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Genetic Difference and Selection in Domestic Cat Populations of the United Kingdom and Former British Colonies

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Summary. Domestic cat populations of former British colonies provide a unique set of data with which to evaluate the historical/immigration hypothesis because such populations are believed to sample an evolving parental United Kingdom stock at various times over the last three centuries. A regression of f coefficients upon separation time between founding populations, as inferred from historical records, is statistically significant. Selection is indicated as the mechanism underlying allele frequency change.

Introduction

Present day allele frequencies in populations of *Felis catus* that reside within nations that were former European colonies are believed to approximate those of Europe at the time the cats were first exported with waves of human migration (Todd, Fagen, and Fagen 1975). This hypothesis suggests that colonial cat populations have undergone relatively little genetic evolution when compared to those of the mother country. Such populations should present a genetic profile approximating that of the founding population during its period of initial and presumed rapid expansion to a condition characterized by genetic equilibrium and panmixia. This model has been used to explain the genetic profiles which characterize Hobart (Dartnall and Todd 1975), the maritime provinces of Canada (N.B. Todd personal communication), Vancouver (Blumenberg, Lowry, and Blumenberg 1977), and colonial America (Costello and Blumenberg 1976).

More than a dozen cities have been surveyed whose founding cat populations are predominantly United Kingdom in origin. These localities may be grouped into three subsets, each of which is characterized by a distinct date for the initial period of rapid population growth. Boston/Salem, New York City, and Philadelphia are believed to sample the United Kingdom population circa 1650; Charlottetown, Frederickton, and Halifax according to the hypothesis would sample the same population circa 1750; Adelaide, Brisbane, and Hobart would therefore represent a mid 19th century sampling and Vancouver a late 19th century sample. Consult Clark (1973) plus the references given in the paragraph above for detailed discussions of the relevant historical data. According to the model, these colonial populations may be thought of as evolutionary lines which take an essentially horizontal path upon branching off from the central evolutionary track which is represented by the United Kingdom *F. catus* populations. In view of their common geographic origin, these populations provide a unique set of data with which to substantiate or refute, in a quantitative manner, the fundamental premise of the historical/immigration hypothesis. This model predicts that the amount of genetic separation between any two populations of common geographic origin should be proportional to the separation in time between their respective founding populations. For example, the amount of genetic difference between the *F. catus* populations of New York and Philadelphia should be insignificant because both cities had an early history dominated by an initial period of large scale immigration from the British Isles in the middle of the seventeenth century. On the other hand, the hypothesis predicts that substantial diffference should be demonstrable between the cats of colonial America and those of Australia whose founding British populations underwent their initial expansion in the middle of the nineteenth century.

Methods

The measure of genetic difference adopted herein is that developed by Kidd and Cavalli-Sforza (1974) and

Table 1. Allele frequencies for mutations affecting pelage in domestic cat populations of the United Kingdom and former British colonies

Population	n^1	0	a	t^b	d	S	c.d.^{2}
Boston/Salem	387	.209	.691	.419	.419	.403	.371
New York City	206	.145	.752	.473	.443	.470	.455
Philadelphia	202	.274	.705	.449	.500	.421	.354
Pooled "1650"	779	.212	.712	.439	.446	.424	.380
Charlottetown	88	.281	.790	.447	.460	.342	.396
Frederickton	97	.285	.764	.500	.388	.357	.418
Halifax	132	.320	.788	.573	.450	.379	.404
Pooled "1750"	303	.307	.782	.517	.436	.362	.402
Adelaide	482	.191	.779	.710	.326	.295	.582
Brisbane	234	.143	.815	.685	.455	.408	.558
Hobart	731	.217	.758	.813	.244	.386	.630
Pooled "1850"	1467	.202	.779	.744	.325	.359	.588
Vancouver	193	.174	.809	.612	.439	.333	.429
Dublin	137	.14	.83	.73	.28	.36	.692
London	560	.107	.762	.814	.142	.343	.751
S. England	406	.189	.795	.838	.260	.315	.673
York	352	.20	.81	.78	.27	.33	.664
Pooled "1950"	1318	.149	.792	.820	.228	.347	.708

1 - average sample size over the five loci considered
2 - coefficient of darkness = $0^+ d^+ (a^+ t^b + a)$ according to Todd (1969).
Data taken from Blumenberg, Lowry, and Blumenberg (1977); Clark (1973); Costello and Blumenberg (1976); Dartnall and Todd (1975); Metcalfe and Turner (1971); Moffat (1968); Robinson and Silson (1969); Searle (1949); Todd (1964, 1966, 1976, personal communication)

the reader is referred to that paper for a theoretical derivation of the relationships. The angular transformation is chosen because the variance of θ is essentially independent of the mean gene frequency.

$$\cos\theta_{12} = \sum_{i=1}^{k} \sqrt{p_{i1}\, p_{i2}} \tag{1}$$

where p_{i1}, p_{i2} are the frequencies of the ith allele in populations 1 and 2 respectively for a locus of k alleles. An estimate of the variance for all k alleles at one locus becomes:

$$f_\theta = \frac{4(1 - \cos\theta_{12})}{k - 1} \tag{2}$$

An estimate of f over several loci can be obtained as the weighted average of the f values at each locus:

$$\bar{f}_\theta = \frac{\sum_i 4(1 - \cos\theta_i)}{\sum (k_i - 1)} \tag{3}$$

f_θ values are affected by a bias due to random sampling variance which can be computed from the Bhattacharya-Matousek distribution to be $(N_1 + N_2)/4N_1N_2$.

Six mutant alleles in the genetic system of *F. catus* (0, a, t^b, d, l, S) fit the requirements for this analysis; i.e. they are characterized by frequencies within the range 0.05-0.95. In view of the difficulties in

Table 2. Genetic difference and f coefficients: comparisons with colonial American populations

Locus	SB-NYC	SB-PH	SB-Hal	SB-Adel	SB-Van	SB-Lond	NYC-Ph
Orange	.003539	.002893	.007985	.000253	.000991	.010003	.012812
Nonagouti	.002320	.000116	.006147	.004997	.009386	.003182	.001398
Bl. tabby	.001476	.000458	.011930	.044098	.018820	.087258	.000290
Dilute	.000294	.003308	.000489	.004639	.000204	.050033	.001631
Piebald	.002284	.000167	.000302	.006446	.002638	.001927	.001216
$\Sigma(1 - \cos\theta)$	.009913	.006943	.026854	.060433	.032039	.152403	.017347
f_θ	.007931	.005554	.021483	.048347	.025631	.121922	.013877
samp. error	.001860	.001884	.002540	.001165	.001941	.001138	.002451
corrected f	.006071	.003671	.018943	.047182	.023890	.120784	.011426

Table 3. Genetic difference and f coefficients: comparisons with Canadian maritime and

Locus	Ch-Fred	Ch-Hal	Ch-Van	Fred-Hal	Fred-Van	Hal-Van
Orange	.000010	.000905	.008235	.000726	.008813	.014581
Nonagouti	.000488	.000003	.000282	.000414	.001511	.000343
Bl. tabby	.001409	.007973	.013756	.002682	.006373	.000788
Dilute	.002657	.000050	.000223	.001976	.001342	.000061
Piebald	.000124	.000743	.000045	.000260	.000319	.001155
$\Sigma(1 - \cos\theta)$	.004688	.009674	.022541	.006060	.018358	.016927
$\bar{f}_\theta$	.003751	.007739	.018033	.004847	.014686	.013542
samp. error	.005418	.004735	.004136	.004471	.003873	.003189
corrected f	.0+	.003005	.013896	.000376	.010813	.010353

achieving a reliable diagnosis of the long hair phenotype (Todd and Todd 1976), it is quite probable that the many literature reports of the frequency of this mutant in various populations are at best only poor approximations of the true level of this allele. For this reason, long hair allele frequencies will not be considered in this paper.

Results

Table 1 gives the allele frequencies and coefficient of darkness for all surveys dealt with in this study and the pooled regional gene frequencies which are believed to represent the genetic profile of United Kingdom *F. catus* populations at various times during the past three centuries. Tables 2 and 3 give genetic difference calculations for 28 pairwise comparisons between eleven cities. The individual surveys for these comparisons were chosen, whenever possible, on the basis of large sample size (so as to minimize sampling bias) and presumed origin in one major founding population whose arrival from the United Kingdom can be reliably documented historically. Data from Melbourne were not used because of the small sample size (n = 84) when compared to other Australian cities (Moffat 1968). Data from Charlottetown were used (n = 88), however, because of the relatively small sample sizes of all the Canadian Maritime surveys; see Table 1. Data from Dunedin, New Zealand (Marples 1967), which could have been pooled with that from Vancouver for the 1875 time point, were not used because the allele frequencies have been secondarily derived from verbal descriptions and are not considered reliable (N.B. Todd personal communication).

Discussion

The model predicts that the genetic difference between pairs of populations should increase as the separation time between founding populations increases. As shown in Table 4, this prediction is confirmed although the standard deviations of the separation times characterizing a particular range of f values are enormous. It should be noted that due to the requirements of equation (3), the f coefficients in this analysis are 0.8 of the summed genetic difference across the five loci considered for each pairwise comparison. A least

NYC-Hal	NYC-Adel	NYC-Van	NYC-Lond	Ph-Hal	Ph-Adel	Ph-Van	Ph-Lond
.022098	.001900	.000786	.001647	.001268	.004857	.007264	.023593
.000916	.000508	.002379	.000068	.004574	.003590	.007417	.002082
.005023	.029557	.009780	.066414	.007722	.035648	.013426	.075311
.000025	.007263	.000008	.057882	.001254	.015750	.001869	.078561
.004247	.016373	.009819	.008397	.000919	.008866	.004132	.003228
.032308	.055601	.022772	.134408	.015737	.068530	.034108	.182775
.025847	.044481	.018217	.107527	.012590	.054824	.027289	.146220
.003108	.001732	.002509	.001660	.003132	.001756	.002533	.001684
.022739	.042748	.015708	.105867	.009498	.053068	.024754	.144536

Australian populations

Ad-Hob	Ad-Hal	Ad-Van	Hob-Van	Hal-Lond	Ad-Lond	Van-Lond
.000520	.011075	.000242	.001473	.035703	.007079	.004705
.000310	.000060	.000689	.001922	.000485	.000204	.001643
.007370	.010273	.005380	.025261	.034893	.007370	.025261
.004141	.008134	.006786	.021472	.060266	.024389	.056539
.004625	.003959	.000839	.001526	.000703	.001327	.000056
.016966	.033501	.013936	.051655	.132050	.040370	.008204
.013574	.026800	.011147	.041324	.105640	.032296	.070563
.000861	.002413	.001814	.001637	.002340	.000965	.001742
.012713	.024388	.009334	.039687	.103299	.031307	.068822

Table 4. Relationship between f and separation time

f	t(yrs)	n
$0 <\ \ < .015$	42 ± 58	12
$.015 \leqslant\ < .030$	142 ± 68	6
$.030 \leqslant$	190 ± 97	10

$f = .000282(t) + .000997$ $r = .538014$ $p < .01$

f - An estimate of the variance of all k alleles over several loci according to Kidd and Cavalli-Sforza (1974). See Tab. 2 and 3
t - Mean separation time between the founding populations when pairs of populations are compared
n - Number of pairwise population comparisons

squares linear regression of the f values given in Table 2 and 3 against separation time results in a correlation coefficient which is statistically significant ($p < .01$) as shown in Table 4. Therefore, as the separation time between any two founding populations increases, the genetic difference between two populations increases at a rate which may be best described as linear. The essential premise of the historical/immigration hypothesis appears to be substantiated.

The reverse hypothesis that gene frequencies have been stable in Britain since 1650 and changes have occurred in the new environments in proportion to the time separation is considered unlikely for two reasons. 1) Fragmentary data from Bloemfontein (Dreux 1969) indicate a genetic profile not significantly different from that of New York City for three of the four loci which show systematic clinal variation (see below). The founding cat population of Bloemfontein must have been recruited from the Cape Colony which was established in the mid seventeenth century. It seems highly improbable that the environments of New York City and Bloemfontein have evolved in identical directions over the last three hundred years. 2) The cline map of $\underline{t}^b$ for Europe takes the form of a series of smooth elliptical regions of ever decreasing allele frequency spreading outward from Britain (Dreux and Todd 1974). Such a pattern strongly implies that $\underline{qt}^b$ has not been stable in the United Kingdom over the last few centuries and has, in fact, been steadily rising.

As to whether selection or drift is responsible for the genetic profiles which characterize these localities, some preliminary observations may be made. Selection is indicated by a comparison of observed with theoretical variance according to Lewontin and Krakauer (1973) which is given in Table 5. Clark (1976) reached a similar conclusion when applying this analytical approach to various cat populations in Scotland. Selective forces also appear to operate upon the cats of York (Metcalfe and Turner 1971). The lack of heterogeneity within the spectrum of F_c values may indicate that the selective forces involved are now applying approximately equal pressure to each of the five mutants examined.

Figure 1 plots the time course of change for four of the five loci studied ($\underline{O}$, $\underline{a}$, $\underline{t}^b$, $\underline{d}$) and the coefficient of darkness. These alleles show systematic clinal variation over much of the New and Old World (Dreux and Todd 1974; Todd, Glass, and Creel 1976). The gene frequency difference for $\underline{a}$ between the 1650 and 1750 time points is significant ($\chi^2 = 9.06$ for 1 d.f.). Table 1 and Fig. 1 illustrate an overall darkening of

Table 5. Test for heterogeneity of $\hat{F}_c$

Locus	N	$\hat{F}_c$	$S^2{}_F$	$\sigma^2(10^{-8})$	S^2/σ^2	p
Orange	14	.0001455	.0000224	33	6788	$<.001$
Nonagouti	14	.0001371	.0000240	29	8276	$<.001$
Bl. tabby	14	.0002789	.0000577	1.2	4815	$<.001$
Dilute	14	.0002404	.0000458	64	7156	$<.001$
Piebald	13	.0001488	.0000345	37	9324	$<.001$

$F_c = \dfrac{S^2 p}{\bar{p}(1-\bar{p})}$ where $\hat{F}_c$ is an estimate of effective inbreeding; $S^2 p$ is the variance in frequency of one of two alternative alleles from population to population; and $\bar{p}$ is the mean frequency of the allele over the ensemble of populations

$\sigma^2 = \dfrac{k\bar{F}^2}{n-1}$ where k = 2.0 when the underlying distribution of p is binomial. The ratio $S^2{}_F/\sigma^2$ is distributed as a χ^2/d.f.

According to Lewontin and Krakauer (1973)

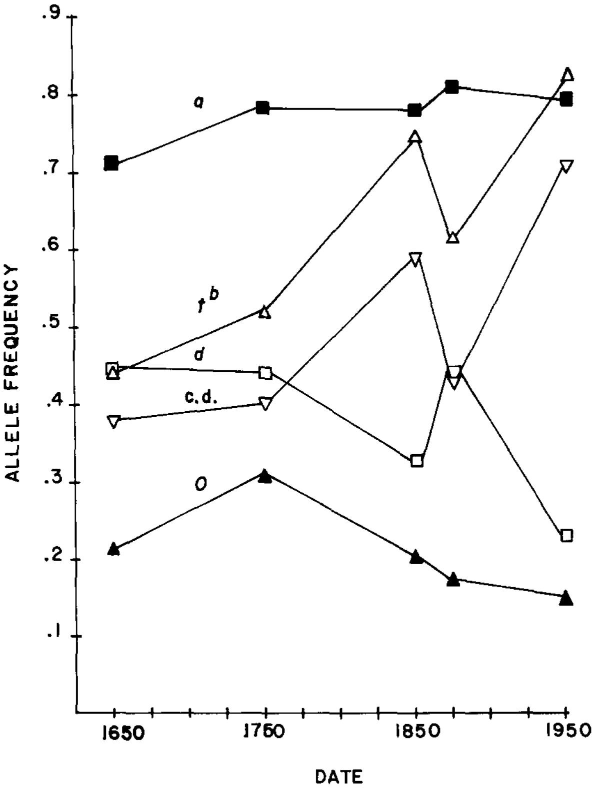

Fig. 1. Time course of allele frequency change: United Kingdom and former colonies. See discussion and Tab. 1

the phenotype as measured by the coefficient of darkness through the last three centuries as first pointed out by Todd (1969). The contribution of an ever increasing frequency of the blotched tabby mutant appears to be the key factor influencing the direction of this change. Such an observation suggests a response of the gene pool conditioned by cumulative urban pressure. Studies are underway to examine the correlation between allele frequency and the degree of urbanism of specific environments.

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