

A New Hypothesis on the Origin of Tortoiseshell Male Cat

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The inheritance of yellow, black and tortoiseshell color in cats and its interpretation

The data concerning the inheritance of these colors may be summarized as follows:

(O=yellow, B=black, T=tortoiseshell)

| Mother | | Father | = | Daughters | + | Sons |
|--------|---|--------|---|-----------|---|-------|
| B | × | B | = | B | + | B |
| B | × | O | = | T | + | B |
| O | × | O | = | O | + | O |
| O | × | B | = | T | + | O |
| T | × | B | = | B, T | + | O, B |
| T | × | O | = | O, T | + | O, B. |

Most of the previous authors, e.g. Little (1912), Doncaster (1913), Whiting (1915) and Wright (1918), regard B and O as sexlinked allelic factors, and T their heterozygote. Some, for hold different views. Ibsen (1916), for instance, postulates a factor pattern formation T which is closely linked with the sex-linked allelic color factors B and b (=O). T restricts the area of black color, and produces tortoiseshell. Thus, black is BtBt (♀), Bt (♂), yellow bTbT (♀), bT (♂), and tortoiseshell BtbT. Doncaster (1912) and Little (1919) also have suggested that O is sex-linked, while B is present in all gametes. As Bamber (1927) states, the ordinary facts of inheritance of these colors summarized above, may be explained in various ways, and there is no established theory. The alleged sex-linkage of O and B is still open to question.

In my opinion, this question can be definitely settled by examining the sex-ratio among each color type. If O is sex-linked, there must be many more males than females among yellow cats, because, whereas only one O factor is enough for producing a yellow male, two O's

are needed for a yellow female, the heterozygote being a tortoiseshell. In Table 1 is presented the result of such a census recorded on Japanese cats in a Japanese book (Isida 1910).

Table 1. The results of a census among various color types of Japanese cats

| Coat color | Male | Female |
|------------------|------|--------|
| Yellow and white | 18 | 103 |
| Black and white | 59 | 45 |
| Tortoiseshell | 86 | 4 |

Thus it is clear that there are many more males than females among yellow cats, while no such disparity is found among blacks. Both Darwin (1868, 1871) and Doncaster (1904) recognize the preponderance of male sex among yellow cats. This very plainly shows that yellow is due to a sex-linked factor, while black, as also its alleles tabby and blue, is due to an autosomal factor. Black behaves as if it were allelic to yellow, simply because it is the commonest 'wild-type' color of the domestic cat, and appears when she carries no yellow factor. A homo- or hemi-zygous yellow is epistatic to black, as well as tabby or blue, but a heterozygous yellow covers black only partially, and produces tortoiseshell. The original wild-type color in cat is unknown. The domestic cat is generally colored, if not yellow or tortoiseshell, black, tabby or blue. Thus, if the color types are to be designated by symbols, they should be: O/O b/b (yellow female), O b/b (yellow male), O^+/O^+ b/b (black female), O^+ b/b (black male), O/O^+ b/b (tortoiseshell female); the tabby tortoiseshell is O/O^+ b^t/b^t or O/O^+ b^t/b .

The tortoiseshell male

The mode of inheritance of the color-types stated above has some exceptions. Especially noteworthy is the occasional appearance of a male tortoiseshell; and the sterility of such a male is another significant fact. The origin of such an exceptional tortoiseshell male and its sterility were subjects of great discussion among geneticists till about twenty years ago. Various theories have been proposed, postulating (1) break of sex-linkage of the color factor (Doncaster 1913), (2) a modifying factor influencing the size of the color pattern (Whiting 1915, 1918), (3) a crossing over between the X and Y chromosomes, producing a color-gene-bearing Y (Doncaster 1912, Hayes 1923; Tjebbes and Wriedt 1927, Crew 1927, Plate 1933), (4) a crossing over between

the color and pattern genes on the X-chromosome (Ibsen 1916), (5) non-disjunction of the X-chromosome (Little 1919), (6) an especially powerful male gene in female chromosome complex (Ohsihma and Oyama 1925, Bonnevie 1925, Tanaka 1943), (7) free-matin phenomenon (Doncaster 1920) (for details of these theories see Bamber 1927 and Tanaka 1943). None of these, however, has become an established theory, and the question of the origin of this enigmatic male remains as unsettled to-day as it was in 1914 when its sterility was first noticed by Doncaster and Cutler.

To answer this question, accurate records of the parents of such an individual are indispensable. In Table 2 are presented such data as are available in the literature.

Table 2. Records of parents and siblings (excluding the propositus) of tortoiseshell males gathered from literature

| Mother | Father | Siblings | | | Author |
|--------------|--------|----------|--------|----------------|-----------------|
| | | Male | Female | Sex unrecorded | |
| B | O | | T | B | Doncaster |
| T | B | | T | | " |
| T | O | | | | " |
| T | O | | | | " |
| T | O | | | | " |
| Blue | Blue | 1 T | 2 T | | Bonhote |
| T | ? | | 2 T | O | Ohsima & Oyama |
| B (Siamese) | O | 1 T | 1 T | | Bamber & Herdan |
| T | O | 3 O | 1 T | | Isida |
| T (nearly B) | ? | 4 T, 1 B | 2 B | 4 B | " |

The two cases recorded in the last two lines in Table 2 are from Japanese sources. Especially, the one in the last line is highly remarkable, since as many as five tortoiseshell males were borne of a mother. This occurred in a farmer's home in the suburb of Tiba near Tokyo. The mother was nearly black and white, but had yellow hair scattered on her belly and legs. She gave birth to three male tortoiseshells, together with two black females and one black male in 1936, and two tortoiseshell males together with four black males and females in 1935 (Isida 1936). The authenticity of the record, at least on the litter of 1936, has been verified by my special inquiry.

A new hypothesis accounting for the origin of tortoiseshell male and its sterility

As stated above, yellow is a sex-linked gene, and it is apparently very closely linked with a powerful gene for the female sex. If an 'unequal crossing over' like that known in the case of *Bar* in *Drosophila* (Sturtevant 1925, '27) takes place in this region, between the two X's of a tortoiseshell mother, and the two sets of color and sex genes come together on the same X, the son that gets this X will become tortoiseshell. At the same time, its sexuality will be shifted toward the female side into a kind of intersex, since its X chromosome bears two powerful female genes instead of one. This hypothesis can account for the origin of a tortoiseshell male and its sterility. According to this hypothesis, the mother of a tortoiseshell male should be tortoiseshell herself. This is exactly what is found in Table 2. In the same table, however, there are a few cases where the mother is recorded as black or blue. In these cases, it may be noticed that the tortoiseshell son has usually tortoiseshell brothers. This fact can be explained by assuming that the black or blue mother was in reality a tortoiseshell having two X's of which one bears double sets of color and sex genes and the other a single set of these genes. Such a female had received from either her father or mother an X chromosome in which the duplication of color and sex genes had already taken place. The mother of the five tortoiseshell males mentioned above was such a tortoiseshell. Accordingly, she must have been $OO^+/O^+ b/b$.

If such a female possessed in her ordinary X chromosome a yellow gene instead of a wild-type gene, she must look almost yellow. The 'anomalous yellow' female described by Bamber and Herdman (1927) was probably such a female. According to these authors, they bred, by crossing a tortoiseshell female and a yellow male, an anomalous female which was almost yellow at birth, but developed small black spots on her right paw when she was four months old. This female was mated with her yellow father, and gave birth to an anomalous yellow male which looked like herself, besides two yellow females and three yellow males. This 'anomalous yellow' female presumably carried yellow and wild-type genes and duplicate sex genes on one of her X's, and a yellow gene on the other X. The former X was transmitted to her anomalous yellow son and the latter to her normal sons. Her symbol therefore should be $OO^+/O b/b$. Nearly all other unexpected breeding records that puzzled previous authors also can be

accounted for by this hypothesis. The few cases which apparently disagree with it are doubtful records.

* In conclusion I record here my indebtedness to Dr. James V. Neel for valuable criticisms.

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(A complete bibliography up to 1927 may be found in Bamber 1927; for Japanese literature see Komai 1946; the rest are given below.)

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