

## THE MALE TORTOISESHELL CAT

BY RUTH C. BAMBER, M.Sc. (Mrs BISBEE).

IN 1920 Professor Doncaster published a paper in the *Journal of Genetics*(1) in which he suggested that the occasional male tortoiseshell cats which unexpectedly appear, may perhaps be explained in the same way as the freemartins amongst cattle.

Female tortoiseshell cats are common: they are apparently the heterozygous female progeny of parents carrying the factors for black and yellow respectively. The corresponding male progeny of such parents are yellow, but that they are heterozygous is beyond doubt as shewn by their behaviour in breeding: very rarely, however, they are tortoiseshell.

The tortoiseshell colouration is not a sex-linked character in the usual meaning of the term. The factor for yellow is apparently sex-linked in the male but not in the female. The cross yellow male  $\times$  black female gives tortoiseshell females and black males; whereas the reciprocal cross, yellow female  $\times$  black male gives yellow males and tortoiseshell females; also a tortoiseshell female crossed with a black male gives tortoiseshell females, yellow males, and black males and females. From this it appears that the yellow males and tortoiseshell females are both heterozygous, but in the male yellow is dominant to black whereas in the female it is incompletely dominant.

Nevertheless, occasionally a tortoiseshell male appears, and, to account for these exceptions, several suggestions have been put forward along the lines of failure of sex-linkage, non-disjunction, etc.(2).

Last year Professor Doncaster suggested an explanation along entirely different lines. He had previously(3) recorded the fact that male tortoiseshell cats are usually sterile, and he conceived the idea that these males are possibly females which have been turned during development to the male condition, in the same way as the freemartin.

In cattle, when a male and a female are born as twins, the female, called a freemartin, is often imperfect sexually, shewing varying degrees of maleness and femaleness in different cases. F. R. Lillie(4) has shewn, beyond question, that the freemartin is a female which during develop-

ment has been intimately associated with a developing male due to confluence of blood vessels in their fused chorions. He suggested that this fusion of blood vessels allows hormones from the male embryo to pass into the female embryo, and so to inhibit the development of femaleness.

Professor Doncaster suggested that a similar confluence of blood vessels may occur in cats and may account for the tortoiseshell males, these having been turned even further towards the male condition than is the case in the most male freemartins, but usually not far enough to be fertile males.

Simultaneously with the publication of this suggestion he began an examination of all pregnant female cats available. He had examined fourteen when he died, and I have continued his observations up to the present time. Altogether, seventy cats have been examined, giving a total of two hundred and fifty-three kittens, and so far no case of confluence of blood vessels has been found. There have been two cases which could not be reported on with certainty. In one there was a slight attachment of the chorions of two adjacent embryos, but unfortunately it was impossible to settle definitely by injection whether or not the blood vessels were confluent, for by an accident the kittens were moved in my absence and the two had separated. The area of attachment was carefully examined under the microscope and shewed no break anywhere. It is almost certain that this was a case of simple adhesion and not of fusion. In the second case two nearly full time embryos were so tightly packed in the uterus that one was pushed under the placenta of the other, carrying the two chorions before it. The chorions were here so closely adherent that, as the specimens were not fresh, but had been preserved in formalin, it was impossible to say with certainty that there was no fusion. However, several similar cases have been found in fresh specimens where there was certainly no fusion, so that it is probable that in the formalin specimens it was again a case of simple adhesion.

There seems to be no reason however why this adhesion should not occasionally be carried a stage further, giving fusion and thus confluence of blood vessels. It can only be said that at present we have no record of such confluence. Lillie, discussing the probability of confluence occurring in other groups than cattle, remarks that "the highly localized" type of placenta found in carnivores makes it unlikely that confluence occurs in that group. But the chorion is very vascular quite outside the placental region, and fusion of the chorions apart from the actual placentas could conceivably give a large degree of confluence of the two embryonic blood streams. There seems no reason however why the

placentas themselves should not sometimes fuse, for they are by no means always in the typical central position on the chorions, being very often nearer to one end than the other. Sometimes the placenta even forms a cap over one end of the chorion, particularly where it is pressed against the distal end of the uterus. If pressure induces this condition fusion of the placentas of adjacent embryos is not at all unlikely. However it has certainly not been found, and at present the parallel between the tortoiseshell tom cat and the freemartin remains an open question until further observations throw more light on the subject.

It seems possible however that the tortoiseshell male may still be a case of sex reversal quite apart from confluence of embryonic blood streams. Recent work by Riddle on pigeons(5), and by Goldschmidt(6) and Harrison(7) on moths has brought to light the fact that, apart from any possible connection between male and female embryos through fusion of foetal membranes, certain fertilized eggs, apparently predestined by their chromosome content to develop into one sex, can be made to develop more or less completely into the opposite sex. It has also been shewn that animals are not quite so sharply separated into males and females as has been commonly believed, but that there are degrees of maleness and femaleness.

Riddle has shewn that in pigeons "generic crosses produce from their 'stronger' germs—those of spring and early summer—nearly all males. If however the birds of such a generic cross be made to 'overwork at egg production'—i.e. if their eggs are taken from them as soon as laid, and given to other birds for incubation—then the same parents which in spring threw all or nearly all male offspring may be made to produce all or nearly all female offspring in late summer and autumn." Riddle's evidence against selective maturation seems sound, and one is almost forced to the conclusion that some eggs, which normally would have developed into one sex, have been induced by special circumstances to develop into the opposite sex.

Moreover amongst the females Riddle finds a series ranging from those which, though females anatomically, are distinctly male in instincts and relative weights, to those which are excessively female, even to the extent of retaining both ovaries in the adult, whereas only one is normally present. When judged by weight the males gave a similar series, but apparently were too pugilistic to give evidence in regard to instinct.

It seems clear that not only may a "predestined" male become a female, or *vice versa*, but also that there are varying degrees of maleness and femaleness.

Now in the light of these facts it seems possible to account theoretically for the tortoiseshell male cat, even apart from confluence of embryonic blood streams. There is no evidence, so far as I know, to suggest that the cause—whatever it may be—which is able to reverse the sex of the embryo completely or partially in birds and in moths cannot also work in mammals. If by this agency a fertilized egg which would normally develop into a tortoiseshell female, be turned from its original “intention” and transformed into a male, then the unexpected tortoiseshell male cat would be produced, just as he might be by hormones due to confluence of blood vessels during development. Also it is equally conceivable, on either hypothesis, that he might be sterile—as is known to be often the case—due to the interference not having been quite strong enough to overcome entirely the original female tendency.

If the tortoiseshell males be comparable to some of the animals in Riddle's series, whose sex has been reversed (or less closely to Goldschmidt's intersexes), one would expect to find a tendency to produce unisexual families in those strains in which they occur. I have not been able to obtain very full information on this point, but the following facts seem significant. Of the four or five tortoiseshell males whose records are available, one was produced by the cross black female  $\times$  yellow male, and this black female had previously, by different sires, produced only male kittens. By this sire she produced one tortoiseshell male, one tortoiseshell female, and a black kitten of unknown sex. Two other tortoiseshell males are recorded<sup>1</sup> from the mating tortoiseshell female  $\times$  yellow male and in each case every kitten in the litter was tortoiseshell: it follows therefore that in each case every kitten except the recorded tortoiseshell male was a female. If the records of these last two males are to be trusted, they could not, of course, possibly have arisen due to confluence of blood vessels, as in neither case was there a male in the family with which they could have been united during development. The three records given above provide dangerously scanty evidence, but so far as it goes that evidence supports the hypothesis here suggested that the tortoiseshell males are due to some cause within the fertilized egg, tending to reverse the sex of certain individuals, and so to produce, in extreme cases, unisexual families, as in Riddle's pigeons and Goldschmidt's and Harrison's moths<sup>2</sup>.

There are however two separate possibilities to be kept in view. Is

<sup>1</sup> *Fur and Feather*, May 10, 1912.

<sup>2</sup> I find that Professor Dakin, thinking along separate lines, has concluded that possibly the tortoiseshell male may be comparable to Goldschmidt's intersexes.

the tortoiseshell male necessarily always a female turned more or less completely towards the male condition, or may he be sometimes a male which has been turned slightly towards the female condition—enough in most cases to make him sterile, but never enough to mask his essential maleness?

The answer to these questions seems to depend on the exact Mendelian constitution of a yellow male, a tortoiseshell male and a tortoiseshell female.

There is no evidence that a tortoiseshell male is different from a yellow male in his Mendelian factors. There is, however, very little evidence to shew how a tortoiseshell male transmits factors to his offspring. Fertile tortoiseshell males are very rare, and when they do occur they are nearly always mated with tortoiseshell females in the hope of obtaining other tortoiseshell males. This mating does not test the constitution of the male. There is only one doubtful record of the mating of a tortoiseshell male with a black female, which is of course the one required, and this gave the same result as the cross yellow male  $\times$  black female. If ever I am fortunate enough to find a fertile tortoiseshell male I hope to test the matter more thoroughly. At present the very slender evidence from breeding suggests that the yellow male and the tortoiseshell male behave alike in the transmission of factors to their progeny. In origin they are also the same, with one exception. Tortoiseshell males are recorded from the cross black male  $\times$  tortoiseshell female and from yellow male  $\times$  tortoiseshell female: yellow males are also produced from these matings. There is however one record of a tortoiseshell male from the cross yellow male  $\times$  black female. A yellow male could not have been produced from this mating apart from a breaking down of sex-linked inheritance, and it has been suggested(8) that this breaking down is the cause of the tortoiseshell male. In regard to the tortoiseshell female it seems almost certain that she has the same constitution as the yellow male as far as the factor for yellow is concerned (both arise from the cross, yellow female  $\times$  black male), but whether the complete dominance of yellow over black in the male, and its incomplete dominance in the female is due to some other sex-linked colour factor, or whether it is due to the different physiological conditions of the two sexes seems uncertain. If the female possesses some colour factor not present in the male, then one is forced to conclude that if the tortoiseshell male is the result of sex reversal at all he can only be a female turned to the male condition and never the reverse. But may it not be possible that the tortoiseshell colour of the female and the yellow colour of the male are

simply the result of different reactions of the same Mendelian factors to the different physiology of the two sexes? The male physiology may be favourable to the dominance of yellow over black, and the female physiology not so favourable. If this be possible, then a tortoiseshell male may equally well be a male with a very slight female tendency, or a female turned almost entirely to the male condition. In either case he would be a "not very male male," and this may account both for his characteristically female colouration and for his usual sterility<sup>1</sup>.

In other cases where a character usually found in one sex appears in the opposite sex the animals shewing this abnormality have also been shewn to be sterile<sup>2</sup>, e.g. birds and moths; and it is tempting to suggest that these more normal cases of the apparent breaking down of sex-linkage are also in reality examples of sex reversal. The unexpected black female cats which occasionally appear from the cross yellow male  $\times$  black female may also be accounted for in the same way.

The cause underlying this reversal of sex has deliberately not been discussed here; but quite apart from any theory, the fact itself has been unmistakably demonstrated by Riddle in pigeons and by Goldschmidt and Harrison in moths, and it is here suggested that the tortoiseshell male cat is another example of the same phenomenon. Whether the reversal in this case must always be from female to male, or whether it can be in either direction, is not clear until further evidence throws more light on the subject.

#### LITERATURE CITED.

1. DONCASTER, L. "The Tortoiseshell Tom Cat. A Suggestion." *Journal of Genetics*, Vol. IX. 1920.
2. A fuller discussion of the inheritance amongst cats of the colours yellow, black and tortoiseshell, will be found in the following papers :
  - i. DONCASTER, L. "On the Inheritance of tortoiseshell and related colours in Cats." *Proc. Camb. Phil. Soc.* Vol. XIII. p. 35, 1904.

<sup>1</sup> If the colour be a matter of sex physiology then by castrating a very young yellow male and grafting ovaries it might be possible to bring up the black to some extent later. Similarly by grafting a functional testis into a newly born tortoiseshell male it might be possible to inhibit the development of black in future coats. There is not very much hope of success in these experiments, for after birth it seems late to attempt to alter such a well-fixed character as coat colour. Still, birds from which ovaries have been removed develop male plumage, and castrated deer cease to grow their horns. Administration of extracts of the endocrine glands and transfusion of blood might also give interesting results. I hope to attack the problem along these lines in the near future.

<sup>2</sup> See Literature cited 3 i and ii.

- ii. DONCASTER, L. "Sex-limited Inheritance in Cats." *Science*, N.S. Vol. xxxvi. p. 144, 1912.
- iii. —. "On Sex-limited Inheritance in the Cat and its bearing on the Sex-limited transmission of certain Human Abnormalities." *Journal of Genetics*, Vol. iii. p. 11, 1913.
- iv. IBSEN, H. L. "Tricolor Inheritance. III. Tortoiseshell Cats." *Genetics*, Vol. i. p. 377, 1916.
- v. LITTLE, C. C. "A Preliminary Note on the Occurrence of a Sex-limited Character in Cats." *Science*, N. S. Vol. xxxv. p. 784, 1912.
- vi. —. "Colour Inheritance in Cats, with special reference to the colours black, yellow, and tortoiseshell." *Journal of Genetics*, Vol. viii. p. 279, 1919.
- vii. —. "Is the Fertile Tortoiseshell Tom Cat a Modified Female?" *Journal of Genetics*, Vol. x. p. 301, 1920.
- viii. WHITING, P. W. "The Tortoiseshell Cat." *Amer. Nat.* Vol. xlix. p. 518, 1915.
- ix. —. "Inheritance of Coat-Colour in Cats." *Journ. Exp. Zool.* Vol. xxv. p. 539, 1918.
- x. WRIGHT, S. "Colour Inheritance in Mammals. X. The Cat." *Journ. Heredity*, Vol. ix. p. 139, 1918.
- 3<sup>1</sup>. i. DONCASTER, L. "A possible connection between Abnormal Sex-limited Transmission and Sterility." *Proc. Camb. Phil. Soc.* Vol. xvii. p. 307, 1914.
- ii. —, and CUTLER, D. W. "On the Sterility of the Tortoiseshell Tom Cat<sup>2</sup>." *Journal of Genetics*, Vol. v. p. 65, 1915.
4. LILLIE, F. R. "The Free-Martin ; A Study of the Action of Sex-hormones in the Foetal Life of Cattle." *Journ. Exp. Zool.* Vol. xxiii. 1917, p. 371.
5. RIDDLE, O. "Sex Control and known Correlations in Pigeons." *American Naturalist*, Vol. l. 1916, p. 385.

<sup>1</sup> Little's theory of non-disjunction has not yet, to my knowledge, been tested experimentally: it remains therefore as a fascinating possibility. There are however several difficulties. As Little himself points out, it does not account for the production of a tortoiseshell male from the mating black male  $\times$  tortoiseshell female, as reported by Doncaster. Little suggests that the breeders' records may have been at fault; and that of course is possible. If records are to be trusted at all however, another difficulty seems to arise in the case of the black female, referred to elsewhere in the present paper. When crossed with a yellow male she produced a tortoiseshell male, a tortoiseshell female and a black of unknown sex: previously, mated with many different males, she had produced male offspring only. This would not be expected on the theory of non-disjunction; unless, indeed, the females referred to by Little, "with peculiar gametic conditions," prove to be males.

<sup>2</sup> I have had the opportunity of dissecting Professor Doncaster's tortoiseshell tom cat. Anatomically he was typically male; but microscopic examination of the testis shewed the left remaining one to be like the right one previously described by Professor Doncaster: there was a large amount of interstitial tissue, and well-developed seminiferous tubules but no spermatozoa.

6. i. GOLDSCHMIDT, R. "Experimental Intersexuality and the Sex-problem." *American Naturalist*, Vol. L. 1916, p. 705. (A short account in English.)  
ii. ——. "Mechanismus und Physiologie der Geschlechtsbestimmung." Berlin, 1920. (Full account in German.)
7. HARRISON, J. W. H. "Studies in the Hybrid *Bistoninae*. IV. Concerning the Sex and related problems." *Journal of Genetics*, Vol. IX. 1919, p. 1.
8. DONCASTER, L. "On Sex-limited Inheritance in the Cat, and its bearing on the Sex-limited Transmission of certain Human Abnormalities." *Journal of Genetics*, Vol. III. 1913, p. 11.