

New data on allele frequencies of coat phenotypes of cats from Madeira and Azores islands (North Atlantic, Portugal)

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To determine allele frequencies, surveys of coat phenotypes of domestic cats were conducted in Madeira Island (Madeira archipelago) and Flores Island (Azores archipelago). The samples fitted a 1:1 sex ratio and panmictic populations were assumed based on the analysis of the *O* locus. The genetic profiles were compared to those from other Atlantic littoral populations and a marked deviation was detected at Flores Island referring to very high values of *d*, *W* and *l* alleles. The differences were interpreted as indicating that cats from Flores may reflect the condition of continental cats in former times. The Madeira population is more similar to Western Europe probably due to more close and continual contact in recent years.

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Introduction

Domestic cat coat polymorphism has been studied in many places. Lloyd and Todd's catalogue (1989) can be used as a reference work, since it contains the results of the surveys conducted worldwide until that date. Moreover, they also summarise the main effects responsible for deviations in gene frequencies among the different populations and give information on genetic control of coat colour and pattern polymorphism.

However, very few studies referred to island populations (eg Robinson 1972, Todd *et al.* 1975, Todd and Lloyd 1984, Ruiz-Garcia 1994).

Data herein presented were obtained in Madeira, the main island in the Madeira archipelago (30°N latitude and 17°W longitude), approximately 860 km from the coast of mainland Portugal and 660 km from North Africa, and in Flores, one of the most western islands of the Azores (40°N latitude and between 20° and 30°W longitude), which lies approximately at half way between Europe and North America.

Since their discovery, by Portuguese navigators in the 15th century, these islands have been at the centre of an intense international commerce, particularly Madeira, and can be assumed to have received a continuous flow of cats from diverse regions (eg Todd 1977). Cats are rarely confined and their breeding is unrestrained, being much less dependent on man than most domestic animals, so their populations can be treated as natural and essentially panmictic (eg Searle 1959, Robinson 1987).

These observations are relevant to the main objectives of this study which are: (1) to record the coat gene frequencies of Madeira and Flores domestic cats, (2) to understand their origin and dispersal, and (3) to compare our data with findings about other Atlantic populations.

Material and methods

Sampling

The total sample in the present census consisted of 177 live-cats, 124 from Madeira and 53 from Azores. Cats from Madeira archipelago were mostly from the capital, the city of Funchal ($n = 60$), although animals from different rural localities were also included in the analysis ($n = 64$). In Azores, all cats were surveyed in and around Santa Cruz, the main town of Flores Island ($n = 53$).

Cats were observed on streets, open spaces and private gardens, and in addition, in Funchal, some animals were also surveyed in a cat rescue centre. Screening activities in both islands were performed during short periods and precautions were taken so that the same cat could not be scored twice. Only cats which proximity or handling allowed sex determination were considered.

Screening and analysis of coat variations

The genes scored were those controlling the common coat colour, pattern and texture polymorphism (eg Robinson 1977), including sex-linked orange (O) and the autosomal loci non-agouti (a), blotched-tabby (t^b), blue dilution (d) and dominant white (W). The alleles responsible for the extent of white spotting (S) and the coat length (l) were also scored. As the number of loci involved is small, with a little practice the phenotypes produced are easily scored into groups: black vs orange, agouti vs non-agouti, striped tabby vs blotched tabby, intense vs dilution, entirely white vs pigmented and white-spotted vs non-spotted.

The degree of piebald white spotting exhibited by each cat was estimated using Dreux's method (1967) on a scale ranging from absent or restricted (ϵ) to over 90%, excluding dominant white. When screening for white spots, comparisons were made with the white spotting patterns illustrated by Pontier (1984). Moreover, for comparative purposes and as suggested before by Searle (1949), cats were redistributed on the basis of the quantity of white in a four-point scale: S_0 - no white spotting, S_1 - less than one third white, S_2 - one third to two thirds white, and S_3 - over two thirds white but not all white. Restricted white spotting (ϵ) was included in the grade S_0 in order to reduce possible misclassifications because very small patches on the chest are not always visible on agouti backgrounds, and hence tend to be classified as not present.

Estimates of gene frequencies for recessive phenotypes (a , t^b , d and l) were calculated as the square root of their proportion in the sample (q), and for dominant mutants (S and W) this was one minus the square root of the proportion of the recessive phenotype (p). The standard error of these estimates was taken as the square root of the variance of both estimates: $p = (1 - q^2) / 4n$ (recessive alleles) or $q = (2 - p) p / 4n$ (dominant alleles), n being the number of observations (eg Robinson and Manchenko 1981, Todd and Lloyd 1984, Robinson 1987).

As each sample was scored for sex, the frequency of the sex-linked orange gene was found by counting the number of *O* alleles over all phenotypes and dividing by 2n (Robinson 1987).

Randomness of mating was determined by comparing the observed frequencies of the orange (*O* and *OO*) and tortoiseshell (*O+*) phenotypes, with those expected if the *O* gene is in Hardy-Weinberg equilibrium. Lack of deviation indicates random mating and represent valid estimates of the autosomal frequencies (Robinson 1987).

Heterogeneity among samples was examined by χ^2 tests (eg Zar 1984). To understand the genetic relationships between the different cat populations a phenetic approach (UPGMA algorithm) was performed with the NTSYS-pc package (1.80 version, Rohlf 1993), considering the gene frequencies and applying the Euclidean distance coefficient (Sneath and Sokal 1973). Similarity indexes (*I*) and minimum genetic distances (*D*) were calculated by the method of Nei (1972, 1978).

Results

Distribution of phenotypes and gene frequencies

No significant deviation from a 1:1 sex ratio was observed in Flores ($\chi^2 = 1.32$, $df = 1$, $p > 0.05$) nor in the rural cats from Madeira ($\chi^2 = 0.08$, $df = 1$, $p > 0.05$) but a slight excess of females was found in the Funchal cats ($\chi^2 = 6.60$, $df = 1$, $0.01 > p > 0.05$). However, since no heterogeneity was detected when the two samples from Madeira are pooled ($\chi^2 = 2.44$, $df = 1$, $p > 0.05$) equality of sexes was assumed in both islands.

The observed frequencies at the sex-linked orange locus were similar to the ones expected on the Hardy-Weinberg equilibrium (Table 1), indicating panmixia, except for Madeira, when considering simultaneously urban and rural cats. In that island the deviation observed is apparently due to a paucity of tortoiseshell phenotypes and may reflect a human preference for orange cats and a non-preference for tortoiseshell cats, as observed elsewhere (eg Todd *et al.* 1975, Dards and Robinson 1983).

In any case, the frequencies for sex-linked orange in the two samples from Madeira (Funchal and rural localities) do not differ significantly ($\chi^2 = 4.47$, $df = 1$, $p > 0.05$), and therefore no special concern was given to the apparent discrepancy,

Table 1. Correspondence of frequencies at the sex-linked locus (*O*) to Hardy-Weinberg ratios (Test of randomness of mating).

Sampling sites	Sex	Sample size	Phenotype Obs. (Exp.)			χ^2 (df = 2)	<i>p</i>
			+	+ <i>O</i>	<i>O</i>		
Funchal	F	40	22(22.5)	13(15.0)	5(2.5)	5.18	> 0.05
	M	20	18(15.0)		2(5.0)		
Madeira	F	74	45(43.1)	19(26.8)	10(4.7)	9.99	0.05 > <i>p</i> > 0.01
	M	50	42(38.2)		8(11.9)		
Flores	F	15	8(7.7)	5(6.1)	2(1.2)	0.80	> 0.05
	M	23	17(16.5)		6(6.5)		

Table 2. Phenotypic proportions and allele frequencies of cats from Madeira and Flores Islands. *n* – sample size.

Allele	Madeira Island			Flores Island			Heterogeneity	
	<i>n</i>	Phenotype frequency (%)	Gene frequency (%)	<i>n</i>	Phenotype frequency (%)	Gene frequency (%)	χ^2 (df = 1)	<i>p</i>
<i>a</i>	107	56.1	74.9 ± 3.2	45	60.0	77.4 ± 4.7	0.199	> 0.05
<i>O</i>	124	58.2	23.7 ± 3.8	38	51.3	28.4 ± 9.0	0.074	> 0.05
<i>t^b</i>	65	40.0	63.3 ± 9.5	22	27.3	52.2 ± 18.2	1.145	> 0.05
<i>d</i>	113	14.2	37.6 ± 4.3	47	23.4	48.4 ± 6.4	2.023	> 0.05
<i>S</i>	113	59.3	36.2 ± 3.6	48	52.1	30.8 ± 5.2	0.715	> 0.05
<i>W</i>	124	8.9	4.5 ± 1.3	53	9.4	4.8 ± 2.1	0.014	> 0.05
<i>l</i>	124	2.4	15.6 ± 4.4	53	43.4	65.9 ± 5.2	49.751	< 0.001

particularly since this kind of human selection, as already referred to by others (eg Todd *et al.* 1975), does not appear to have a permanent effect. Therefore, both populations, ie from Flores and as well from Madeira, were assumed as randomly mating.

Estimates of frequencies of the seven genes scored are shown in Table 2. In general, results can be viewed as congruent with other surveys (see references in Table 6), as far as the alleles responsible for coat colour and pattern are concerned, with non-agouti and blotched-tabby showing the highest frequencies and orange and dominant white denoting the lowest values.

Significant differences are, however, detected for other loci (Table 2). Cats from Flores show a significant higher frequency of long hair than the ones from Madeira.

However, frequencies from Flores show only four out of 21 possible differences significant at the probability level when compared with the ones previously

Table 3. Heterogeneity tests of gene frequencies estimates of Azorean cat populations (Flores vs São Miguel, Terceira and Faial/Pico).

Gene	São Miguel		Terceira		Pico/Faial	
	χ^2 (df = 1)	<i>p</i>	χ^2 (df = 1)	<i>p</i>	χ^2 (df = 1)	<i>p</i>
<i>a</i>	5.399	0.05 > <i>p</i> > 0.01	3.285	> 0.05	9.235	0.01 > <i>p</i> > 0.001
<i>O</i>	0.110	> 0.05	0.617	> 0.05	0.004	> 0.05
<i>t^b</i>	0.037	> 0.05	2.354	> 0.05	1.880	> 0.05
<i>d</i>	4.228	0.05 > <i>p</i> > 0.01	4.277	0.05 > <i>p</i> > 0.01	3.529	> 0.05
<i>S</i>	0.064	> 0.05	5.031	0.05 > <i>p</i> > 0.01	0.213	> 0.05
<i>W</i>	11.206	< 0.001	0.987	> 0.05	5.012	0.05 > <i>p</i> > 0.01
<i>l</i>	67.855	< 0.001	60.154	< 0.001	43.721	< 0.001

obtained for other Azorean islands (São Miguel, Terceira and Pico/Faial) by Todd and Lloyd (1984) (Table 3). Three of them refer to the long hair mutant allele (Flores vs São Miguel, Terceira and Pico/Faial) and another to the dominant white (Flores vs São Miguel). Other marginal differences are observed for agouti, dilution and piebald, but no consistent pattern of variation was identified.

Piebald white-spotting

In accordance with Dreux's scale (1967), the distribution of piebald spotting is shown in Fig. 1 and, following Searle's grouping proposal (1949), the percentage of white exhibited by cats is shown in Table 4.

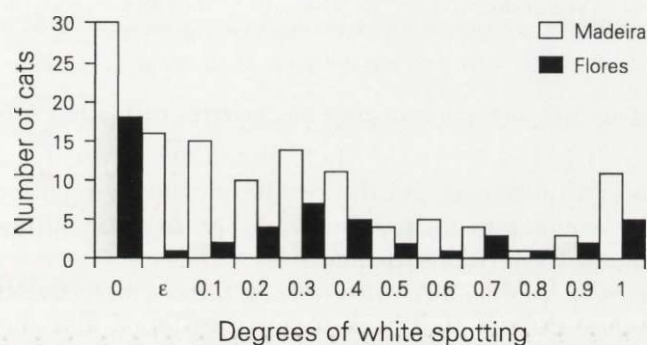


Fig. 1. The distribution of piebald white spotting in cats from Madeira and Flores estimated using Dreux's method (1967). ϵ - restricted white spotting.

Almost half of the cats from both islands have no white spots or just a restricted patch; of the remaining the majority show less than 30 per cent white. Cats with extensive white spotting were rare.

Considering Flores against Madeira some variation is observed in the amount of white but differences are not significant ($\chi^2 = 1.661$, $df = 3$, $p > 0.05$).

Although white is more obvious on dark phenotypes (black, blue and tabby) than on lighter ones (orange plus tortoiseshell), the incidences of white on dark vs. light patterns within or between each island are not significantly different ($\chi^2_{MD} = 2.195$, $df = 1$, $p > 0.05$, $\chi^2_{FL} = 1.485$, $df = 1$, $p > 0.05$) for the former and considering either the dark and the light patterns ($\chi^2 = 0.045$, $df = 1$, $p > 0.05$) or each of the different phenotypes referred above ($\chi^2 = 1.003$, $df = 4$, $p > 0.05$) for the later (Table 5).

Table 4. Percentage of white spotting (S).

White spotting grade	n	S_0	S_1	S_2	S_3
Madeira	113	40.7	34.5	17.7	7.1
Azores, Flores	46	41.3	28.3	17.4	13.0

Table 5. Percentage of white-spotted cats for each of the main phenotypes scored.

Phenotype	Madeira (<i>n</i> = 77)	Flores (<i>n</i> = 33)
Dark patterns	58.4	60.6
Black	46.7	55.0
Blue	6.7	10.0
Tabby	46.7	35.0
Light patterns	41.6	39.4
Orange	40.6	46.2
Tortoiseshell	59.4	53.9

Comparison of Madeiran and Azorean gene frequencies with other Atlantic localities

In Table 6, gene frequencies for the Madeira and Azores archipelagos, including both the data herein presented and the results previously reported by Todd and Lloyd (1984), are compared with those for other Atlantic littoral localities of Western Europe and Eastern North-America.

The estimates of *S* in Madeiran and Azorean (Flores plus São Miguel, Terceira and Pico/Faial) cats are similar to the frequencies found elsewhere, the values

Table 6. Gene frequencies estimates in Atlantic populations (the dark mark indicates the highest values and the light one the lowest).

Localities	Alleles							References
	<i>a</i>	<i>O</i>	<i>t^b</i>	<i>d</i>	<i>S</i>	<i>W</i>	<i>l</i>	
Reykjavik	0.600	0.130	0.530	0.440	0.490	0.010	0.140	Todd <i>et al.</i> 1975
London	0.740	0.250	0.690	0.290	0.280	0.030	0.500	Dyte 1974 in Robinson 1987
Portsmouth	0.770	0.060	0.640	0.060	0.250	–	0.140	Dards and Robinson 1983
York	0.810	0.200	0.780	0.270	0.330	0.010	–	Metcalfe and Turner 1971
Bordeaux	0.734	0.061	0.559	0.221	0.284	–	0.221	Todd and Lloyd 1984
Porto	0.768	0.142	0.429	0.296	0.290	0.008	0.234	Todd and Lloyd 1984
Lisboa	0.653	0.069	0.446	0.274	0.213	0.017	0.088	Todd and Lloyd 1984
Cadiz	0.707	0.155	0.447	0.248	0.235	0.008	0.000	Todd and Lloyd 1984
Marseille	0.720	0.080	0.680	0.340	0.290	0.003	0.270	Dreux 1975 in Pontier 1983
Rabat	0.810	0.090	0.380	0.380	0.270	0.010	0.090	Todd and Lloyd 1984
Madeira	0.749	0.237	0.635	0.376	0.362	0.045	0.156	New data
São Miguel	0.632	0.234	0.503	0.338	0.293	0.003	0.112	Todd and Lloyd 1984
Terceira	0.665	0.307	0.368	0.337	0.450	0.028	0.158	Todd and Lloyd 1984
Pico/Faial	0.571	0.252	0.381	0.340	0.337	0.009	0.166	Todd and Lloyd 1984
Flores	0.774	0.284	0.522	0.484	0.308	0.048	0.659	New data
New York	0.752	0.145	0.473	0.443	0.471	0.013	0.130	Todd 1969
Boston	0.642	0.193	0.443	0.426	0.430	0.022	0.302	Todd 1969

obtained falling within the range in other Atlantic populations. However, all the other values represent either the highest or the lowest found among those populations.

The frequencies for dominant white, particularly in Madeira and Flores, differ from the 1–3% levels commonly found in free-ranging populations; the highest and the lowest estimates of W are found among the Azorean populations, with the highest frequency recorded in Flores island. The a and t^b alleles attained the lowest values respectively in Pico/Faial and Madeira. For the remaining alleles (O , d and l), maximum values were recorded in Azores, notably for l which frequency is exceptionally high in Flores.

The variation in gene frequencies in the island populations of Madeira, São Miguel and Pico/Faial reveals a more or less consistent pattern in which alleles can be ordered, from high to low, as: $a > t^b > d > S > O > l > W$. With very small adjustments this pattern occurs in other Atlantic populations, at least in what concerns the highest frequencies consistently attained by a followed by t^b and the lowest by W . Exceptions are recorded in Terceira ($a > S > t^b > d > O > l > W$) and Flores ($a > l > t^b > d > S > O > W$), due to the high frequencies of S and l , respectively.

Trying to identify relationships among the named Atlantic populations, similarity was calculated on the basis of the Euclidean distance of the gene frequencies scored for all the variants (Fig. 2). The most contrasting result was the dissimilarity of Flores from all the other samples, mainly due to the frequency

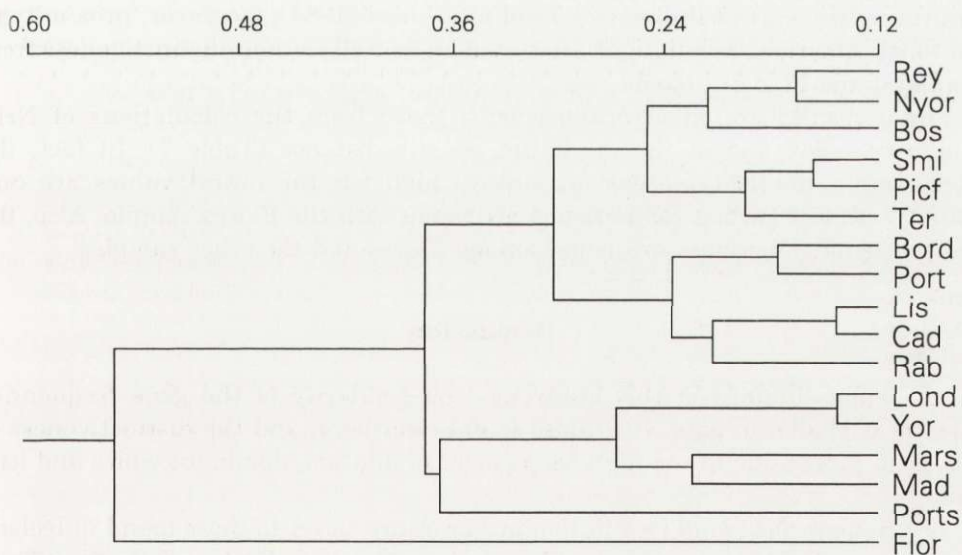


Fig. 2. Relationships among Atlantic domestic cats populations based on the Euclidean distance (Rey – Reykjavik, Lond – London, Ports – Portsmouth, Yor – York, Bord – Bordeaux, Port – Porto, Lis – Lisbon, Cad – Cadiz, Mars – Marseille, Rab – Rabat, Mad – Madeira, Smi – São Miguel, Ter – Terceira, Picf – Pico/Faial, Flor – Flores, Nyor – New York, Bos – Boston).

Table 7. Similarity (I – top right of diagonal) and minimum genetic distance (Dm – bottom left) for comparison of gene frequency profiles in 17 Atlantic populations (Abbreviations as in Fig. 2).

	Rey	Lond	Ports	Yor	Bord	Port	Lis	Cad	Mars	Rab	Mad	Smi	Ter	Picf	Flor	Nyor	Bos
Rey	–	0.91	0.89	0.94	0.94	0.95	0.95	0.94	0.96	0.94	0.98	0.97	0.97	0.98	0.89	0.99	0.98
Lond	0.09	–	0.93	0.91	0.96	0.96	0.93	0.9	0.97	0.9	0.95	0.95	0.91	0.94	0.97	0.91	0.96
Ports	0.12	0.08	–	0.97	0.98	0.95	0.96	0.95	0.96	0.92	0.94	0.93	0.88	0.89	0.84	0.9	0.88
Yor	0.06	0.09	0.03	–	0.97	0.94	0.98	0.98	0.96	0.94	0.98	0.97	0.92	0.93	0.83	0.94	0.91
Bord	0.06	0.04	0.02	0.04	–	0.99	0.99	0.97	0.99	0.96	0.98	0.97	0.93	0.95	0.91	0.96	0.95
Port	0.05	0.04	0.06	0.06	0.02	–	0.99	0.97	0.97	0.98	0.98	0.98	0.96	0.97	0.94	0.98	0.97
Lis	0.05	0.07	0.04	0.03	0.01	0.02	–	0.99	0.98	0.99	0.98	0.98	0.94	0.96	0.89	0.97	0.95
Cad	0.07	0.11	0.05	0.02	0.04	0.03	0.01	–	0.95	0.98	0.98	0.98	0.94	0.95	0.85	0.96	0.92
Mars	0.04	0.03	0.04	0.04	0.01	0.03	0.02	0.05	–	0.9	0.98	0.92	0.82	0.87	0.93	0.87	0.87
Rab	0.06	0.11	0.09	0.07	0.04	0.02	0.01	0.02	0.11	–	0.96	0.97	0.95	0.96	0.88	0.98	0.95
Mad	0.02	0.05	0.06	0.02	0.02	0.02	0.02	0.02	0.02	0.04	–	1	0.97	0.98	0.91	0.98	0.97
Smi	0.03	0.06	0.07	0.03	0.03	0.02	0.02	0.02	0.09	0.04	0	–	0.97	0.99	0.91	0.98	0.97
Ter	0.04	0.09	0.13	0.09	0.08	0.04	0.07	0.06	0.2	0.05	0.03	0.03	–	0.99	0.91	0.98	0.98
Picf	0.02	0.06	0.12	0.07	0.06	0.03	0.05	0.05	0.14	0.05	0.02	0.01	0.01	–	0.94	0.98	0.99
Flor	0.11	0.03	0.18	0.19	0.09	0.06	0.12	0.17	0.07	0.12	0.09	0.09	0.09	0.07	–	0.86	0.93
Nyor	0.01	0.09	0.1	0.06	0.04	0.03	0.03	0.04	0.14	0.02	0.02	0.02	0.02	0.02	0.15	–	0.98
Bos	0.02	0.05	0.13	0.1	0.05	0.03	0.06	0.08	0.14	0.06	0.03	0.03	0.02	0.01	0.07	0.02	–

of the l allele. There was a close similarity among the other Azorean samples, confirming the earlier findings of Todd and Lloyd (1984); moreover, proximity to the North American populations seem evident as well as their distinctiveness from mainland and Madeira island.

These results are in accordance with those from the calculations of Nei's similarity index and of the minimum genetic distance (Table 7). In fact, the inter-sample similarity values are always high but the lowest values are consistently attained when comparisons are made with the Flores sample. Also, the highest genetic distances are found among Flores and the other samples.

Discussion

The main findings of this study are the similarity of the gene frequencies pattern of Madeiran cats with those found elsewhere, and the distinctiveness of cats from Flores due to the high frequencies of dilution, dominant white and long hair.

The frequencies found for dilution in Flores are closer to those found in Iceland (Reykjavik) (Todd *et al.* 1975) and North America (New York and Boston) (Todd 1969). It is known that, for instance, the American grey short hair has a European origin (Pugnetti 1990). Therefore, the similarity between Flores and North America frequencies may indicate that dilution was previously higher in Western

Europe and has only fallen recently. Moreover, while Madeira island and some Azorean islands, for example São Miguel, have always had close political and economical links with mainland Portugal, emigration to the New World countries has been very common during the last century in the less developed islands of Azores. Since this is the situation of Flores (Arruda 1932, Frutuoso 1983), a North American influence should be taken into consideration.

The frequencies for dominant white and long hair attain undoubtedly very high values, most likely due either to random sampling (founder effects), novelty selection or environmental selection, eg predation pressure. The same applies to dominant white estimate in the Madeiran sample, where the value found is the second highest among the Atlantic populations analysed.

Although a deeper study based on larger samples should be carried out, from the present results several hypothesis concerning the origin and dispersion of Madeiran and Azorean cats can be drawn: (1) the founding populations of Madeira and Flores islands must have been derived largely from Western Europe; (2) human preferences may have resulted in a selection of some coat colour patterns to be introduced on the islands; (3) in early times, some restriction of gene flow between the original and the derived populations could have occurred, followed by more recent and continuous input from Europe and North America; (4) cats of Flores could represent the least disturbed population.

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