothesis no orange females should result.

Tortoiseshell ♀, Bt bT
Tortoiseshell ♂, BT —

F_1 $\left\{\begin{array}{l} Bt.BT, \text{ tortoiseshell } ♀ \\ bT.BT, \text{ tortoiseshell } ♀ \\ Bt.\text{—, black } ♂ \\ bT.\text{—, orange } ♂ \end{array}\right.$

It will be noted, however, that the second type of tortoiseshell female in the F_1 generation has a double dose of T and a single dose of B. It may be possible that the extra T restricts the black to such an extent that the animal appears to be an orange instead of a tortoiseshell. This is offered only as a suggestion.

A further test of the hypothesis would be to determine what kind of offspring are obtained from the F_1 females resulting from the tortoise-shell × tortoiseshell cross. By hypothesis one-half of their male offspring should be tortoiseshells no matter what the color of the male is to which they are mated. There appears to be no record of a mating of this type.

We may next consider how the black females in matings No. 1 and 3 may have been formed. It will be remembered, that when crossing over takes place in the tortoiseshell female, the two kinds of crossover gametes formed are BT and bt, and that no matter whether the male parent is black or orange the male offspring are $BT.$—, tortoiseshell, and $bt.$—, orange. The $bt.$— orange male is different from other orange males in that b is not linked with the T factor. By the mating of this sort of orange male with (1) a black or (2) a tortoiseshell female we should obtain black females which are otherwise unexpected in matings No. 1 and 3.

(1)   Black ♀, Bt Bt
      Orange ♂, bt —

F_1 $\left\{\begin{array}{l} Bt.bt, \text{ black } ♀ \\ Bt.\text{—, black } ♂ \end{array}\right.$

(2)   Tortoiseshell ♀, Bt bT
      Orange   ♂, bt —

F_1 $\left\{\begin{array}{l} Bt.bt, \text{ black } ♀ \\ bT.bt, \text{ orange } ♀ \\ Bt.\text{—, black } ♂ \\ bT.\text{—, orange } ♂ \end{array}\right.$

It is to be regretted that DONCASTER does not give the offspring from individual matings. If this had been done it would have been possible to test more thoroughly that part of the hypothesis dealing with the unexpected black females. It will be noted that when black females are mated to *bt.*— orange males all the offspring should be black. There is no way of determining from DONCASTER's data whether or not this ever happens. Moreover, when tortoiseshell females are mated to *bt.*— orange males none of the female offspring should be tortoiseshells.

Part of DONCASTER's data were obtained from BONHOTE. These are now given separately in BONHOTE's (1915) recent book. Here the individual matings are presented and it is possible to trace the offspring of three orange males. Two of the males had the usual tortoiseshell and orange daughters when mated to either black or tortoiseshell females, while the third had 1 orange, 3 *black,* 6 *blue* and 7 tortoiseshell female offspring when similarly mated. This last mating does not fit in at all with the theory that the orange male parent was *bt.*—. It should be pointed out, however, that, as BONHOTE states, he always selected tortoiseshell mothers carrying a large amount of black, which would facilitate the production of tortoiseshell daughters with large amounts of black also. Some of these daughters might therefore have the appearance of blacks. It will also be noted that many (6) of the blacks were dilute and hence classified as blues. I have noticed in dilute tortoise guinea-pigs that it is much more difficult to detect the small yellow (dilute red or orange) spots surrounded by dilute black hair, than it is to detect the small red spots surrounded by deep black hair. It is therefore possible that in this way also animals which should have been classified as tortoises have been called blacks (blues).

The crossover (*bt.*—) orange male should be as rare as the tortoiseshell male. The latter is often sterile and it is possible the *bt.*— orange male is sometimes sterile also. Taking all this into consideration it is probable that matings between either black or tortoiseshell females and *bt.*— orange males are comparatively infrequent; thus it is quite possible that DONCASTER has no record of this type of mating.

If such matings occur, however, the black female offspring would be of the formula *Bt.bt.* These bred to either orange or black males should have orange and black sons in equal proportions. The orange sons would be *bt.*—. On WHITING's hypothesis the unexpected black females should have orange and black sons also, but the orange sons should be *bT.*—. DONCASTER states that he knows of "no satisfactory record of a yellow male mated to a black female having yellow sons." From this

one may infer that there have been cases reported in which a black female had orange sons, but none of them so far have been thought reliable. A larger number of records may furnish some reliable cases.

I have tried so far to account for the tortoiseshell males and the unexpected black males. The three tortoiseshell females in mating No. 5 remain to be explained.

BARTON (1908), writing for the fancier, states, "If there is no white [in a tortoiseshell], then the amount of black hair should be small, compared with the red [orange] and yellow [dilute orange] markings." According to DONCASTER the three tortoiseshell females in mating No. 5 come from one mating. It is therefore possible that in selecting for a tortoiseshell female with the requisite small amount of black spotting one was obtained showing so little black that it appeared to be an orange. Mated to a true orange male this should produce some tortoiseshell female offspring. WHITING has given essentially the same explanation in his 1915 paper.

While it must be admitted that the foregoing hypothesis is not entirely satisfactory, and carefully controlled experiments are necessary for its substantiation, it still has two decided advantages, (1) it is quite definite, thereby tending to be comparatively easy to prove or disprove, and (2) it violates none of the accepted tenets of genetics.

GENERAL COMPARISON OF TRICOLOR IN GUINEA-PIGS, BASSET
HOUNDS AND CATS

In parts I, II and III of the present series characteristics of the tricolor coats of guinea-pigs, Basset hounds and tortoiseshell cats have been considered separately with little reference to their resemblances or differences. They will now be considered briefly from this general comparative viewpoint. We shall first take up the spotting characters themselves, after which their factorial relations will be discussed.

The tricolor coats of guinea-pigs, and tortoiseshell cats show a much greater resemblance to each other than do either of them to the tricolor coat of Basset hounds. They will therefore first be compared with each other and then both can be compared with the Basset hound coat.

Since white spotting tends to mask the true black-red relationship, it is better first to consider black and red alone in their relation to each other, and then to take up white spotting as it affects both of them. In both cats and guinea-pigs the black spotting is variable in amount and is quite irregularly distributed. In both, black may be so far extended that

the animal looks like a self black or so little extended that it resembles a self red. Where the animals differ from each other is in the white spotting. In tortoiseshell cats, as bred by the fanciers, this is small in amount and has therefore little chance of blotting out all of the orange (red) or all of the black. In guinea-pigs, on the other hand white varies greatly in amount and distribution. It can therefore at times blot out either the black or the red and in this way produce red-and-whites or black-and-whites instead of the usual tricolors. Thus we see in guinea-pigs that the variability in amount and distribution of both the black and the white spotting help to produce the unusual color types, while in cats this is affected only by the black spotting. Because of this, cats tend to have fewer of the unusual types than do guinea-pigs.

Basset hounds differ decidedly in several respects from both tortoise-shell cats and tricolor guinea-pigs in that black is localized on the back, so that if there were no white present the entire head, legs and belly would presumably be tan in color, making the animal a black-and-tan. There is no chance here for the black to be so far extended that the animal appears to be a self black or so little extended that it appears to be a self red. The distribution of the white is also somewhat different. In both guinea-pigs and dogs, as well as in mammals in general, pigmen-tation tends to recede toward definite centers, and each of these centers may become entirely devoid of pigmentation. The order in which the centers become pigmentless seems to be quite irregular in guinea-pigs, while in dogs there is greater regularity. The point that concerns us in the present instance is that the aural patches are the last from which pigmentation entirely recedes, and as already noted, these patches in the Basset are always tan. As a consequence the dog may be entirely white except for these tan patches covering the ears. Such an animal is a tan-and-white. Black-and-whites never occur since black pigmentation is never found on the head in Bassets.

Summarizing, we find that in cats white spotting plays a very unim-portant rôle in the production of red-and-whites and black-and-whites; black spotting is perhaps occasionally responsible for these color types. In guinea-pigs black spotting and white spotting are co-equal in their effects, while in Basset hounds white spotting is chiefly instrumental in the production of tan-and-whites, the black spotting merely being pas-sive and aiding only by its position.

So far we have been considering in the three species only the visible relations of black and of white spotting to red. We may next take up

their factorial bases. The white spotting factors in the three animals may have some resemblances so far as we know, but since white spotting has not as yet been adequately treated in a factorial manner, we are not in a position to discuss them. The black spotting factor, on the other hand, can be more definitely discussed.

In guinea-pigs this is called the partial-extension factor (e^p) and is the middle term of a triple allelomorphic series of which entire extension (E) and non-extension (e) are the two extremes. It is therefore recessive to entire extension. In cats on the other hand the factor for black spotting is assumed to be a dominant partial-restricting factor (T), sex-linked, and also closely linked to the orange factor (b). Here it is dominant to entire extension of black. In Basset hounds two factors have to be considered. E is present just as in guinea-pigs, but black spotting here is not due to a modification of E as it is in guinea-pigs. Instead we have a new factor (T) which is not found in either guinea-pigs or cats. The T in cats and the T in dogs are two entirely different factors. As found in dogs it is the factor for the self-colored condition. In its absence (t) the animal is bi-colored. Since a bi-colored animal may be a red-and-lemon as well as a black-and-tan we see that t differs from e^p in guinea-pigs and T in cats in that it has to do with spotting with red as well as spotting with black or chocolate. In order to get dogs spotted with black but not with red, E and T must both be present.

We thus see that though characters in different animals may show some resemblances, they may differ entirely in their factorial analysis.

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