

GENE FREQUENCIES IN LONDON'S CATS

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During the summer of 1947 I examined 700 cats, which had been destroyed at three of the main animal clinics in London, in order to estimate the frequencies of known genes in the city's cat population.

It will be desirable to give a résumé of the known facts of cat genetics. Whiting (1918) divided tabby cats into three categories: lined (usually described by breeders as Abyssinian), striped and blotched, with dominance in the order given. Sewall Wright (1917) analysed the tabby pattern, pointing out that the banding of individual hairs to form the light stripes is due to a gene which acts only on black, as in the agouti-coloured rodent. He said that the width of these 'agouti' bands varies independently of the character of the black stripes. Action of the 'non-agouti' gene gives solid black, which is recessive to tabby (Doncaster, 1904). The tabby stripes can still be seen occasionally in black kittens. Solid white is due to a dominant gene (Sewall Wright, 1917).

Doncaster (1912) concluded that yellow was sex-linked, and this is the accepted view. Bamber (1927) gave a comprehensive review of previous literature on the yellow and the tortoiseshell cat, normally a female heterozygous for yellow. She pointed out that the rare tortoiseshell male had been accounted for by failure of sex-linkage, non-disjunction or sex-reversal. Sewall Wright thought the tortoiseshell male had a pair of X-chromosomes like the normal female, but some other influence had over-balanced the sex-determining mechanism. This problem is not yet settled.

Tjebbes (1924) worked on Siamese cats, and found that their pattern was due to a gene for 'weakened chromogen' acting on chocolate-black. The latter appeared in full intensity in crosses introducing normal chromogen, and was then epistatic over tabby. The gene for 'weakened chromogen' could be combined with tabby to give a 'striped Siamese'. Keeler & Cobb (1933) showed that this Siamese dilution was recessive to silver, and allelomorphous with it. These alleles are regarded as members of an albino series, other possible members being Burmese (included by Castle, 1940) and full albino (reported by Bamber & Herdman, 1931). No adequate analysis of white-spotting has been made, but the genes involved seem on the whole dominant. A number of loci are probably concerned, as in other mammals studied.

The gene for dilution is recessive (Doncaster, 1904). Bamber (1927) thought polydactylism dominant over normal, and this has been confirmed by Danforth (1947). Manx tail seems to be incompletely dominant, and long hair to be recessive (Bamber, 1927), but it seems likely that several genes are concerned.

CLASSIFICATION

We may take as our standard the short-haired striped tabby, with a fair amount of yellow in the banded hairs, a normal tail and digits. This striped pattern resembles that of *Felis silvestris*. Colour genes can be classified as follows:

L. *Abyssinian* (Whiting's 'line'). Stripes very fine and close together, except on the legs, tail and nose. The first impression is of a uniform agouti cat, but it has a dark vertebral line.

+. *Striped tabby*. I found two major variations of the normal pattern, which may be due to modifiers at other loci.

b. *Blotched tabby*. Stripes very wide, few in number and much broken up. Prof. Haldane states that the type of blotched tabby commonest in America is decidedly different from the English type, so there may be other allelomorphs.

a. *Non-agouti*. Cats with a/a are black. The tabby pattern was sometimes seen, but no attempt was made to distinguish different types.

W. *White*. All white cats seen had yellow eyes.

B. *Chocolate-black*. I found this only in the Siamese cat, when combined with c^s (see below).

y. *Yellow*. This is a sex-linked gene, y males and y/y females being yellow, $+/y$ females tortoiseshell. Gene a has no effect on y and y/y cats. On the other hand, the tabby genes can be distinguished, for the light agouti stripes of the tabby cat are replaced by light yellow stripes composed of uniform hairs. On $+/y$ cats the effect of a is very clear. But the different types of tabby in the tabby-tortoiseshell are sometimes rather hard to distinguish; in three cats (classified $+/y$ t ?) the exact pattern could not be definitely determined.

d. *Dilute*. Gives Maltese blue (dilute tabby), Russian blue (dilute black), and cream (dilute yellow).

c^{sh}. *Silver*. Removes yellow from the banded hairs, but Dr Spurway points out that c^{sh} does not affect the yellow areas in a tortoiseshell. I found intermediates between the clear-cut silver tabby and normal; possibly there are several slightly different c^{sh} genes, as in the rabbit.

c^s. *Siamese dilution*. c^sB phenotype is the Siamese cat. This is born white; later the tips of the tail, limbs and nose colour up to a greater or less degree, depending on external temperature (Iljin & Iljin, 1930).

S. *White-spotting*. Since the amount of white varied continuously between 0 and 100% I classified the cats as follows: S_0 , no white-spotting; S_1 , less than $\frac{1}{3}$ white; S_2 , $\frac{1}{3}$ to $\frac{2}{3}$ white; S_3 , over $\frac{2}{3}$ white, but not all white.

Other characters noted were:

Hair length. Long hair is said to be recessive, but there were several different grades of hair length, depending perhaps on modifiers of the main gene. I classified for medium hair and long hair (half-Persian and full Persian).

Tail length. The Manx character is dominant, there is no definite evidence on whether the homozygote is viable. Intermediate tail lengths were found.

Polydactylism. Dominant. More than one additional digit may occur; fore- and hind-limbs may be unequally affected.

Eye-colours were not noted on the whole sample as pupils were often so dilated by death that no accurate observations could be made.

The significance boundary for χ^2 tests is taken at $P=0.05$.

RESULTS

I examined 700 cats in all, of which 454 were seen at clinic 'A', of the Animal Rescue League (R.S.P.C.A.), Islington; 202 at clinic 'B', of Our Dumb Friends' League, Victoria; 44 at clinic 'C', the Mayhew Home (R.S.P.C.A.), Willesden. Some had been stray cats, and others unwanted or ill, collected from surrounding districts.

There were 356, or 50.9%, male cats. Five hundred were classified for age and male castration (δ) in adults. Results were as follows:

Adults	♀ 165	♂ 90	♂ 87
Kittens	94	64	

There is thus a significant tendency ($\chi^2=5.04$) to abandon female rather than male kittens. The frequency of male castrates is here 49.1%, and may well be higher in the total population, as they are probably less likely to stray.

The numbers of cats falling into the classes of coat pattern are shown in Table 1. Included in the striped tabby group (+) are sixteen cats with modified patterns. Nine of these (three males and six females) had thin broken stripes. The other seven (five

Table 1. *Coat patterns found, with the degree of white-spotting*

Phenotype	S_0	S_1	S_2	S_3	Totals
W ♂	1	—	—	—	1
W ♀	5	—	—	—	5
t^b ♂	1	0	0	0	1
+					
♂	18	19	6	3	46
♀	16	16	2	2	36
t^b ♂	27	35	11	13	86
t^b ♀	36	27	9	6	78
a ♂	71	73	19	15	178
a ♀	69	63	22	9	163
y ♂	5	6	3	0	14
y ♀	1	2	0	0	3
$t^b y$ ♂	10	12	4	2	28
$t^b y$ ♀	1	3	0	0	4
+/ y ♂	0	1	0	0	1
+/ y ♀	1	4	1	1	7
+/ $y t^b$ ♀	4	6	2	0	12
+/ $y t^2$ ♀	1	1	0	1	3
+/ $y a$ ♀	11	14	3	4	32
$c^s B$ ♂	1	—	—	—	1
$c^s B$ ♀	1	—	—	—	1
Totals	280	282	82	56	700

Table 2. *Distribution of the diluting gene*

Phenotype	S_0	S_1	S_2	Totals
+				
♂	1	0	0	1
♀	0	2	0	2
t^b ♂	0	1	0	1
a ♂	0	4	0	4
a ♀	1	2	1	4
+/ y ♀	0	2	0	2
Totals	2	11	1	14

males and two females) had a fairly uniform appearance, with faint stripes, sometimes broken, on the trunk, and darker stripes on head, legs and tail. This was reminiscent of Siamese dilution, but the only undoubted striped Siamese which I have seen had no sign of stripes on the trunk, which was almost pure white. So I have not classified these seven cats under c^s .

Included in the y phenotype cats are two with broken stripes, and one of the +/ y phenotype had broken stripes.

Other genes whose effects were seen are:

c^{ch}. Six male and five female silver tabbies were seen, but seven others seemed intermediate between these and normal.

d. Table 2 gives the distribution of the diluting gene.

Hair-length. Sixteen males and thirty-three females had medium hair, seven males and six females had long hair. Results with classified adults and male castrates (δ^c) were:

	Short	Medium	Long	Totals
♀	146	15 (9.1%)	4 (2.4%)	165
♂	84	3 (3.3%)	3 (3.3%)	90
δ^c	74	10 (11.5%)	3 (3.4%)	87
Totals	304	28	10	342

There is no significant difference between the results for long hair. But there is a significant tendency ($\chi^2=4.36$) for male castration to increase hair length from short to medium. Medium hair length seems commoner in females than in functional males ($\chi^2=2.86$). It is well established that castration inhibits baldness in Man.

Tail length. Four males and one female had Manx tails. Six males and three females had short tails, apparently not accidental.

Polydactylism. One male had an enlarged thumb on the front paws, and an extra digit on the hind paws. One male and two females had an extra digit on each paw. One female had two extra digits on the hind paws and one extra on the front paws.

GENE FREQUENCIES

The following is a classification with respect to *y*:

	+ / + or +	+ / y	y / y or y	Total
♀	277 (269.6)	54 (64.5)	7 (3.9)	338
♂	311 (315.3)	1?	42 (37.8)	354

White and Siamese cats are omitted as unclassifiable for presence or absence of *y*.

These figures can be used both to estimate the gene frequency and to check the hypothesis of random mating. If *x* be the frequency of *y*, we expect females to be in the ratio $(1-x)^2 + / + : 2x(1-x) + / y : x^2 y / y$, and males $(1-x) + : xy$ (omitting the tortoiseshell male). There were $2 \times 277 + 54 + 311$, or 919 + genes, and $54 + 14 + 42$, or 110 *y* genes; that is, 110 out of 1029, or 10.69% *y* genes.

The expected values worked out from this frequency are shown in brackets above. There are rather too many yellow and too few tortoiseshell females, suggesting a slight degree of selective mating, but the divergences from expectation were not significant ($\chi^2=4.90$ with 3° of freedom) and the hypothesis can be accepted as reasonably accurate.

Table 3. *Gene frequency estimations*

Character	No. classifiable	Phenotype no.	Phenotype frequency (%)	Gene frequency (%)
<i>W</i>	700	6	0.9	0.4
<i>l^L</i>	296	1	0.3	0.2
<i>+</i>	296	99	33.6	18.5 ± 2.3
<i>l^b</i>	296	196	66.4	81.4 ± 2.3
<i>a</i>	643	373	58.0	76.2 ± 1.7
<i>y</i>	692	—	—	10.7 ± 1.2
<i>d</i>	694	14	2.0	14.2 ± 1.3
<i>c^{ch}</i>	270	11	4.1	20.2
<i>S</i>	692	420	60.7	—

Table 3 shows other gene frequency estimates. On the assumption of random mating, recessive gene frequencies are taken as the square root of the phenotype frequency.

Standard errors have been calculated where numbers justified this. In Table 3, cats classified for tabby patterns do not include tabby-tortoiseshells, since the type of tabby pattern could not be determined in three cats of that group.

TESTS FOR HOMOGENEITY AND INDEPENDENCE

Tests for homogeneity were carried out between the three clinics. Sex ratios were as follows:

	A	B	C
♀	246	79	19
♂	208	123	25

The differences between A and C are not significant, but there is a significantly greater proportion of females at A than at B ($\chi^2=12.6$). This may be due to human preferences.

The numbers of cats falling into the main colour groups were also compared. These are shown in Table 4.

Table 4. *Comparisons of phenotype numbers*

Phenotype	Clinic		
	A	B	C
+	49	25	9
t^b	106	42	16
a	233	94	14
y and $t^b y$	26	19	4

Table 5. 2×2 tests

Characters compared	χ^2
Sexes $\times A, a$	0.17
Sexes $\times S, s$	1.19
+, $t^b \times A, y$	0.02
$S, s \times A, a$	0.12

The differences between A and B are not significant ($\chi^2=4.14$ with 3° of freedom). The differences between A and C are significant ($\chi^2=9.47$), but the population sample at C was statistically inadequate.

2×2 tests for independence were made on the whole sample, to reveal associations between characters, which would imply lack of randomness in mating, or human selection. Table 5 shows characters compared, with values of χ^2 found. None was significant, so no associations were found.

Age. For the last 500 cats, which had been classified for age, a comparison was made between the numbers of kittens and adults in the main coat-colour classes. Results were:

	+	t^b	a	All y	All +/ y	Total
Kittens	18	44	73	7	15	157
Percentage	11.47	28.03	46.50	4.46	9.55	
Adults	40	67	178	26	25	336
Percentage	11.91	19.94	52.97	7.74	7.44	

Comparing figures for t^b and a , $\chi^2=3.92$ which is significant for $P=0.05$. The higher percentage of blotched tabby and the lower percentage of black in the kitten population, compared with adults, seem to indicate the working of human selection. For this is exercised mainly on the young progeny, the kittens here being those which have been selected against and destroyed, while the adults are those which have escaped this early selection. So black kittens appear to be favoured, and therefore less liable to destruction than blotched tabby. Similarly, yellow kittens seem to be preferred to tortoiseshell ($\chi^2=2.28$).

Castration. A comparison was made between castrated and functional adult males in the main coat-colour classes. Results were:

	+	<i>b</i>	<i>a</i>	All <i>y</i>	Total
Castrated	11	17	45	12	85
Functional	12	18	51	8	89

There are no significant differences between these figures. So there is no evidence that any type of cat is more likely to be made sterile than any other.

DISCUSSION

We have been dealing here with a sample from a polymorphic population, maintained thus by human selection. Yet it is very seldom that man has any direct influence on the cat's choice of a mate, although, by castration, he reduces the male breeding population by about half, and the female by an unknown amount. Darwin (1859) remarked on the difficulty of pairing cats, 'owing to their nocturnal rambling habits', and in this matter cats are certainly the most independent of all domestic breeds of animal. Calculations made on the present sample, based on numbers of yellow and tortoiseshell, and on comparisons between different combinations of characters, show fairly conclusively the randomness of mating. Human selection is exercised mainly on the progeny, demonstrated here by the large number of kittens destroyed, the greater proportion of females among them, and other divergences from the make-up of the adult population.

But the fact of random mating indicates that a city's cat population is a less artificial assembly than a similar population of other domestic breeds. Individuals are less isolated and less protected from the hazards of the environment. Phenotypic differences in fitness can therefore show themselves more easily, keeping some types rare despite human preferences. Wholly white cats are uncommon, for instance, although some degree of white-spotting is very common. The former might well be favoured by human selection, but it is already known that nearly all white cats with blue eyes are handicapped by deafness. Blotched tabby and black are both very common, with gene frequencies markedly above that for the wild type pattern. We have seen that black kittens appear to be favoured by human selection, having the advantage of being considered lucky by common superstition. They, and blotched tabby, may well have other special advantages in industrial areas.

The biological significance of the different gene frequencies cannot be assessed, however, until comparisons can be made with results from elsewhere. It is certain that other populations have a very different composition; until data are available from them no important conclusions can be drawn from this investigation.

SUMMARY

1. The results are given of a survey of inherited characters in 700 London cats.
2. The hypothesis of random mating was tested by using the results for yellow and tortoiseshell, and was found satisfactory.
3. Gene frequencies were estimated on this hypothesis, and are given in Table 3.
4. There was a significant tendency for male castration to increase hair length.

I should like to thank Prof. J. B. S. Haldane, who suggested this investigation, for the great interest he has shown in it, and for his constant help and encouragement. I also thank Major G. Hancock, Chief Veterinary Officer of the R.S.P.C.A., and Mr W. E. Murts, Veterinary Officer of Our Dumb Friends' League, for permitting me to work at clinics under their charge.

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