

Gene Frequencies and Body Weights of Feral Cats, *Felis catus* (L.), from Five Australian Localities and from Macquarie Island

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Abstract

Frequencies of seven pelage-related genes and a coefficient of darkness were scored on groups of feral cats collected from five localities in south-eastern Australia and from Macquarie Island. There were significant differences in the frequencies of some of these genes and the coefficient of darkness between the various groups of cats. These differences were presumed to have been caused by the combined effects of natural selection, gene flow from surrounding domestic populations, and the founder effect. Significant differences in body weights of cats between some localities and for one coat colour allele were also found.

Introduction

In general terms feral cats, *Felis catus* (L.), may be defined as domestic cats which survive and reproduce without a close association with man. However, their status is very variable and some populations may be regarded as more 'feral' than others. The two extremes are represented by populations in remote or sparsely settled areas, which obtain their food predominantly by hunting naturally occurring prey and maintain their numbers through reproduction, and urban populations of stray cats, which obtain much of their food by scavenging human food scraps and maintain their numbers by some interbreeding with domestic cats, or by the recruitment of strays from the domestic population. The situation is further complicated by the existence of semi-domesticated farm cats and roaming pet cats, so no precise definition of feral cats is possible.

Domestic cats are polymorphic for genes affecting coat colour, coat pattern and hair characteristics. For feral cats originally derived from domestic cats, the frequencies of some of these genes might vary in response to surrounding domestic populations, particular habitats, or according to their 'feral' status. This paper reports the frequencies of seven pelage-related genes, a coefficient of darkness, and body weights for six groups of feral cats, collected from differing habitats and areas of varying human density.

Methods

Between December 1973 and March 1975 feral cats were collected from Macquarie I., mainly for a dietary study (Jones 1977). Some additional specimens were collected in the following (1975-76) summer. Between April 1977 and March 1981 feral cats were collected from various localities in south-eastern Australia for dietary and other studies (Jones and Coman 1981, 1982a, 1982b). For all localities other than the eastern highlands most cats were collected by spotlight shooting; cats from the eastern highlands were caught by leghold trapping.

The sex and weight as collected were determined and the following pairs of alleles were scored for each cat heavier than 1000 g: striped (t^+) versus blotched (t^b); agouti (a^+) versus non-agouti (a); orange (O) versus non-orange (O^+), a pair of sex-linked alleles in which the heterozygote (O^+O) is a female

tortoiseshell; dominant piebald spotting (S) versus non-spotted (s^+); dominant white (W) versus pigmented (w^+); intense (d^+) versus dilute (d); short hair (l^+) versus long hair (l). The modes of inheritance of these alleles are reviewed by Robinson (1977).

Recessive mutant frequencies (q) were obtained by taking the square roots of the corresponding phenotype frequencies, and dominant mutant frequencies (p) were then derived from $(1 - q)$. Standard errors were calculated from the expression: $\pm \sqrt{[(1 - q^2)/4N]}$ (Saliternik and Todd 1977). In the case of sex-linked orange, the allele frequencies were calculated directly because the three female genotypes non-orange (O^+/O^+), orange (O/O) and tortoiseshell (O^+/O), and the two male genotypes non-orange (O^+/Y) and orange (O/Y), are easily identified. Dominant piebald spotting was calculated on the assumption that the s/s genotype produces a grade O (Dreux and Legel 1973); restricted white spotting was ignored. Striped and blotched were scored on both agouti and orange (but not on tortoiseshell) cats from all localities except Macquarie I., where striped and blotched were scored only on agouti cats. Long hair was not scored on Macquarie I. cats. It should be noted that dominant white is epistatic to all other coat colour genes, non-agouti is epistatic to tabby, and sex-linked orange is epistatic to agouti. A 'coefficient of darkness', defined as the frequency for males of the darker phenotypes controlled by alternative alleles at the O, a, t and d loci (Todd 1969), was also calculated for each group of cats.

Finally, mean body weights of male cats 3400 g and heavier and non-pregnant females 2400 g and heavier (approximating the initial attainment of sexual maturity at an estimated age of 12 months; Jones and Coman 1982a) were obtained for each locality and for various coat colour phenotypes. Two-way analyses of variance were conducted to test the effects of locality and sex on weight and effects of coat colour alleles (t, a, O, S) and sex on weight.

Table 1. Sex ratios and phenotypes of feral cats from five localities in south-eastern Australia and from Macquarie Island

n.d., not determined

Phenotype	Western N.S.W.	Hattah-Kulkyne	Mallee farmland	Settled rural	Eastern Highlands	Macquarie Island
Total males	34	46	32	60	128	50
Total females	29	40	35	37	29	24
Striped tabby	52	54	28	28	44	11
Blotched tabby	5	10	13	13	56	18
Black	1	11	15	28	48	4
Striped orange	4	6	8	11	3	39
Blotched orange	0	2	0	1	3	
Tortoiseshell	1	3	1	12	3	2
Dominant white	0	0	2	4	0	0
Dilute	0	0	1	3	0	0
Long hair	0	0	7	9	0	n.d.
Piebald spotting	15	37	30	35	36	0
Sample size	63	86	67	97	157	74

Cats were obtained from the following six areas:

Western New South Wales. Specimens were collected mainly from Kinchega National Park (area 70 000 ha) in the south-western region of New South Wales. Others were collected from remote station country approximately 100 km north of the Park. The area surrounding the park is semiarid with a human density of <1 per square kilometre.

Hattah-Kulkyne Park. Situated in the semiarid north-western Mallee region of Victoria, the Park has an area of 48 000 ha.

Mallee farmland. The area sampled was the north-western area of the Victorian Mallee, contiguous with but south of the Hattah-Kulkyne Park. Used mainly for cereal cropping and sheep grazing, the area is semiarid with a human density of 1-3 per square kilometre.

Settled rural. Cats were collected from the more settled areas of north-central Victoria, and from isolated rubbish tips adjacent to small country towns. The human density was 3-25 per square kilometre.

Eastern Highlands. This area consists of mountainous country covered with wet and dry open sclerophyll forests and has a human density of 1–3 per square kilometre.

Macquarie Island. A subantarctic island of 120 km² with no permanent human settlement.

Due to the distribution of human settlement, the feral status of some cats from the settled rural and, to a lesser extent, the Mallee farmland groups, may have been in doubt.

Table 2. Assortment of the O gene and test for random mating

Expected values are shown in parentheses. Mainland cats treated as a single group with orange and tortoiseshell females combined ($\chi^2_3 = 9.69$, $P < 0.05$). Macquarie I. cats treated separately ($\chi^2_1 = 22.6$, $P < 0.001$)

Phenotype	Western N.S.W.	Hattah- Kulkyne	Mallee farmland	Settled rural	Eastern Highlands	Macquarie Island
Non-orange male O ⁺ /Y	30 (32.2)	38 (42.0)	24 (29.1)	45 (45.2)	122 (121.9)	19 (25.0)
Non-orange female O ⁺ /O ⁻	28 (25.9)	37 (33.3)	32 (27.2)	24 (24.2)	26 (26.3)	14 (6.0)
Tortoiseshell female O ⁺ /O	1 (3.0)	3 (6.4)	1 (5.5)	12 (11.5)	3 (2.7)	2 (12.0)
Orange male O/Y	4 (1.8)	8 (4.0)	8 (2.9)	11 (10.8)	6 (6.1)	31 (25.0)
Orange female O/O	0 (0.1)	0 (0.3)	0 (0.3)	1 (1.4)	0 (0.1)	8 (6.0)
Sample size	63	86	65	93	157	74

Table 3. Mutant allele frequencies and coefficients of darkness for feral cats from five localities in south-eastern Australia and from Macquarie I.

Standard errors in parentheses. Similar superscripts link values which are not significantly different. n.d., not determined

Allele	Western N.S.W.	Hattah- Kulkyne	Mallee farmland	Settled rural	Eastern Highlands	Macquarie Island
Blotched t ^b	0.286 ^A (0.061)	0.408 ^{AB} (0.054)	0.515 ^B (0.061)	0.514 ^B (0.059)	0.746 ^C (0.032)	0.788 ^C (0.057)
Non-agouti a	0.131 (0.065)	0.383 ^A (0.053)	0.518 ^{AB} (0.057)	0.637 ^B (0.046)	0.569 ^B (0.034)	0.348 ^A (0.082)
Orange O	0.054 ^A (0.020)	0.087 ^A (0.022)	0.092 ^A (0.026)	0.192 ^A (0.031)	0.048 ^A (0.012)	0.500 (0.050)
Spotted S	0.127 ^{BC} (0.031)	0.245 ^A (0.035)	0.266 ^A (0.042)	0.210 ^{AB} (0.032)	0.122 ^C (0.019)	0
White W	0 ^A	0 ^A	0.015 ^A (0.011)	0.021 ^A (0.010)	0 ^A	0 ^A
Dilute d	0 ^A	0 ^A	0.124 ^{AB} (0.062)	0.180 ^B (0.051)	0 ^A	0 ^A
Long hair l	0 ^A	0 ^A	0.323 ^B (0.058)	0.305 ^B (0.048)	0 ^A	n.d.
Coefficient of darkness	0.092	0.263 ^A	0.415 ^B	0.440 ^B	0.667	0.333 ^{AB}

Results

The sex ratios and phenotypes of all groups of collected cats are presented in Table 1. There was a significant excess of males in the overall sample ($\chi^2_1 = 36.2$, $P < 0.05$), but when the eastern highlands group was excluded from the test, there was no significant difference in the sex ratio ($\chi^2_1 = 7.3$, $P > 0.05$). Eastern highlands cats were the only ones collected by leghold trapping. This would have biased the collected sex ratio if a behavioural difference made males more susceptible to trapping than females.

The observed and expected numbers of cats of each phenotypic class at the sex-linked orange locus are presented in Table 2. The deviation from a Hardy-Weinberg equilibrium

was tested firstly on the mainland cats as a single group and with the orange and tortoiseshell females combined (because of the low frequency of O), and secondly on the Macquarie I. cats. A significant deviation from equilibrium was found in both the mainland ($\chi^2_3 = 9.69$, $P < 0.05$) and Macquarie I. ($\chi^2_4 = 22.6$, $P < 0.001$) cats, in both cases due to an excess of males and a deficiency of females carrying the O gene.

Mutant gene frequencies and the coefficient of darkness for all groups of cats are presented in Table 3. Student's *t*-test (at 5% confidence limits) was used to determine the significance of variations in the frequencies of each gene and the coefficient of darkness, or for each group of cats. There was no significant difference in the frequency of any gene scored for the coefficient of darkness between Mallee farmland and settled rural cats. Also, there was no significant difference in the frequency of dominant white between any of the groups and no significant difference in the frequency of sex-linked orange between any of the mainland groups. However, significant differences were evident in all other gene frequencies and the coefficient of darkness, between the various groups of cats.

The mean body weights of cats from the various localities and of various coat colour phenotypes are presented in Table 4. A two-way analysis of variance showed a highly significant difference ($P < 0.001$) in weight between the sexes and between different

Table 4. Mean weights of feral cats from six localities, and with different coat colour phenotypes from the six localities combined

Values are in grams. Differences in weight between sexes and localities were highly significant ($P < 0.001$). The effect of the O allele on body weight was highly significant ($P < 0.001$) and sex-dependent (O males heavier than O⁻ males; O females lighter than O⁺ females); the effects of the other alleles tested were not significant

	Males		Females	
	Mean $\pm$ SE	N	Mean $\pm$ SE	N
Area				
Western N.S.W.	4535 $\pm$ 126	27	3469 $\pm$ 103	24
Hartah-Kulkyne	4734 $\pm$ 127	28	3197 $\pm$ 91	18
Mallee farmland	4631 $\pm$ 135	24	3059 $\pm$ 80	22
Settled rural	4197 $\pm$ 97	37	2946 $\pm$ 93	24
Eastern Highlands	4410 $\pm$ 58	107	3235 $\pm$ 96	23
Macquarie I.	4459 $\pm$ 87	35	2946 $\pm$ 93	12
Coat colour phenotype				
Striped t ⁻	4531 $\pm$ 73	98	3223 $\pm$ 59	65
Blotched t ^b	4452 $\pm$ 79	61	3131 $\pm$ 106	27
Agouti a ⁺	4447 $\pm$ 55	147	3185 $\pm$ 51	86
Non-agouti a	4343 $\pm$ 63	66	3100 $\pm$ 90	15
Non-orange O ⁺	4415 $\pm$ 43	213	3146 $\pm$ 53	101
Orange O	4642 $\pm$ 94	44	2858 $\pm$ 108	6
Non-spotted	4392 $\pm$ 38	154	3202 $\pm$ 62	62
Spotted S	4593 $\pm$ 82	69	3156 $\pm$ 65	49

localities. There were no effects of the t, a, or S alleles on body weight, but the effect of the O allele was highly significant ($P < 0.001$) on weight, and this was sex-dependent (O males were heavier than O⁺ males, O females were lighter than O⁺ females).

Discussion

Differing factors associated with the collection areas could have influenced the gene frequencies of the various cat populations. Scavenged human food scraps made up a large part of the diet of settled rural cats (E. Jones, unpublished data), but the diets of the other groups consisted mainly of naturally occurring food; smaller mammals (particularly European rabbits *Oryctolagus cuniculus*), birds and reptiles (Jones 1977; Jones and Coman 1981). A winter nutritional stress was indicated as a population-limiting mechanism for the

cats on Macquarie I. (Jones 1977) and in the Hattah-Kulkyne Park (Jones and Coman 1982b). Natural selection under those conditions would tend to favour individuals with the best survival attributes, and coat colour may play a large part in hunting success. However, the greater dependence of settled rural cats on human food scraps would tend to reduce the effect of this particular pressure upon them. Also, because the Mallee farmland and settled rural areas had higher human densities than the other areas, they contained in consequence a greater number and variety of domestic cats. Thus the greater genetic diversity displayed by Mallee farmland and settled rural cats in comparison to the other groups could be explained in part by an increase in the number and variety of genes flowing from the surrounding domestic populations, coupled with a slower rate of removal of less fit genes due to a reduction in the pressure of natural selection.

The excess of males and the deficiency of females carrying the O allele may have been a result of non-random mating or, more likely, could indicate selection at this locus. An excess of orange males and a deficiency of tortoiseshell females have been reported in studies of domestic cats. Selection was indicated as the cause in one instance (Metcalf and Turner 1971), but human preference (Robinson and Silson 1969; Dreux and Legel 1973) and misdiagnosis of the tortoiseshell phenotype (Clark 1976) have also been suggested as possible causes.

Clines in some coat colour alleles have been found and mapped in domestic cat populations (Todd 1977). If clines exist in the domestic cat populations of Australia, then they could be reflected in part, by the gene frequencies of the corresponding feral cat populations through either gene flow or a founder effect. Although gene frequencies have been determined for the domestic cats of Brisbane and Melbourne (Moffatt 1968), Melbourne (Kinnear 1979), Adelaide (Clark 1973), Darwin (Dartnall 1977) and Hobart (Dartnall and Todd 1975), and for feral cats from rural Tasmania (Dartnall 1975), no information is available on the gene frequencies of domestic cats from the same general areas as the feral cats sampled here.

The significance of the founder effect on the gene frequencies of the more isolated feral cat populations in mainland Australia is unknown, but for feral cats on islands it is important. The founder effect has influenced the gene frequencies of feral cats on subantarctic Kerguelen and Marion Is (Dreux 1974; van Aarde and Robinson 1980). The Macquarie I. population was characterized by very high frequencies for blotched (0.788) and sex-linked orange (0.500); presumably the founder effect must have played a role in this. The absence of piebald spotting and dilute in the Macquarie I. population could also have been caused either by a lack of these genes in the founder population or by their subsequent loss. However, dilute appeared to have been present in at least one cat sighted but not collected. For Marion I. cats sex-linked orange was absent, the frequency of blotched was 0.592, that of non-agouti was 0.908 and piebald spotting (0.171) and dilute (0.143) were also present (van Aarde and Robinson 1980). They also had a higher incidence of non-agouti and lower incidences of piebald spotting and dilute than domestic cats of Pretoria. This led van Aarde and Robinson (1980) to suggest that a darker phenotype was better adapted to a colder environment by acting to mitigate a presumed cold stress. However, there was no significant difference in the coefficient of darkness between Macquarie I. cats and those from the semi-arid Hattah-Kulkyne Park where a cold stress was non-existent. Also, eastern highland cats were significantly darker than those from Macquarie I., where such a presumed cold stress would be greater. Finally, the founding population of Marion I. cats is known, and the present population can be explained entirely by a founder effect.

In some domestic cat populations a progressive increase in the coefficient of darkness with increasing urbanization has been demonstrated (Todd 1969; Clark 1975, 1976). This could be the result of pleiotropic effects of the mutant alleles on endocrine function enabling cats to tolerate higher population densities and, as a consequence, produce a darker coat (Clark 1976; Todd 1978). On Marion I. male cats carrying the t^+ allele were significantly heavier than those carrying the alternative allele, there appeared to be a positive effect of the

S allele on body weight in males, and an allometric relationship between body weight and adrenal weight was indicated (van Aarde and Blumenberg 1979). Thus it has been suggested that the genotype best adapted to higher densities would be $aat^{bt}bs^{+}s^{+}$, which may give the smallest, darkest animal (van Aarde and Blumenberg 1979; Blumenberg and Lloyd 1980). Our results give no clear confirmation of this. The estimated density of Macquarie I. cats was 2–7 adults per square kilometre (Jones 1977); we considered that settled rural cats lived at somewhat higher densities. The mean summer and winter densities of Hattah–Kulkyne cats were 2.4 and 0.74 km^{-2} respectively (Jones and Coman 1982b); we considered that the remaining groups lived at slightly lower densities. There was a cline in the coefficient of darkness for western New South Wales through to settled rural cats and there existed a corresponding demographic cline. Also, the mean body weights of settled rural cats (which we considered lived at the highest densities) were significantly lower than those from some of the other localities. However, this cline was reversed by the high degree of phenotypic darkening present in eastern highlands cats, where the human density was comparable to the Mallee area. In this case the forest habitat may have favoured a darker coat.

The positive effect of the O allele on body weight of male cats and its negative effect on females may explain the suspected selection pressure at this locus, indicated by the deviation from the Hardy–Weinberg equilibrium.

Table 5. Gene frequencies of feral and domestic cats from various Australian localities

Location	Blotched	Non-agouti	Orange	Spotted	White	Dilute	Long hair
Adelaide	0.71	0.78	0.19	0.29	0.02	0.33	0.38
Darwin	0.78	0.74	0.33	0.44	0.03	0.31	0.33
Brisbane	0.68	0.81	0.14	0.41	0.02	0.47	—
Hobart	0.81	0.76	0.22	0.39	0.04	0.24	0.46
Rural Tasmania	0.84	0.63	0.11	0.21	0	0.13	0.18
Melbourne 1964	0.61	0.85	0.14	0.21	0.04	0.47	—
Melbourne 1977	0.71	0.73	0.17	0.32	0.04	0.34	0.39
Settled rural	0.51	0.64	0.19	0.21	0.02	0.18	0.31
Mallee farmland	0.52	0.52	0.09	0.27	0.02	0.12	0.32
Eastern highlands	0.75	0.57	0.05	0.12	0	0	0
Hattah–Kulkyne	0.41	0.38	0.09	0.25	0	0	0
Western N.S.W.	0.29	0.13	0.05	0.13	0	0	0

A comparison of the gene frequencies of domestic cats in urban areas of Australia with those of feral populations in rural areas (Table 5) suggested some reversion to wild type (lower frequencies of blotched, non-agouti, sex-linked orange, white-spotting and dilute). This reversion was almost complete in western New South Wales, where human influence would be least. The low frequencies of blotched and non-agouti are highly significant, since these genes were invariably common in the more settled areas sampled. A founder effect is unlikely to explain such a marked reversion to wild type in all genes, thus it may be concluded that this effect is a result of strong selection pressure against mutations which are maintained in the majority of urban cat populations. For eastern highland cats the high frequencies of blotched and non-agouti (compared to western New South Wales and Hattah–Kulkyne cats) may have come about by natural selection maintaining these genes at levels comparable to those in the more urban populations.

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