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SHORT COMMUNICATION

Microspatial genetic heterogeneity and gene flow in stray cats (*Felis catus* L.): a comparison of coat colour and microsatellite loci

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Abstract

We analysed levels of genetic differentiation between nine local urban colonies of stray cats using eight coat colour and nine microsatellite loci. Both types of markers revealed a strong differentiation between colonies (F_{ST} = 0.15 and 0.09 for coat colour and microsatellite loci, respectively). Three coat colour loci showed extreme levels of genetic differentiation comparatively to other loci and are strongly suspected to be under divergent selective pressures. Microsatellite loci showed significant heterozygote deficiency within colonies (F_{IS} = 0.14), suggesting that coat colour loci are not appropriate to investigate genetic structure at a fine scale because coat colour allele frequencies are based on Hardy–Weinberg equilibrium. The reported pattern conformed to that predicted from the social structuring of cat colonies: aggressive exclusion of immigrants, inbreeding and very low dispersal rate.

Keywords: coat colour markers, *Felis catus*, *F*-statistics, microsatellite markers, population differentiation

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Introduction

In the domestic cat (*Felis catus*), the intraspecific genetic variability of coat colour and length of fur is well documented, as well as the relative contribution of evolutionary processes that change allele frequencies at a macrogeographical scale. Throughout most of Europe, the frequency of coat genes shows clines that have been interpreted as reflecting origin of the mutations and their subsequent spread through Europe (Todd 1977). Low population genetic subdivision has been found and attributed to both high rates of migration due to human intervention and to high effective population sizes (Todd 1977; Ruiz-Garcia & Klein 1997). Detailed analyses of events that could be directing the allelic frequencies at a microgeographical level are scarce. A rural–urban dichotomy has been highlighted, the orange allele being more frequent in rural cat populations than in the nearest urban ones (Manchenko & Balakiriev 1981; Pontier *et al*. 1995) whereas the nonagouti allele, at the opposite, is more frequent in urban populations (Metcalfe & Turner 1971; Blumenberg 1977). Interpretation of these effects came from observations of behavioural differences between cats carrying different coat genes (Pontier *et al*. 1995, 1998; Mendl & Harcourt 2000) and their subsequent impact upon social structure (Pontier *et al*. 1995). However, we still do not understand clearly the consequences of the establishment of social groups of stray cats in urban environments on the intensity of gene flow and on the distribution of genetic variability (Ruiz-Garcia & Alvarez 2000). In cities, distribution of stray cats is highly discontinuous because resources, either food or shelters, are highly aggregated (Calhoon & Haspel 1989; Pontier 1993). Suitable habitats such as parks, cemeteries, individual gardens or small waste grounds are generally isolated from one another by highways and stray cats do not inhabit buildings and then large areas of cities. In suitable habitats, cats form highly socially structured multimale/

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multifemale groups called colonies (Natoli & De Vito 1991). Home ranges of cats belonging to the same colony are small and largely overlapping (see Liberg *et al*. 2000 for a review). A dominance hierarchy exists among males (Natoli & De Vito 1991; Say *et al*. 2001), but high-ranking males are unable to monopolize access to the females, leading to a promiscuous mating system (Natoli & de Vito 1991; Yamane 1998; Say *et al*. 1999). In addition, a low rate of physical aggression by dominant males (Natoli & De Vito 1991), low reproductive skews in male breeding success (Say *et al*. 2001) and strong urban environmental constraints lead to an extremely weak dispersal among colonies of both adult and juvenile males and females (Devillard *et al*. 2003). Fights are observed with nonresident individuals and very few of them are able to settle for long in a colony (Natoli 1985). However, nonresident males can reproduce successfully within colonies, but always at very low rates (Say *et al*. 1999). Because juvenile mortality is very high in urban populations (approximately 70%, Say 2000), few of those young sired by nonresident cats will reach sexual maturity. Consequently, gene flow among colonies of cats is expected to be low. Additionally, low gene flow and genetic drift should lead to a significant genetic differentiation between colonies of cats in the urban environment.

To test for these predictions, we used eight coat colour and nine microsatellite loci to investigate the genetic structure among nine colonies of stray cats within 4 km of each other. Partitioning of genetic variance between and within colonies was compared between the two types of markers. All previous studies in the domestic cat have used coat colour genetic markers (e.g. Todd 1977; Pontier *et al*. 1995; Ruiz-Garcia & Alvarez 2000) because of their relatively well-known inheritance and simple assessment of phenotype (Todd 1977). However, these markers are dominant and some of them are suspected strongly to be under divergent selective pressures in the urban environment (Metcalfe & Turner 1971; Blumenberg 1977; Pontier *et al*. 1995; Mendl & Harcourt 2000). Perhaps more importantly, allele frequencies at all coat colour loci except for the orange locus were estimated under the strong assumption of Hardy–Weinberg equilibrium (HWE). Using more neutral and polymorphic markers such as microsatellites in combination with coat colour loci offers an opportunity to investigate the usefulness of coat colour loci in analysing the influence of cat social organization on the genetic structure of the population at a fine local scale.

Materials and methods

Population samples

Nine colonies (representing 187 cats) dispersed over the city of Nancy (Northeastern of France) were monitored for 2 years (1994 and 1995, Xémar 1997). The distance separating neighbouring colonies varied from 720 to 4030 metres, a distance that can be covered by an individual during dispersion (Liberg *et al*. 2000). We recognized all individuals visually by their coat colour pattern and hair length. The number of cats per colony varied from 14 to 43 (Table 1). Each cat has been assigned to a colony without any ambiguity by extensive behavioural observations of individuals and by interviews with people taking care of them. One hundred and fifty-three cats were captured using baited traps. No cats assigned to a given colony have been observed or captured in any other colony during the whole study period. The percentage of cats captured varied from 53 to 100% depending on the colony (mean 82%, see Table 1). It was independent of colony size (Xémar 1997). Upon capture, cats were anaesthetized with an intramuscular injection of ketamin chlorhydrate (Imalgène 1000 15 mg/kg, Rhône Mérieux) and acepromazin (Vétranquil 5.5% 0.5 mg/kg, Sanofi), and marked permanently using an electronic passive integrated transponder (pit-tag) and a coloured collar. Hair samples were taken from all captured animals. Cats were then released.

Genotype determination

Genotypes of the 187 cats were recorded directly from observation of individuals for seven coat gene loci. The

Table 1 Number of cats (n) living in the colony and number of cats n_{capt} belonging to the colony that has been trapped, number of alleles n_{all} per colony, observed H_O and expected H_E heterozygosity and multilocus F_{IS} estimated per colony using microsatellite loci

	Colonies									
	L	C	D	F	J	K	M	O	V	Total
n	27	43	17	14	20	15	15	19	17	187
n_{capt}	22	23	15	14	20	14	15	17	13	153
n_{all}	5.89	7.44	5.33	4.67	7.78	5.78	4.89	6.78	4.38	
H_E	0.70 ± 0.09	0.75 ± 0.08	0.64 ± 0.21	0.67 ± 0.10	0.78 ± 0.08	0.67 ± 0.18	0.69 ± 0.09	0.79 ± 0.10	0.60 ± 0.21	
H_O	0.57 ± 0.13	0.63 ± 0.09	0.56 ± 0.25	0.55 ± 0.11	0.66 ± 0.12	0.56 ± 0.12	0.68 ± 0.13	0.69 ± 0.15	0.60 ± 0.34	
F_{IS}	0.190	0.165	0.125	0.188	0.158	0.171	0.019	0.138	0.011	0.140
P-value	< 0.001	0.038	< 0.001	< 0.001	< 0.001	< 0.001	0.31	< 0.001	0.35	< 0.001

mutant alleles at these loci are the sex-linked orange (*O*) and the autosomal nonagouti (*a*), chinchilla (C^{ch}), blotched tabby (t^b), long-hair (*l*), white (*W*), piebald white spotting (*S*) and dilute (*d*) (Robinson 1977). Total DNA from the hair sample of each of the 153 captured cats was extracted with a Chelex-based method. DNA amplification was carried out for nine microsatellite loci by polymerase chain reaction (PCR) using the fluorescent labelled primers fca23, fca43, fca45, fca77, fca78, fca90, fca96, fca8 (Menotti-Raymond & O'Brien 1995) and fca37 (Menotti-Raymond, pers. comm.). PCR temperature cycles were preceded by a denaturation for 3 min at 94 °C and followed by an extension for 5 min at 72 °C. A PCR amplification of 25–30 cycles was carried out with an annealing temperature of 55–58 °C depending on locus. PCR products were resolved on a 6% denaturing polyacrylamide gel on a Pharmacia Automatic Sequencer (ALFexpress). Data collection and analysis were perfomed using Fragment Manager software supplied with the sequencer. More details are given in Say *et al*. (1999).

Genetic analysis

Allelic frequencies, genetic diversity and HWE test. Allele frequencies at all coat colour loci except for the orange locus were estimated under the assumption of HWE as presented in numerous previous studies of other cat populations (e.g. Pontier *et al*. 1995). Tests of HWE, as well as F_{IS} estimations, could be based potentially on the codominant orange locus for which it is possible to recognize heterozygote from homozygote females (Robinson 1977), but there were too few cats carrying the orange allele within the studied colonies to perform HWE tests. To estimate within-population genetic variability from microsatellite loci, we looked at the mean number of alleles per locus, observed (H_O) and expected (H_E) heterozygosities for each locus and each colony. The departure from HWE was estimated by F_{IS} values according to Weir & Cockerham (1984) and tested with a 5000 permutations procedure.

Genetic structure among colonies. Genetic differentiation across all colonies was calculated using an estimator of F_{ST} as described by Workman & Niswander (1970) and used in previous studies by different authors for mutant allele of each coat colour loci. Significance of F_{ST} values was tested according to Workman & Niswander (1970) using χ^2 tests. Genetic differentiation across the entire set of colonies was estimated from the microsatellite loci according to Weir & Cockerham (1984). Variance of F_{ST} over loci and colonies was estimated by a jackknife procedure and significance of these values was tested with 5000 permutations. A Mann–Whitney *U*-test was used to assess differences in multilocus F_{ST} estimates computed over the entire set of populations for the two classes of genetic markers. In order to detect outlying values of F_{ST}, we pooled the two types of markers into a single group and used an exploratory data analysis (see Ross *et al*. 1999 for a similar approach). We calculated the mean and variance of the F_{ST} distribution and defined as outliers the loci for which the F_{ST}-value estimate was associated with a *P*-value less than 10%, assuming a normal distribution of F_{ST}.

χ^2 tests for significance of coat colour F_{ST} values and Mann–Whitney *U*-tests were performed using SPLUS (StatSci Mathsoft) software. All other analyses were performed using GENETIX 4.0 (Belkhir *et al*. 1996–2000)

Results

Genetic diversity and HWE test

No consistent linkage disequilibria between microsatellite loci were detected in the nine colonies (data not shown). Mean number of alleles (*mna*) varied from 4.38 to 7.78 according to colony. Mean observed (H_O) heterozygosities ranged from 0.45 ± 0.10 to 0.70 ± 0.15 according to locus, and ranged from 0.55 ± 0.11 to 0.69 ± 0.15 according to colony (Table 1). Heterozygosity found here falls within the range of values reported in two other cat colonies (*mna* = from 3 to 9 and $H_O = 0.70$, Yamane 1998; *mna* = 7.89 and $H_O = 0.67$, Say *et al*. 2001). Except for fca43 ($P = 0.45$), the single-locus F_{IS} values differed from zero ($P < 10^{-4}$). Multilocus F_{IS} values ranged from 0.011 ($P = 0.35$) to 0.190 ($P < 10^{-4}$), depending on colony (Table 1). F_{IS} values showed a significant departure from HWE, caused by a heterozygote deficiency in seven colonies (Table 1). Multilocus F_{IS} across all samples also differed significantly from 0 and was equal to 0.140 ± 0.019 ($P < 10^{-4}$).

Genetic structure

Single–locus F_{ST} values estimated from the entire set of colonies ranged from 0.04 ($P = 0.07$) for the agouti locus (*a*) to 0.26 ($P < 10^{-4}$) for the orange locus (*O*) (Table 2). They ranged from 0.05 ± 0.02 ($P < 10^{-4}$) to 0.10 ± 0.05 ($P < 10^{-4}$) depending on the microsatellite locus (Table 2), showing significant differentiation among colonies. The overall multilocus F_{ST} values estimated for coat colour loci (0.15 ± 0.10, $P < 10^{-4}$) and microsatellites (0.09 ± 0.01, $P < 10^{-4}$) were not significantly different ($P = 0.12$) and indicated that colonies are differentiated from each other. In addition we re-estimated allelic frequencies of coat colour loci, and thereafter F_{ST} values, according to equilibrium frequencies estimated with a F_{IS}-value of 0.14 (F_{IS} value found using microsatellite loci). The re-estimated multilocus F_{ST} value was then 0.10 ± 0.06 ($P < 10^{-4}$). Microsatellite loci did not show any disparity in F_{ST} values, whereas three coat colour loci exhibited either a low (agouti locus) or a high (dilution and orange loci) levels of genetic differentiation. When

Table 2 Single and multi locus F_{ST} estimates using microsatellite and coat colour loci

Coat colour loci		Microsatellite loci	
Locus	F_{ST} (*P*-value)	Locus	F_{ST} (*P*-value)
a	0.037 (0.07)	Fca8	0.090 (< 0.001)
d	0.236 (< 0.001)	Fca23	0.049 (< 0.001)
t^b	0.069 (0.001)	Fca37	0.081 (< 0.001)
O	0.258 (< 0.001)	Fca43	0.083 (< 0.001)
W	0.097 (< 0.001)	Fca45	0.102 (< 0.001)
C^{ch}	0.128 (0.07)	Fca77	0.085 (< 0.001)
S	0.193 (< 0.001)	Fca78	0.104 (< 0.001)
l	0.190 (< 0.001)	Fca90	0.104 (< 0.001)
		Fca96	0.093 (< 0.001)
Multilocus value	0.151 (< 0.001)	Multilocus value	0.092 (< 0.001)

these three loci were removed from the analysis, the overall multiloci F_{ST} became 0.13 ± 0.05 when allelic frequencies of dominant coat colour allele was estimated without correction by the *F*-value found with microsatellite data and 0.09 ± 0.05 when this correction was taken into account.

Discussion

Our main findings are (1) that the influence of social organization of stray cats in highly fragmented urban environment on the genetic structure of the colonies is relatively strong (F_{ST} ranging from 0.09 to 0.15 depending on the type of marker) and (2) that the deviation from HWE revealed by microsatellites calls into question the appropriateness of using coat colour loci (assumed to be under HWE) to investigate population structure at this spatial scale.

Aspects of the social structure that can contribute to significantly differentiate the colonies are an absence of monopolization of resources (food and mates) by the dominant individuals (Say *et al*. 1999, 2001); a low level of aggressiveness among members of the colony (Natoli & De Vito 1991; Say 2000) that allows subordinates to remain within the social group (Natoli & De Vito 1991) and reproduce successfully (Say *et al*. 1999); and an intense defence of the territory of the colony by aggressive exclusion of immigrants of both sexes (Tabor 1983; Natoli & De Vito 1991) that decreases the probability of reproduction considerably among nonresident males and thus reduces gene flow between colonies. In addition, a part of the recorded genetic substructure could be due to a founder effect and subsequent genetic drift. Colonies are founded typically by a single or a low number of female cats (Tabor 1983) and founder effect is maintained through a high philopatry of both sexes (Devillard *et al*. 2003).

F_{IS} values within most (seven of the nine studied) social groups are significantly positive. Using the same microsatellite loci, no problem of genetic mismatch was recorded with the genotype of more than 350 known mother/young pairs in a previous parentage study (Say *et al*. 1999). This result suggests that the F_{IS} positive values recorded here are not due to the presence of null alleles or allelic dropout and make urban stray cats relatively unusual among social mammals. Indeed, populations of many social mammals are generally subdivided into behaviourally segregated breeding groups characterized by a large within-group variance of the male reproductive success and maintained by philopatry of one sex and dispersal of the other one (Greenwood 1980; Chepko-Sade & Halpin 1987). Both theoretical works (Chesser 1991a,b) and empirical studies (see van Staaden 1995; Storz 1999 for reviews) have shown that this pattern leads to a significant genetic structure among groups associated with negative F_{IS}-values indicating a within-group excess of heterozygotes relative to Hardy–Weinberg expectations. Genetic results reported here appear similar to the ones found within and among coteries of prairie dog *Cynomys ludovicianus* in isolated conditions (Chesser 1983). The high fragmentation of the urban environment, combined with the existence of barriers (mainly heavy-traffic roads, road accident being the first cause of mortality in cats, Pontier 1993) lead to a low dispersal rate both for males and females between colonies (Devillard *et al*. 2003). Consequently, mating between relatives occurs in urban cat colonies. They can constitute more than 10% of copulations (Ishida *et al*. 2001; Devillard, Say and Pontier, unpublished data) and this may explain the positive F_{IS} values reported here if a colony corresponds to the juxtaposition of several affiliative groups (Castric *et al*. 2002). Under less extreme conditions, as in the rural environment, the domestic cat (like the prairie dog, Foltz & Hoogland 1983) conforms to the pattern exhibited by other social mammals: the male-biased dispersal pattern in combination with a polygynous mating system prevents substantial genetic structuring and results in negative F_{IS} values (up to −0.15 according to the year in a French rural population, Pontier 1993).

We have no other choice but to assume that the coat colour loci conform to the HWE model in order to be able to estimate the proportions of the different genotypes for each loci. The violation of this assumption (as observed from the microsatellite loci) leads to over-estimate the F_{ST} using coat colour loci. Moreover, the consistency of single-locus F_{ST} estimates was greater for microsatellites than for coat colour loci. The highest amount of among-loci variability for coat colour loci could be due in part to the incapacity to obtain direct genotypic information, because all but one (the orange locus) are dominant markers (Lynch & Milligan 1994; Latta & Mitton 1997; Ross *et al*. 1999), and possibly to the higher polymorphism of microsatellite markers (Charlesworth 1998). Among the coat colour loci showing disparities, the agouti and orange markers are both suspected strongly to be affected by divergent selection pressures in the urban conditions, the nonagouti allele being favoured (Metcalfe & Turner 1971; Blumenberg 1977) and the orange allele counter-selected (Pontier *et al*. 1995, 1998; Mendl & Harcourt 2000). Such a divergent selection is likely to give biased estimates of some genetic parameters. Thus, codominant multiallelic neutral markers (Lynch & Milligan 1994; Bossart & Pashley Prowell 1998) such as the microsatellites markers studied here should be preferred.

To conclude, a social structure involving resident males and females, the exclusion of immigrants and limited dispersal due to the patchy distribution of suitable habitat promote strong genetic subdivision and inbreeding in urban stray cats. However, as these colonies are relatively small it is difficult to distinguish between the effects of genetic drift and limited dispersal. Such structuring of the population into genetically heterogeneous small groups might have exposed a greater proportion of the genome to selection (Wright 1980), rapidly purging deleterious recessives, and may have provided the means by which the species has been able to adapt to the urban environment. Both coat colour and microsatellite markers performed well in detecting the effect of cat social organization on genetic variability but microsatellites should be preferred to describe the genetic structure. However, the existence of a link between some coat colour genetic markers and individual life history traits (Pontier *et al*. 1995, 1998) offers a unique opportunity to understand the selective processes in progress in this species in the different types of environment colonized.

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