

# Molecular and behavioural analyses reveal male-biased dispersal between social groups of domestic cats<sup>1</sup>

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**Abstract:** We investigated the natal dispersal pattern between social groups within an urban colony of domestic cats, *Felis catus*, using both population assignment index for multilocus microsatellite genotypes and behavioural observations. Males had a significantly lower assignment index than females, suggesting a male-biased dispersal between social groups, as expected for a polygynous/promiscuous mating system. Behavioural observations were highly consistent with a male-biased dispersal pattern and also showed that natal dispersal is rare within this colony. Details of the analysis, combined with previous results from this species, revealed that the sexes probably disperse at different spatial scales. Females disperse over greater distances outside the colony, whereas males disperse between social groups within the colony. **Keywords:** *Felis catus*, genetic assignment, natal dispersal, sex bias.

**Résumé :** Nous avons étudié le patron de dispersion après la naissance des groupes sociaux composant une colonie de chats errants, *Felis catus*. Nous avons utilisé, d'une part, un indice d'appartenance à une population basé sur les génotypes individuels à plusieurs loci microsatellites et, d'autre part, les localisations des individus au cours de sessions de captures successives. Les mâles ont un plus petit indice d'appartenance au groupe social dans lequel ils ont été échantillonnés que les femelles. Ce résultat suggère une dispersion plus importante des mâles et est en accord avec les attentes théoriques pour un système d'appariement de type polygyne/promiscuiste. Les observations comportementales supportent également l'hypothèse d'une dispersion plus importante chez les mâles mais révèlent que la dispersion est rare dans cette colonie après la naissance. Certains détails de l'analyse combinés à des résultats antérieurs révèlent que mâles et femelles ne se dispersent probablement pas à la même échelle spatiale : les femelles quittent la colonie tandis que les mâles se dispersent entre les groupes sociaux composant la colonie.

**Mots clés :** assignation génétique, biais sexuel, dispersion, *Felis catus*.

**Nomenclature:** Nowak, 1991.

## Introduction

Sex-biased dispersal has received a lot of interest in the last two decades, and many comparisons covering a wide range of taxa in mammals and birds have shown large intra- and inter-specific variability in patterns of dispersal (Greenwood, 1980; Dobson, 1982; Chepko-Sade & Halpin, 1987; Pusey & Packer, 1987; Johnson & Gaines, 1990; Stenseth & Lidicker, 1992; Waser, 1996; Van Vuren, 1998; Clobert *et al.*, 2001). These results came from two main methods of dispersal estimation (Slatkin, 1985): direct observations from long-term monitoring of marked animals (reviewed by Bennetts *et al.*, 2001) and indirect estimation based on genetic data (reviewed by Prugnolles & De Meuwis, 2002).

Feral cats are well suited for combining both demographic and genetic approaches of dispersal study at different spatial scales, because cats show a large flexibility of social and spatial structure depending on the environment (Liberg, 1980; Say, Pontier & Natoli, 1999; Liberg *et al.*, 2000). Such a variability leads to distinct dispersal

patterns (Liberg *et al.*, 2000; Devillard, Say & Pontier, 2003). Previous results in the urban environment suggested that strong constraints, such as clumped distribution of abundant food resources and high traffic roads, lead to a weak dispersal among cat colonies and that females predominantly disperse at this scale (Devillard, Say & Pontier, 2003 take a demographic approach). This result is unexpected for a promiscuous/polygynous mammal species (Greenwood, 1980; Dobson, 1982; Perrin & Goudet, 2001). However, urban cat colonies are generally structured into several spatially distinct social groups organized around feeding points (called feeding groups; Izawa, Doi & Ono, 1982; Yamane, Ono & Doi, 1994; Say, 2000), and the dispersal pattern between social groups within a colony had not yet been studied in this species.

Here, we analysed the dispersal pattern within a structured urban colony of domestic cats using both a genetic approach based on multilocus microsatellite genotypes and a behavioural approach using resighting of individuals during successive trapping occasions. The number of works using a genetic approach to study dispersal processes has increased rapidly since the work of Paetkau *et al.* (1995). In their paper, the authors proposed the use

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of an assignment index ( $AI$ ) to determine the geographical origin of animals based on their multilocus genotype. Favre *et al.* (1997) extended the method and provided a test for sex-biased dispersal dealing with the sex-specific mean values of  $AI$  across populations. Their test is based on allelic frequencies; it has been argued that Bayesian methods of  $AI$  estimation perform better than the original frequency-based methods (Rannala & Mountain, 1997; Cornuet *et al.*, 1999; Pritchard, Stephens & Donnelly, 2000; Manel, Berthier & Luikart, 2002). Whatever the method of estimation, all assume that sex-biased dispersal occurs between distinct geographical populations if an inter-sexual difference in the mean  $AI$  value exists for the population in which animals were sampled. We applied the Favre *et al.* (1997) approach to assess the dispersal pattern between the two social groups of the urban colony under study. Accordingly, with the promiscuous mating system shown by urban cat colonies (Natoli & De Vito, 1991; Yamane, 1998; Say, Pontier & Natoli, 1999), we expected a lower mean  $AI$  value for males than for females, indicating a male-biased natal dispersal pattern between social groups within the colony. In addition, we tested whether genetic results are in agreement with behavioural observations.

## Methods

### THE STUDY COLONY

Our study was conducted in the Croix-Rousse Hospital park in the centre of Lyon (France). This urban cat colony resides in a 7.2-ha park bounded by walls, buildings, and busy roads (Figure 1), leading to a weak dispersal among colonies (Devillard, Say & Pontier, 2003). Cats were mainly fed with canteen surplus by the hospital staff at specific locations. Groves and the basement of the hospital are used as shelters by the cats. The spatial distribution of food resources and shelters, as well as the presence of a large trench, resulted in a spatial differentiation between two social groups of cats in the hospital area: the north group and the south group, located about 500 m away from each other. Cats have been monitored for demography and spacing pattern since 1993 (Courchamp, 1996; Say, 2000) and were live-trapped using double-door metal traps in March and in September. The Croix-Rousse colony was nearly closed to immigration, as sug-

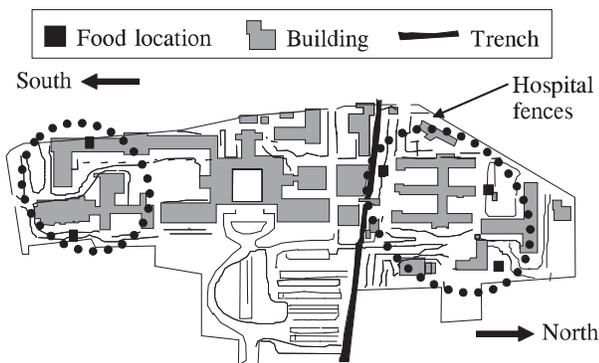


FIGURE 1. Croix-Rousse hospital map. Dotted lines show the locations of the two social groups within the colony.

gested by the low number of permanent immigrants into the colony during the study period (fewer than 10 individuals in 9 y, mainly surgically sterilized individuals).

During each trapping session, hair samples were taken after cats were anaesthetized with an intramuscular injection of Ketamin Chlorhydrat (Imalgène 1000 15 mg·kg<sup>-1</sup>, Rhône Merieux, Lyon, France) and Acepromazin (Vétranquil 5.5% 0.5 mg·kg<sup>-1</sup>, Sanofi, Paris, France). A permanent subcutaneous electronic device (TROVAN transponder, AEG & TELEFUNKEN Electronic, Weilerswist, Germany) and a coloured collar were fitted at first capture for subsequent identification of each individual. Previous results showed that the mating system is promiscuous (Say, Pontier & Natoli, 1999), and that relationships between members of the colony were mainly amicable, with a low level of aggressiveness (Say, Pontier & Natoli, 2001). Moreover, few behavioural interactions occurred between members of the two social groups (Say, 2000; S. Devillard, unpubl. data), and home-ranges of the cats belonging to different social groups overlapped little (Say, 2000), as shown in other colonies (Izawa, Doi & Ono, 1982).

### GENOTYPING INDIVIDUALS

Because the test for sex-biased dispersal assumes that individuals are sampled after juvenile dispersal (Favre *et al.*, 1997; Goudet, Perrin & Waser, 2002), we recorded the north/south location of each individual at their first capture as an adult (animal > 1-y old) during 4 y (1994–1998). Only 10 individuals, five females and five males, temporarily dispersed (*i.e.* were trapped only once in the social group where they were not born) during the entire study period (1993–2002), suggesting strong fidelity to the social group as adults (Say, 2000). For all the individuals, DNA was extracted from hair samples 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 (M. A. Menotti-Raymond, pers. comm.). The PCR products were resolved on a denaturing polyacrylamide gel on a Pharmacia Automatic sequencer (ALFexpress, Buckinghamshire, England). Data collection and analysis were done using Fragment Manager software supplied with the sequencer. The genotype of each individual was determined at each of the nine loci (details in Say, Pontier & Natoli, 1999).

### STATISTICAL ANALYSIS

#### GENETIC ANALYSIS

Allele frequencies, observed ( $H_o$ ) and expected heterozygosity ( $H_s$ ), and mean number of alleles per locus were calculated for the whole colony. Genotypic proportions within each of the two social groups of the colony were compared to their Hardy-Weinberg expectations with a randomization test (1,800 randomizations), and we calculated the multilocus  $F_{is}$  values according to Weir and Cockerham (1984). We also evaluated the between-social-groups differentiation by calculating  $F_{st}$  (Weir & Cockerham, 1984), using the log-likelihood statistic  $G$  over loci (Goudet *et al.*, 1996). Between-sex difference in  $F_{is}$ , calcu-

lated for the whole colony, and between-sex difference in  $F_{st}$  were also assessed. Calculations and statistical tests were done using the randomization-based tests implemented in the program FSTAT 2.9.3.2 (Goudet, 2001). In accordance with Goudet, Perrin, and Waser (2002), we expected both a lower  $F_{st}$  and a higher  $F_{is}$  for males than for females.

The between-social-groups dispersal pattern was assessed using the assignment index  $AI$  (Paetkau *et al.*, 1995; Favre *et al.*, 1997; Goudet, Perrin & Waser, 2002) calculated from the multilocus genotype of each individual using GENECLASS software (Cornuet *et al.*, 1999). We calculated  $AI$  by applying the partially Bayesian method, which performs better in situations where there are many rare alleles (Rannala & Mountain, 1997). We used the “leave one out” method, which removed each individual from a given data set to calculate the allele frequencies in this data set. We standardized  $AI$  to  $A_{Ic}$  by log-transforming the data and subsequently subtracting the mean of the social group from which the individual was sampled to allow us to compare social groups. Thus,  $A_{Ic}$  values averaged zero for each social group, and individuals having lower probabilities than average to be born in the social group were characterized by negative values of  $A_{Ic}$ . Under male-biased dispersal, we expected that males would show a lower mean  $A_{Ic}$  than females for a given social group (Favre *et al.*, 1997; Goudet, Perrin & Waser, 2002). Moreover, a higher variance of  $A_{Ic}$  was also expected in the dispersing sex, because a mixture of philopatric and emigrant individuals should occur in the dispersing sex. We calculated the  $A_{Ic}$  values for each social group separately. We then tested for between-sex differences in mean and variance  $A_{Ic}$  values, first with mean and variance of  $A_{Ic}$  calculated for the pooled social groups and then with mean and variance calculated for each social group separately. We used the Wilcoxon test and the  $F$ -ratio test (SPLUS software, Venables & Ripley, 1999), respectively for mean and variance tests.

#### BEHAVIOURAL ANALYSIS

Throughout the study period (1993-2002), we recorded the social group at birth and location of first capture as adult (at most 6 months after their sexual maturation: 8 months for females, 12 months for males; Say, Pontier & Natoli, 1999) of 111 individuals. We estimated the natal dispersal rate in each sex as the proportion of individuals who changed social group before and after their sexual maturation.

## Results

#### GENETIC ANALYSIS

We typed 109 adult cats for nine polymorphic loci, 24 females and 22 males in the south group and 33 females and 30 males in the north group. Substantial variation occurred at each locus with respect to number and frequencies of alleles and observed  $H_o$  and expected  $H_s$  heterozygosity (Table I). We showed a slight differentiation between the two social groups ( $F_{st} = 0.009$ ,  $P = 0.001$ ). The south group showed a significant deficit in heterozygosity ( $F_{is} = 0.055$ ,  $P = 0.019$ ) contrary to the north group ( $F_{is} = 0.029$ ,  $P = 0.11$ ).

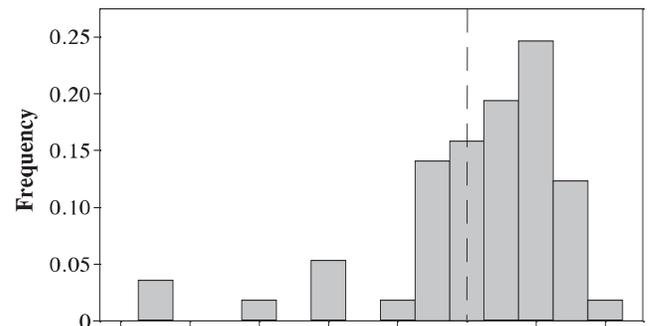
Males had a significantly lower mean  $A_{Ic}$  than females (mean  $\pm$  SE:  $-0.41 \pm 2.45$  and  $0.37 \pm 2.72$ , respectively; Wilcoxon test, one-tailed  $P = 0.007$ , Figure 2), whereas no between-sex difference occurred in the variance of  $A_{Ic}$  (one-tailed  $P = 0.77$ ) when the two social groups were pooled. In agreement with the  $A_{Ic}$  results, males had a lower  $F_{st}$  than females ( $P = 0.027$  for the between-sex difference;  $F_{st} = 0.003$ ,  $P = 0.43$  for males versus  $F_{st} = 0.018$ ,  $P = 0.002$  for females). Contrary to what is expected,  $F_{is}$  (0.043 for males versus 0.037 for females,  $P = 0.43$ ) did not differ between sexes when data were pooled for the two social groups. Although the results are not significant, the same trends are shown when between-sex differences in mean and variance of  $A_{Ic}$  were tested in each social group separately (Table II).

However, two females in the north group and one male in the south group presented extremely low  $A_{Ic}$ ,

TABLE I. Number and frequency of alleles per locus and observed  $H_o$  and expected  $H_s$  heterozygosity per locus for the whole population.

Locus	Number of alleles [range of allele frequencies]	$H_o$	$H_s$
Fca8	12 [0.005-0.384]	0.714	0.794
Fca23	11 [0.005-0.584]	0.575	0.610
Fca37	8 [0.005-0.412]	0.719	0.714
Fca43	8 [0.005-0.280]	0.730	0.792
Fca45	9 [0.014-0.406]	0.659	0.771
Fca77	7 [0.009-0.495]	0.639	0.677
Fca78	9 [0.005-0.272]	0.788	0.808
Fca90	7 [0.005-0.335]	0.819	0.794
Fca96	9 [0.009-0.653]	0.602	0.558

#### a) Females



#### b) Males

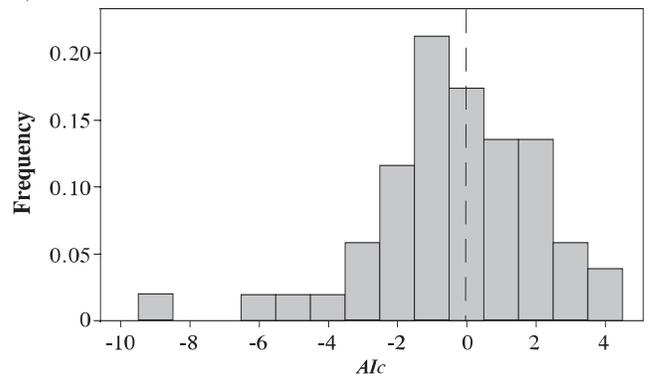


FIGURE 2. Frequency distributions of  $A_{Ic}$  for a) females and b) males for the overall colony after pooling the  $A_{Ic}$  values for the two social groups.

TABLE II. Between-sex differences in mean and variance of *Aic* values for each social group.

Social group	North		South	
	Mean	Variance	Mean	Variance
Males	-0.363	5.30	-0.474	7.28
Females	0.333	8.85	0.435	5.71
<i>P</i> -values	0.29	0.91	0.087	0.035

which could suggest these individuals are long-distance immigrants from a non-sampled colony (Figure 2). Because of the low sample size, these three particular individuals had a high weight in mean and variance values of *Aic* and thus could bias the results. Performing the analysis without these three individuals led to the same conclusions as above for the mean ( $P = 0.004$ ) as well as for the variance ( $P = 0.37$ ) of *Aic* when the two social groups were pooled.

#### BEHAVIOURAL ANALYSIS

Among the 111 cats (54 males and 57 females) for whom we recorded both the social group at birth and the social group to which they belonged soon after their sexual maturity, 15 dispersed. Thirteen were males and two were females. Males had a higher dispersal rate than females over the study period (0.241 *versus* 0.035,  $\chi^2 = 10.8$ ,  $P = 0.001$ ).

### Discussion

Both genetic and behavioural results showed a male-biased dispersal pattern between the two social groups in this promiscuous cat colony. In addition, natal dispersal rates were low over the study period, as shown by the behavioural data. To our knowledge, the *Aic* approach is typically used between populations rather than between groups within a population as we used it in this cat colony. Here, we were able to detect a male-biased dispersal without a strong apparent genetic differentiation between the two social groups within the colony ( $F_{st} = 0.009$ ). This general pattern seems replicated in the two social groups (Table II) and confirmed by the behavioural observations. Genetic differentiation between groups, *i.e.*, high  $F_{st}$  and weak, but biased dispersal are the main conditions for the *AI* to perform well (Cornuet *et al.*, 1999; Goudet, Perrin & Waser, 2002; Manel, Berthier & Luikart, 2002) and thus to detect sex-biased dispersal. The violation of these conditions could lead to the assignment of some individuals in one or the other group simply by chance. In this respect, a low genetic differentiation should be conservative when testing for a sex-biased dispersal. Although low, the  $F_{st}$  value between the two social groups is significant when tested with the *G*-test (Goudet *et al.*, 1996), probably because we used nine highly variable microsatellite loci (Wright, 1978; Charlesworth, 1998; Balloux & Lugon-Moulin, 2002) with a large genetic sample (more than 50 individuals per sex). The biological meaning of a low but significant  $F_{st}$  should be always questioned because of the extreme statistical power of randomization-based tests (Goudet *et al.*, 1996).

Permanent immigration events into the colony being rare, as suggested by the fact that only three individuals were assumed to be immigrants (Figure 2) and by the

long-term monitoring of this colony (Say, 2000), our results can thus be viewed as a consequence of dispersal events within the colony rather than immigration from non-sampled colonies. Natal dispersal between the two social groups appears to be male-biased, in agreement with the theoretical expectation for a promiscuous/polygynous mating system (Greenwood, 1980; Dobson, 1982; Perrin & Goudet, 2001). This male bias is nonetheless surprising in light of the low level of local mate or resource competition between males in this colony (Say, Pontier & Natoli, 1999; 2001). Indeed, high-ranking males do not defend access to females, and young males can successfully reproduce as soon as they reach physiological sexual maturity, leading to a high rate of multi-paternity in high-density urban colonies (Natoli & De Vito, 1991; Yamane, Doi & Ono, 1996; Say, Pontier & Natoli, 1999; 2001). Inbreeding avoidance could thus play a role, and future field investigations are needed in this area.

Contrary to what is expected for a male-biased dispersal pattern (Favre *et al.*, 1997; Goudet, Perrin & Waser, 2002), no between-sex differences occurred in *Fis* values and variance of *Aic*. As in other species (like the white-footed mouse, *Peromyscus leucopus*: Mossman & Waser, 1999), the absence of a between-sex difference in the variance of *Aic* suggests that the two sexes disperse. In the domestic cat, the two sexes may not disperse at the same spatial scale, females dispersing further than males. Indeed, previous results have shown that females are the predominant dispersers outside the colony, probably in response to a higher level of local resource competition between matriarchies for shelters and parturition sites, which appear to be limiting resources (Yamane, Ono & Doi, 1994; Devillard, Say & Pontier, 2003). A similar dispersal pattern has recently been shown in river otters, *Lontra canadensis* (Blundell *et al.*, 2002), another social carnivore where both sexes are mainly philopatric but with shorter and more frequent movements by males and longer and less frequent movements by females. A between-sex difference in the social and spatial structures in this species leads to a gender effect in mean dispersal distances (Blundell *et al.*, 2002), because females have to move further than males to find vacant habitats. Such results in river otters and cats underline the necessity to take into account different spatial scales to describe the dispersal pattern in a population. Several authors have suggested that long-distance dispersal events are often missed (Koenig, Van Vuren & Hooge, 1996), but increasing the spatial scale of the study to have a better understanding of dispersal could also lead to missing fine-scale dispersal events when populations are sub-divided.

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