Journal of Heredity 2005:96(5):557–565
doi:10.1093/jhered/esi072
Advance Access publication July 1, 2005

Mutant Allele Frequencies in Domestic Cat Populations in Arkansas and Tennessee

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We conducted surveys of mutant allele frequencies of four cat populations in Arkansas and Tennessee during 2002. Our calculations and analyses support that Southwestern cat populations were relatively more genetically similar to each other than compared to cat populations in other areas of North America. However, the cat population of Fort Smith is slightly different from the other cat populations studied in the Southwestern United States. Although there is a clear significant spatial geographic pattern for many mutant coat allele frequencies in the United States and Canada cat populations (*d*, *I*, *S*, and *W*), our results revealed that there is not a significant isolation-by-distance model affecting these cat populations. Our data also support the historical migration hypothesis because our calculated allele frequencies were genetically similar to cat populations located in ancestral areas of Europe. Different phenograms, including new European cat genetic profiles, showed that the Southwestern cat populations studied are of a clear British origin. Therefore, migration routes of early Arkansas and Tennessee settlers help explain the similarities of allele frequencies among domestic cat populations.

Since 1947, numerous domestic cat population surveys have been conducted around the world (Hoger 1994; Klein et al. 1988; Ruiz-Garcia 2000; Wagner 1996). Data from these surveys support that the cat populations around the world vary in polymorphic gene coat frequencies (Lloyd 1987). Some of this variation has been claimed by some authors to be attributed to environmental variables, such as temperature. For example, in Brazil, Watanabe (1984) showed a possible significant correlation between long hair and temperature. However, Ruiz-Garcia (2000) and Ruiz-Garcia and Alvarez (2003) demonstrated that this correlation could be explained by a particular migration scheme from Europe to Brazil without the explicative need of natural selection. Moreover, environmental variables do not explain variances in other polymorphic coat gene frequencies besides long hair. Therefore, other explanations have been suggested to help explain differences in polymorphic coat gene frequencies. One such explanation called the historical migration hypothesis (Todd 1977) suggests that present-day domestic cat gene frequencies have been determined by human migration and settlement patterns. To test the historical migration hypothesis, we surveyed four cat populations in Arkansas and Tennessee and compared their allele frequencies with other North American cat populations and with their possible ancestral populations in Europe.

To our knowledge, no studies have dealt with gene frequencies of cat populations in these areas. Other objectives of our study were (1) to determine if the mutant allele frequencies of cat populations in Little Rock, Fort Smith, Jonesboro, and Memphis were significantly different among each other; (2) to determine if geographical distance between cat populations (isolation by distance) is an important factor that can explain differences in allele frequencies between cat populations in North America and if there is some evidence of significant spatial geographic pattern in the seven mutant allele frequencies analyzed by means of a spatial autocorrelation analysis; and (3) to determine if the migration process from Europe to the Americas produced the same allele frequency variances in the Southwestern U.S. and Latin American cat populations.

Materials and Methods

We surveyed the Southwestern U.S. cat populations of Little Rock (AR), Fort Smith (AR), Jonesboro (AR), and Memphis (TN). A total of 1,200 domestic cats were scored, 300 from each of the four cities. The Italian cat populations of Napoli ($n = 104$), Terrassa ($n = 117$), Reus ($n = 175$), Valencia ($n = 214$), as well as Cartagena ($n = 145$) in the Mediterranean area of Spain were also sampled and analyzed.

The genetic nomenclature used in this study is in accordance with the Committee on Standardized Genetic Nomenclature for Cats (1968). The phenotypes scored were: sex-linked orange versus nonorange (O, o); agouti versus nonagouti (A, a); full color versus dilute (D, d); short hair versus long hair (L, l); presence or absence of piebald spotting (S, s); tabby pattern abyssinian, striped, or blotched (T^a, T, t^b); and dominant white versus pigmented (W, w). Descriptions of these traits have been published elsewhere (Robinson 1977). Piebald spotting was also scored on a scale of 0 (no white spotting) to 9.5 (white extending over most of the body) (Dreux and Legel 1973). The frequency of the O allele was calculated directly from the phenotypes. We calculated other allele frequencies assuming Hardy-Weinberg equilibrium. Standard errors were calculated by using the equations $\sqrt{1 - (q^2)/4N}$ and $\sqrt{([2 - p]p)/4N}$ for the recessive and dominant alleles, respectively. Chi-square tests were used to test for random breeding at the O and S loci. Two-by-two chi-square contingency tests were also used to compare the phenotypic frequencies between the four Southwest cat populations surveyed in this study. The Nei's (1972) genetic distance and the Cavalli-Sforza and Edwards's (1967) chord distance were used to compare our survey data with 32 other U.S. and Canadian populations and with European cat surveys previously analyzed. These genetic distance matrices were used to generate phenograms with the UPGMA algorithm. Bootstraps (Felsenstein 1985) were performed to determine the consistence of the nodes on the trees obtained. Nonmetric multidimensional scaling analyses were carried out, and minimum spanning trees were superimposed.

Frequency data were used to calculate genetic heterogeneity and theoretical gene flow estimates among the four cat populations and other Southwestern U.S. cat populations by means of the Wright's F_{ST} statistic and Nm (Slatkin 1987; Weir and Cockerham 1984). These estimates were compared with those obtained for the same mutant alleles for a set of Latin American cat populations (Ruiz-Garcia et al. in preparation). This comparative analysis is useful to understand if the migration process from Europe to different regions of America has caused the same degree of allele variance for each of the markers analyzed. This could be meaningful to determine if the premigrative selection of these characters was the same from different points of Europe and/or if the effects of genetic drift during the colonization process differentially affected each one of these loci in diverse parts of America.

Moran's *I* index (Moran 1950) spatial analysis was used to identify significant spatial autocorrelations for each one of the seven allele frequencies (by means of correlograms). To compute the spatial autocorrelation coefficients, one must hypothesize a scheme for connecting the populations being sampled. A variety of such schemes (networks) have been proposed (Tobler 1975). The Gabriel-Sokal network (Gabriel and Sokal 1969; Matula and Sokal 1980) was used in this study. Additionally, we computed spatial autocorrelation coefficients to measure spatial interactions for sets of population pairs at specified geographic distance classes (DC). Here, we selected four DC, with 1 DC = 0–896 km, 2 DC = 896–1,472 km, 3 DC = 1,472–2,170 km and 4 DC = 2,170–4,877 km, being the number of populations pairs in each DC about 157–158. We used Bonferroni's procedure (Oden 1984) to determine the statistical significance of the autocorrelation coefficients and overall correlograms, and we used Slatkin's test (1993) to analyze the existence of possible isolation by distance from the population of Little Rock in regards to the other North American cat populations studied. This method is based on the regression equation between the gene flow matrix estimated (Nm = M; Cockerham and Weir 1993) among locality pairs from the F_{st} statistic corrected by sampling size (Weir and Cockerham 1984) and the geographic distances among the same localities.

Table 1. Chi-square test for random breeding at the O locus

	Fort Smith observed	Expected	Little Rock observed	Expected
Phenotype				
O/O	25	16.77	21	22.78
O/−	45	50.33	29	28.20
O/+	49	55.80	46	55.80
+/+	77	67.11	98	103.70
+/−	87	88.00	89	104.80
χ^2_3	6.89		14.10	
p	$.25 > p > .10$		$.01 > p$	
	Jonesboro observed	**Expected**	**Memphis observed**	**Expected**
Phenotype				
O/O	12	15.25	15	7.76
O/−	19	28.20	27	29.93
O/+	54	55.80	43	46.59
+/+	104	103.70	100	95.70
+/−	95	104.80	108	105.06
χ^2_3	4.66		7.57	
p	$.50 > p > .25$		$.25 > p > .10$	

Results

Female cats outnumbered male cats in all four cities surveyed with an average male:female ratio of 1:1.31. In the city of Jonesboro, female cat numbers were almost 50% greater than male numbers.

Random breeding tests (Table 1) at the O locus supported the hypotheses of random breeding at Fort Smith ($\chi^2 = 6.89$; $.10 < p < .25$), Jonesboro ($\chi^2 = 4.66$; $.25 < p < .50$), and Memphis ($\chi^2 = 7.57$; $.10 < p < .25$). Random breeding could not be confirmed for the Little Rock population, which had a high significant number of orange females compared to predicted numbers. Tests for panmixia at the S locus supported random breeding in the Fort Smith, Little Rock, and Memphis populations (Table 2).

There were significant differences in *d*, *l*, *O*, and *S* allele frequencies among the four cat populations (Table 3). The frequency of *O* was greatest in Fort Smith (0.333) and least in Jonesboro (0.214). The allele frequency of *l* was significantly

Table 2. Chi-square for random mating at the S locus

	Fort Smith observed	Expected	Little Rock observed	Expected
Phenotype				
s/s	147	147	149	149.12
S/s	109	113.93	109	107.58
(1–5)				
S/S	27	22.07	24	19.41
p(S)	0.279		0.273	
χ^2_2	1.31		0.50	
p	$.25 < p < .50$		$.25 < p < .50$	
	Jonesboro observed	**Expected**	**Memphis observed**	**Expected**
Phenotype				
s/s	154	154	121	121
S/s	125	110.26	126	120.70
(1–5)				
S/S	5	19.74	40	35.30
p(S)	0.263		0.35	
χ^2_2	12.97		0.80	
p	$.001 > p$		$.25 < p < .50$	

highest in Fort Smith (0.474) and decreased in an eastward direction, with lowest values in Memphis (Tables 3 and 4). The Memphis population had a significantly greater piebald allele frequency compared to the other three populations (Tables 3 and 4). The allele frequency of *d* was significantly greatest in the Little Rock population (Tables 3 and 4). There were no significant differences in frequencies of *a*, t^b, or *W* among populations (Tables 3 and 4). Dominant white (W) was rare in all four populations (Table 4).

The Nei's genetic distance (D) between Little Rock and the three cat populations surveyed in our study were very small, with an average of 0.005. Figure 1 shows the UPGMA tree with the Nei's genetic distance (cophenetic correlation coefficient, $r = 0.7091$, $t = 7.2245$, $p = .0000$, 5,000 Monte Carlo permutations, $5{,}000 < z, 0 = z, 0 > z, p = .0004$) with the four populations studied plus 32 other North American cat populations. Duluth was the most differentiated North America cat population. From the four populations studied here, Fort Smith was that most differentiated from the others, whereas Memphis and Jonesboro were the most related. The four populations were mainly related with populations such as St. Louis, Halifax, Portland, Lawrence, or Salem and were more related with cat populations of Anglo origin than to populations that could have a Spanish/Anglo origin or to the populations of Texas, Colorado, and California, which have a Spanish origin (Ruiz-Garcia 1990a).

Table 3. Chi-square comparison of cat phenotypes in Arkansas and Tennessee cat populations: Summary of loci that differ ($p < .05$)

Location	Fort Smith	Little Rock	Jonesboro	Memphis
Fort Smith	_____	d, O	l, O	l, S, O
Little Rock	d, O	_____	d	d, l, S
Jonesboro	l, O	d	_____	S
Memphis	l, S, O	d, l, S	S	_____

Figure 2 presents an UPGMA tree with the Nei's genetic distance with the 4 populations studied and 46 European populations (cophenetic correlation coefficient, $r = 0.65925$, $t = 13.5732$, $p = .0000$; 5,000 Monte Carlo permutations, $5{,}000 < z, 0 = z, 0 > z, p = .0004$). Clearly, our samples were more related to the British and French cat populations than to other European cat populations. Diverse multidimensional scaling analyses (not shown here) also showed the same relationships between the four Southwestern U.S. and European cat populations. The minimum spanning tree superimposed with the Nei genetic distance related all the Southwestern U.S. populations to each other as well as related Memphis with Lyon (France).

The mean value of F_{ST} was 0.0414 ± 0.0456 (Table 5), which signified that cat populations on average contained more than 96% of the total genetic variability found in all the U.S. region studied. All estimates of Nm from Fort Smith, Little Rock, Jonesboro, and Memphis populations were greater than 1.00, with an average of 13.05 ± 9.38 (Table 6), which is in full agreement with high levels of gene flow in the area studied. When other areas of America (in Latin America) are compared for these statistics, the overall mean values were extremely similar ($F_{ST} = 0.0526 \pm 0.0442$, $Nm = 8.40 \pm 7.98$), although the Latin American geographical area is considerably more extended than that of the Southwestern United States. However, the F_{st} magnitudes for the different loci were extremely different for some genes. The F_{st} values among the Southwestern United States and Latin American regions were not extremely different at *O*, *a*, t^b, and *S* loci, but were noteworthy different at *d*, *l*, and *W*. Genetic heterogeneity was considerably higher at *d* (0.071 versus 0.028) and at *l* (0.142 versus 0.017) loci in Latin American compared to Southernwestern U.S. cat populations. However, the genetic heterogeneity at *W* was much higher in the Southwestern United States than in Latin America (0.137 versus 0.0098).

The spatial autocorrelation analysis, with the Moran's *I* index showed a significant overall pattern at *d*, *l*, *S*, and *W* loci (Table 6). There were very similar monotonic clinal patterns for *d*, *l*, and *S* at the first 2,170 km of separation among the populations studied. At the first 896 km, the genetic similarity among the populations within this distance class was significantly higher than that expected by random, but the population pairs were significantly less similar than expected between 1,472 and 2,170 km. At the *S* locus, the overall pattern was a monotonic cline in all 4,877 km comprised by the study. The population pairs at the first 1,472 km presented more similar p(S) frequencies than that expected by random. Otherwise from 2,170 to 4,877 km, the population pairs were significantly different than that expected by random. The other three alleles, *O*, *a*, and t^b did not show any significant spatial pattern. Altogether the seven alleles support a significant overall genetic spatial geographic pattern for the North American cat populations. The percentage of significant autocorrelation coefficients

Table 4. Mutant allele frequencies of Arkansas, Tennessee, and other selected cat populations

Location	O	a	t[b]	d	I	S	W	Source
North America								
Fort Smith	0.313	0.784	0.523	0.442	0.474	0.313	0.005	This study
Little Rock	0.251	0.783	0.577	0.542	0.404	0.362	0.009	This study
Jonesboro	0.203	0.760	0.562	0.428	0.371	0.384	0.012	This study
Memphis	0.214	0.801	0.546	0.439	0.318	0.379	0.012	This study
Phoenix, AR	0.231	0.698	0.565	0.439	0.509	0.228	0.067	Todd et al. 1976
Humbolldt C., CA	0.269	0.748	0.510	0.350	0.290	0.220	0.034	Blumenberg 1986
San Fran., CA	0.271	0.778	0.333	0.324	0.363	0.311	0.027	Blumenberg 1976
Denver, CO	0.205	0.839	0.257	0.377	0.345	0.288	0.007	Morrill and Todd 1978
Duluth, MN	0.100	0.791	0.840	0.609	0.441	0.341	0.029	Klein et al. 1988
Cleveland, OH	0.233	0.743	0.615	0.413	0.254	0.351	0.021	Blumenberg & McDonald 1978
Rapid City, SD	0.220	0.800	0.150	0.521	0.400	0.230	0.029	Klein et al. 1988
Stevens County, MN	0.292	0.780	0.251	0.500	0.382	0.272	0.012	Klein et al. 1988
St. Paul, MN	0.250	0.742	0.471	0.633	0.501	0.280	0.010	Klein et al. 1986
Winnipeg, Canada	0.190	0.730	0.640	0.511	0.510	0.332	0.025	Klein et al. 1988
Polk County, WI	0.262	0.750	0.438	0.586	0.394	0.289	0.017	Kerr 1984
Quad Cities, IA	0.289	0.776	0.266	0.464	0.512	0.334	0.026	Dunn et al. 1989
Omaha, NE	0.346	0.810	0.351	0.529	0.371	0.200	0.039	Halpine and Kerr 1986
Dallas, TX	0.252	0.673	0.277	0.317	0.435	0.182	0.000	Gerdes 1973
Houston, TX	0.247	0.691	0.286	0.287	0.345	0.186	0.005	Gerdes 1973
Lubbock, TX	0.306	0.789	0.358	0.332	0.439	0.236	0.004	Gerdes 1973
Mineral Wells, TX	0.308	0.726	0.344	0.285	0.523	0.204	0.005	Gerdes 1973
Denton, TX	0.252	0.897	0.267	0.326	0.464	0.217	0.008	Gerdes 1973
Lawrence, KS	0.220	0.722	0.440	0.401	0.440	0.250	0.011	Glass and Todd 1976
St. Louis, MO	0.299	0.787	0.507	0.427	0.481	0.384	0.016	Dorn 1973
Champaign, IL	0.320	0.780	0.317	0.452	0.344	0.268	0.022	Fagen 1975
Chicago, IL	0.225	0.715	0.340	0.455	0.370	0.310	0.020	Todd 1969a
Columbus, OH	0.289	0.637	0.312	0.501	0.394	0.300	0.007	Tinney and Griesmeyer 1968
Boston, MA	0.193	0.642	0.443	0.426	0.302	0.436	0.022	Todd 1964
New York, NY	0.146	0.752	0.473	0.443	0.130	0.470	0.013	Todd 1966
Philadelphia, PA	0.274	0.705	0.449	0.500	0.198	0.421	0.012	Todd 1969a
Salem, MA	0.220	0.776	0.435	0.401	0.498	0.345	0.038	Blumenberg 1977
Halifax, Canada	0.323	0.788	0.573	0.450	0.476	0.379	0.032	Todd and Todd 1976a
Atlanta, GA	0.228	0.653	0.464	0.426	0.305	0.314	0.032	Todd 1969b
Portland, ME	0.291	0.785	0.537	0.478	0.435	0.437	0.029	Blumenberg et al. 1977
Vancouver, Canada	0.160	0.811	0.681	0.439	0.260	0.331	0.010	Blumenberg et al. 1979
Reno, NV	0.200	0.766	0.381	0.509	0.390	0.255	0.050	Anderson and Jenkins 1979
Europe								
Austria (lower)	0.161	0.809	0.381	0.156	0.154	0.270	0.008	Hoger 1994
Austria (upper)	0.157	0.687	0.422	0.180	0.237	0.276	0.004	Hoger 1994
Edinburgh (Scotland)	0.200	0.780	0.750	0.350	0.300	0.280	0.030	Clark 1976
Glasgow (Scotland)	0.200	0.800	0.800	0.260	0.300	0.200	0.000	Clark 1975
London (England)	0.105	0.762	0.814	0.142	0.330	0.313	0.004	Searle 1949
Newcastle (England)	0.160	0.800	0.770	0.300	0.360	0.340	0.010	Symmonds unpublished
Southern England	0.189	0.795	0.838	0.260	0.317	0.315	0.014	Robinson and Silson 1969
Dublin (Ireland)	0.115	0.824	0.744	0.290	0.329	0.306	0.020	Todd and Lloyd 1979
Chamonix (France)	0.100	0.750	0.690	0.400	0.320	0.220	0.014	Dreux 1971
Marseille (France)	0.080	0.720	0.680	0.340	0.270	0.290	0.000	Dreux 1975
Paris (France)	0.060	0.710	0.780	0.330	0.240	0.240	0.011	Dreux 1967
Lyon (France)	0.110	0.780	0.650	0.390	0.370	0.220	0.030	Pontier 1983
Budapest (Hungary)	0.080	0.600	0.000	0.270	0.090	0.330	0.001	Davis and Davis 1977
Rimini (Italy)	0.127	0.677	0.380	0.407	0.224	0.264	0.012	Ruiz-Garcia 1997
Rome (Italy)	0.090	0.660	0.490	0.340	0.100	0.310	0.010	Lloyd et al. 1983
Venice (Italy)	0.107	0.557	0.267	0.338	0.186	0.204	0.014	Ruiz-Garcia 1997
Napoli (Italy)	0.223	0.686	0.275	0.197	0.000	0.317	0.000	Ruiz-Garcia (new data)
Brzesko (Poland)	0.042	0.487	0.132	0.110	0.110	0.369	0.000	Wagner and Wolsan 1987
Olecko (Poland)	0.056	0.703	0.312	0.000	0.000	0.430	0.000	Wagner and Wolsan 1987
Warsaw (Poland)	0.037	0.623	0.346	0.254	0.220	0.325	0.000	Wagner and Wolsan 1987
Lisbon (Portugal)	0.071	0.666	0.447	0.283	0.074	0.215	0.012	Todd et al. unpublished
Porto (Portugal)	0.142	0.768	0.429	0.296	0.234	0.290	0.008	Todd and Lloyd 1984
Barcelona (Spain)	0.159	0.701	0.275	0.266	0.136	0.266	0.004	Ruiz-Garcia 1991
Girona (Spain)	0.216	0.665	0.242	0.121	0.145	0.290	0.003	Ruiz-Garcia et al. 1995

Table 4. Continued

Location	O	a	t[b]	d	l	S	W	Source
Tarragona (Spain)	0.209	0.678	0.379	0.152	0.000	0.291	0.000	Ruiz-Garcia 1990b
Alicante (Spain)	0.230	0.775	0.497	0.244	0.000	0.306	0.006	Ruiz-Garcia 1990b
Murcia (Spain)	0.184	0.742	0.619	0.080	0.078	0.377	0.012	Ruiz-Garcia 1991
Palma Maj. (Spain)	0.196	0.719	0.354	0.350	0.270	0.228	0.004	Ruiz-Garcia 1994
Ibiza (Spain)	0.256	0.770	0.311	0.254	0.216	0.287	0.013	Ruiz-Garcia 1994
Ciudadela (Spain)	0.213	0.727	0.220	0.348	0.078	0.268	0.004	Ruiz-Garcia 1994
Mahon (Spain)	0.300	0.804	0.176	0.379	0.122	0.145	0.003	Ruiz-Garcia 1994
Reus (Spain)	0.166	0.607	0.358	0.080	0.176	0.268	0.012	Ruiz-Garcia (new data)
Cartagena (Spain)	0.165	0.715	0.476	0.254	0.084	0.327	0.007	Ruiz-Garcia (new data)
Terrassa (Spain)	0.178	0.725	0.177	0.255	0.229	0.224	0.017	Ruiz-Garcia (new data)
Valencia (Spain)	0.192	0.731	0.516	0.000	0.000	0.262	0.002	Ruiz-Garcia (new data)
Reykjavik (Iceland)	0.135	0.604	0.528	0.438	0.170	0.493	0.015	Todd et al. 1975
Switzerland	0.155	0.746	0.358	0.400	0.101	0.429	0.010	Kerr 1983
Bitola (Jugoslavia)	0.283	0.729	0.280	0.333	0.277	0.478	0.024	Wagner 1996
Ohrid (Jugoslavia)	0.296	0.659	0.108	0.278	0.145	0.548	0.000	Wagner 1996
Struga (Jugoslavia)	0.211	0.593	0.226	0.229	0.081	0.656	0.000	Wagner 1996
Utrech (Netherlands)	0.220	0.820	0.560	0.300	0.160	0.310	0.010	Lloyd 1982
Amsterdam (Netherlands)	0.130	0.740	0.570	0.250	0.150	0.320	0.010	Lloyd 1982
Rotterdam (Netherlands)	0.160	0.740	0.540	0.170	0.100	0.310	0.010	Lloyd 1982
Athens (Greece)	0.146	0.719	0.296	0.336	0.123	0.264	0.008	Todd and Kunz 1977
Chios (Greece)	0.239	0.680	0.245	0.257	0.104	0.407	0.000	Todd and Todd 1976b
Istanbul (Turkey)	0.186	0.631	0.282	0.355	0.353	0.386	0.005	Todd and Todd 1976b

was 35.71%, which is significantly different from the 5% type I error ($\chi^2 = 8.146$, 1 df, $p < .05$).

When an isolation by distance Slatkin (1993) test, between the Little Rock population and all the other North American cat populations studied, was performed, the following equation was obtained

$$\mathrm{Log}_{10}(M) = 0.585 - 0.148 \log_{10}$$

(Sphuler geographical distance) with a correlation coefficient of $r = -0.1506$.

Although the b coefficient was negative (a requirement for isolation by distance) it was not statically significant ($t = -0.875$, 33 df, $p = .324$). Therefore, there is no strong evidence of isolation by distance globally for these coat genes, although a significant spatial pattern affects these variables. Thus, certain routes for gene flow (historical migration hypothesis) rather than isolation by distance help explain genetic variability in this study.

Discussion and Conclusions

The mean values of F_{ST} and Nm agree quite well with relative low levels of genetic heterogeneity among the cat populations studied in the Southernwestern United States. Furthermore, all of our estimated values of Nm were above 1.00, which indicated that gene flow prevented genetic drift from causing local genetic differentiation in these populations (Slatkin 1987). However, significant differences in the *d*, *l*, *O*, and *S* alleles in Southwestern cat populations are consistent with some remarkable differences probably due to founder effect at the moment the cat populations were formed. Nevertheless, globally these differences are relatively low. When these statistics were compared with those found for a set of Latin American cat populations (Ruiz-García et al. in preparation), we detected that the cat populations in North and South America are characterized by relatively high levels of gene flow and relatively moderate levels of gene divergence, at least for the coat genes studied.

However, several alleles showed a very noteworthy population genetic heterogeneity between these two American areas. The genetic heterogeneity for *d* and *l* in Latin America was considerably higher than in the Southwestern United States. This could reflect that in the European areas (mostly Spain and Portugal), where the cats were obtained for the Latin American colonization, these characters were more heterogeneous in their frequencies than in the British and French areas, which provided cats for North America. Other alternative explanations could be as follows. It is also possible that preferences for these traits were more homogenous by the British compared to the Iberian people prior to the migrations. Even if some traits were very rare in parts of the Iberian peninsula, they could have been introduced to new areas through novelty selection by human colonizers and thus cause high frequency levels in Latin America. However, in areas of Iberia where these alleles were totally absent, novelty selection could not be a factor, and the Latin American populations founded throughout these Iberian areas would have null or very low frequencies. On the contrary, if the frequencies of *d* and *l* were relatively similar and elevated in the original British areas, this novelty selection could be absent, and all the new colonies in North America could have similar frequency levels of these traits.

Fort Smith was the most differentiated of the cat populations studied. In fact, Fort Smith showed more genetic resemblance with St. Louis, Halifax, and Portland than

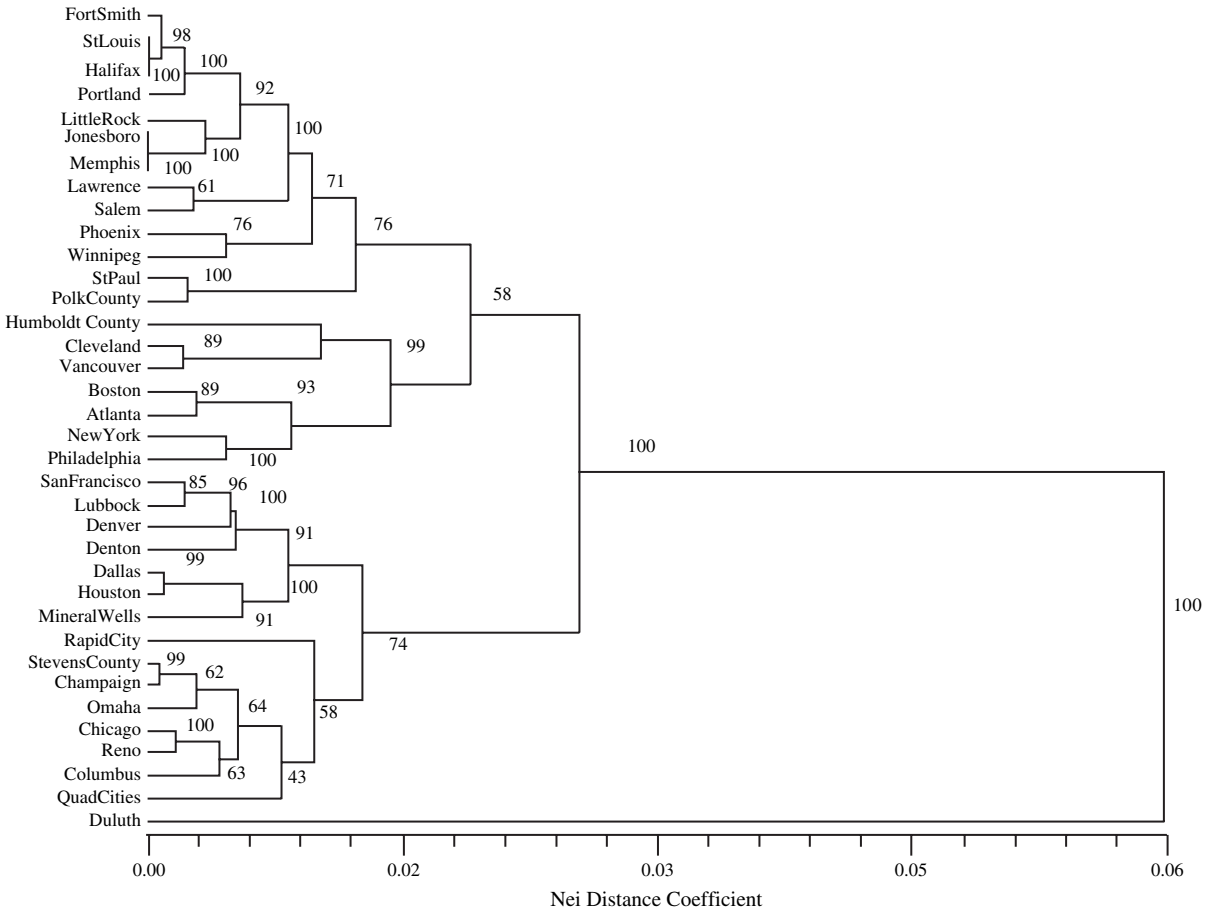

Figure 1. UPGMA tree with Nei's (1972) genetic distance of the four Southwest U.S. populations studied plus 32 other North American cat populations. The numbers on the nodes are the bootstrap percentages.

with the other Southwestern U.S. populations. The genetic relationship among Jonesboro and Memphis was outstanding. The four populations were clearly more related to Eastern North American and those populations of indubitable Anglo origin. It is remarkable that the present cat populations surveyed did not show any Hispanic influence, such as it was presented in the populations of California, Texas, and Colorado or, partially, in the populations of the Midwest.

The Slatkin's (1993) test between Little Rock and the other North American cat populations analyzed in this study did not detect a significant isolation by distance. Genetic distance increased as the geographical distance between cities increased, but the correlation obtained was not significant, and thus a clear isolation by distance model cannot be supported. In fact, the significant correlograms for *d*, *l*, *S*, and *W* showed a monotonic clinal pattern but not the typical correlogram shape for isolation by distance. The variables that showed global significant spatial correlograms are likely explained by migration patterns of people and accompanying cats rather than specific geographical distances.

Based on the historical migration hypothesis, frequencies of alleles in current feline populations should be similar to ancestral populations. To test this hypothesis, we researched settlement patterns into Arkansas and Tennessee. The earliest settlers of Arkansas (1686) chose to live in or near fortified areas that served as protection against Native Americans. Documentation of cats in forts in other North American areas, such as at Fort Clarke in Des Moines (Thwaites 1904a), Iowa, support the likelihood that other settlement areas such as the Arkansas Post also contained cats, even though there are no written records supporting this claim. Wagon migrations from Missouri into Fort Smith (Southwest Trail) help explain the strong genetic relationship found between the cat populations of these cities. Until 1840 it was easier to travel into and through Arkansas by water. There is evidence of cats aboard a vessel in 1811 that navigated the Missouri River in Missouri, a state that provided a source of earlier immigrants to Arkansas (Thwaites 1904b). Steamboats became the preferred way of travel (1820), transporting people and their possessions among Little Rock, New Orleans, Cincinnati, Louisville, Pittsburgh, Florence, and Wheely. Later development of well-established railroads (1850s) and highways among early cities (Memphis, Charleston, Savannah; Little Rock and St. Louis) provided greater corridors of gene flow and thus influenced cat population

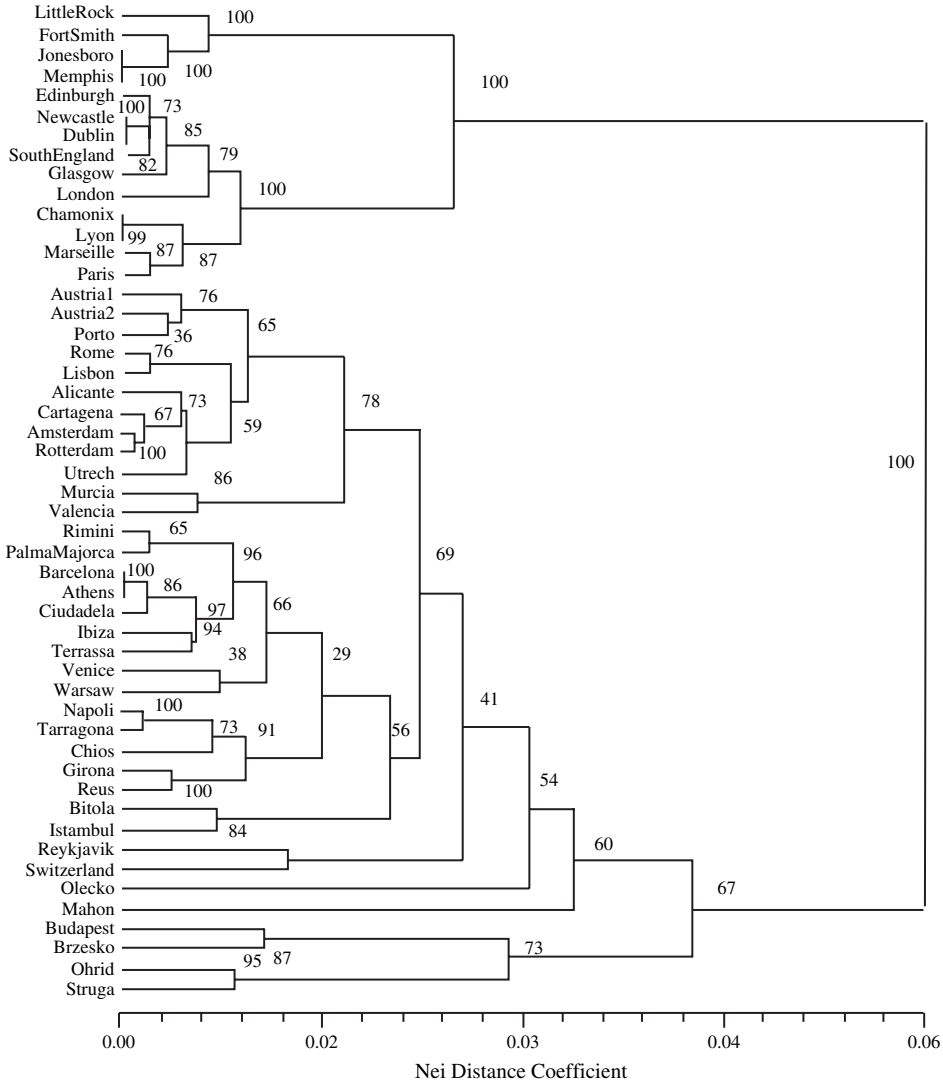

Figure 2. UPGMA tree with Nei's (1972) genetic distance of the four Southwest U.S. populations studied plus 46 European cat populations. The numbers on the nodes are the bootstrap percentages.

genetics, creating one large interbreeding population that currently extends across multiple states.

Arkansas received settlers indirectly from several European countries, including France, Ireland, England, Scotland, Switzerland, Italy, Poland, and Germany. After their arrival to the East Coast, immigrants would move to any of a number of state destinations prior to their eventual settlement in Arkansas. We compared the mutant allele frequency data of

Table 5. Comparative estimated F_{ST} and Nm (population size times migration rate) statistics for Southwest U.S. (TX, AR, KS, and MO) cat populations and for a set of 50 cat populations of Latin America

	Southwest cat populations		Latin American cat populations	
Allele	F_{ST}	Nm	F_{ST}	Nm
O	0.0092	26.990	0.0231	10.572
a	0.0181	22.8675	0.0367	6.562
t[b]	0.0608	3.8606	0.0510	4.652
d	0.0279	8.7096	0.0710	3.271
l	0.0167	14.7437	0.1425	1.504
S	0.0194	12.6271	0.0345	6.996
W	0.1376	1.5673	0.0098	25.260
Mean	0.0414 ± 0.0456	13.052 ± 9.388	0.0526 ± 0.0441	8.402 ± 7.982

Table 6. Spatial autocorrelation correlograms using the Moran's *I* index of the seven coat mutant allele studied in 36 North American cat populations for four identical distance classes (in km)

Loci	896	1,472	2,170	4,877	CgramProb.
O	0.02	−0.07	−0.02	−0.04	0.928
a	−0.01	0.07	−0.17*	−0.00	0.063
t[b]	−0.07	0.04	−0.05	−0.04	0.556
d	0.38**	−0.13	−0.26**	−0.10	0.000**
l	0.14**	−0.01	−0.18**	−0.06	0.013*
S	0.23**	0.16**	−0.01	−0.50**	0.000**
W	0.20**	−0.12	−0.19**	−0.00	0.000**

Notes: CgramProb = Overall correlogram probability. *$p < .05$. **$p < .01$.

the cat populations we surveyed in Arkansas and Tennessee to cat populations that resided in ancestral locations in Europe (Table 4). Our results demonstrated the British-French origins (even the Switzerland link with Memphis for the minimum spanning tree with the Cavalli-Sforza and Edwards genetic distance) of the four populations studied. Therefore, our data support the historical migration hypothesis that current populations are similar to populations in countries where immigrants originated.

It is important to note that domestic cat populations residing in some locations in Poland (an ancestral country) were not genetically similar to cat populations in Arkansas and Tennessee areas, although a certain considerable Polish fraction of immigrants arrived in these states. We have two explanations for this exception. First, Poland has a gradient of allele frequencies that reflect influence from Ukraine and other Eastern areas as well as from Western Europe (Wagner and Wolsan 1987). Cat populations in Bialowieza and Warsaw in central eastern Poland have Nei index values of 0.971 and 0.948, respectively. Comparatively, cat populations in Olecko and Chybie have Nei index values of 0.887 and 0.877. These analyses support that early Arkansas/Tennessee settlers were more probably from central eastern areas of Poland than from other areas of Poland, although its genetic influences are of minor relevance. Second, Wagner and Wolsan (1987) did not test for panmixia because of their small sample sizes. Thus, their calculated frequencies may not reflect those of the true domestic cat populations in Poland. Similarly, no relevant contributions from Italy, Spain, Portugal, Greece, Netherlands, Germany, and the Eastern European countries were detected in the genetic composition of the four Southwestern U.S. cat populations studied here.

Interestingly, the majority of current immigrants (1 million per year) into the United States are from Asia, Latin America, and the Caribbean rather than from Europe (Alba 1999). Therefore, we may begin to observe a change in the frequency distributions of domestic cat population alleles over time that would include lower frequencies of W (more like Latin America). In addition, introgression of oriental "purebreds" would most likely result in frequency changes of the *O* (lower), *S* (lower), and *a* (higher) alleles (Halpine and Kerr 1986). As the influx of oriental breeds increases, population geneticists should revisit the question of whether it is appropriate to exclude "purebreds" from their calculations.

Acknowledgments

Julie Staudinger is an undergraduate student at the University of Central Arkansas, Conway, AR. The authors thank Dr. Masatoshi Nei for his help in the calculation of Nei's genetic distances and Dr. Sylvia Kerr for her assistance in data analysis.

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Received June 30, 2004
Accepted March 25, 2005

Corresponding Editor: Stephen O'Brien