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Mutant gene frequencies in cats of the Greater London Area

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Summary. The frequencies of seven mutant genes of the domestic cat have been estimated by sampling the population of greater London, specific areas of the capital and adjoining counties. An attempt was made to diversify the method of sampling by concentrating upon certain categories of cats. In addition to the usual sightings of cats in streets and open spaces, surveys were made of cats attending a veterinary clinic, those staying at a boarding cattery, those exhibited in the household pet classes at a cat show and those in rescue centres. Although there are inconsistencies, the general impression from frequencies in present and earlier observations is that the lighter phenotypes (mackerel tabby, blue dilution and orange) are favoured by human preference, as opposed to the darker phenotypes (blotched tabby, black and non-orange). Reasons are discussed for thinking that, while human preference may be a factor in the evolution of the feline polymorphism, it is not the fundamental cause.

Key words: *Felis catus* – Cat genetics – Gene frequencies – Colour polymorphism

Introduction

The domestic cat population of London is polymorphic for a number of colour and coat mutant genes and presents an interesting problem in applied population genetics. The number of genes involved is few and the phenotypes produced by the genes are easily scored with a little practice. The first survey of the cats of London was that of Searle (1949), who was able to show that the population is essentially mating at random. For this purpose, Searle analysed the frequency distribution of the sex-linked gene orange (*O*), which produces six genotypes, each of which is phenotypically distinct. The test is that of checking if the observed frequencies of phenotypes agree with those expected with Hardy-Weinberg equilibrium. The finding of panmixia for cat populations has subsequently been confirmed by similar analyses with a number of electrophoretic variants (Spencer 1979; Auer and Bell 1981; Weghe et al. 1981; Brown and Brisbin 1983; Ikemoto et al. 1985). The significance of these later studies is that electrophoretic variants, unlike colour genes, are not likely to be influenced by human preferences. That cat populations are essentially panmictic is perhaps not surprising since cats are rarely confined and their breeding is unrestrained. Panmixia of populations means that the gene frequencies can be easily estimated.

The cat population of London has been sampled by Robinson and Silson (1969) and this work continued intermittently until 1984. It is the purpose of this paper to present and discuss these subsequent observations in relation to the earlier work.

Materials and methods

The majority of cat populations are heterozygous for seven mutant genes. In brief, these are non-agouti (*a*), dilution (*d*), long hair (*l*), orange (*O*), white spotting (*S*), blotched tabby (t^b) and solid white (*W*). Except for the gene for hair length, all of the genes modify colour; while *O* is additionally sex-linked. Full details of the primary phenotypes and interactions between the genes may be found in Robinson (1977).

The previous report of Robinson and Silson (1969) dealt with cats observed on the streets, gardens and open spaces; the present Ealing, London, (E83) sample was collected in a similar manner. However, an attempt was made to diversify the sampling as much as possible. The two Enfield, London, (E75 and E79) samples were obtained from a veterinary clinic for cats which were brought for neutering. Five samples were obtained from the domestic pet entries at major cat shows in the London area (F69, K77, N76, N81 and N84). The Crawley, Sussex, (C69) sample was obtained from a prominent cat boarding establishment. The Biggins Hill, Kent, (B71) and Wickford, Sussex, (W71) samples were obtained from cat rescue centres. The numbers attached to the reference letters indicate the year of sampling. Therefore, if cats observed on the streets, etc., represent an "random" sample, those from a veterinary clinic, cat shows and a boarding cattery could represent "wanted" animals, while those from rescue centres could represent "unwanted" or "stray" animals. The first and perhaps the last category will doubtless be composed of both wanted and unwanted cats, which will confuse matters, but nevertheless differences may be apparent.

Estimates (q) of the gene frequency were derived by the method of maximum likelihood. For recessive genes, this is the square root of the proportion of the recessive phenotype in the sample, with the error variance of $(1-q^2)/4n$, where n is the number of observations. For dominant genes, this is one minus the square root of the proportion of the recessive phenotype, with the error variance of $q(2-q)/4n$. Procedure for estimation of the frequency of the sex-linked O gene will depend upon whether or not the sample is scored for sex. If so, the frequency is found by counting the number of O genes over all phenotypes and dividing by $2n$, with the error variance of $2q(1-q)/3n$. When the sample is not scored for sex, the frequency may be approximated by $(2a+b)/2n$, where a and b are the number of orange (O and OO) and tortoiseshell ($O+$) phenotypes in the sample, with the approximate error variance of $q(2-3q)/(3-4q)n$. The frequencies in this paper have been derived from a maximum likelihood computer programme.

Results

All of the samples provided estimates of frequencies of the seven genes described above, with the exception of C79 (where the long haired (l) cats were not scored) and W69 (where no white (W) cats were observed, probably because of the small number of animals examined). The estimates of gene frequencies are shown by Table 1.

The observed frequencies of the orange (O and OO) and tortoiseshell ($O+$) phenotypes may be compared with those expected, if the O gene is in Hardy-Weinberg equilibrium, as a test for random mating. The results of these calculations are shown by Table 2. All of the samples display frequencies in keeping with expectation, except for W69 which is formally significant at the 5% level. It is probable that the deviation is due to the small size of the sample since the χ^2 value is not overly large. It is concluded that all of the samples are representative of panmictic populations.

Tests were performed for between sample heterogeneity for each gene and the results are shown by Table 3. The χ^2 values indicate that the estimates for genes a and W do not display excessive variability and the value for the estimates of S just exceeds the 5% level of significance. All of the χ^2 values for the other genes are highly significant. The heterogeneity for t^b is due to the unusually low gene frequency shown by sample

Table 1. Gene frequency estimates in percentages and sample sizes for 7 genes of 11 populations

Gene	E83	E75	E79	N76	N81	N84	K77	F69	C79	B71	W69
a	77.0±2.7	75.0±2.0	76.7±2.4	77.9±1.6	76.7±2.0	70.1±2.8	70.4±3.2	81.7±2.4	76.6±2.0	78.1±3.6	79.5±4.9
	(140)	(270)	(178)	(402)	(257)	(161)	(123)	(141)	(269)	(77)	(38)
d	20.9±3.9	18.3±2.8	15.7±3.5	31.7±2.7	24.5±2.9	23.2±2.9	22.4±3.8	27.7±3.7	33.5±2.8	25.2±5.3	20.4±7.1
	(161)	(300)	(202)	(477)	(317)	(278)	(140)	(169)	(294)	(83)	(48)
l	31.3±3.7	18.3±2.7	29.6±3.3	31.7±2.2	47.3±2.4	47.7±2.6	43.2±3.8	47.0±3.3	–	30.7±5.3	50.0±6.3
	(163)	(310)	(202)	(494)	(331)	(290)	(145)	(181)		(85)	(48)
O	15.6±2.4	17.9±1.8	18.1±1.8	25.0±1.7	25.8±2.1	26.6±2.3	23.2±3.2	15.7±2.3	23.8±2.1	14.8±3.3	16.7±4.4
	(163)	(174)	(129)	(477)	(317)	(278)	(140)	(169)	(294)	(83)	(48)
S	32.7±2.9	34.7±2.2	36.9±2.7	31.9±1.7	31.2±2.0	29.5±2.1	23.5±2.7	35.2±2.9	31.2±2.1	28.0±3.8	40.5±5.8
	(161)	(270)	(262)	(477)	(317)	(278)	(140)	(169)	(294)	(83)	(48)
t^b	74.5±3.5	73.5±2.8	77.9±3.2	72.4±2.3	72.0±2.7	76.7±2.7	72.8±3.8	83.9±3.2	54.0±3.4	83.6±5.0	75.6±7.1
	(90)	(148)	(178)	(233)	(160)	(141)	(83)	(71)	(269)	(28)	(21)
W	0.6±0.4	1.6±0.7	1.0±1.0	1.7±0.4	2.1±2.1	2.9±0.7	1.7±0.7	3.3±1.0	1.0±0.4	1.2±0.8	0
	(163)	(310)	(206)	(494)	(331)	(295)	(145)	(181)	(300)	(85)	

Table 2. Distribution of gene O phenotypes and a test for random mating for eleven populations. The expected frequencies are shown in *brackets*

Population	O	$O+$	$++$	χ^2 for 1 *df*
E83	17 (14.5)	18 (21.2)	126 (125.2)	0.92
E75[a]	3 (4.8)	52 (48.3)	174 (173.9)	0.50
E79[a]	3 (2.9)	33 (33.1)	93 (93)	0
N76	75 (74.5)	89 (89.4)	313 (313.1)	0.01
N81	60 (51.4)	48 (60.7)	209 (204.9)	4.18
N84	47 (46.9)	54 (54.3)	177 (176.9)	0
K77	20 (20)	25 (25)	95 (95)	0
F69	21 (15.3)	15 (22.3)	133 (131.3)	4.53
C79	47 (43.3)	48 (53.3)	199 (197.3)	0.87
B71	9 (7.1)	8 (10.5)	66 (65.5)	1.11
W69[a]	3 (1.3)	3 (6.5)	10 (8.3)	4.5

[a] Test based upon female frequencies

Table 3. Tests of heterogeneity between gene frequencies estimates for the 11 populations. *NS*: not significant; *JS*: just significant; *S*: significant

Gene	Heterogeneity χ^2	*df*	Status
a	15.76	10	NS
d	34.20	10	S
l	67.51	9	S
O	44.49	20	S
S	19.87	10	JS
t^b	55.23	10	S
W	16.40	10	NS

Table 4. A comparative summary of gene frequency estimates (percentages) in cat populations of Southern England. Sources: *TP*: this paper. *D73*: London (Dyte 1974). *E69*: Ealing; *H*: Hertfordshire; *K*: Kent (Robinson and Silson 1969). *S49*: London Searle (1949). *C*: Cambridge (Todd et al. 1969). *BC*: Bristol clinic; *BS*: Bristol streets (Gruffydd-Jones et al. 1979)

Gene	TP	D73	E69	S49	H	K	C	BC	BS
a	76	74	78	76	78	82	81	79	76
d	24	29	22	14	29	22	29	33	24
l	47	50	25	33	33	31	29	38	32
O	25	25	13	11	23	19	25	21	20
S	32	28	31	27	31	34	29	31	38
t^b	75	69	83	81	86	80	73	68	80
W	2	3	1	1	1	–	1	1	1

Table 5. Comparison of gene frequencies in "wanted" (samples C79, D74, E75, E79, F69, K77, N76, N81 and N84), "unwanted" (samples B71, S49 and W69) and "random collected" (samples E69, E83, H and K) cats. See text for definitions and qualifications. *NS*: not significant; *S*: significant. χ^2 based upon a 2×2 comparison of observed numbers, with 1 *df*

Gene	Wanted	Unwanted	χ^2	Status	Random
a	76.0±0.7	76.6±1.2	0.14	NS	78.3±1.4
d	26.7±1.0	15.6±1.7	24.64	S	24.0±2.1
l	48.2±1.0	34.9±2.2	56.81	S	31.3±2.0
O	23.6±0.5	12.2±0.7	77.28	S	18.4±1.0
S	32.0±0.7	36.8±1.4	9.91	S	32.0±1.6
t^b	71.7±1.0	81.5±1.6	24.42	S	80.1±1.9
W	0.5±0.2	0.2±0.2	19.08	S	0.9±0.3

C79. Eliminating this estimate from the heterogeneity test gives the insignificant χ^2 of 14.41 for nine *df*. The heterogeneity shown by O is curious; it is as if the samples are drawn from two distinct populations, one with a mean frequency of about 18.2% and another of about 25.3%. However, a partial explanation for this may be found for two of the samples, namely E75 and E79. The sex ratios in the samples were unbalanced, with a significant excess of female cats. The gene O frequencies differed between the sexes as follows: E75, 21.4±3.7 for males and 16.7±1.2 for females; E79, 28.8±5.3 for males and 15.2±2.2 for females. The other samples were not scored for sex and could not be examined for a comparable sex difference. The heterogeneity for d and l showed no readily obvious trend.

Discussion

The present compilation invites comparison with previous surveys and a summary is presented by Table 4. The frequencies of the table may be compared with those shown in Table 1. In as much as it is possible to assess the implications of the different methods of sampling, human preference would seem to be in the direction of favouring the lighter phenotypes, a finding first made explicit by Clark (1975) with sociological questionaires.

An attempt has been made assess the extent of human preference by pooling the samples belonging to the wanted and unwanted categories as defined above. The results are shown by Table 5. There is no significant difference of mean frequency between the categories for gene a. There is a significant difference for d but, if the unusually low frequency shown by sample S49 is removed from consideration, the difference is no longer significant (the mean becomes 22.7±4.5 for the unwanted category and a χ^2 of 0.69). If the unusually low frequency for t^b shown by sample C79 is removed from consideration, the mean becomes 78.5±0.7 for the wanted category but the difference remains significant, with a χ^2 of 7.46. The table suggests that human preference is for the lighter phenotypes, certainly for mackerel tabby and orange and probably for blue dilution and white. Somewhat surprisingly, piebald animals apparently are not favoured. Long haired cats are preferred upon this showing. The last column of Table 5 shows the mean gene frequencies for the pooled samples of random collected cats. There appears to be a small tendency for the means to resemble those of the unwanted category. It is tempting to infer that the majority of cats ordinarily observed are unwanted in the sense that deliberate choice of colour of ordinary domestic cats is only exercised by a minority of people.

The Bristol observations may be germane in the present context because two different contemporary samples were obtained: one (BC) consisting of cats brought to a veterinary clinic and another (BS) consisting of cats observed on the streets and open spaces (see Table 4). The former may be depicted as wanted animals and the latter as a mixture of wanted and unwanted animals. The interesting aspect is that a similar pattern of preferences is manifested as noted above. The preferences are even more evident in the samples of Clark (1975), who surveyed and compared the results for two distinct sociological areas of Glasgow, an upper and a lower in terms of economic status. If the assumption is made that the households of the former are likely to be marginally more discriminative in choice of cat than the latter, the frequencies for all of the lighter phenotypes are reported as greater in the sample, even for *a* and *S*.

The point may be made that epistasis between the genes can interfere with staightforward human selection. For example, *O* is epistatic to *a* hence, if orange or ginger cats are favoured, effectively there will be no selection for or against *a*. Again, *O* is partially epistatic to t^b. The grey agouti coloration is removed but the blotched tabby pattern will remain. Indeed, if the intensity of the orange colour is an incentive in the preference for the colour, blotched orange is redder than mackerel orange. It is well-known that while black tortoiseshells are easily scored, this is not so for tabby tortoiseshells. It is easy to overlook small or diffused areas of the orange pattern, especially for the uninitiated.

Metcalfe and Turner (1971) were able to demonstrate that either artificial or natural selection is acting upon the *O* locus although the nature of this is obscure. Blumenberg's (1977) analyses are revealing in that the selective forces have probably been acting for some considerable time. Gene *a* had probably attained high frequency some 300 years ago and had increased only slowly, but significantly, in more recent times. On the other hand, the frequency of gene t^b had increased more dramatically over the same period. Conversely, the frequencies of genes *d* and *O* have declined over the same period but not so dramatically. Gene *S* appears to show a stable frequency.

Notwithstanding the above conclusions, it would seem unwise to place too much weight upon the human preference factor in explaining the coat colour polymorphism of cats. One aspect of human preference must be mentioned, however, and this is the novelty element. An unusual colour may be retained in preference to others for a while until the novelty wears off. In this manner, a new mutation could gain a foothold which it might otherwise fail to do. Yet this aspect is insufficient by itself to guarantee an increase in frequency. A pertinent case is that of the all-white cat which finds favour in human preference but which in all samples consistently recurs at a very low frequency due to the inherent disadvantage of the *W* gene (Robinson 1970; Bergsma and Brown 1971).

Two potentially fruitful explanations have been proposed for the high frequencies of the *a* and t^b genes. The first rests upon the hypothesis of Keeler (1942) that the *a* gene in mammals has a docility effect, so that the animal is less fearful. The t^b gene, as a melanotic mutant, may have a similar effect but docility alone may not be sufficient to account for the rapid rise in frequency of the gene during the last 300 years. The second explanation postulates that the advantage of t^b is density dependent, so that the rise coincided with the increase in human population density (which implies an increase in cat population density). The higher frequencies of t^b are associated with urban conurbations, where such conditions prevail, and should the gene confer a greater tolerance of close proximity of other cats in comparison with the mackerel wild type, the allele would be at an advantage (Robinson 1982).

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