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Supplementary Notes on the Genetics of Tortoiseshell Male Cat*

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Genetics of common coat colors

As has been pointed out elsewhere (Komai 1952a, b, 1956a, b, Komai and Ishihara 1956), the gene for orange (yellow) color is sex-linked, whereas the gene for black or tabby color is autosomal. The effect of the gene for orange, in the homozygous or hemizygous state, is perfectly epistatic to that of the gene for black or tabby, and the orange color completely covers the black or tabby color. However, the effect of the former gene is only incompletely epistatic to that of the latter in the heterozygous state of the gene, and a tortoiseshell coat is produced. The validity of this interpretation is plainly indicated by the results of census of cats with respect to coat colors and sexes (Searle 1949, Komai 1952a, Suzuki 1953). All these results perfectly agree with the presumption stated above. One thing which is apparent to even a casual observation of these results, is the distinct sexual disparity among orange cats—there are always many more males than females among these cats, whereas no such striking disparity is seen among black or tabby cats. Darwin apparently knew this, as he stated, "The peculiar colour called tortoiseshell is very rarely seen in a male cat, the males of this variety being of a rusty tint" (Darwin 1868, II, p. 61). Doncaster (1904) also describes: "Orange females are very rare, although males are common" (1904, p. 36). It is known to many cat lovers too. This fact may be clearly understood by the assumption given above, much the same way as for the distinct sexual disparity among color-blind people. The gene which is allelic to the sex-linked gene for orange (O) is the one for non-orange or wild-type of orange (O^+), and not the gene for black (b) or tabby (b^+) which is located on one of the autosomes. It is rather striking that this plain fact has escaped notice of some recent geneticists including Sprague and Stormont (1956). This basic fact on the location of genes for common coat colors is important for understanding the origin of tortoiseshell males.

Origin of tortoiseshell males

It had been stated in some of my previous papers (1946, 1947) that the mothers

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Table 1. Records of tortoiseshell males collected by the writer:
 B-black, O-orange, T-tortoiseshell, T(b)-black tortoiseshell,
 T(ta)-tabby tortoiseshell, Ta-tabby.

Specimen no.	Tortoiseshell ♂	Mother	Father	Litter mates
1	T (b)	T (ta)	O (or B)	B ♀, T ♀, O ♂
2	T (b)	T (b)	O	T ♀, O ♂2, B ♂2
3	T (ta)	T (ta)	?	
4	T (ta)	T (b)	O	B ♀, B ♂, O ♂
5	T (ta)	T (b)	T a	T ♀, B ♂
6	T (b)	T (b)	?	O ♂2
7	T (ta)	T (b?)	O?	
8	T (b)	T (b)	B	O ♂, B ♂
9	T (b)	T (b)	B?	T ♀, T a ♀, White ♀
10	T (b)	B	O?	T (b) ♀, B ♂
11	T (b)	O	?	T a ♀ 2
12	T (b)	O	?	T (b) ♀, O ♂
13	T (b)	T (b)	B (or O)	B ♂
14	T (ta)	T (ta)	?	T ♀, T a ♀, ♂
15	T (b)	T (b)	?	T ♀3, T a ♀
16	T (b)	T (b)	B?	B ♀, T a ? ♂
17	T (b)	T (b)	?	T ♀4
18	T (b)	T (b)	O?	T ♀2, O ♂
19	T (b)	?	?	?
20	T (b)	B	O?	B ♀, B ♂
21	T (b)	O	?	?
22	T (ta)	T a	?	T ♀, O ♂, B?
23	T (b)	T (b)	?	O ♀
24	T (b)	B	O	T (b) ♀2
25	T (ta)	T (ta)	B	O ♂, B ♂, T a ♂
26	T (ta)	T (ta)	O	?
27	T (b)	?	?	?
28	T (b)	T (b)	O	T ♀, O ♂2, Gray ♂
29	T (b)	B	B?	B ♂2
30	T (ta)	T (b)	?	T ♀2, B ♀, B ♂
31	T (ta)	T a	?	T ♀, B ♂, T a ♂
32	T (b)	O	B?	T ♀6
33	T (b)	T (b)	?	?
34	T (b)	T (b)	O	T ♀2, O ♀, B ♂
35	T (b)	?	?	?
36	T (ta)	T (b)	?	B ♀, T a ♂
37	T (b)	T (b)	?	T ♀, B ♀, B ♂
38	T (b)	T (b)	?	T ♀2
39	T (ta)	?	?	?
40	T (b)	B	O?	T (b) ♀, B ♂2
41	T (b)	T (ta)	B	T (ta) ♀, B ♂
42	T (b)	T (b)	B (or O)	O ♂
43	T (b)	T (b)	O?	T ♀
44	T (b)	T (b)	O	O?
45	T (b)	T (b)	O?	O?
46	T (b)	B	O?	B ♂3
47	T (b)	T (b)	B	T ♀, O ♀, O ♂
48	T (b)	T a	?	B ♀, T ♀
49	T (b)	O	B	O ♂5
50	T (b)	T (b)	?	O ♀3
51	T (b)	B	O	B ♂2
52	T (b)	T (ta)	?	T ♀, B ♀, B ♂
53	T (ta)	T (ta)	T a	T (ta) ♀2, O ♂3
54	T (b)	T (b)	?	?

Specimen no.	Tortoiseshell ♂	Mother	Father	Litter mates
55	T (b)	T (ta)	?	T (♀)2, B ?
56	T (b)	?	?	?
57	T (b)	T	B (or O)	B ?
58	T (b)	B	O ?	O ♀
59	T (b)	?	?	?
60	T (b)	T (b)	?	T ♀
61	T (b)	B	?	?
62	T (b)	T (b)	?	B ♂
63	T (b)	B	?	T ♀
64	T (b)	T (ta)	B	O ♀, B ♀, B ♂
65	T (ta)	?	?	?

of all tortoiseshell male cats are tortoiseshells. This has been revealed as erroneous by further records of the births of such cats obtained from various parts of Japan. Records of 65 such specimens were available (Table 1). Since such records were obtained mostly by questionnaire methods from owners of cats, most of them are incomplete, and ought to be used with some precaution. Still they clearly show that the mother of a tortoiseshell male can be of any color. This implies that she might carry either O or O^+ in her X-chromosome and either b or b^+ in one of her autosomes. But, the sex-linked gene possessed by her and that possessed by her mate should be in a heterozygous relation O/O^+ . These facts are indicated in Table 1. It is thus obvious that the tortoiseshell male is heterozygous for O and O^+ , much like the female tortoiseshell.

Since the tortoiseshell male cats are males, they should be hemizygotic. But they should be heterozygous for O . To reconcile this apparent contradiction, it seems appropriate to assume that the Y-chromosome in such exceptional males carries O or O^+ . This would be possible if crossing-over between X and Y chromosomes takes place in a germ cell of the father of the cat, and transfers the O or O^+ from X to Y.

All the workers on the cytology of cat recognize the presence of a Y-chromosome in the male cell. Koller (1941), one of workers, has revealed the details of the structure of X and Y-chromosomes, and found that both of these are differentiated into pairing and differential segments, and chiasma may be formed between the pairing segments of the two chromosomes. Thus, it is very likely that crossing-over takes place between X and Y. If, by this process, the sex-linked gene O or O^+ is transferred from X to Y, the latter will get the gene in question. Then, there would be no difficulty to assume that occasionally a male heterozygous for O may be produced.

There remains another important question to answer which concerns the sterility of tortoiseshell males which is almost without exception. For this, I assume the presence of a gene or gene complex for fertility of the male in the Y-chromosome and its transfer by crossing-over to X, reciprocal to the transfer of O from X to Y. In case this interpretation is unlikely, it might be equally well

to assume that the crossing-over somehow upsets the sex-differentiation mechanism of Y-chromosome which acquires some female-determining gene present on a neighboring locus of *O*. It seems to me that this is about the right explanation of the origin of tortoiseshell male and its sterility, even though it might be revealed to be wrong in details by a future study.

Fertile tortoiseshell males

As indicated elsewhere (Komai and Ishihara 1956), I have been able to find three specimens of tortoiseshell males which are probably fertile (Table 2). Two of these were histo-cytologically examined by Ishihara, my co-worker in the National Institute of Genetics. The testes of these cats were revealed to be perfectly normal and apparently fertile. No breeding data have been available for these cats. The third specimen has provided such data which show its fertility almost certainly (for further details *op. cit.*).

Table 2. Records of apparently fertile tortoiseshell males collected by the writer, with those of similar males in the literature.

Specimen no.	Owner	Parents		Progeny
		♀	♂	
5	Mr. Hasioka	O T(ta)	B T(ta) ¹	T(ta)♂ ¹ , T(ta)♀, B♂ T(ta)♂, T♀, O♀ ²
12	Mr. Noda	O	B?	T(b)♂, T(b)♀, O♂
65	Dr. Tanaka	?	?	?
Sir S. C. Alexander Bamber & Herdman		T B O T	T T(ta) ² T(ta) ² T(ta) ²	T, O, B B♂ ¹³ , T♀ ¹⁴ , B♀ ¹ O♂ ⁹ , O♀ ⁸ , Anom. ♂ ¹ B♂ ¹ , O♂ ¹ , O♀ ⁵ , T♀ ² , Anom. ♀ ¹

Anom. — Orange with slight mixture of black. The same male is indicated by the same numeral.

For the origin of such fertile tortoiseshell males, it might be assumed that the crossing-over between X and Y had failed to remove from Y the gene complex for fertility of the male, even though it did transfer *O* from Y to X. Then the fertile tortoiseshell son should produce among its progeny some tortoiseshell males like itself. The specimen 3 may represent such an example.

In the literature there are on record three such examples as far as I know. For one of these, there is no breeding record. Of the rest, the one reported by Cutler and Doncaster (1915, 1932) might have been originated by a crossing-over process suggested above. However, for the last specimen of which the breeding record is most complete and reliable, this theory meets some difficulties. Rather, as pointed out by Bamber and Herdman (1932), this male was a genetic orange in spite of its tortoiseshell appearance, but the covering effect of the gene for orange

had become incomplete by the presence of a modifying gene or by some other cause. No. 3 specimen in my collection might be accounted for by this hypothesis as well.

Discussion

Obviously, it would be very difficult to present any cytological evidence for the crossing-over hypothesis on the origin of tortoiseshell male cat. Because, owing to the sterility of the gonad, few mitotic or meiotic figures are seen in it. Perhaps tissue culture of some somatic tissue will provide mitotic figures. Still, it will be very hard to make out any change in the structure of the Y-chromosome as compared with its normal structure. On the other hand, negative genetic evidence against this hypothesis might be more easily given, if there be an indisputable case where more than one such male were born of the same mother preferably sired by different males. So far, no such evidence has been available (Komai and Ishihara 1956).

The several hypotheses proposed by previous authors on this problem have been criticized by subsequent authors (for details, see Bamber 1927), and they would scarcely need any further comment. One of them, the freemartin hypothesis, has been revived by Sprague and Stormont (1956), and may deserve a short discussion. This hypothesis postulates the occurrence of anastomoses of chorionic circulations between embryos of different sexes. Such anastomoses were actually observed in cat embryos by Bissonnette (1928). However, it would be too long way, based on such observation, to try to explain the sterility of tortoiseshell males. In this connection, it may be emphasized that the sterile gonads of these males show no sign of intersexuality, much less their original femaleness, as already pointed out by Wislocki and Hamlett (1934).

Summary

1. Census of cat populations offer clear evidence for the sex-linkage of the gene for orange color and the non-sex-linkage of the gene for black or tabby color.
2. The records of 65 tortoiseshell males collected by the writer indicate that the mother or such a male can be of any color. They also show that such males are heterozygous for the gene for orange (Table 1).
3. A crossing-over between the pairing segments of X- and Y-chromosomes in the father is probably responsible for the production of a tortoiseshell male. The sterility of these cats is probably caused by a transfer of a gene complex for fertility of the male from Y to X by the same crossing-over process.
4. Three tortoiseshell males which seem to be fertile are included in this list. A few similar cats have been recorded in the literature (Table 2). Some, at least, of these cats are perhaps of different origin from the sterile tortoiseshell males, being genetic oranges in which the covering effect of the gene for orange is imperfect and allows the black to appear partially.
5. A short discussion of the freemartin hypothesis for the sterility of tortoiseshell male cats revived by Sprague and Stormont (1956).

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