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Mutant Gene Frequencies in Cats of Southern England

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Summary. Three areas in Southern England have been sampled for frequency of nine mutant genes among the domestic cat population. The significance of the derived estimates are discussed and a brief comparison is made with the earlier estimate obtained by SEARLE. The frequencies seem comparable in the two surveys except for genes *O* and *d*. The estimates of these from the present study are significantly higher than those found earlier. Tentatively, it is proposed that human preference for orange cats may be responsible for the increase in *O*. No obvious reason exists for the higher frequency of *d*.

The present study sets forth an analysis of mutant gene frequencies for cats observed in three areas of Southern England. Only one area is well defined, that of Ealing and District, a suburb in West London. The other areas may be defined as the Hertfordshire (Herts.) where the majority of cats were observed in Berkhamsted, Hemel Hempstead, Tring and other less well-known localities within the general area, and the Kent, where the majority of cats were observed in Farningham, High Halden and Ramsgate. A small number of observations were made in Guildford and in Southampton. These have been included in the Kent sample. Herts. lies about 30 miles to the north of London, while Kent lies about 70 miles to the south-east. The Herts. and Kent samples were taken by M.S. and the Ealing by R.R. No fancy cats are knowingly included; the few Siamese observed did not seem to be under restraint although these may be fancy bred. The inclusion or exclusions of these animals do not materially affect the results.

Material and methods

Most cat populations be examined for the frequency of nine or ten mutant genes although, of course, not all samples need contain this number. The following genes were found in the present study:

Mutant gene	Phenotype and remarks
a	Non-agouti; epistatic to t^b
c^{ch}	Silver or smoke
c^s	Siamese
d	Dilute
l	Long hair
O	Orange (sex-linked); epistatic to *a*
S	White spotting
t^b	Tabby, blotched
W	White (yellow or blue eyed); epistatic to all other coat colour genes.

The orange gene was formerly known as yellow (*y*) but has now been renamed in the interests of a consistent nomenclature (Committee on standardized nomenclature for cats 1968). The wild type tabby cat possesses vertical striping and is designated as striped or mackerel. White spotting may be due to more than one gene but it is probable that only one major gene (*S*) is involved. A comprehensive account of the various mutants and phenotypes may be found in ROBINSON (1959).

The data were compiled by observations of cats on the streets and in open spaces. The frequencies of the more important phenotypes are arranged in tables 1, 2, and 3 for the three areas sampled. The first seven entries of the table sum to the total number of observations (but see later) while the remaining entries show some of the data re-arranged to facilitate further computation. In addition to those listed, the following cats were seen. For the Herts. sample: 5 Siamese (4 black and 1 red) and 8 white. For the Ealing sample: 3 white. For the Kent sample: no additions. Thus, the sample sizes are 198, 128, and 82, respectively, giving a total of 408 cats. The observations were made for the years 1966 to 1968. No kittens were recorded for the Ealing sample but 14 and 16 per cent were noted for the Herts. and Kent samples, respectively. These are distributed at random among the phenotypes and are thought to be too few to warrant separate consideration.

The three tables also show the distribution of white spotting relative to the phenotypes in the left hand column. The grade of white is based on the figure given by ROBINSON (1959; p. 301) and it may be noted that the amount shows no obvious association with any particular phenotype. Each cat was scored for as many relevant features as possible but, because of the nature of the observations, it was not always possible to score every animal completely. Sex and the type of tabby were particularly affected in this respect. For those cats which were sexed, the Herts. sample consisted of 59 males and 58 females while the Kent sample consisted of 17 males and 19 females. Apparently, the sexes are evenly distributed. Also, it was not always practicable to ascertain the presence (or amount) of white spotting on the stomach. This meant that the frequencies of white spotting grades 1 (spot on centre of stomach) and 2 (blotch on stomach) may be under-represented in the tables.

All of the mutants listed above, with the exception of *O*, are inherited autosomally. All three samples give no reason for thinking that mating is not essentially at random, so estimates of the frequencies for the recessive genes may be found as square roots of the proportions of the appropriate phenotypes. The absence of information on sex for many individuals means that straightforward estimation of the frequency of *O* is impossible unless the non-sexed observations are arbitrarily apportioned. However, maximum likelihood estimates were derived from the following expectations:

$$\underset{\frac{q(1+q)}{2}}{OO} \qquad \underset{(1-q)\,q}{O+} \qquad \underset{\frac{(2-q)(1-q)}{2}}{++}$$

The above formulae assume equal numbers of the sexes, an assumption which seems valid in the present case since (as noted above) no departure from equality was observed for those cats which were sexed.

Table 1. *Distribution of the more important phenotypes in combination with degree of white spotting. Herts. survey*

Phenotype	Non-White	Amount of white 1	2	3	4	5	6	7	8	Total
Tabby, striped	4	2	2	2	2	.	.	.	.	12
Tabby, blotched	16	2	2	5	2	.	.	.	.	27
Tabby, undiagnosed	12	1	1	2	2	.	.	.	.	18
Non-agouti	41	17	6	14	12	4	1	1	1	97
Orange, striped	3	.	1	1	1	.	.	.	.	6
Orange, blotched	8	3	6	1	.	1	.	1	.	20
Orange, undiagnosed	3	.	1	.	.	.	.	1	.	5
Tortoiseshell	12	3	1	4	4	1	.	.	.	25
Dilute	9	1	1	2	2	.	.	.	.	15
Silver	1	.	.	.	.	.	.	.	.	1
Smoke	1	.	.	.	.	.	.	.	.	1
Long hair	12	.	2	5	4	1	.	.	.	24

Table 2. *Distribution of the more important phenotypes in combination with degree of white spotting. Ealing survey*

Phenotype	Non-White	Amount of white 1	2	3	4	5	6	7	8	Total
Tabby, striped	8	.	4	2	.	.	.	.	.	14
Tabby, blotched	14	1	6	4	4	1	1	.	.	31
Non-agouti	31	6	11	8	7	4	.	1	.	68
Orange, striped	2	.	.	.	.	.	1	.	.	3
Orange, blotched	5	1	1	.	2	.	.	.	.	9
Tortoiseshell	5	1	1	2	1	1	.	.	.	11
Dilute	2	.	1	1	1	1	.	.	.	6
Long hair	4	.	2	1	1	.	.	.	.	8

Table 3. *Distribution of the more important phenotypes in combination with degree of white spotting. Kent survey*

Phenotype	Non-White	Amount of white 1	2	3	4	5	6	7	8	Total
Tabby, striped	2	2	1	1	.	1	.	.	.	7
Tabby, blotched	7	1	2	.	2	.	.	1	.	13
Tabby, undiagnosed	4	.	.	.	.	.	.	.	.	4
Non-agouti	17	7	10	6	6	1	.	1	.	48
Orange, striped	4	.	.	.	.	.	.	.	.	4
Orange, blotched	1	.	1	1	1	.	.	.	.	4
Orange, undiagnosed	1	.	.	.	.	.	1	.	.	2
Tortoiseshell	5	1	3	2	1	.	.	.	.	12
Dilute	2	.	1	1	.	.	.	.	.	4
Long hair	3	2	1	1	1	.	.	.	.	8

The analysis

The most interesting frequency is that for *O*. This gene is sex-linked and, if sex can be ascertained for every cat, all five phenotypes are readily identifiable. However, if sex cannot be determined in all cases, the frequency can still be calculated from the expectations given earlier for the orange, tortoiseshell and type animals. The frequency of *O* is given in table 4 for the three samples and for the samples combined. The frequencies seem to be rather divergent but a heterogeneity test based on the combined estimate of 0.189 failed to reach significance. The heterogeneity χ^2 between samples is 5.71 with two degrees of freedom.

The three classes of young provide a χ^2 for one degree of freedom, after the frequency is calculated, and this may be used to test for randomness of mating. Table 4 presents the results of the comparison. The results indicate that the distribution of the three classes do not strictly accord with the frequencies expected on the basis of random mating. The trend is discernible for all three samples but only emerges as significant when these are combined. Apparently, that there are too many orange cats or too few tortoiseshell.

It is instructive to examine the London data of SEARLE (1949) on the *O* gene in this respect. His data were fully sexed and he compared the five phenotypes for agreement with expectation. Some disagreement was apparent but was statistically insignificant. If, however, sex is ignored, SEARLE's data reduce to 49 orange, 54 tortoiseshell and 588 type. These figures give a frequency for *O* of 0.105 $\pm$ 0.010. The expected frequencies would be 40 orange, 65 tortoiseshell and 586 type. The χ^2 test gives a value of 3.9, on the borderline of significance. Thus, the same pattern emerges (indeed, as noted by SEARLE). It seems possible, therefore, that orange cats may be favoured by human selection because of their bright colour or that tortoiseshells are discriminated against because these are females. In SEARLE's data, there are 354 males and 338 females, figures which do not represent a significant divergence from equality. Thus, there is no evidence of discrimination against females. SEARLE's subsequent comparison of adult versus kitten populations is suggestive that orange is favoured but unfortunately the data are insufficient to establish this with certainty.

Table 4. *Assortment of the O gene and a test for random mating for the three samples. The figures in brackets indicate the theoretical frequencies*

Area	Phenotype *OO*	*O+*	*++*	χ^2 test for random mating
Herts.	32 (26)	25 (33)	133 (131)	3.35
Ealing	12 (9)	11 (15)	102 (101)	2.08
Kent	10 (9.5)	12 (12.8)	60 (59.8)	0.93
Combined	54 (45)	48 (61)	295 (291)	4.63

Despite the hint of a small amount of human preference in the distribution of the *O* gene, random mating may be reasonably assumed for the derivation

Table 5. *Sample sizes and gene frequency estimates for the nine genes scored in three areas of Southern England*

Gene	Herts.		Ealing		Kent		Combined	
	No.	Freq.	No.	Freq.	No.	Freq.	No.	Freq.
a	158	0.779 ± 0.024	113	0.776 ± 0.030	72	0.817 ± 0.034	343	0.795 ± 0.016
c^{ch}	117	0.131 ± 0.046		—		—		—
c^{s}	190	0.162 ± 0.036		—		—		—
d	190	0.290 ± 0.035	125	0.219 ± 0.044	82	0.221 ± 0.040	397	0.260 ± 0.024
l	198	0.255 ± 0.033	128	0.250 ± 0.043	82	0.312 ± 0.052	408	0.317 ± 0.024
O	190	0.225 ± 0.026	125	0.132 ± 0.026	82	0.193 ± 0.037	397	0.189 ± 0.017
S	185	0.314 ± 0.027	125	0.307 ± 0.022	82	0.337 ± 0.041	392	0.038 ± 0.018
t^{b}	64	0.857 ± 0.032	57	0.834 ± 0.036	30	0.796 ± 0.055	151	0.838 ± 0.022
W	198	0.020 ± 0.007	128	0.012 ± 0.007		—	408	0.014 ± 0.004

of frequencies of the other mutant genes. The evidence for this is shown by the random combination of grade of white spotting with the various phenotypes (tables 1, 2 and 3) and the absence of significant associations between the majority of phenotypes (analysis of table 6). The gene frequency estimates for the nine genes scored in the present survey are given in table 5. All the appended standard errors are based upon maximum likelihood formulae. The various estimates seem to be reasonably consistent between samples and call for no special comment.

Table 6 presents a series of 2 × 2 tests for association (with YATES' correction) between phenotypes. Tests are only performed where the numbers are adequate. With one exception, no significant association can be seen and this may be held to support the assumption of random mating. The exception is that of an association between *a* und *O*. Specifically, there are too many black tortoiseshells as opposed to tabby tortoiseshells. The association is consistently manifested in all three samples and becomes significant in the combined data. The association could be due to chance, since numerous associations are calculated and allowance must be made for this. Alternatively, there could be human preference for black versus tabby tortoiseshells. A further possibility is that, if the amount of orange pattern is small or occurs merely as small intermingled patches, these can be easily overlooked against a tabby background and the animal would be erroneously classified as an ordinary tabby. The effect of this would be two-fold, (1) to reduce the number of tabby tortoiseshells observed and (2) to reduce the number of tortoiseshells in the sample. If this sort of error recurs, it would be a partial explanation, at least, for the deficiency of tortoiseshells when a comparison is made between the expected and observed numbers of phenotypes for the *O* gene.

Table 6. *Tests of association between phenotypes as indicated by their respective genes. In the case of the O gene, the orange and tortoiseshell classes are pooled*

Genes	χ^2 Value			
	Herts.	Ealing	Kent	Combined
a–*d*	0.01	0.01	—	1.17
a–*l*	1.60	0	—	1.05
a–*O*	1.31	1.33	2.81	6.89
a–*S*	1.89	0.02	0	0.51
a–♂	0.19	—	1.30	0.61
d–*l*	0.10	—	—	0
d–*O*	0.45	—	0.22	0.05
d–*S*	0.61	0.10	—	0.18
d–♂	0.13	—	—	0.01
l–*O*	0.49	0	1.29	3.14
l–*S*	0.01	0.06	0.02	0
l–t^{b}	0	—	—	0.06
l–♂	0.31	—	—	0.55
O–*S*	0	0.04	0.49	0.19
O–t^{b}	0.44	0	0.13	0.03
S–t^{b}	0.17	0.17	0.14	0.12
S–♂	0.01	—	—	0.07
t^{b}–♂	0.29	—	—	0.35

Discussion

The present observations invite comparison with those of SEARLE (1949) which were executed in 1947, some 20 years earlier, although, strictly, only the Ealing sample is comparable. Several points of difference may be seen but it is doubtful if many of these are of real significance. In this respect, the frequency of genes *a*, *l*, *S* and t^{b} are in good or fair agreement in the two surveys (the frequency of *l* and *S* are calculated from SEARLE's data to be 0.333 and 0.373, respectively). The c^{ch} gene may seem to differ in frequency (allowing for variation in expression, the frequency may range from 0.203 to 0.260 for SEARLE's tabby data) but, in view of the variable expression in the amount of yellow pigmentation shown by the silver and the deficiency of yellow shown by some type animals which can simulate a tawny silver, the comparison cannot be pressed too far. *W* occurs at a low frequency and a comparison of frequencies would be of dubious utility. The c^{s} animals may not be part of the domestic population although it must be only a matter of time before they form a minute fraction of the gene pool. The Siamese is a popular fancy breed and some intermating with domestic cats may occur at a low frequency. The gene frequency is included for this reason but with due reservation.

The frequency of *O* would seem to differ between the two samples. If human preference for orange

cats does exist (as discussed earlier) this could lead to a slow increase in keeping with that observed. However, it could lead merely to cyclic fluctuation of gene frequency, depending how consistently the preference is maintained. These speculations cannot be carried too far at this time but they emphasise that a long-termed study of a single cat population may be rewarding. SEARLE's comparison of the adult and kitten populations showed that black (non-agouti) may also be favoured by human preference. This being so, an increase in *a* may be anticipated. There is indeed an increase for the present survey (compared with 0.762 in SEARLE's data) but this is far from being significant. On the other hand, the frequency of *a* is already at a high level, so that further increments may be small. This is another aspect which could be monitored by a long-termed study.

The frequency of *d* was found by SEARLE to be 0.142, apparently significantly lower than that of the present samples. It is uncertain if the difference has any meaning except perhaps to signify that the earlier survey happened to produce an unusually low estimate. This suggestion is only justified in that DREUX (1967, 1968) has observed frequencies of 0.330 and 0.286 for Paris and Laval (Mayenne), respectively. There is no reason, of course, to expect that the cat populations of London, Paris and Laval need have similar frequencies for *d* but they may not diverge so greatly as the earlier English sample would indicate.

Six polydactylous cats were observed in the Ramsgate sample. The owner of one polydactylous female stated that the animal had produced a total of 9 normal and 7 polydactyl offspring (presumably by a normal male). Typical dominant heredity (ROBINSON 1959) is thus indicated and a "pocket" of the polydactyl gene is probably subsisting in the area.

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Zusammenfassung

In drei Gebieten Südenglands wurden Beobachtungen über die Häufigkeit von 9 Genmutanten bei Hauskatzen angestellt. Die Signifikanz der aus den getroffenen Feststellungen abgeleiteten Voraussagen wird besprochen und kurz mit durch SEARLE vorgenommenen Schätzungen verglichen. Die Häufigkeiten scheinen in beiden Fällen vergleichbar mit Ausnahme der Gene *O* (orange) und *d* (dilute). Die Vorhersagen für diese Gene sind nach der gegenwärtigen Untersuchung signifikant höher als die früher gefundenen. Es könnte die Möglichkeit bestehen, daß für die Steigerung der Häufigkeit des Gens *O* die menschliche Vorliebe für orangefarbene Katzen verantwortlich ist. Für die größere Häufigkeit des Gens *d* liegt kein offensichtlicher Grund vor.

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