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Frequencies of Mutant Alleles in the Cat Populations of Cape Town and Pretoria, South Africa

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The genetic profiles of the domestic cat populations of Cape Town and Pretoria have been determined. That for the Cape Town population satisfies two tests for panmixia, whereas the Pretoria population meets one of two such criteria. The relative affinities of each locality with various populations in England, the Netherlands and the New World are discussed with reference to the historical immigration hypothesis.

Die genetiese profiele van Kaapstad en Pretoria se huiskatbevolkings is bepaal. Die bevolking van Kaapstad beantwoord aan twee toetse vir panmiksie, terwyl dié van Pretoria aan een van twee sulke maatstawwe voldoen. Die relatiewe affiniteit van elke plek teenoor verskillende katbevolkings in Engeland, Nederland en die Nuwe Wêreld word met verwysing na die historiese immigrasiehipotese bespreek.

Frequencies of mutant alleles that control various characteristics of the pelage of domestic cats, *Felis catus*, have been reported for more than 150 urban populations scattered throughout the world. In spite of the diverse geography of these data,[1] only a single paper,[2] based upon a rather small sample, has reported the genetic profile of an African cat population south of the Sahara. The present communication provides information on the genetic profiles of the cat populations of Cape Town and Pretoria.

Although not precisely documented, it can be assumed that the transportation of domestic cats to South Africa coincided with the early exploration and settlement of the subcontinent by Europeans during the middle of the seventeenth century. Todd[3] and Todd *et al.*[4] have suggested that colonial cat populations were directly drawn from 'European countries originally active in a given overseas region'. In the case of South Africa, therefore, the countries of interest are Britain, France and the Netherlands. *F. catus* migrates almost exclusively in association with man, and 'what are water barriers to most animals become veritable highways to cats'.[5] The relationship between European cat populations and their colonial counterparts has received much attention.[3,4,6-8] A statistically significant linear relationship has been derived between genetic difference and separation time from their country of origin for thirteen populations of cats originally from the United Kingdom.[6]

Study areas

Cape Town is a thriving metropolis with a municipal area of 30 000 hectares and a human population of about 890 000.[9] The city is situated at the southern tip of the African continent and is the oldest port in South Africa. The establishment of a settlement at the Cape in 1652 by the Dutch East India Company followed several visits by both the Portugese and Dutch. In 1795, the Cape Colony was annexed by the British but was restored to the Batavian Republic eight years later. It became a British possession once again in 1806 and British settlers arrived in substantial numbers in 1820/21, mainly to live in the eastern Cape Province.[10]

Situated 1500 km north of Cape Town, Pretoria was a slowly developing city and retained a rural atmosphere for many years. Established as a town in 1856, its present municipal area is 58 850 hectares and its human population 650 000.[9] Little more than a century ago, this part of South Africa (Transvaal) was virtually uninhabited by Europeans, and the establishment of the city resulted from the settlement of groups of 'Voortrekkers' (Settlers) who had left the Colony of the Cape of Good Hope. It is reasonable to assume that Pretoria's founder cat population was drawn from the Cape Colony.

No information is available on the numerical status of the cat populations of these two cities. However, a growing body of data on the dynamics of cat populations indicates that they may approach 20% of the human population in some urban localities.[11]

Assessment of coat colour allele frequencies

The alleles assessed in this study include those for sex-linked non-orange, orange (O^+, O), and the autosomal mutants agouti, non-agouti (a^+, a); Abyssinian, striped and blotched tabby (t^A, t^+, t^b); intense, blue dilution (d^+, d); non-spotted, piebald spotted (s^+, S); short hair, long hair (l^+, l); and pigmented, dominant white (w^+, W). The mode of inheritance of these alleles is well understood and has recently been reviewed.[12]

Field data were accumulated from surveys of areas frequented by cats such as streets, parks, food dumps, and the kitchen doors of restaurants and hotels. Additional information was obtained from samples of unwanted cats found at local offices of the Society for the Prevention of Cruelty to Animals. Only single individuals from sibling groups were noted, and pedigreed 'fancy' cats were excluded from calculations of allele frequency. The sex of many animals

Table 1. Observed and expected frequencies of the phenotypes non-orange (+/?), tortoiseshell (+/O) and orange (O/?) in the Pretoria and Cape Town cat populations. (m = maximum likelihood estimate of the proportion of males.)

	Pretoria		Cape Town	
Phenotypes	Observed	Expected	Observed	Expected
Non-orange	185	178.5	99	99.5
Tortoiseshell	20	32.5	23	21.9
Orange	29	22.7	16	16.4
m	0.692		0.478	
$\chi^2(m)$	34.51		0.836	
$q(0)$	0.167 ± 0.032		0.199 ± 0.042	
$\chi^2(0)$	6.79		0.064	

Table 2. A test for panmixia based on the piebald spotting locus partition according to the nine-point scale of Dreux.[19]

(a) *Heterozygote-homozygote boundary between S4 and S5.*

	Pretoria		Cape Town	
Phenotype	Observed	Expected	Observed	Expected
s^+s^+	125	120.6	60	59.4
s^+S	86	94.8	61	62.3
SS	23	18.6	17	16.3
	$\chi^2 = 2.00$		$\chi^2 = 0.060$	

(b) *Heterozygote-homozygote boundary between S5 and S6.*

	Pretoria		Cape Town	
	Observed	Expected	Observed	Expected
s^+s^+	125	125.7	60	66.1
s^+S	93	91.6	71	58.8
SS	16	16.7	7	13.1
	$\chi^2 = 0.054$		$\chi^2 = 5.915$	

could not be determined and thus estimates of the frequency of sex-linked orange were based upon maximum likelihood formulae.[13] On the assumption of Hardy-Weinberg equilibria, recessive allele frequencies (q) were taken as the square root of phenotype frequencies, and dominant allele frequencies as $1 - q$. Standard errors were computed from $\sqrt{(1-q^2)/4N}$ and $\sqrt{\{(2-p)p\}/4N}$ for recessive and dominant alleles, respectively. Phenotypic observations at each locus for Cape Town and Pretoria were compared by means of contingency tables.

Calculation of genetic distance

Nei's method of calculating genetic distance was adopted because (*a*) it places no restriction upon the numerical range of allele frequency that may be considered as data input; and (*b*) it appears to be the only conceptualization of a genetic distance between populations that relates directly to gene structure and thereby permits estimation of the number of codon differences per locus between populations.[14,15] If x_i and y_i are the frequencies of the ith alleles in populations X and Y respectively, then the probability of the identity of two randomly chosen alleles is $j_x = \Sigma x_i^2$ in population X; $j_y = \Sigma y_i^2$ in population Y; and $j_{xy} = \Sigma x_i y_i$ between populations. No assumptions are required about selection, mutation and migration. The arithmetic means of j_x, j_y and j_{xy} over all loci considered are designated J_x, J_y and J_{xy}, respectively. The standard genetic distance is given by $D = D_{xy} - \{(D_x + D_y)/2\}$, where $D_x = -\ln J_x$, $D_y = -\ln J_y$ and $D_{xy} = -\ln J_{xy}$. The criterion adopted here for 'close' relationships is $D \leq 0.20$.

Results and discussion

Panmixia. According to the procedure of Robinson,[13] the maximum likelihood estimate of $q(0)$ in the Pretoria population was 0.167. The expected proportions of the three phenotypes at this locus (+/?, +/0, 0/?) differed significantly from those observed ($\chi^2 = 6.79$ for 1 d.f.; Table 1). This result, along with the maximum likelihood estimate of 0.692 for the proportion of males ($\chi^2 = 34.5$ for 1 d.f.), suggests a departure in this population from Hardy-Weinberg equilibria and panmixia. This phenomenon has been encountered before,[16,17] and can sometimes be explained by difficulty in distinguishing tortoiseshell phenotypes (+/0) that exhibit very small areas of orange from various non-orange agouti individuals. Such a diagnostic error in the field would presumably result in a deficiency of females (tortoiseshell) and an excess of males in the sample.

Using phenotypic observations at the S locus partitioned according to the nine-point scale of Dreux, a second test for panmixia may be performed on the field data.[18,19] Non-spotted and S6-S9 phenotypes were taken to represent the homozygous recessive and dominant classes, respectively. The S1-S5 phenotypes were thus assumed to represent the heterozygotes. Expected frequencies of all genotypes could then be calculated from the binomial expansion of the allele frequencies. Using the S5/S6 boundary between heterozygote and homozygote dominant classes, a good statistical fit was obtained between observed and expected frequencies ($\chi^2 = 0.054$ for 1 d.f.; Table 2).

Blumenberg[7] has stated that the best position for the homozygote-heterozygote boundary remains to be determined on a wide regional basis and indeed may fluctuate from region to region owing to the presence of different modifier alleles in different localities.[16,19,20] The best statistical fit for this boundary has been shown to lie between S4 and S5 for Portland, Maine, southern New Hampshire, Massachusetts, and Karachi;[7,16,20] between S5 and S6 for Providence, Rhode Island, and Quetta, Pakistan;[16,20] and between S6 and S7 for Vancouver, Islamabad, Peshawar, Rawalpindi and Sahiwal.[6,16] This list of examples is by no means exhaustive.

In Cape Town, the maximum likelihood prediction for the proportion of males did not differ significantly from that expected

Table 3. Autosomal mutant allele frequencies for the Pretoria and Cape Town cat populations.

			Cape Town		Pretoria	
Locus	Phenotypes	Genotype	Number observed	Allele frequency	Number observed	Allele frequency
a	Non-agouti	*a/a*	64	$q(a) = 0.759 \pm 0.031$	136	$q(a) = 0.819 \pm 0.020$
	Agouti	$a^+/-$	47		67	
t	Blotched tabby	t^b/t^b	36	$q(t^b) = 0.688 \pm 0.042$	22	$q(t^b) = 0.479 \pm 0.045$
	Abbyssinian tabby	$t^A/-$	–		3	$p(t^A) = 0.016 \pm 0.009$
	Striped tabby	$t^+/-$	40		71	
d	Dilute	*d/d*	11	$q(d) = 0.282 \pm 0.041$	18	$q(d) = 0.277 \pm 0.031$
	Intense	$d^+/-$	127		216	
l	Long hair	*l/l*	8	$q(l) = 0.237 \pm 0.041$	8	$q(l) = 0.176 \pm 0.031$
	Short hair	$l^+/-$	135		249	
S	Piebald	*S/−*	78	$p(S) = 0.341 \pm 0.032$	109	$p(S) = 0.269 \pm 0.022$
	Non-spotted	s^+/s^+	60		125	
W	Dominant white	*W/−*	5	$p(W) = 0.018 \pm 0.008$	23	$p(W) = 0.046 \pm 0.009$
	Pigmented	w^+/w^+	138		234	

Table 4. Genetic profiles of selected cat populations.

Population	*O*	*a*	t^b	t^A	*d*	*l*	*S*	*W*
Pretoria	0.167	0.819	0.479	0.016	0.277	0.176	0.269	0.046
Cape Town	0.199	0.759	0.688	0.000	0.282	0.237	0.341	0.018
Hobart	0.217	0.758	0.813	0.000	0.244	0.460	0.386	0.039
Bristol	0.200	0.760	0.800	0.000	0.240	0.320	0.380	0.013
S. England	0.189	0.795	0.838	0.000	0.260	0.210	0.315	0.014
Rotterdam	0.140	0.744	0.538	0.000	0.169	0.097	0.306	0.005
Amsterdam	0.146	0.739	0.573	0.000	0.249	0.150	0.321	0.010
Boston/Salem	0.212	0.691	0.441	0.000	0.419	0.395	0.403	0.028
New York	0.146	0.752	0.473	0.000	0.443	0.130	0.470	0.013
Kingston	0.163	0.809	0.645	0.000	0.335	0.322	0.317	0.037

Data taken from this paper and Blumenberg[7]; Blumenberg and Lloyd[1]; Dartnall and Todd[21]; Gruffyd-Jones *et al*[22]; Ref. 23 and Robinson and Silson.[24]

from a 1 : 1 sex ratio (Table 1). Using $q(O) = 0.199$, the fit between observed and predicted phenotypes at the orange locus was good ($\chi^2 = 0.064$ for 1 d.f.; Table 1), indicating no departure from panmixia. The best fit for the heterozygote-homozygote boundary at the *S* locus was between S4 and S5 (Table 2), thereby providing a second confirmation of panmixia.

Autosomal mutant allele frequencies. Assuming Hardy-Weinberg equilibria, the autosomal mutant allele frequencies are presented in Table 3. Considering that Pretoria was founded by 'Voortrekkers' from the Cape Colony, one would expect the genetic profiles of the two cat populations would resemble each other. That prediction is supported by the lack of significant differences in allele frequency between the two populations at the loci *O*, *a*, *d*, *l*, *S*, and *W*. (All $\chi^2 \leq 3.4$ as judged by contingency table analysis). The frequency for blotched tabby, however, was significantly higher in Cape Town than Pretoria ($\chi^2 = 10.4$ for 1 d.f.), an observation which cannot yet be explained. No explanation is readily available to explain the presence of t^A in Pretoria, an allele that commonly reaches such levels only in south Asia.[16]

Genetic distance relationship. Table 4 gives mutant allele frequencies at seven loci for eight populations deemed appropriate for comparison with the two South African surveys. Table 5 presents a genetic distance matrix for Nei's *D* statistic. Cape Town shows close relationships with Bristol, southern England, Rotterdam and Amsterdam, results that accord with the known history of the English and Dutch influence at the early Cape Colony. Pretoria shows close relationships with Rotterdam and Amsterdam, an observation that illustrates the predominent Afrikaner (i.e. Dutch) influence on its founding population.

The lack of affinity between Cape Town and Pretoria and colonial America (Boston and New York) is not surprising (Table 5). While each colony was founded in the mid-seventeenth century, the English contribution to the Cape Colony was diluted by significant waves of migration from several other countries, a circumsance that is not characteristic of Boston. New Amsterdam (i.e. New York City) represents the dilution of a small Dutch founder population of cats by large numbers of English immigrants, a circumstance that is again different from that describing either Cape Town or Pretoria. In terms of the historical immigration hypothesis,[3,4,6,7] the same point in time is being sampled through the populations of colonial America and the Cape Colony but the geographic sources of these animals differ in the two cases. The resemblance of Hobart to Pretoria is not readily explicable, for Hobart is presumed to represent a mid-nineteenth-century British population,[6,21] yet this analysis raises the possibility that the influence of an early Dutch cat population in Van Diemen's Land is still detectable. The close relationships between Cape Town, Pretoria and Kingston presumably reflect the drawing of the founder population of each locality from the same group of channel ports in southern England and Holland.

Future surveys of the gene profiles of cat populations of other ports of entry may shed further light on the occurrence of t^A in the Pretoria population.

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Table 5. Genetic distance matrix (Nei's *D* statistic).

	Pretoria	Cape Town	Hobart	Bristol	S. England	Rotterdam	Amsterdam	Boston/Salem	New York
Cape Town	0.0112								
Hobart	0.0447	0.0152							
Bristol	0.0289	0.0049	0.0040						
Southern England	0.0259	0.0050	0.0145	0.0038					
Rotterdam	0.0058	0.0119	0.0476	0.0273	0.0237				
Amsterdam	0.0040	0.0053	0.0345	0.0185	0.0163	0.0020			
Boston/Salem	0.0230	0.0249	0.0405	0.0380	0.0502	0.0362	0.0251		
New York	0.0166	0.0225	0.0620	0.0427	0.0425	0.0219	0.0149	0.0182	
Kingston	0.0108	0.0036	0.0145	0.0089	0.0114	0.0192	0.0101	0.0171	0.0232

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