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ORIGINAL PAPER

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Genetic structure of the feral cat (*Felis catus* L.) introduced 50 years ago to a sub-Antarctic island

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Abstract Information about the invasion dynamics and demographic status of invasive species is essential to choose the optimal control options of population numbers. While long-term direct demographic and historical records are generally lacking, the analysis of the genetic variability of a current population might supply information about past and current demographic processes. In this study, we analysed the genetic variability of the cat population living on the main island of the Kerguelen archipelago. Genetic diversity was consistent with the introduction of a very small number of individuals followed by a demographic explosion of the cat population. Significant genetic structure among sites ($F_{st} = 0.06 \pm 0.005$) and absence of isolation by distance could indicate that the initial phase of fast colonisation is now over. Estimates of individual relatedness indicated a significant kin structure. Overall data suggested that the cat population of the main island has probably reached carrying capacity.

Introduction

Cats (*Felis catus* L.) introduced to sub-Antarctic islands are held responsible for major perturbations of host ecosystems (Nogales et al. 2004). Yet, sub-Antarctic islands are made up by less diversified communities than on the mainland, with simplified trophic webs. Cats have been shown to have the highest detrimental impact on native seabird colonies, especially colonies of ground-nesting species lacking efficient anti-predator behaviour (Pascal 1980; Jouventin et al. 1984; Johnstone 1985). While complete removal of this alien predator has been achieved on several small sub-Antarctic islands (Nogales et al. 2004), a long-term control program of cat numbers is difficult to implement on large and/or remote insular complexes. Moreover, in large islands biodiversity and endemism levels are highest, which complicates the community structure (Zavaleta et al. 2001). Thus, the use of control strategies needs to be placed in the whole ecosystem context to avoid unexpected changes to other ecosystem components when several alien prey and predators have been introduced (Zavaleta et al. 2001; Shea and Chesson 2002; Simberloff 2003). For example, on the Kerguelen Islands, the eradication of cats could have a disastrous effect on some seabird populations due to a possible demographic expansion of the rabbits (*Oryctolagus cuniculus*) (see Soulé et al. 1988; Courchamp et al. 1999). On these islands, rabbits, the major prey of cats (Pontier et al. 2002), have a high impact on soil erosion and then on the ability of burrowing seabirds to nest. Information about the invasion dynamics and demographic status of invasive species is essential to choose the optimal control options of population numbers (Simberloff 2003). Concerning the cat, long-term direct demographic data are generally lacking, and historical information for islands is scattered (Nogales et al. 2004). An analysis of cat population genetic variability might supply information on the current demographic processes (Cavalli-Sforza 1986; Slatkin 1993; Gonser et al. 2000).

Here, we used genetic data and historical information about the invasion of cats on a very large sub-Antarctic island, the main island of Kerguelen archipelago, to assess the current invasion dynamics. More specifically, we investigated whether the cat population has reached a steady state or not. Although several waves of cat importation took place during the ninteenth and early twentieth centuries, most were unsuccessful, so the current cat population is believed to derive from at most four cats introduced in the 1950s (Derenne 1976; Pascal

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1984). Two cats from France were first introduced in 1951 to control rodents (*Mus musculus* and *Rattus* sp.) and rabbits, at the research station of Port-aux-Français, established the year before. The cats disappeared from the station in the following years, but there is no evidence that the species had become extinct. A male cat from Madagascar and a female cat from Cape Town were then introduced at Port-aux-Français in 1956 (Pascal 1984). This latter introduction led to an exponential increase in the number of cats (Pascal 1980). By 1974, 20% of the main island was already colonised. The population size was estimated at 1,750 in 1971, 2,500 in 1974 (Derenne 1976) and 3,500 in 1977 (Pascal 1980), which corresponds to a mean growth rate of 33% per year. The colonisation probably succeeded thanks to the availability of native (seabirds) and also introduced prey (rodents and rabbits), the latter providing an alternative food source all year round (Johnstone 1985; Pontier et al. 2002), and to the absence of competitors and the usual pathogens harmful to cats (Fromont et al. 2001). The impoverished genetic polymorphism for alleles governing coat-colour (Dreux 1974) is consistent with the foundation-explosion scenario described above. All cats carry a black or black and white coat-colour phenotype.

We analysed genetic variability of the Kerguelen cat population at four sites using nine microsatellite loci. It has been hypothesised that the current cat population originated from <4 individuals (Pascal 1984). We first checked for the consistency of this hypothesis by comparing the estimates of mutation rate derived from the observed allelic diversity at microsatellite loci to those usually reported. We further evaluated whether the cat population is still expanding or has reached carrying capacity using traditional genetic differentiation *F*-statistics (Wright 1969). *F*-statistics can indeed be useful in such a test because an absence of correlation of genetic differentiation with geographical distance can reflect either (1) discontinuities in the colonisation process (see Leblois et al. 2000 for an example in cane toad *Bufo marinus* presently colonising Australia) or (2) a spatially or socially structured population (Chesser 1998). In addition, a high genetic similarity of individuals within a site is expected to indicate a structured population. Indeed, within-population genetic differentiation might be the consequence of social and/or spatial structures in a population close to saturation (Chesser 1991a, b).

Materials and methods

Population sample collection

The Kerguelen archipelago is a French territory located 49°20′ S, 70°20′ E in the Southern Indian Ocean. The archipelago is composed of a main island (6,600 km^2) partly covered by an ice cap, and over 300 secondary islands and islets for a total surface of 7,200 km^2. The climate is cold, wet and windy. Temperatures average 1–2°C during the year with the exception of the summer season, which has an average of 8°C (Météo-France, Port-aux-Français). For practical reasons, we collected samples near human settlements

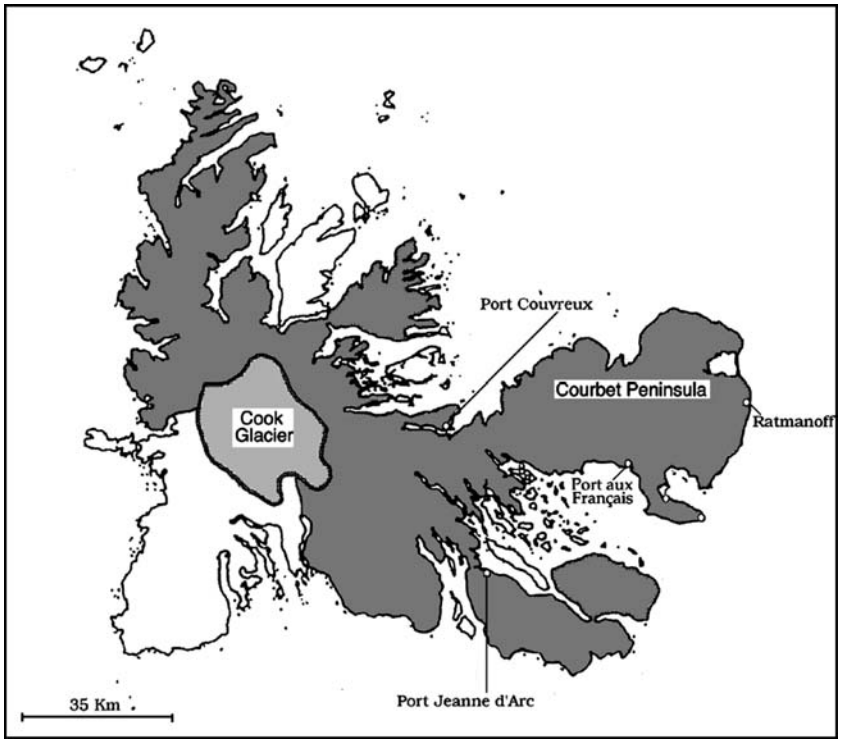

Fig. 1 Location of sampled sites in the main island (Kerguelen, Grande-Terre): Port-Jeanne d'Arc (PJDA), Port-aux-Français (PAF), Port-Couvreux (PCX) and Ratmanoff (RAT). The centre of the island is occupied by an ice cap. The *streaked lines* denote the distribution range of cats on Grande Terre

on the main island (Fig. 1): (1) the Norwegian whaling station Port-Jeanne-d'Arc (PJDA, 21 cats) on the southeastern peninsula was settled in 1920 and used until 1930, (2) the French scientific station Port-aux-Français (PAF, 126 cats) was established in 1950, 100 km northeast of PJDA, following the coastal line, (3) the 1930–1932 farmer settlement of Port-Couvreux (PCX, 8 cats), and (4) Ratmanoff (RAT, 37 cats) on the Courbet peninsula. The pairwise distances between sites range from 20 to 140 km. The short vegetation (tussok grass *Poa cookii*, mosses *Azorella selago* and *Acaena adscendens*) is the same across sites, while sites differ in terms of the number of prey species available (Pontier et al. 2002). All cats were introduced to PAF (Derenne 1976; Pascal 1984; 1995).

Cats were live-trapped between 1994 and 1997, anaesthetised and marked using an electronic device (Transponder). This permanent individual identification ensures that all samples come from different individuals. We collected hair samples from all adult animals. Hair samples were then stored in envelops at current ambient temperature in a dry place.

Isolation and resolution of microsatellite loci

DNA extraction

Total DNA from the hair was extracted using a Chelex-based method. Approximately 15–20 hairs were placed in 500 µl of 10% Chelex resin, 30 µl extraction buffer (pH = 8, 0.1 M EDTA, 0.05 M Tris HCL, 1% SDS) and 15 µl proteinase K (20 mg/ml) in a 1.5-ml tube and incubated for 45 min at 56°C. Extracts were centrifuged at 12,000 *g* for 2–3 min and then incubated for 20 min at 72°C.

Polymerase chain reaction

Selective amplification was carried out by polymerase chain reaction (PCR), using the nine microsatellite primers fca23, fca43, fca45, fca77, fca78, fca90, fca96, fca8 (Menotti-Raymond and O'Brien 1995) and fca37 (M.A. Menotti-Raymond, personal communication). PCR reactions were in a total volume of 20 µl containing 0.13 mM of each primer (one of the locus-specific flanking primers was fluorescently labelled), 1.6 µl of Pharmacia Biotech dNTP (2 mM of each nucleotide), 2 µl of GibcoBRL 10×buffer, 1 µl of GibcoBRL MgCl2 (50 mM), 0.2 µl of GibcoBRL DNA polymerase (5 U/µl) and 5 µl of DNA as described above. PCR was conducted in 96-well microtitre plates using a 9600 Perkin–Elmer thermal cycler. PCR temperature cycles (25–30 cycles: with 94°C/30 s, 55–58°C/30 s depending on locus and 72°C/30 s denaturing, annealing and extension temperatures) were preceded by a denaturation step of 3 min at 94°C and finished by an extension step of 3 min at 100°C.

DNA visualisation

PCR products were resolved on a 25 ml 6% denaturing polyacrylamide gel on a Pharmacia Sequencer at 45°C together with 100 and 300 bp internal size markers (5 fmol/µl). Data collection and analysis, as well as automatic sizing of bands, were performed using the Fragment Manager software supplied with the sequencer.

DNA of all analysed samples was successfully extracted and amplified. Some individuals have been analysed five times to test the reliability of the method.

Mutation rates of microsatellite loci

To check for the consistency of the reported demographic history (foundation-explosion), we derived a rough microsatellite mutation rate estimation from the observed allelic diversity, given the demographic curve of the introduced population, and compared this estimated mutation rate to values found in the literature. Two to four cats are thought to be at the origin of the current cat population (Derenne 1976; Pascal 1984), which corresponds to an initial number of alleles, Y, varying from one (if all founder cats were homozygotes and carried the same allele) to eight (if the four founder cats were heterozygotes and carried different alleles). Under the hypotheses that (1) alleles above Y resulted from new mutations, and (2) all alleles initially present became established within the population [as proposed by Ewens (1979) and Villablanca et al. (1998), exponential growth after a founder event increases the probability of establishment of founder alleles but also the probability of establishment of new mutations], we estimated a mean overall per generation mutation rate for the nine microsatellite loci. This rate is expressed as the ratio of the *per locus* number of newly arisen alleles x to the number of meioses having occurred since foundation in the gene lineages leading to the sample observed:

$$\frac{x}{Gn_{\mathrm{a}}}$$

where n_{a}, the number of independent allelic lineages in the sample, was estimated as $n_{\mathrm{a}} = 2N/(1 + F_{\mathrm{is}})$, N is the number of individuals typed and G is the number of generations. Because of overlapping generations, G was estimated as $50/\overline{T}$ with $\overline{T}$ the generation time (*sensu* Leslie 1966). We took into account extreme estimates of $\overline{T}$ reported for mainland cat populations living in rural environment (3–4 years, Pontier 1984). Fifty represents the maximum number of years since the introduction of cats to Kerguelen Islands (1951). Obviously, Gn_{a} may be overestimated because all allelic lineages were not independent during the very first generations. However, a very fast expansion is likely to have occurred at the beginning (Derenne 1976), so that n_{a} in the third generation, for instance, was likely to be higher than 100 or

more, according to the demography of the species: cats are seasonal polyoestrians with up to two litters of 3–5 kittens each per year, as stated by Derenne (1976). These estimates of mutation rate are imprecise. In particular, they assume an Infinite Allele Model for mutation which leads to an underestimation of mutation rate (under this model, a mutation involves any number of tandem repeats and always results in allelic states not previously encountered in the population, Kimura and Crow 1964) but, if in a reasonable range, they will add support to the foundation-explosion scenario.

Polymorphism analysis

For each of the four sites, linkage disequilibrium was assessed following the method of Black and Krafsur (1985), and tested by 5,000 random permutations over individual genotypes. To correct for multiple tests, *P*-values were adjusted according to the sequential Bonferroni procedure. Within the site, genetic variability was estimated by the mean number of alleles per locus (n_a), as well as heterozygosities observed (H_{cal}) and expected (H_{exp}). We also gave the allelic richness R_s, which is a measure of the number of alleles independent of sample size (El Mousadik and Petit 1996). The allelic richness R_s was estimated according to the rarefaction method (El Mousadik and Petit 1996) as implemented in the program FSTAT 2.9.3 (Goudet 2001). The departure from Hardy–Weinberg Equilibrium (HWE) was estimated by Wright's fixation index F_{is}. We analysed whether groups of related individuals occurring within our samples could explain any departures from panmixia that were encountered. For that purpose, we computed the mean and variance of the *r* coefficient of Queller and Goodnight (1989) expressed at a given locus as

$$r_{xy} = \frac{\sum_j n_{jy}(n_{jy} - 2p_j)}{\sum_j n_{jx}(n_{jx} - 2p_j)}$$

where n_{jx} is the number of copies of allele *j* in individual *x*, p_j the sample frequency of allele *j*, a symmetric estimate being obtained as $1/2(r_{xy} + r_{yx})$, and the multilocus estimate being obtained by weighting as shown in Lynch and Ritland (1999). We tested for departure from the null hypothesis of no kinship between individuals by comparing the values observed with the distribution obtained performing 5,000 permutations of multilocus genotypes, using the Identix2.0 software (Belkhir et al. 2002).

Genetic differentiation across sites was estimated according to the Weir and Cockerham (1984) estimator of among population fixation index F_{st}. Variance of F_{is} and F_{st} over loci and populations was estimated by a Jacknife procedure. Significance of these values was tested by permutations using 5,000 runs. All analyses were performed using GENETIX 4.0 (Belkhir et al. 2000).

Results

Genetic diversity

The nine loci showed no linkage disequilibrium at the four sites, which is not surprising since these loci belong to different linkage groups (Menotti-Raymond et al. 1999). Each microsatellite locus was polymorphic (Table 1), with the number of alleles per locus ranging from 4 (locus fca96) to 11 (locus fca8). The number of different alleles per locus R_s standardised to the smallest sample size ($N = 8$ in PCX) using the rarefaction method (Table 1) did not show large variation of the allelic richness among sites. However, alleles not recorded in the large sample of PAF (the introduction site) were detected in PJDA (one private allele at locus fca90) and RAT (two private alleles at locus fca23). The overall heterozygosity observed was 0.50 ± 0.09 (mean $\pm$ SD) for PAF, 0.52 ± 0.08 for PJDA, 0.53 ± 0.19 for PCX and 0.56 ± 0.12 for RAT (Table 2).

Mutation rates of microsatellite loci

The average number of newly arisen alleles per locus *x* ranges from 6.33 to 0.56 according to our two extreme hypothesised values for *Y* (1 and 8, respectively). The mean IAM mutation rate for the microsatellite loci thus ranges from 1.28×10^{-4} mutations per generation ($x = 6.33$) to 1.45×10^{-3} ($x = 0.56$) mutations per generation ($G = 14$, $N = 192$, multi-locus $F_{is} = 0.23$). Locus-specific estimates of mutation rate vary from 6.40×10^{-4} (fca96) to 2.37×10^{-3} (fca8) with $Y = 1$, and from 0 (all loci but fca8, fca23 and fca37) to 0.71×10^{-3} (fca8) with $Y = 8$.

Relatedness among individuals

The F_{is} values were 0.28 ± 0.001 ($P < 0.0001$) for PAF, 0.17 ± 0.002 ($P < 0.0001$) for PJDA, 0.14 ± 0.007 ($P < 0.0001$) for PCX and 0.11 ± 0.003 ($P = 0.008$) for RAT. Using the same protocol (same microsatellite loci, same number of hairs per individual), no genetic mismatch problem was recorded with the genotype of >350 known mother/young pairs, in a previous parentage study (Say et al. 1999). The null allele or allelic drop-out hypothesis is highly improbable. Thus, F_{is} results show a significant departure from HWE resulting in heterozygote deficiencies (Table 2). Small F_{is} values could be created if locally sampled cats are not a random sample of unrelated individuals, but are made up of one or several groups of kin. The variance of Queller and Goodnight (1989) *r* coefficient was significantly different from its null distribution in the PAF, PJDA and PCX samples (corresponding *P*-values after 5,000 permutations $P < 0.001$ in all cases) but not in the RAT ($P = 0.22$) sample.

Table 1 Allele frequencies, observed (H_{obs}) and expected (H_{exp}) heterozygosities, and allelic richness (R_s) at nine microsatellite loci in four sites located on the main island

N	PAF 126	PCX 8	PJDA 21	RAT 37
fca8				
117	0.004	0	0	0
123	0.07	0.188	0.048	0
125	0.23	0.063	0.143	0.056
129	0.012	0	0	0
133	0.049	0.063	0.048	0.111
135	0.09	0.5	0.191	0.319
137	0.344	0.125	0.429	0.139
139	0.176	0.063	0.143	0.375
143	0.012	0	0	0
145	0.008	0	0	0
153	0.004	0	0	0
n_a	11	6	6	4
H_{exp}.	0.782	0.688	0.735	0.723
H_{obs}.	0.566	0.625	0.619	0.722
R_s	5.626	6	5.144	4.457
fca37				
131	0.021	0	0.024	0
133	0.033	0	0.024	0.014
135	0.113	0.188	0.095	0
137	0.383	0.438	0.571	0.23
139	0.079	0	0	0.23
141	0.217	0.313	0.286	0.135
143	0.104	0.063	0	0.351
145	0.017	0	0	0.014
147	0.033	0	0	0.027
n_a	9	4	5	7
H_{exp}.	0.773	0.672	0.582	0.752
H_{obs}.	0.55	0.5	0.429	0.73
R_s	5.821	4	3.627	4.73
fca45				
152	0.049	0	0	0.027
154	0.16	0	0.119	0.068
156	0.422	0.375	0.381	0.243
158	0.307	0.625	0.476	0.595
160	0.041	0	0	0.068
162	0.021	0	0.024	0
n_a	6	2	4	5
H_{exp}.	0.697	0.469	0.613	0.577
H_{obs}.	0.418	0.25	0.381	0.351
R_s	4.296	2	3.304	3.813
fca23				
132	0	0	0	0.027
134	0.12	0	0	0
136	0.136	0.125	0	0.027
138	0.508	0.813	0.595	0.622
140	0	0	0	0.081
142	0.054	0	0.024	0.027
146	0.054	0	0	0
148	0.017	0.063	0	0
150	0.112	0	0.381	0.216
n_a	7	3	3	6
H_{exp}.	0.69	0.32	0.5	0.558
H_{obs}.	0.43	0.25	0.619	0.487
R_s	5.088	3	2.381	3.934
fca43				
120	0.269	0.063	0.024	0.068
122	0.252	0.313	0.167	0.216
126	0.143	0.063	0	0.041
128	0.202	0.5	0.548	0.257
132	0.042	0	0	0.014
134	0.076	0.063	0.262	0.405
146	0.013	0	0	0
152	0.004	0	0	0
n_a	8	5	4	6
H_{exp}.	0.795	0.641	0.603	0.717
H_{obs}.	0.681	0.875	0.524	0.622
R_s	5.378	5	3.355	4.439
fca77				
138	0.024	0	0	0
140	0.173	0.313	0.167	0.095
142	0.23	0.188	0.333	0.541
144	0.21	0	0	0.054
146	0.073	0.438	0.095	0.068
148	0.29	0.063	0.405	0.243
n_a	6	4	4	5
H_{exp}.	0.783	0.672	0.688	0.632
H_{obs}.	0.484	0.5	0.619	0.595
R_s	4.965	4	3.842	4.174
fca78				
185	0.012	0	0.167	0
191	0.008	0	0	0
193	0.73	0.438	0.643	0.73
199	0.163	0.563	0.191	0.257
201	0.087	0	0	0.014
n_a	5	2	3	3
H_{exp}.	0.433	0.492	0.523	0.401
H_{obs}.	0.397	0.625	0.476	0.541
R_s	3.028	2	2.962	2.212
fca96				
202	0.202	0.625	0.357	0.243
206	0.093	0.063	0.191	0.176
208	0.657	0.313	0.452	0.581
210	0.048	0	0	0
n_a	4	3	3	3
H_{exp}.	0.516	0.508	0.632	0.572
H_{obs}.	0.444	0.5	0.524	0.514
R_s	3.335	3	2.987	2.964
fca90				
77	0	0	0.048	0
91	0.296	0.188	0.167	0.194
93	0.06	0	0	0
101	0.032	0	0	0
111	0.092	0.063	0	0.028
113	0.388	0.5	0.381	0.278
115	0.12	0.25	0.405	0.5
141	0.012	0	0	0
n_a	7	4	4	4
H_{exp}.	0.734	0.648	0.661	0.634
H_{obs}.	0.536	0.625	0.524	0.472
R_s	4.909	4	3.598	3.376

Table 1 (Contd.)

N number of individuals studied, n_a number of alleles for each locus

Population differentiation

Pairwise F_{st} values were all significant and equal to 0.07 ± 0.02 (PAF-RAT, $P < 10^{-3}$), 0.04 ± 0.01 (RAT-PJDA, $P < 10^{-3}$), 0.04 ± 0.01 (PJDA-PAF, $P < 10^{-3}$), 0.08 ± 0.02 (PCX-PAF, $P < 10^{-3}$), 0.05 ± 0.02 (PJDA-PCX, $P < 10^{-2}$) and 0.09 ± 0.02 (RAT-PCX, $P < 10^{-3}$). The extent of genetic differentiation between pairs of sites was not dependent on the geographical distance between them: PAF and RAT, which are the two sites separated by the shortest distance (40 km), exhibited a higher level of differentiation than RAT and PJDA, which are separated by the largest distance (140 km, see Fig. 1). Multilocus F_{st} across all four sites was estimated

Table 2 Average number of alleles per locus (n_a), observed (H_{obs}), and expected (H_{exp}) heterozygosity across loci, F_{is} values for four sites on the main island

N	PAF 126	PJDA 21	PCX 8	RAT 37
n_a	7.00 (2.12)	4.00 (1.00)	3.67(1.32)	4.78 (1.39)
H_{obs}.	0.50 (0.09)	0.52 (0.09)	0.52 (0.20)	0.56 (0.12)
H_{exp}.	0.69 (0.13)	0.62 (0.08)	0.57 (0.13)	0.62 (0.11)
F_{is}	0.28 (0.01)	0.17 (0.03)	0.14 (0.09)	0.11 (0.04)
	$P < 0.001$	$P < 0.001$	$P = 0.07$	$P = 0.002$

Standard error is given in parentheses
N number of cats sampled

to be 0.06 ± 0.005. This value differed significantly from zero ($P < 10^{-3}$).

Discussion

As expected, given the bottleneck at foundation, the genetic variability is lower in the Kerguelen population than in mainland French populations, as measured by the mean number of alleles per locus [7.33 ± 0.75 (SE) in the Kerguelen population versus 8.67 ± 0.50 and 9.11 ± 0.35 reported in Say (2000) for two mainland cat populations with comparable sampling effort, and using the same microsatellite loci]. However, the Kerguelen population showed a remarkably high number of alleles at some loci (up to 11 alleles for fca8). The estimated mean mutation rate of the microsatellite loci studied here (10^{-3}–10^{-4}) falls right in the middle of the range of values generally reported for microsatellite loci (10^{-2}–10^{-5} mutations per generation, Dallas 1992; Weber and Wong 1993; Dib et al. 1996), which is consistent with the foundation-explosion event. The variability in the number of alleles across loci (from 4 to 11) may reflect interlocus discrepancies in initial diversities, mutation rates (Gonser et al. 2000) and/or mutation types. The cat population of the Kerguelen main island thus most probably went through two demographic events of opposite direction: first, a strong bottleneck corresponding to the foundation of the initial population involving very few cats coming from abroad and, second, the subsequent expansion.

Notwithstanding the recent founding event, the sites displayed a significant genetic differentiation ($F_{st} = 0.06$) of magnitude similar to that found in mainland French populations using the same microsatellite markers (F_{st} in [0.06; 0.10], Say 2000). Three possible scenarios for the colonisation of the main island by cats are (1) a fast colonisation from the initial founders, due to a high growth rate of the cat population, together with a high dispersal rate in all directions, (2) a step-by-step progressive colonisation with a low dispersal rate occurring preferentially between neighbouring sites, and (3) a colonisation involving a process of multiple budding; different individuals may have rapidly left the initial founder group and been at the origin of founding events in different parts of the island (Cavalli-Sforza 1986; Leblois et al. 2000). Historical data concerning cat expansion on the main island do not fit the third scenario. Derenne (1976) reported a very fast expansion of cat population, which was continuous and in all directions from the initial site of introduction PAF during the first 20 years. The two remaining scenarios make different predictions on the distribution of the genetic variability within the cat population of Kerguelen: a spatially homogeneous genetic diversity across the main island should result from scenario 1 and persist if a high gene flow between locations exists, whereas allele frequency and genetic diversity gradients are expected with geographic distance under scenario 2 (Malécot 1950; Kimura and Weiss 1964; Slatkin 1993). Our data do not support the second scenario as PAF and RAT, separated by the shortest distance, exhibit a higher differentiation than, for example, RAT and PJDA, which are separated by a much larger distance. Moreover, the founding population PAF is not the most diverse, and RAT is characterised by two alleles absent from PAF. The first scenario describes quite well the first steps of the colonising process in this cat population (Derenne 1976), although the current data do not fit entirely with it because of the existence of a statistically significant genetic structure. This could thus indicate that the initial phase of colonisation (increase of population census size) is now over. All suitable habitats may be now occupied, and prey availability appears as the most likely factor that limits and spatially structures cat numbers (Pontier et al. 2002) as observed on other sub-Antarctic islands (see Johnstone 1985). In these conditions, the genetic structure observed might likely be due to a decrease in the rate (Wright 1951, 1965) and distance of dispersal (Rousset 2001). This may be so because of a reinforcement of the effects of geographic features (such as rivers) that are not strong obstacles to dispersion during the explosion phase but may become efficient barriers once the colonisation process is over, due to a spatial organisation of cats into territories (Wright 1965, 1969) or because of the social structure of the cat population (Chesser 1991a, b; Storz 1999). Immigrants are indeed expected to meet less social resistance in colonising populations than in a spatially and socially structured populations (Pope 1992; Sugg et al. 1996; Say 2000). Social structuring may enhance genetic similarity of individuals creating local genetic substructuring within the populations (Chesser 1991a, b; Say 2000). Although we had a spatially large sampling of adult cats at each site (5–15 km), a part, if not all, of F_{st} values among sites might result from such a social substructuring. The indirect evidence for related individuals in the sample, as highlighted by the mean and variances of the Queller and Goodnight index, reinforces this hypothesis. Moreover, the stability of cat densities over time (around 1.5 cat/km^2, Say et al. 2002) at the different sampling sites suggests that the invasion process is now over. It is expected that because of the reduction of effective migration and social substructuring, genetic

differentiation will slowly build up, while neutral genetic variability will still continue to increase.

From a management point of view, complete cat eradication on a large and inaccessible island such as the Grande Terre of Kerguelen archipelago is a difficult task. Such eradication is especially difficult to achieve because the cat population has now been established for a long time and well spread over the Grande Terre (Simberloff 2003). That this cat population has reached stable numbers with few connections among sites leads to the suggestion that local eradication of cats to protect seabird nesting might be a suitable action.

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