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The mating system of feral cats (*Felis catus* L.) in a sub-Antarctic environment

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Abstract In order to investigate the mating system of domestic cats living in a sub-Antarctic environment, we sampled 40 kittens belonging to 13 litters (from 9 mothers) in the main island of Kerguelen archipelago. We genotyped females and kittens using nine microsatellite markers. Contrary to what has been found in environments under strong human influence where the mating system is polygynous or promiscuous, and where male cats were in general not able to control the access to receptive females, results show that kittens from the same litter were sired by only one male in the Kerguelen population. It is hypothesised that this pattern is the closest to that of the original environment of adaptation.

Introduction

The study of mammalian mating systems based on behavioural observations has revealed the existence of a large variability in mating tactics both within and between populations of a given species (Lott 1991). In the domestic cat (*Felis catus* L.), the mating system ranges from promiscuity to polygyny (Say et al. 1999) according to environmental conditions. At high densities (up to 3,000 cats/km^2, Liberg et al. 2000), cats in the urban environment live in fairly large social groups on small but largely overlapping home ranges (Liberg et al. 2000; Say 2000). Dominant males are not able to monopolise the receptive females, leading to a promiscuous mating system in which both males and females copulate with several mates at each oestrous period (Natoli and De Vito 1991). This promiscuous mating system is then characterised by a high rate of multiple paternity within litters (up to 83%, Say et al. 1999). At low density (100–300 cats/km^2, Liberg et al. 2000), males of rural populations live in individual large home ranges that overlap those of 2 or 3 females (Pontier and Natoli 1996; Liberg et al. 2000). Resident males defend the access to oestrous females during the reproductive period (Liberg 1981), leading to a polygynous mating system (Pontier and Natoli 1996; Say et al. 1999). Nevertheless, as satellite males sometimes copulate with females in the absence of the resident male (Liberg 1981), multiple paternity occurs, but at a low rate (22% of litters, Say et al. 1999).

Domestic cats do not live only in areas under strong human influence. They have been introduced, deliberately or accidentally, in several sub-Antarctic islands, where they represent one of the most important threats to many seabirds reproducing on these islands (Jouventin et al. 1984; Johnstone 1985). This species was introduced to the Kerguelen archipelago in 1951 (Derenne 1976) to control pest species (rabbits, *Oryctolagus cuniculus*, and rodents, *Mus musculus*). Cat density on the main island, around 1.5 cats/km^2 (Say et al. 2001), is one of the lowest reported for a feral population (Liberg et al. 2000). Males and females live in large individual and, for the most of the time, non-overlapping home ranges, as have been hypothesised in other low-latitude insular cat populations (Derenne and Mougin 1976; Jones 1977; van Aarde 1979) and reported for different species of wild small Felidae (Liberg et al. 2000) such as the European wild cat *F. silvestris* (Stahl 1986). Such conditions provide a unique opportunity to analyse the mating system in a cat population living independently from humans, thereby permitting a complete description of intraspecific mating pattern

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variability in this species. Given the very low density of the cat population and their solitary habits on the main island, we can expect competition for access to females through agonistic encounters to be lower than in the rural higher-density cat populations. Accordingly, females in Kerguelen should have less opportunity to mate with several males than females in rural environments. As a result, we expect to find a low rate of multiple paternity in the Kerguelen cat population. Here, by using microsatellite markers, we investigated if multiple paternities occurred in 13 litters (40 kittens) born on the main island of the Kerguelen archipelago.

Materials and methods

Kerguelen archipelago (48°28′–50°S, 68°28′–70°35′E) is in the sub-Antarctic area of the Southern Indian Ocean and is composed of a 6,600 km^2 main island, partly covered by an ice-cap, and over 300 islands and islets making a total surface of 7,200 km^2. It is of volcanic origin, experiencing low temperatures (the mean annual temperature is 4.6°C, Météo-France Port-aux-Français, 1951–1999 records), high precipitation (the total annual rainfall is <800 mm in the eastern part of the main island) and strong winds. Cats have colonised the main island from the research station of Port-aux-Français where a few cats (less than ten) were introduced (Derenne 1976). They are now widely distributed over the main island except in the southwestern part and above 200 m (Derenne 1976) where rabbits are not present because vegetation is sparse or absent. The actual population size is estimated to be around 7,000 individuals (Say et al. 2002). Cats utilise burrows as shelters and hunt solitarily, mainly rabbits and some birds species (*Pterodroma lessonii*, *Procellaria aequinoctialis*, *Pygoscelis papua*, *Pachyptila desolata*) (Pontier et al. 2002). In two sites of the main island (Port-aux-Français, "PAF", and Ratmanoff, "RAT"), 126 (60 males, 66 females) and 37 (20 males and 17 females) adult cats, respectively, have been captured using baited traps since 1996, and then released. Thirteen litters (8 from PAF and 5 from RAT) with a total of 40 kittens were born to 9 females in 1999 and 2000. Litter size varied from 2 to 6 (3.08 ± 1.14). Cat fur was collected from all 40 kittens belonging to 13 litters and from all mothers. Intensive observations on pregnant females during the last days of pregnancy allowed us to be sure of capturing complete litters. Kittens were captured in the burrows where they were delivered, and were collected within 24 h after they were born. In addition, tissues were collected from three pregnant females (and their foetuses) that had been killed by hunters.

Total DNA from the hair 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 and O'Brien 1995) and fca37 (M.A. Menotti-Raymond, personal communication). 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 according to the locus. PCR products were resolved on a 6% denaturing polyacrylamide gel on a Pharmacia Automatic Sequencer (ALFexpress). Data collection and analysis were carried out using Fragment Manager software supplied with the sequencer. More details are given in Say et al. (1999).

No case of inaccuracies in assignment of maternity by genetic analysis was encountered, suggesting that errors in the typing process were infrequent. To search for potential fathers among the sampled males, paternity of each kitten was assigned using genetic data through a paternity exclusion procedure performed with the CERVUS software (Marshall et al. 1998). The CERVUS program carries out a likelihood-based parentage analysis, testing the confidence of each parentage using the results of a simulation analysis. For each offspring tested, an LOD score [i.e. the log (to base e) of the product of the likelihood ratio at each locus] is calculated for each candidate parent; a positive value of LOD score indicates that the candidate parent is more likely to be the true parent than an arbitrary, randomly chosen individual. The difference between the two most likely candidate parents, called Delta, is then used to assess the reliability of assigning parentage to the most likely candidate parent, by comparing it against the Delta distributions obtained by the simulation. CERVUS provides two critical values of Delta corresponding to the 80% and 95% levels of confidence. Additionally, the CERVUS computation program estimates the exclusion probability for each locus (*Pe*) according to formulae given by Chakraborty et al. (1988), as well as the cumulative power of exclusion (*PE*) for all the microsatellite loci.

We tested whether the rate of multiple paternity in Kerguelen varied significantly from that estimated in a rural cat population (22%, 31 litters, Say et al. 1999) using a Fisher exact test on a 2×2 contingency table.

Results

Genetic diversity among adults in the two sites was relatively large: the mean number of alleles per locus was 7.11 and 4.89, and mean heterozygosity was 0.51 ± 0.09 and 0.57 ± 0.11, respectively in PAF and RAT. The exclusion probability for each locus (*Pe*) and the cumulative power of exclusion for the nine loci (*PE*) are shown in Table 1. The most informative loci were *fca8*, *fca37* and *fca43*. These loci had the largest number of alleles

Table 1. Information of polymorphic markers for analysis of cat populations: number and range size (in bp) of alleles per locus, observed heterozygosity, exclusion probability for each locus (*Pe*) and cumulative power of exclusion for all the microsatellite loci (in **bold**, *PE*)

Port aux Francais					Ratmanoff				
Locus	Alleles	Size-range (bp)	Heterozygosity	Pe	Locus	Alleles	Size-range (bp)	Heterozygosity	Pe
fca8	11	117–151	0.541	0.577	fca8	5	125–139	0.707	0.508
fca23	8	120–150	0.418	0.478	fca23	6	132–150	0.524	0.320
fca37	9	131–147	0.594	0.569	fca37	7	133–147	0.762	0.512
fca43	8	120–152	0.682	0.590	fca43	6	120–134	0.619	0.487
fca45	6	152–162	0.415	0.445	fca45	5	152–160	0.357	0.318
fca77	6	138–148	0.511	0.562	fca77	5	140–148	0.619	0.394
fca78	5	185–201	0.396	0.230	fca78	3	193–201	0.548	0.182
fca90	7	91–141	0.522	0.491	fca90	4	91–115	0.512	0.359
fca96	4	202–210	0.401	0.269	fca96	3	202–208	0.500	0.301
	Mean 7.11		**Mean** 0.510	**PE** 0.997		**Mean** 4.89		**Mean** 0.572	**PE** 0.987

Table 2. Genotype of mothers and kittens. Alleles are identified by their size (e.g. "135139" corresponds to an individual heterozygote as the studied locus carries on the alleles "135" for 135pb and "139" for 139pb). Partial genotype of fathers is also indicated

Litter	Site		locus8	locus23	locus37	locus43	locus45	locus77	locus78	locus90	locus96
1	PAF	mother A	135139	138138	141141	122128	154158	144144	193193	091113	208208
		kitten1	135139	138138	135141	122122	154158	144144	193193	091091	208208
		kitten2	135135	138138	137141	122128	158158	144148	193193	113113	208208
		kitten3	135139	138138	137141	122122	158158	144144	193193	113113	208208
		kitten4	135139	138138	135141	122122	158158	144148	193193	091115	208208
		father	135 –	138 –	135137	122 –	158 –	144148	193 –	091115	208 –
2	PAF	mother A	135139	138138	141141	122128	154158	144144	193193	091113	208208
		kitten1	139139	120138	141141	122128	154156	144148	193199	091091	208208
		kitten2	139139	138138	141141	122122	156158	144148	193199	091091	208208
		father	139 –	120138	141 –	122 –	156 –	148 –	199 –	091 –	208 –
3	PAF	mother A	135139	138138	141141	122128	154158	144144	193193	091113	208208
		kitten1	135135	134138	137141	120128	154158	144148	193199	091091	208208
		kitten2	135135	134138	141143	120128	154158	144148	193199	091113	208208
		kitten3	135135	134138	141143	120122	158158	140144	193199	091091	206208
		kitten4	135135	138138	141143	120122	154158	140144	193193	091091	206208
		kitten5	135135	134138	141143	122128	158158	140144	193199	091113	206208
		kitten6	135135	134138	137143	122128	154158	144148	193199	113113	208208
		father	135 –	134138	137143	120 –	158 –	140148	193199	091113	206208
4	PAF	mother A	135139	138138	141141	122128	154158	144144	193193	091113	208208
		kitten1	123139	138138	137141	122128	154158	144144	193193	091113	206208
		kitten2	123139	138138	137141	128128	158158	144144	193193	113113	202208
		kitten3	123139	138138	141143	128128	158158	144148	193193	113113	202208
		kitten4	139139	138138	137141	122128	154158	144148	193193	113113	206208
		father	123139	138 –	137143	128 –	158 –	148 –	193 –	113 –	202206
5	PAF	mother B	125137	138138	137143	120122	154158	144148	193193	091101	208208
		kitten1	125139	138150	137137	120128	158158	142148	193199	091091	206208
		kitten2	125139	138150	137143	122122	158158	148148	193193	101113	206208
		father	139 –	150 –	137(137/143)	122128	158 –	142148	193199	91113	206 –
6	PAF	mother C	125137	136136	141141	120122	152156	142142	193193	091113	208208
		kitten1	125137	136138	137141	122126	156156	142148	193193	113113	208208
		kitten2	137137	136138	137141	120122	156156	142148	193193	091113	208208
		kitten3	137137	136138	137141	122126	156156	142142	193199	091113	208208
		father	137 –	138 –	137 –	(120/122)126	156 –	142148	193199	113 –	208 –
7	PAF	mother C	125137	136136	141141	120122	152156	142142	193193	091113	208208
		kitten1	137137	136136	141141	122128	156156	142148	193193	091113	208208
		kitten2	137137	136136	141141	122128	156156	142148	193199	091113	208208
		kitten3	137137	136136	141141	120134	152158	142148	193199	113113	208208
		kitten4	137137	136136	141141	120134	152158	142148	193199	113113	208208
		father	137 –	136 –	141 –	128134	156158	148 –	193199	113 –	208 –
8	PAF	mother D	135139	138138	137141	122122	158158	144144	193193	113113	208208
		kitten1	135135	138138	137143	122128	158158	144148	193193	091113	208208
		kitten2	135135	138138	137137	120122	158158	140144	193199	091113	208208
		father	135 –	138 –	137143	120128	158 –	140148	193199	091 –	208 –
9	PAF	mother E	135135	138138	137141	122128	158158	144148	193193	113113	208208
		kitten1	135135	134138	137137	120122	158158	144148	193199	091113	206208
		kitten2	135135	138138	137137	120122	158158	144148	193193	113113	208208
		kitten3	135135	134138	141143	120122	158158	144148	193193	091113	208208
		father	135 –	134138	137143	120 –	158 –	(144/148) –	193199	091113	206208
10	RAT	mother F	135135	138138	143147	128134	158158	140146	193199	091115	208208
		kitten1	135139	138142	143147	122128	156158	140142	193199	091113	208208
		kitten2	135135	138142	141147	122128	156158	142146	193199	113115	208208
		father	135139	142 –	141(143/147)	122 –	156 –	142 –	(193/199) –	113 –	208 –
11	RAT	mother G	133137	138150	143143	120122	158158	142144	193199	091113	208208
		kitten1	125137	138138	143143	120128	158158	142148	199199	091115	208208
		kitten2	133139	138150	137143	120128	158158	144148	193199	091115	208208
		kitten3	125133	138150	137143	120128	158158	142148	199199	113115	208208
		father	125139	138 –	137143	128 –	158 –	148 –	199 –	115 –	208 –
12	RAT	mother H	139139	138150	137143	122134	156156	140140	193199	113115	208208
		kitten1	139139	138150	137143	122122	156158	140142	193193	113115	208208
		kitten2	125139	138150	137143	120134	156158	140148	193199	115115	208208
		father	125139	(138/150) –	(137/143) –	120122	158 –	142148	193 –	115 –	208 –
13	RAT	mother I	137137	138138	137143	134134	158158	142148	193199	115115	202206
		kitten1	137137	138138	137139	126134	158158	142148	193199	091115	202202
		kitten2	133137	138150	139143	134134	158158	142142	193193	091115	202208
		kitten3	133137	138150	139143	126134	158158	142148	193201	091115	202208
		father	137 –	138150	139 –	126134	158 –	142 –	193201	091 –	202208

and were characterised by the highest overall heterozygosity. The *PE* reached 0.997 in PAF and 0.987 in RAT (Table 1).

Despite the high cumulative power of exclusion of our 9 loci, the fathers of only 10 kittens (belonging to 3 litters, 1 in RAT and 2 in PAF) were determined reliably: 80% confidence paternities were all secure at 95%. The three different fathers identified each sired all young of a litter. For the other 30 kittens, LOD score values of all candidate fathers were weak, and Delta values did not differ from those obtained for arbitrary, randomly chosen individuals, showing that these kittens were sired by non-sampled males. While paternity has not been assessed for these ten litters, we never found more than two different alleles coming specifically from males within each litter for all loci (Table 2). According to the polymorphism and the number of loci used in our analysis, the existence of multiple paternity is highly improbable. Thus, no case of multiple paternity occurred in any of the 13 litters. This proportion (0%, $N=13$) in Kerguelen was significantly lower than the proportion (22%, $N=31$) of multiple paternity in the rural environment (Fisher exact test, $P=0.035$).

From Table 2, it was possible to determine the partial genotype of the father of each litter. Fathers were indisputably different for ten litters. We could not exclude the possibility that the same non-sampled male sired 3 litters, 1 in 1999 (litter 8, female D) and 2 in 2000 (litters 3 and 9, females A and E, respectively, see Table 2).

Discussion

In spite of the relatively large number of males sampled in each site and the high cumulative power of exclusion of the 9 loci used, paternity has been determined for only 10 (belonging to 3 different litters) of the 40 kittens studied. This result is explained by the large size of the studied areas (approximately 10–15 km^2) which did not permit us to sample all cats (and consequently all putative fathers) living on the 2 sites, and also by the shyness of experienced males (Courchamp et al. 2000) (probably the reproductive males).

The Kerguelen population is the first feral-cat population studied where each litter was sired by only one male. No multiple paternity was detected, unlike cat populations living at higher densities, where the rate of multiple paternity varied from 22% in rural to 83% in urban environments (Yamane 1998; Say et al. 1999). Our results from paternity analyses strongly suggest that in the sub-Antarctic environment, males are able to control the access to receptive females. Thus, the mating system might be polygynous (each male successfully copulates with several females at each oestrus period) as in the rural environment (Say et al. 1999). Nevertheless, while monogamy is not frequent in mammals (Kleiman 1977; Greenwood 1980), several arguments are in favour of a monogamous mating system (each male successfully copulates only with one female at each oestrus period). We repeatedly observed associations between one male and one female during the oestrus period (D. Pontier and L. Say, unpublished data). On the contrary, such behaviour has never been recorded in urban and rural cat populations. Here, we reported only one case where the same male could have monopolised two different females within the same oestrous period. Each of the other 11 litters studied was sired by a different male. Moreover, males living in the Kerguelen archipelago have smaller testes relative to their body mass than males from urban and rural populations (L. Say and D. Pontier, unpublished data), which is also in agreement with a monogamous mating system (Harcourt et al. 1981; Kenagy and Trombulak 1986; Parker 1990a, b). The mating system in the Kerguelen population could thus be confined to monogamy induced by the very low density.

On Kerguelen main island, cats live independently of humans and depend only on natural prey, a context that might be close to the ancestral way of life of cats. Density, social and spatial organisation are different from those reported for urban and rural populations and are closer to those reported for different species of wild, small Felidae, such as the African (*F. lybica*) and European (*F. silvestris*) wild cats (Corbett 1979; Stahl 1986; Liberg et al. 2000), the probable ancestors of the domesticated form (Johnson and O'Brien 1997; Serpell 2000). The study of this population and the results could shed some further light on the evolution of social and mating systems of domestic cats.

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