Gene frequencies in feral cats on Marion Island

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THE DOMESTIC CAT, *Felius catus*, is polymorphic for a number of coat color, texture, and pattern characteristics that can be recognized with relative ease. The inheritance of these traits is well known and has recently been reviewed[9].

With the exception of a note by Dreux[6] and some remarks on the coat color of cats at Cochons Island[4], no published information is yet available on the population genetics of the cats inhabiting several sub-Antarctic Islands. A study of the population genetics of the Marion Island cats is of interest for several reasons. The population originated from a limited stock of which the phenotypical constitution is known. It has existed in isolation from other felids (therefore no interbreeding) under extreme environmental conditions. The lack of potential competitors also may have afforded opportunities not available to cats in continental areas. Furthermore, human preferences would not have influenced the frequencies of the different phenotypes.

The study area and history of the cat population

In evaluating the genetic profile of this population, possible selective environmental factors that might have affected the population must be taken into consideration. Being situated in the sub-Antarctic region ($46°52'S$, $37°51'E$), 2100 km south-southeast of Cape Town (South Africa) the volcanic Marion Island is continuously subjected to low temperatures, strong westerly winds, and high humidity. Rainfall is evenly distributed throughout the year, precipitation being recorded on over 300 days per annum[1].

The introduction of cats to this tundra biome resulted from the establishment of a permanent Meteorological Station during 1948, which followed the annexation of the Island by South Africa in 1947/48. Personal communication with members of the meteorological teams responsible for the introduction of the cats as well as through the use of black and white photographs indicate that two consecutive introductions occurred. The first, early in 1949, comprised a marmalade (orange) striped tabby tom and a nonagouti piebald spotted female; the second introduction followed in August of the same year and was comprised of three siblings—one nonagouti with spotting and two nonagouti kittens.

A photograph of the first litter (F_1) born on Marion Island assisted in the clarification of the genotypic composition of the original adult pair and the siblings (Table I). Some of the offspring of this founder group, then household pets, turned

wild and during October 1951 the first feral cat was observed approximately 12.0 km west of the meteorological station[12].

In 1965, 16 years after their introduction, cats and signs of their activities were present all round the island, indicating an average dispersal rate of 2.0 km per year[12]. Estimates based on information obtained in a study of the biology of this population[11] indicated the presence of approximately 2,200 individuals at the onset of the 1975/76 breeding season. The population was characterised by an intrinsic rate of natural increase of 23.3 percent per year and crude and ecological densities were estimated at 3.65 and 10.61 cats per km^2, respectively[12].

Methods

The results of this study are based on mutant phenotypes recorded for 839 cats comprised of two subsamples. The first, consisting of 656 cats, was classified using binoculars during numerous field excursions. Phenotypical data were recorded for the entire area where cats were known to occur. An attempt was made not to record animals that had previously been scored. The second subsample consisted of 183 animals, which were shot to death as part of an investigation of the reproductive biology of this feral population[11].

Since sex-linked orange is absent in the island population no tests for random mating could be conducted. The use of the piebald spotting locus for the establishment of equilibrium[2] was also confounded since no high-grade piebald spotting occurred. Consequently Hardy Weinberg-equilibrium could only be assumed for the autosomal traits present in this population.

Recessive mutant frequencies, q, were computed for all loci using the square root of the phenotype frequencies and dominant mutant allele frequencies, p, as $1 - q$. Standard errors were computed using

$$\sqrt{\frac{1 - q^2}{4N}} \quad \text{and} \quad \sqrt{\frac{(2 - p)p}{4N}}$$

for the recessive and dominant alleles respectively[10].

Numerous systems have been proposed to categorize the amount of piebald spotting in cats[3,5,9]. Cats scored in the field for the present study were grouped using grades S1-S3, S4, and S5. The animals classified as S4 or S5 formed only 6.87 percent of the total sample of 262 cats scored for this locus. No high-grade piebald spotting (S6-S9) was observed in the island population. Consequently, computations of allele frequencies were established by grouping all grades of piebald white spotting scored against individuals lacking this character. Restricted white spotting, i.e., on the chest or pubic region, was not included in the piebald sample as a second gene may be implicated in its inheritance[9].

Mutants scored for the observed subsample comprised agouti, nonagouti (a^+,a), striped and blotched tabby (t^+,t^b) intense and dilute (d^+,d), dominant piebald spotted and nonspotted (S,s^+). Similar characteristics were recorded for the dead subsample with the addition of short and long fur (l^+,l). The classification of the latter trait in the subsample observed at a distance was thought to be subject to considerable error and was consequently omitted.

Results

The genotypes of the P_1,F_1 and three introduced kittens are presented in Table I. The phenotypes and the allele frequencies

of the eight cats comprising the founder population are shown in Table II. The reduction from nine (Table I) to eight individuals in the founder population is based on the premise that the marmalade tom's contribution extended no further than F_1. This is borne out by the fact that sex-linked orange is absent in the present phenotypical composition of the island's cats.

Chi-square tests of the phenotypic proportions in the dead and viewed subsamples revealed a statistically significant difference only for piebald spotting. However, because it is difficult to score the low grades (S1 and S2) of this character in free-ranging feral cats with an aversion to humans, it may well have been underestimated. Therefore, the apparent statistical significance may result only from a diagnostic error. Consequently, the subsamples were grouped and treated as a single composite sample. Gene frequencies for this grouped sample (observed + dead) are presented in Table IV.

Discussion

An interesting aspect of the Marion Island cat population is that the phenotypical and genetic constitution of the founder population is fully known for two autosomal traits. The absence of tortoiseshell kittens in the first litter implies that all four progeny were males. Furthermore, since no record of sex-linked orange exists for the present linked population, it is probable that the marmalade tom was either castrated following the birth of the F_1 or died prior to the siring of a subsequent litter. An alternative hypothesis, namely that fertilization of the female by another tom had occurred prior to the departure of the cats to Marion Island can be safely discounted. This is supported by the fact that the first litter was born during November 1949, while the introduction occurred in January of that year. Since the gestation period is approximately 65 days[11], conception must have occurred on the island.

A statistical comparison of allele frequencies between the founder and grouped sample is precluded by the sample size ($n = 8$) of the founder population. Standard errors of allele frequencies calculated from the founder population for two

mutants (nonagouti and piebald spotting) suggest ranges that include frequencies for these loci determined from the group sample. There is, therefore, no indication that the present-day population differs from the founder population, suggesting that a founder effect predominates on Marion Island.

In view of the fact that this population was derived as a subsample from South-Africa, it is of interest to compare the Marion population's genetic profile with that of a South-African population, i.e., Pretoria (unpublished data). Such a comparison revealed significant differences with regard to frequencies at the a, d, and S loci; the frequency of the mutant allele (a), conferring a dark phenotype, was significantly higher ($\chi^2 = 23.80$), while the frequency of mutant alleles d and S, which confer lighter phenotypes was significantly lower ($\chi^2 = 18.53$ and 18.76, respectively) in the Marion Island population than in the Pretoria population.

In considering that the comparison is between samples representing populations adapted to sub-Antarctic and temperate environments, it might well be argued that the observed differences are due to differences in the fitness of different phenotypes, i.e., the darker phenotype being better adapted to the colder environment than the lighter phenotypes. Cats inhabiting Marion Island are presumably under severe temperature stress during a large part of the year (annual mean temperature is 5.5°C with the warmest month being February (6.8°C) and the coldest, August (3.6°C)[1]. Innes and Lavigne[8] indicated that melanistic *Sciurus carolinensis* appear to have a lower energy cost for existence during winter than gray morphs. Similarly this may contribute to the apparent superior fitness of nonagouti versus piebald spotting and maltese dilution in the Marion Island population.

Table I. Genotypic constitution of the founder population

P_1	$\delta\ O/Y\ a^+a\ t^+t^b\ s^+s^+$
	$\varphi\ o^+o^+\ aa\ -t^b\ Ss^+$
F_1	$aa\ ??\ s^+s^+$
	$a^+a\ t^+-\ s^+s^+$
	$aa\ ??\ Ss^+$
	$a^+a\ t^bt^b\ s^+s^+$
Second introduction	
	$aa\ ??\ s^+s^+$
	$aa\ ??\ Ss^+$
	$aa\ ??\ s^+s^+$

Table III. Chi-square tests of association between observed and dead subsamples

Locus		Subsamples Observed[†]	Dead[†]	χ^2
Nonagouti	a	530(530.32)	143(142.68)	
	a^+	113(112.68)	30(30.32)	0.005
Tabby	t^b	37(39.51)	13(10.49)	
	t^+	76(73.49)	17(19.51)	1.169
Dilution	d	11(13.34)	6 (3.66)	
	d^+	645(642.66)	174(176.34)	1.946
Piebald	S	192(205.59)	70(56.41)	
	s^+	464(450.41)	110(123.59)	6.077*

* Statistically significant
† Expected values in parentheses

Table II. Autosomal mutant alleles, phenotypes observed and allele frequencies in the founder population

Locus		Individuals diagnosed	Allele frequencies
Nonagouti	+	2	$q_a = 0.866 \pm 0.088$
	a	6	
Piebald	+	5	$pS = 0.209 \pm 0.108$
	S	3	

Table IV. Autosomal mutant alleles, phenotype observed and allele frequencies in the grouped sample (observed + dead)

Locus		Individuals diagnosed	Allele frequencies
Nonagouti	+	143	$q_a = 0.908 \pm 0.007$
	a	673	
Tabby	t^+	93	$q_tb = 0.592 \pm 0.034$
	t^b	50	
Dilution	+	819	$q_d = 0.143 \pm 0.017$
	d	17	
Piebald	+	574	$pS = 0.171 \pm 0.010$
	S	262	

Selection due to the adaptive advantage conferred upon an individual with a dark coat color as opposed to an individual with a light coat color may therefore have resulted in the observed differences in the phenotypic frequencies of the compared populations. This hypothesis is further supported by the absence of the higher grades of piebald spotting (S6-S9) in the phenotypical composition of the present adult population. On the other hand, the prevalence of dark phenotypes may also be ascribed to founder effect.

The only comparable data for a sub-Antarctic island cat population under similar environmental stresses is that published by Dreux for Kergeulen Island[6]. The study based on 36 cats showed that 35 of the sample were black or black with piebald spotting. Only one cat was found to be of the tabby phenotype. Dreux[6] proposed that the population probably arose from a founder group of black cats. The higher grades of piebald spotting were recorded in this small sample. Without further sampling this contradictory situation for the two islands cannot be satisfactorily explained.

An interesting aspect of the phenotypic character of the Marion cat population is that the gene for sex-linked orange was lost within one generation. It is also noteworthy that no fixation has occurred in any of the other coat color loci. This would indicate that a considerable degree of genetic diversity must have been present in the eight animals constituting the founder population.

Summary

Coat color phenotypes were scored for a feral island cat population that was descended from a founder group whose genotypic composition was known. Statistical comparisons between the founder group and the scored samples were precluded by the small sample size of the founder group. However, indications of a strong founder effect were evident for the Marion Island population. The Island's cats are notable for the absence of the higher grades of piebald spotting (S6-S9) and it is hypothesized that individuals possessing a dark coat color may have some adaptive advantage in a subantarctic environment.

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