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Mutant Gene Frequencies in Cats of Cyprus

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Summary. Three areas of the island of Cyprus have been sampled for frequency of nine mutant genes among the domestic cat population. The significance of the observed frequencies are discussed with particular reference to the existence of world-wide clines for O (orange) and t^b (blotched tabby). The frequencies for Cyprus seems to be intermediate to those reported for European and Asian populations and could be part of the proposed East-West cline for the two genes.

The cat population of three areas of Cyprus have been sampled for the presence of mutant phenotypes. The three areas are, (1) Dhekelia, which comprises Dhekelia itself and samples from the surrounding villages of Ormidhia, Pyla and Xylotymbou, plus a small sample from Larnaca, a little further south, (2) Kyrenia and (3) Akrotiri. The three areas are widely separated and are coastal. Dhekelia lies towards the South-east of the island, with Kyrenia to the North, and Akrotiri to the South.

Material and Methods

Most cat populations may be examined for the presence of nine or ten mutant genes although not all the samples need contain this number. The following genes were found:

Mutant gene	Phenotype and remarks
a	Non-agouti; epistatic to T^a and t^b
c^{ch}	Chinchilla
d	Dilute (blue)
l	Long hair
O	Orange; epistatic to a
S	Piebald spotting
T^a	Abyssinian tabby
t^b	Blotched tabby
W	White; epistatic to all other colour genes

A comprehensive account of the mutant genes and phenotypes may be found in Robinson (1959, 1971). The wild type cat is the mackerel or striped tabby, with slightly curving vertical stripes on the body. Piebald spotting may be due to more than one gene but it is probable that only one major gene is involved.

The data were collected in the main by house-to-house surveys during 1968. The frequencies of the more important phenotypes are arranged in table 1. The first seven entries sum to the total number of observations (with two exceptions, see later) while the remaining entries show part of the data re-arranged to facilitate further computation. In addition to those of the table, the following cats were noted. A yellow-eyed all-white animal was observed in Larnaca. It is unknown if this could be an extreme phenotypic variant of S or if it is due to W. Two Abyssinian tabbies were seen; one in Larnaca and one in Kyrenia. These three cats were excluded from the analysis. If these animals are part of the mongrel population, it is clear that the genes T^a and W occur at a low frequency. The three samples consisted of 272, 72 and 21 animals for Dhekelia, Kyrenia and Akrotiri, respectively, making a total of 365. A number of kittens were observed in each sample but only for Dhekelia was the number large enough to warrant separate consideration. The sample for Akrotiri was small but it did not seem legitimate to pool it with one of the others.

The table shows the distribution of piebald spotting in relation to the main phenotypes. There appears to be no obvious association with any particular phenotype. Each cat was scored for as many features as possible but it was not always possible to score every animal completely. Sex and type of tabby were particularly affected in this respect. For those individuals which were sexed, 144 were males and 184 were females. The deviation from expectation is significant ($\chi^2 = 4.88$). However, a preponderance of females is to be expected because of the awareness of the observer that the tortoiseshells are females. If the unsexed cats (37 in number) are taken to be mainly males, the frequencies of the two sexes become roughly equal.

All of the mutants listed above, with the exception of O, are inherited autosomally. On the assumption of random mating, the gene frequencies are estimated as the square root of the appropriate phenotype. Estimation of O is a little more complex but follows that outlined by Robinson and Silson (1969). The results are shown in table 3.

Table 1. *Observed frequencies of the more important phenotypes in conjunction with piebald white spotting*

Phenotype	Dhekelia, adult		Dhekelia, kittens		Kyrenia		Akrotiri	
	S	$+$	S	$+$	S	$+$	S	$+$
Tabby, striped	52	29	12	10	10	23	3	1
Tabby, blotched	4	4	1	0	1	2	0	0
Tabby, undiagnosed	5	9	0	0	0	0	0	0
Non-agouti	63	26	9	12	16	14	2	8
Orange, striped	12	9	1	3	3	2	0	5
Orange, blotched	0	0	0	0	0	0	0	0
Orange, undiagnosed	8	4	0	0	0	0	0	0
Tortoiseshell	32	3	4	8	6	2	0	1
Dilute	13	8	4	4	3	6	1	5
Silver	7	8	2	2	3	3	1	0
Long hair	19	39	2	4	10	10	0	6

The Analysis

The most interesting gene frequency is that for O. The gene is sex-linked and, if sex can be ascertained for every individual, all five genotypes are unambiguously identifiable. A difference of gene frequency between the sexes and a departure from random mating can be detected. However, if sex cannot be determined for every cat, a partial analysis can be made from the frequencies of orange, tortoiseshell and type animals, assuming random mating.

Table 2. *Assortment of the O gene and a test for random mating on the assumption of equality of the sexes ($m = 0.5$). The figures in brackets indicate the theoretical numbers*

Locality	O gene frequency	Phenotypes OO	$O+$	$++$	χ^2
Dhekelia					
Adult	0.218	33(26)	35(35)	157(163)	1.97
Kittens	0.227	4(8)	12(9)	31(30)	2.79
Combined	0.222	37(37)	47(47)	188(188)	0
Kyrenia	0.125	5(5)	8(7.9)	59(59.1)	0
Akrotiri	0.282	6(4)	1(4)	14(13)	3.70
Combined	0.206	48(46)	56(61)	261(258)	0.16

A preliminary check for equality of the sexes for the Dhekelia sample (adults plus kittens) indicated a significant excess of females (males = 97, females = 156, $\chi^2 = 13.76$). The elementary formulae given in Robinson and Silson (1969) cannot be used, therefore, so recourse was made to the maximum likelihood formulae:

$$q = \frac{2a + b}{2n} \quad \text{and} \quad m = \frac{4ac - b^2}{(2a + b)(b + 2c)}$$

where q = proportion of O gene, m = proportion of males, $n = a + b + c$ and a, b, and c are the observed numbers of orange, tortoiseshell and type cats, respectively.

The above formulae were employed to derive estimates of q and m for all four samples. Insertion of the observed frequencies of 33 orange, 35 tortoiseshell and 157 type for the Dhekelia adult data gave $q = 0.196$ and $m = 0.569$. Similarly, for the Dhekelia kitten data, $q = 0.260$ and $m = 0.650$, Kyrenia data, $q = 0.125$ and $m = 0.491$ and Akrotiri $q = 0.310$ and $m = 0.889$. The combined data gives $q = 0.208$ and $m = 0.536$. It may be noted that the distributions of the three phenotypes are suggestive of a higher frequency of males than is borne out by the actual data. However, despite the variation in m, the results of table 2 indicate that approximate equality can be assumed without serious error. Alternatively, if inequality does exist, then the samples are not large enough for the deviation from expectation to be significant. The above values for the frequency of O differ from those obtained by assuming equality of the sexes (Table 2) but not significantly. There is variation of frequency between samples but not enough to suggest heterogeneity (table 3).

Estimates of the frequency of the remaining six genes are shown by table 3. The main point of interest is whether significant differences of frequency may exist between the samples. This aspect is examined by χ^2 tests based on the observed phenotypes. The number of expected mutant phenotypes were too few in the case of the smaller samples for the test to have validity for the genes c^{ch} and t^b. In any event, a comparison of the expected and observed frequencies for each gave no grounds for assuming significant heterogeneity. χ^2 tests for a and l revealed that the observed differences were within the conventional limits of chance variation.

The situation is different for the genes d and S. Significant between sample variation is apparent. In the case of d, the heterogeneity is due to the high frequency for the Akrotiri sample. When this is removed, the remaining three samples are homogeneous ($\chi^2 = 2.88$; df = 2, $P = 0.3-0.2$). Akrotiri is a village in a peninsula called "Cape Gatto", which means "Cape of the Cats". Apparently, large numbers of cats were kept in the area to combat the snakes which were particularly numerous. Legend has it that the majority of cats were blue and this may account for the high incidence of the d gene in the sample (Home 1960; and enquiries conducted by Mrs. Brenda Ollivère).

The heterogeneity associated with S is due to the high frequency recorded for the adult Dhekelia sample. When this sample is deleted, the heterogeneity vanishes ($\chi^2 = 4.1$, df = 2, $P = 0.2-0.1$). Five sub-

Table 3. *Sample size and estimates of gene frequency for mutant genes observed in Cyprus*

Gene	Dhekelia (adults) No.	Freq.	Dhekelia (kittens) No.	Freq.	Kyrenia No.	Freq.	Akrotiri No.	Freq.	Combined No.	Freq.	Heterogeneity χ^2
a	194	0.677 ± 0.026	46	0.668 ± 0.055	65	0.679 ± 0.064	18	0.745 ± 0.079	323	0.716 ± 0.019	0.25
c^{ch}	111	0.368 ± 0.044	25	0.400 ± 0.092	35	0.414 ± 0.077	8	0.345 ± 0.165	179	0.389 ± 0.033	–
d	225	0.306 ± 0.032	47	0.413 ± 0.067	72	0.345 ± 0.055	21	0.535 ± 0.093	365	0.347 ± 0.023	11.2*
l	225	0.508 ± 0.029	47	0.357 ± 0.068	72	0.527 ± 0.050	21	0.535 ± 0.093	365	0.497 ± 0.024	4.81
O	225	0.218 ± 0.023	47	0.227 ± 0.052	72	0.125 ± 0.033	21	0.282 ± 0.084	365	0.206 ± 0.012	5.12
S	225	0.400 ± 0.027	47	0.285 ± 0.064	72	0.264 ± 0.041	21	0.127 ± 0.054	365	0.338 ± 0.018	18.00**
t^b	110	0.270 ± 0.046	27	0.192 ± 0.095	41	0.271 ± 0.075	10	0	188	0.253 ± 0.035	–

* Significant at 5 per cent level; ** significant at 1 per cent level.

samples make up the adult Dhekelia sample and significant heterogeneity is apparent ($\chi^2 = 10.11$, df = 4, $P = 0.05$). The heterogeneity is due to a high frequency of 0.511 for the S gene in 46 individuals from the village of Ormidhia. Eliminating this sub-sample reduces the heterogeneity to a negligible quantity ($\chi^2 = 5.70$, df = 3, $P = 0.2-0.1$). The revised S gene frequency for the whole data (less the Ormidhia) is 0.317 ± 0.018, seemingly the more realistic overall estimate. There is no obvious explanation for the high frequency for Ormidhia, unless it is a chance deviation due to the examination of numerous sub-samples.

Discussion

The recording of cat coat colours for the island of Cyprus is one more brick in the edifice of population genetics which is being erected for the species. Provisionally, Cyprus may be regarded as part of Europe, yet being sufficiently distant to have characteristics of its own.

Among the various mutants, only observations for t^b and O have yielded evidence for systematic variation which could be interpreted as clinal effects (Searle 1959). The frequency of t^b is high in Europe but low in Asia while the frequency of O is conversely low in Europe but high in Asia. Nine groups of data are available for Europe (Searle 1949, 1966, Dreux 1967, 1968, 1969, 1971, Robinson and Silson 1969, Metcalfe and Turner 1971) and two for Asia (Komai 1952, Searle 1959). An analysis of the gene frequencies for these is presented by table 4. The nine samples for the t^b European gene frequencies are not homogeneous as measured by χ^2. However, these divide easily into three groups which are internally homogeneous but with significantly different means. The difference between means for the London group versus the Chamonix group has been ascribed to urbanisation favouring a darker phenotype (i.e., the t^b gene; Dreux 1968) but the data could be indicative of a slope for a cline extending roughly North-east to South-east across Europe. The Venice sample would fit this hypothesis. The still lower value for Cyprus would also fit, if it is assumed that the cline is progressing eastwards, as the still lower estimate for Singapore would imply.

Table 4. *Variation of genes t^b and O for European and Asian populations*

t^b mean frequencies	
Europe	
London, Paris, S. England, York	0.804 ± 0.009
Chamonix, Hague, Laval, Marseilles	0.631 ± 0.012
Venice	0.480 ± 0.038
Cyprus	0.253 ± 0.035
Asia	
Singapore	0.113 ± 0.025
O mean frequencies	
Europe	
Hague	0.215 ± 0.012
S. England, York	0.188 ± 0.010
Laval	0.148 ± 0.008
London	0.107 ± 0.007
Chamonix, Marseilles, Paris, Venice	0.066 ± 0.005
Cyprus	0.206 ± 0.012
Asia	
Singapore	0.315 ± 0.017
Gotemba	0.395 ± 0.016
Mishima	0.252 ± 0.022

The observed frequencies for O do not present such a coherent picture. There is considerable heterogeneity between the European samples, so much so, that only the Chamonix group of four (see table) are homogeneous. The London sample differs from the others in time by about 20 years and this could be the explanation for the low frequency recorded (the gene may have increased in frequency in the interim, for Metcalfe and Turner (1971) have shown that the allele is subject to selection). Even so, the other samples differ significantly among themselves. However, taking the European data as a whole, all have frequencies which are significantly lower than the Asian. The three Asian frequencies are not homogeneous – not even the two Japanese. The Gotemba sample is not thought to be as accurately scored as might be desired and this may account for the heterogeneity. The difference between the Singapore and Mishima estimates could indicate differently constituted gene pools, as may be anticipated by the considerable distance which separates the two cities.

Despite the heterogeneity, the frequency of O is clearly different between the European and Asian cat populations. The O frequency for Cyprus is close to that for the Hague and possibly for Southern England and York but, otherwise, it occupies a roughly intermediate position between those of Europe and Asia. The analysis for t^b are more clear-cut in this respect and it is reasonable to emphasize that the results for both t^b and O should be viewed together.

The above speculations are suggestive, especially as pointers for future studies. It would be instructive if cat gene frequency data could be obtained for areas of Europe so far unsampled, such as the Eastern region and the Balkan peninsula. Areas of Turkey and the Middle East particularly deserve attention in order to determine if the clines discussed above are extending eastwards into Asia. Assuming the existence of these clines, it may be that they are not smoothly continuous but may have one or more saltations. These could follow from variation in local climatic conditions, urbanisation or human preference for particular colour types. All of these aspects require investigation.

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