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Linking genetic diversity and temporal fluctuations in population abundance of the introduced feral cat (*Felis silvestris catus*) on the Kerguelen archipelago

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Abstract

Linking temporal variations of genetic diversity, including allelic richness and heterozygosity, and spatio-temporal fluctuations in population abundance has emerged as an important tool for understanding demographic and evolutionary processes in natural populations. This so-called genetic monitoring was conducted across 12 consecutive years (1996–2007) at three sites for the feral cat, introduced onto the Kerguelen archipelago fifty years ago. Temporal changes in allelic richness and heterozygosity at 18 microsatellite DNA loci were compared with temporal changes in the adult population abundance index, obtained by typical demographic monitoring. No association was found at the island spatial scale, but we observed an association between genetic diversity and adult population indices from year to year within each study site. More particularly, the magnitude of successive increases or decreases in the adult population abundance index appeared to be the major factor linking the trajectories of genetic diversity and adult population abundance indices. Natal dispersal and/or local recruitment, both facilitated by high juvenile survival when the adult population size is small, is proposed as the major demographic processes contributing to such an observed pattern. Finally, we suggested avoiding the use of the harmonic mean as an estimator of long-term population size to study the relationships between demographic fluctuations and heterozygosity in populations characterized by strong multiannual density fluctuations.

Keywords: *Felis silvestris catus*, feral cat, genetic diversity, population abundance, temporal variation

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Introduction

Genetic monitoring, *sensu stricto* the quantification of temporal change in population genetic metrics (Schwartz *et al.* 2007), has recently been highlighted as a major topic allowing new insights into demographic and microevolutionary processes in natural populations, complementing the more traditional study of the spatial partitioning of genetic variability. Indeed, temporal changes in genetic structure and diversity are of both fundamental and practical interest to evolutionary biologists as they provide information on the genetic background underlying microevolutionary changes (Lessios *et al.* 1994). Multiple factors can affect the temporal stability of allelic frequencies and genetic diversity, and most of the theoretical models have focused on the genetic consequences of bottlenecks, founder events and large population size fluctuations, stressing the importance of population size on genetic diversity. Resulting from these models, the magnitude of loss of genetic diversity is expected to be directly related to the severity of the decrease in population (Chakraborty & Nei 1977; Hedrick & Miller 1992; Wang & Caballero 1999), and fluctuating or cyclic populations are expected to show more reduced genetic variability than stable

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populations owing to strong genetic drift during the low phases (Nei *et al.* 1975; Wright 1978; Motro & Thomson 1982; Whitlock 1992).

Different approaches have been attempted to evaluate these hypotheses in wild populations of animals by, for example, contrasting the genetic diversity of a given population before and after a documented demographic bottleneck (e.g. Gallardo *et al.* 1995; Busch *et al.* 2007), comparing the genetic diversity of same-species populations with contrasting population sizes and amplitudes of population fluctuations (e.g. Ortego *et al.* 2007; White & Searle 2007; Ehrich *et al.* 2009), but also by carrying out meta- and interspecific analyses (e.g. Frankham 1996). However, results from wild populations are balanced between those supporting and those inconsistent with the theory. Populations known to have experienced a drastic reduction in population size have shown reduced genetic diversity in a number of taxa (e.g. Ethiopian wolf *Canis simensis*, Gottelli *et al.* 1994; tropical butterfly *Drupadia theda*, Gallardo *et al.* 1995; Fauvelot *et al.* 2006; greater prairie chicken *Tympanuchus cupido*, Bouzat *et al.* 1998; African elephant *Loxodonta africana africana*, Whitehouse & Harley 2001; northern elephant seal *Mirounga angustirostris*, Hoelzel *et al.* 2002; lake trout *Salvelinus namaycush*, Guinand *et al.* 2003). There have also been studies where no reduction in genetic diversity was observed (e.g. coyote *Canis latrans*, Williams *et al.* 2003; Kerguelen mouflon *Ovis aries*, Kaeuffer *et al.* 2007; wild striped bass *Morone saxatilis*, Waldman *et al.* 1998; banner-tailed kangaroo rat *Dipodomys spectabilis*, Busch *et al.* 2007; sea trout *Salmo trutta*, Campos *et al.* 2007). In addition, highly fluctuating or cyclic populations often maintained high genetic diversity despite successive phases of low population abundance (e.g. snowshoe hare *Lepus americanus*, Burton *et al.* 2002; lemmings *Lemmus* and *Dicrostonyx* species, Ehrich & Jorde 2005; fossorial water vole *Arvicola terrestris*, Berthier *et al.* 2006). These deviations from theoretical expectations have often been attributed to dispersal, most likely density-dependent (Matthysen 2005), by helping populations to recover or by preventing the loss of genetic diversity (Hansson *et al.* 2000; Hedrick 2000; Keller *et al.* 2001; Ehrich & Jorde 2005; Fauvelot *et al.* 2006; Ortego *et al.* 2007) or, more recently, to selection (Kaeuffer *et al.* 2007).

Most of these studies have been carried out using both contemporary and historical samples for assessing a large timescale variation of genetic diversity and do not take into account variation at very fine timescales. How genetic variability varies with population abundance at such fine timescale (i.e. a few generations) remains poorly described (but see Nussey *et al.* 2005; Xie & Zhang 2006; Ortego *et al.* 2007; Ehrich *et al.* 2009) but may be partly responsible for recorded discrepancies between theoretical predictions and empirical data. Fine timescale studies may allow conservation and evolutionary biologists to grasp the ecological processes (e.g. unstable environment, Østergaard *et al.* 2003) and disturbance factors such as hunting (Scribner 1993) that generate yearly changes in demographic processes (e.g. population cycles, strength of density dependence, social structure, variance in reproductive success) and hence in the genetic diversity of natural populations. Thus, there is a need for both conservation and evolutionary biologists to compile much more information about the relationship between temporal changes in population abundance and genetic diversity, in numerous socio-ecological contexts and over different timescales and, in particular, for fine timescales.

Feral cats (*Felis silvestris catus*) introduced into the Kerguelen archipelago provide an ideal case scenario, because population abundance has shown both marked temporal and spatial fluctuations in a rather simple ecosystem with a reduced food chain. Taking advantage of 12 years (1996–2007) of genetic ($n = 18$ microsatellite loci) and demographic monitoring (transect counts) of cats in three different sampling sites, we seek (i) to describe and understand how year-to-year changes in genetic diversity are related to year-to-year changes in population abundance at two spatial scales: the global island scale by merging the three sites and the local scale within each study site and (ii) to assess how yearly genetic diversity within one study site is related to local population dynamics, described both by the harmonic mean of local population abundance that measures the intensity of genetic drift (Motro & Thomson 1982) and by the coefficient of variation of local population abundance that measures the intensity of population fluctuations. Heading these two specific objectives is the question of whether population abundance fluctuations occurring at this both fine timescales (i.e. a few generations) and spatial scales are large enough to cause permanent or temporary changes to genetic variability in wild populations.

Materials and methods

Study sites and species

The Kerguelen archipelago (48°28′–50°S, 68°28′–70°35E) is located in the southern Indian Ocean and constitutes one main island, called 'Grande Terre' (6600 km^2), and about 300 small islands. It covers a total surface area of 7200 km^2. The sub-Antarctic climate is characterized by high precipitation (mean 783 mm/year), low temperatures (the monthly mean varied from 4.8 to 11.9 °C from 1951 to 2001, Météo France Port-aux-Français, PAF) and continuous wind. The seasonal subdivision of

years is based on climatic data. The summer of year t corresponds to the period ranging from November 1st of the year $t - 1$ to April 30th of the year t. Cats were introduced during the 1950s to control pest species (rabbits *Oryctolagus cuniculus*, rats *Rattus rattus* and mice *Mus musculus*, Pascal 1980). The present population was founded by a few individuals (around 5), introduced to the scientific station PAF, from where they colonized a large part of Grande Terre (Derenne 1976; Pascal 1980). The present population size is estimated at around 7000 individuals, close to the estimated carrying capacity (Pontier *et al.* 2005), with a very low density of 1.5 cats/km^2 (Say *et al.* 2002b). Cats are mainly solitary, holding large territories (Derenne & Mougin 1976; Say *et al.* 2002b; 0.65 km^2, Martin J., Pons J.B., Chagneau G. and Pontier D. unpublished), and the mating system appears to be close to monogamy (Say *et al.* 2002a). Individuals use rabbit burrows as shelters, and their diet is based mainly on rabbits and seabirds with relative proportions depending on the availability of the prey (Pontier *et al.* 2002). Sampling was conducted at three sites in coastal regions of Grande Terre where cats are generally more abundant (Derenne 1976): PAF, Cape Ratmanoff (RAT) and Port-Jeanne-d'Arc (PJDA; Fig. 1). The coastline distance between study sites ranged from 35 to 108 km. The three sites were assumed to be spatially independent with respect to feral cat movements and consisted of the same habitat type of short vegetation (tussock grass, *Poa cookii*, *Azorella selago* and *Acaena adscendens*). We established one permanent transect at each site. The transect at PAF (4.5 km) was oriented inland. Transects at RAT (5 km) and PJDA (2.7 km) were oriented along the coastline at <500 m from the sea. Transects were linear, and stations were identified with numbered and coloured posts at 50-m intervals.

Estimating temporal fluctuations of the cat population abundance index

Typically, a transect count was conducted over a 7- to 10-day counting session at different times of the day (between 04.30 h at sunrise and 17.30 h at sunset) at approximately two-monthly intervals between field sessions from February 11th 1996 to August 17th 2007. Transect surveys were conducted at least twice a day, except during rain or snow. There were always more than 2 h between transects. We considered that this time lapse was sufficient to avoid nonindependence in the data. Therefore, we did not test for autocorrelation in our data set. Only adult cats were counted. Overall, 1332 transect counts were performed during the study period (250 at PAF, 509 at PJDA, 573 at RAT). We pooled these counts into 24 time intervals, corresponding to the successive summer and winter seasons, ranging from the 1996 summer to the 2007 winter (e.g. the 1998 summer encompasses counts performed between November 1st 1997 and April 30th 1998; consequently, the winter of year t corresponds to the period ranging from May 1st to October 31th of the year t). Raw data were the number of cats seen during a given session at

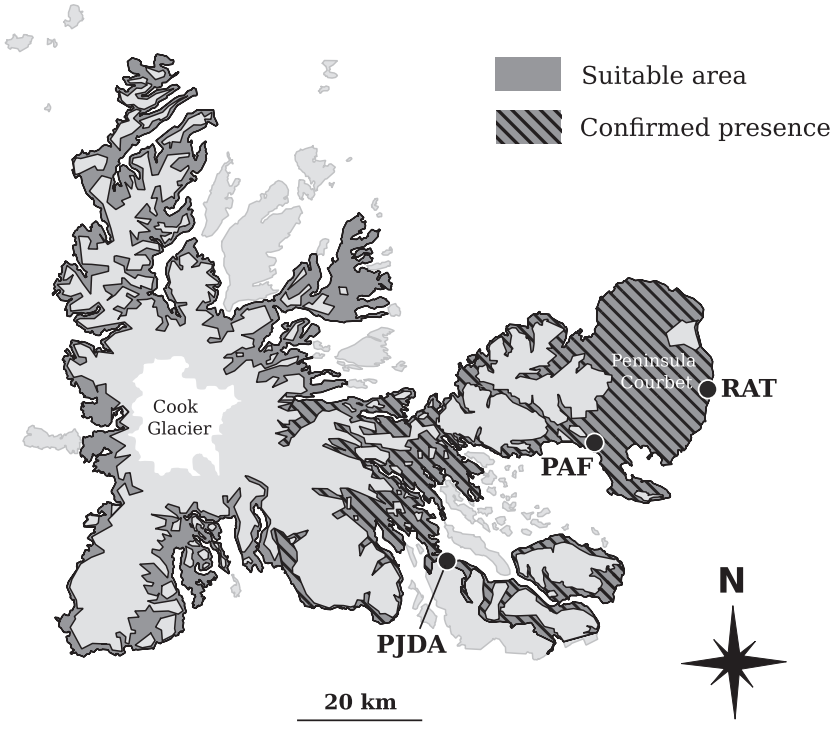

Fig. 1 Location of study sites on the main island (Kerguelen, Grande-Terre): Port-aux-Français (PAF), Cape Ratmanoff (RAT) and Port-Jeanne d'Arc (PJDA).

Table 1 Mean number of transects performed and mean number of adult cats counted per season at each study site

	PAF		PJDA		RAT		All sites	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Mean number of transects per season	14	6.83	28.92	13.5	28.75	19	71.67	39.33
Mean number of cats per km and per season	0.47	0.36	1.46	0.86	0.27	0.32	0.67	0.41
HMa	0.38	—	0.90	—	0.20	—	—	—
CVa	0.49	—	0.61	—	0.57	—	—	—

PAF, Port-aux-Français; PJDA, Port-Jeanne-d'Arc; RAT, Cape Ratmanoff.
Harmonic mean (HMa) and coefficient of variation (CVa) of summer population abundance are also given.

a given transect at a given study site and for a given season. The mean number of transects performed at each study site during each season, as well as the mean number of cats per km counted per study site and season, is provided in Table 1. It should be noted that no transect was performed during the winter of 1999.

To describe the average time variations in adult cat abundance at the three study sites, we fitted a hierarchical generalized linear mixed model (*glmm*) that predicted the mean number of cats ($\hat{\mu}_{ij}$) per km observed during the j^{th} season at site i (see Appendix S1, Supporting information for details of the model). Owing to over-dispersion of the data, the *glmm* was fitted in a 'QuasiPoisson' framework, and parameter estimates were obtained using the *glmmPQL* R function implemented in the *MASS* package (Venables & Ripley 2002) for R software (Ihaka & Gentleman 1996; R Development Core Team 2009). We derived two indices of population abundance. We first considered the three study sites combined and estimated $\hat{\mu}_j^{M2}$, which is a kilometre abundance index (Appendix S1, Supporting information); we term it hereafter the island population abundance index N^I that reflects average time variation in abundance of cats for a 'standard' site and time period, i.e. at the global island scale. Such pooling of abundance estimates makes sense in the context of temporal variability in population abundance, because a large part of the temporal variation in cat population abundance is shared among the three study sites ($R^2 = 0.84$, Santin-Janin 2010). Second, we estimated $\hat{\mu}_{ij}^{M1}$ that is also an abundance index per kilometre (Appendix S1, Supporting information), hereafter termed the local population abundance index N^l, reflecting average time variations in abundance of cats at the local scale, i.e. at each study site.

We used the temporal series of summer population abundance indices N_s^l and N_s^I ($n = 12$ years from summer 1996 to summer 2007) rather than the winter population abundance indices because reproduction occurs mainly during the summer.

Molecular sampling and DNA analysis

Concomitantly, but independently of transect sampling, cats were trapped using baited traps at the three study sites during each field season from 1996 to 2007. At PAF, individuals were trapped around the scientific station in deserted buildings or refuse dumps in an area covering about 9 km^2. At RAT, cats were trapped along the 5-km coastal transect in a 500-m-wide band. At PJDA, cats were trapped both along the 2.7-km transect and around the abandoned whaling station. Hair samples were taken from each captured cat following anaesthesia with an intramuscular injection of Ketamin Chlorhydrat (Imalgène 1000 15 mg/kg; Rhône Merieux, Lyon, France) and Acepromazin (Vétranquil 5·5% 0·5 mg/kg; Sanofi, Paris, France). Hair samples were stored in individual envelopes. Age (in months) was estimated by trained observers from body mass and dentition (Pascal & Castanet 1978) for individuals of more than 1 year of age and trapped for the first time. Age was known precisely for cats trapped for the first time as juveniles.

For each individual, 20–80 ng/μL of total genomic DNA was extracted using DNeasy Tissue Kits (Qiagen) from a sample of more than 50 hair bulbs. Selective amplification was carried out for 18 microsatellite loci (Table 2) divided into three PCR multiplexes by polymerase chain reaction (PCR). PCR was conducted in 10 μL volumes containing 6 μL of PCR Multiplex Master MIX (2x; Qiagen), 0.3 μL of each primer (10 mM; one of the locus-specific flanking primers was labelled with a fluorescent marker) and 2 μL of the extraction product. PCR was conducted in 96-well microtitre plates using a Bioblock PTC 100 thermal cycler and the following programme: 95 °C/15 min; 30 cycles with 94 °C/30 s, 57 °C/1.30 min and 72 °C/1 min denaturing, annealing and extension temperatures, respectively; and finally, 60 °C/30 min. The sizes of PCR amplified products were resolved by Genoscreen (http://www.genoscreen.fr/) using an Applied Biosystems 3730xl

Table 2 Number of alleles, observed heterozygosity H_O, expected heterozygosity H_E, and allelic richness standardized by sample size A per locus

Locus	Number of alleles	H_O	H_E	A
Fca8	9	0.607	0.672	2.433
Fca23	5	0.427	0.499	2.421
Fca24	4	0.386	0.562	2.136
Fca26	4	0.321	0.361	2.257
Fca37	8	0.756	0.769	3.507
Fca43	7	0.648	0.659	3.088
Fca45	6	0.252	0.313	2.061
Fca58	7	0.561	0.635	3.381
Fca77	5	0.590	0.672	3.134
Fca78	7	0.396	0.454	2.433
Fca85	14	0.695	0.730	4.672
Fca90	9	0.463	0.712	3.356
Fca96	5	0.428	0.433	2.215
Fca124	5	0.824	0.758	3.999
Fca547	4	0.558	0.571	2.739
Fca577	6	0.172	0.168	1.706
Fca668	5	0.742	0.763	3.940
Fca675	6	0.203	0.199	1.865

Estimates are provided at the island scale and averaged over the 12 years.

DNA Sequencing Analyzer. Microsatellite DNA fragments were independently amplified up to 10 times for the 18 microsatellite loci, from the same DNA extraction product of seven individuals and in all cases the genotypes matched.

Determining the year of conception

Overall, 281 cats were genotyped (115 from PAF, 92 from RAT and 74 from PJDA). For each cat, we estimated their date of conception by counting back their estimated age plus the gestation length (65 days) from their date of capture. Based on their date of conception, each cat was assigned to a summer season to match the temporal series of population abundance data. In the Kerguelen archipelago, the main mortality period has been found to be the first 3 months of the winter season (May, June and July, Devillard 2004). Consequently, adult population abundance decreases are expected to occur mostly from one summer to the next. Reproduction occurs during summer so that the gene pool of year t is composed of the adult population during the summer t. Hence, a cat conceived before August in a given year t has most likely been conceived by the same gene pool as a cat conceived in the previous summer season (November year $t - 1$ to April year t) and was thus assigned to the summer of the year t. Similarly, a cat conceived between August and October of year t should be assigned to the following summer season (November year t to April year $t + 1$), i.e. after the main mortality period. Following this rule, we were able to assign each cat to a year of conception, thereby building a 12-year-long temporal series of genetic diversity indices (from summer 1996 to summer 2007, Table 3).

Temporal variability in genetic diversity indices

As for the estimation of cat population abundance indices, we derived both global (i.e. at the island scale) and local (i.e. site-specific) yearly estimates of genetic diversity indices. At the island scale, we calculated the expected H_E and observed H_O heterozygosities and the allelic richness A for each locus and temporal sample t (i.e. all individuals conceived during the summer of a

Table 3 Cohort size by year and study site, summer population abundance index estimated at the island scale N_s^I and observed heterozygosity H_O, expected heterozygosity H_E, and allelic richness standardized by sample size A averaged over locus (± SE) per year and over all study sites

Year of conception	PAF	PJDA	RAT	Total	N_s^I	H_O	H_E	A
1996	9	5	10	24	0.313	0.531 ± 0.24	0.453 ± 0.17	2.01 ± 0.45
1997	14	7	5	26	0.250	0.545 ± 0.22	0.502 ± 0.17	2.17 ± 0.48
1998	31	5	5	41	0.502	0.519 ± 0.22	0.500 ± 0.17	2.20 ± 0.50
1999	21	5	4	30	0.450	0.497 ± 0.24	0.452 ± 0.19	2.09 ± 0.50
2000	7	4	5	16	0.727	0.464 ± 0.20	0.459 ± 0.17	2.13 ± 0.49
2001	6	4	0	10	0.268	0.378 ± 0.25	0.364 ± 0.22	2.09 ± 0.63
2002	4	9	3	16	0.319	0.430 ± 0.31	0.343 ± 0.24	1.94 ± 0.48
2003	15	9	9	33	0.588	0.446 ± 0.22	0.458 ± 0.17	1.95 ± 0.36
2004	7	12	16	35	0.249	0.512 ± 0.28	0.422 ± 0.21	1.97 ± 0.35
2005	2	12	18	32	1.049	0.454 ± 0.24	0.418 ± 0.19	2.13 ± 0.46
2006	0	2	4	6	0.928	0.428 ± 0.28	0.360 ± 0.18	2.02 ± 0.36
2007	0	0	13	13	0.796	0.492 ± 0.27	0.421 ± 0.21	1.89 ± 0.72

PAF, Port-aux-Français; PJDA, Port-Jeanne-d'Arc; RAT, Cape Ratmanoff.

given year) on the entire data set. Allelic richness was corrected for unequal sample size using the rarefaction method (Hurlbert 1971; El Mousadik & Petit 1996; Petit *et al.* 1998; Leberg 2002). We standardized the measure of allelic richness to a common sample size of six individuals for the global scale and two individuals for the local scale, i.e. the smallest sample sizes observed in our data set (Table 3). Then, H_E, H_O and A were averaged across all loci to derive yearly mean indices of genetic diversity, and we computed their yearly rate of increase as $\lambda_{It} = \log(I_t/I_{t-1})$, where I can be either H_E, H_O, or A. At the local scale, H_E, H_O and A were computed for each locus in each study site for a given temporal sample t (i.e. all individuals conceived during the summer of the year t at a given study site). We also computed the yearly rate of increase in genetic diversity indices from year $t-1$ to year t for each locus and study site.

All computations were carried out using the *adegenet* package (Jombart 2008) for R software (R Development Core Team 2009), and specific R functions were developed for calculating A.

Linking temporal change in population abundance and genetic diversity indices at the island scale

To test for significant changes in genetic diversity from 1 year to the next, we quantified the degree of genetic differentiation between the 12 temporal samples at the island scale by computing temporal F_{ST} using Weir & Cockerham's (1984) estimates. Significance of genetic differentiation was tested using the G-test (Goudet *et al.* 1996; 9999 permutations) implemented in the software FSTAT (Goudet 2001). Spearman's correlation coefficient ρ between yearly values of genetic diversity indices (H_E, H_O and A) and yearly values of summer population abundance index N_s^I were tested using R software. We then performed a linear regression using the yearly rates of increase in genetic diversity indices against the population abundance index growth rate $\lambda_{N_S^I}$ to quantify the relationship between the magnitude of change in population abundance and the magnitude of change in genetic diversity indices over all loci at the global island scale.

Linking temporal change in population abundance and genetic diversity indices at the local scale

We used linear models to assess the effect of different explanatory variables and factors on time variations of both the genetic indices (H_E, H_O, or A) and their yearly rate of increase (λ_{H_E}, λ_{H_O}, or λ_A). First, in order to account for different levels of diversity among loci, locus was included in all models as a fixed factor effect (L). Because H_E and H_O are not corrected for sample size, contrary to A, we also included the sample size (SS) on which these genetic indices were computed as an explanatory variable in the model. When the rates of increase in these genetic indices were used as response variables, the yearly rate of increase in SS (λ_{ss}) was used as an explanatory variable instead. Second, we included the summer local population abundance index N_s^l and the respective rate of increase in summer local population abundance index $\lambda_{N_S^l}$ in the models when H_E, H_O and A were used as response variables because these are both central explanatory variables of interest in our study. Note that when the rates of increase in the genetic indices were used as response variables, we only included $\lambda_{N_S^l}$ as an explanatory variable. Finally, the amplitude of the multiannual fluctuations in abundance indices was estimated as the coefficient of variation of the summer abundance index per study site (CVa). To estimate site-specific abundance, we used the harmonic mean of the summer abundance index for each year (HMa). Both CVa and HMa were included in all models. The full model for each genetic diversity index was thus

$$I \sim L + N_s + \lambda_{N_s^i} + \mathrm{CVa} + \mathrm{HMa} \quad \text{when } I = A$$

and

$$I \sim L + \mathrm{SS} + N_s + \lambda_{N_s^i} + \mathrm{CVa} + \mathrm{HMa} \quad \text{when } I = H_E, \text{ or } H_O$$

and for the rate of increase in each genetic diversity index

$$\lambda_I \sim L + + \lambda_{N_s^i} + \mathrm{CVa} + \mathrm{HMa} \quad \text{when } I = A$$

and

$$\lambda_I \sim L + \lambda_{SS} + \lambda_{N_s^i} + \mathrm{CVa} + \mathrm{HMa} \quad \text{when } I = H_E, \text{ or } H_O$$

H_E, and H_O were *arcsine-square-root*-transformed in all analyses. Linear models with different combinations of explanatory variables were compared using AICc (Tables S1 and S2, Supporting information). Models with $\Delta\mathrm{AICc} < 2$ were considered equally adequate (Burnham & Anderson 2002), and the model with the fewest number of parameters was retained.

Results

Description of temporal variation of population abundance and genetic diversity indices at the island scale

The summer island population abundance index (N_s^I) increased from 1996 to 2007 (slope = 0.049 after log transformation of the population abundance index,

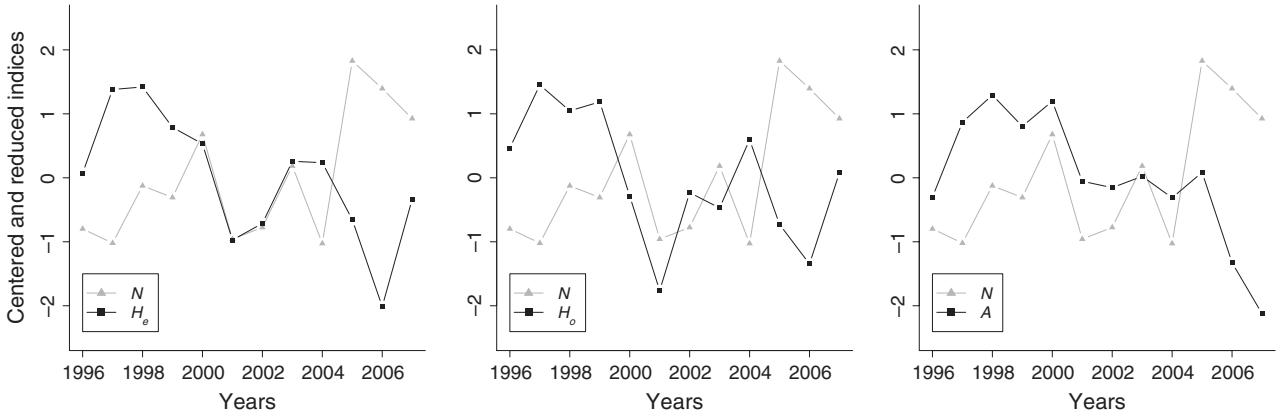

Fig. 2 Temporal variation (1996–2007) of genetic diversity indices (A, H_E and H_O) and the summer island population abundance index N_s^I. For the sake of simplicity, the yearly mean values of all indices over locus and study sites are displayed. All indices are centred and reduced to allow graphical display of the temporal series, expressed in different units.

P-value = 0.03, R^2 = 0.33) but showed large fluctuations around this positive trend (Fig. 2, Tables 3 and 4).

Mean values of genetic indices also fluctuated over time (Fig. 2, Tables 3 and 4), and the genetic differentiation between temporal samples (over all study sites and loci) was significant (temporal F_{ST} = 0.038, P-value < 0.0001). We plotted both the island summer population abundance index N_s^I and the genetic indices time series (A, H_O and H_E), after having centred and reduced them (Fig. 2). We found that all genetic indices fluctuated more or less concomitantly with the population abundance index, an observation that called for a more detailed statistical analysis. Nonetheless, none of the Spearman's correlation coefficients between the genetic diversity indices and the population abundance (all P-values > 0.51) or between the population abundance growth rate and the genetic diversity index growth rates (all P-values > 0.23) were significantly different from zero.

Linking temporal change in genetic diversity indices and population abundance at the local scale

As expected, A, H_E and H_O differed between loci (coefficients not shown), contrary to λ_{H_E}, λ_{H_O}, and λ_A that appeared to behave similarly, independently of locus. Only H_E and λ_{He} were sensitive to sample size because, for no other response variable, was SS or λ_{ss} included in the most appropriate model based on AICc (Tables S1 and S2, Supporting information, Table 5). As expected, H_E and λ_{H_E} were positively related, respectively, to sample size and rate of change in sample size from year to year (Table 5).

All response variables showed a parameter linked to summer local population abundance (N_s^I and/or $\lambda_{N_s^I}$) in their most parsimonious model (Tables S1 and S2, Supporting information, Table 5). In all cases (Table 5), coefficient estimates for the effect of summer local population abundance (N_s^I for A and H_E) or rate of increase in summer local population abundance ($\lambda_{N_s^I}$ for A, H_O

Table 4 (a) Standardized allelic richness A, observed and expected heterozygosities H_O and H_E averaged across loci, and summer population abundance index N_s^I averaged over years for each study site (±temporal SE). (b) Mean, temporal range and coefficient of variation of the standardized allelic richness A, observed and expected heterozygosities H_O and H_E and the yearly population abundance index N_s^I averaged over years and study sites

	(a)			(b)		
	PAF	PJDA	RAT	Mean	Temporal range	CV (%)
A	2.14 ± 0.12	2.04 ± 0.08	2.02 ± 0.19	2.054	1.898–2.204	4.76
H_O	0.474 ± 0.06	0.451 ± 0.06	0.514 ± 0.07	0.471	0.411–0.544	10.3
H_E	0.448 ± 0.12	0.418 ± 0.06	0.441 ± 0.06	0.493	0.417–0.556	7.8
N_s^I/N_s^I	0.464 ± 0.23	1.460 ± 0.89	0.269 ± 0.15	0.537	0.247–1.049	52.2

PAF, Port-aux-Français; PJDA, Port-Jeanne-d'Arc; RAT, Cape Ratmanoff.

Table 5 Parameter estimates from the most adequate linear models (chosen on the basis of AICc) for the effect of different explanatory variables on genetic diversity indices

Response variable	Effect	Estimate	SE	*P*-value
A	N_s^I	**0.114**	**0.056**	**0.041**
	$\lambda_{N_S^I}$	0.022	0.04	0.584
	CVa	**−1.902**	**0.614**	**0.002**
H_E	SS	**0.008**	**0.002**	**$<10^{-3}$**
	N_s^I	**0.053**	**0.022**	**0.017**
	HMa	**−0.133**	**0.048**	**0.006**
H_O	$\lambda_{N_S^I}$	0.027	0.021	0.198
	HMa	**−0.135**	**0.055**	**0.015**
λ_A	$\lambda_{N_S^I}$	0.025	0.028	0.28
λ_{H_E}	λ_{SS}	**0.111**	**0.031**	**$<10^{-3}$**
	$\lambda_{N_S^I}$	0.0007	0.027	0.979
λ_{H_O}	$\lambda_{N_S^I}$	**0.088**	**0.037**	**0.018**

Locus was always included as an additional effect in the model (coefficients or intercept not shown). Significant effects are shown in bold.

and λ_I) were positive. This suggests that the indices of genetic diversity measured for a given summer are higher when summer local population abundance is high (A, Fig. 3a, and H_E) or when the rate of increase in summer local population abundance from the previous summer is positive (A and H_O, Fig. 3c) and vice versa. In addition, the greater the decrease in summer local population abundance from one summer to the next, the greater the genetic diversity lost during this interval. Nonetheless, the size effect was small as only three of the eight coefficient estimates were significant (Table 5).

Interestingly, A, H_E and H_O were significantly related to site-specific parameters, i.e. the coefficient of variation in summer local population abundance over the 12-year period (CVa for A, Table 5, Fig. 3b) and the mean level of summer local population abundance assessed by the harmonic mean (HMa for H_E and H_O, Table 5). As expected, the more significant the summer local population abundance fluctuations, the lower the allelic richness ($\beta = -1.902$, Table 5, Fig. 3b). More surprisingly, genetic diversity, assessed by both H_E and H_O, was higher for sites with lower mean summer population abundance ($\beta = -0.133$ and $\beta = -0.135$ for H_E and H_O, respectively, Table 5). However, it would be somewhat inappropriate to disentangle the biological effects of CVa and HMa, as both parameters are correlated between the three study sites: PJDA, which is the site where the summer local population abundance was the highest, is also the site showing the highest coefficient of variation of summer local population abundance (Table 1).

Discussion

The pattern of covariation between genetic variability and population abundance at both fine time scales (i.e. a few generations) and spatial scales remains poorly described (but see Nussey *et al.* 2005; Xie & Zhang 2006; Ortego *et al.* 2007; Ehrich *et al.* 2009). It is unclear whether population abundance fluctuations (especially population decreases) occurring at these scales are sufficient to cause permanent or temporary changes to genetic variability in wild populations. Most of the theoretical predictions have been developed and tested in a historical context over several hundred generations, so that their applicability for shorter periods can be questioned. We used 'genetic monitoring' (*sensu* Schwartz *et al.* 2007) to investigate the pattern of covariation between genetic variability and population abundance at a very fine spatial and temporal scale,

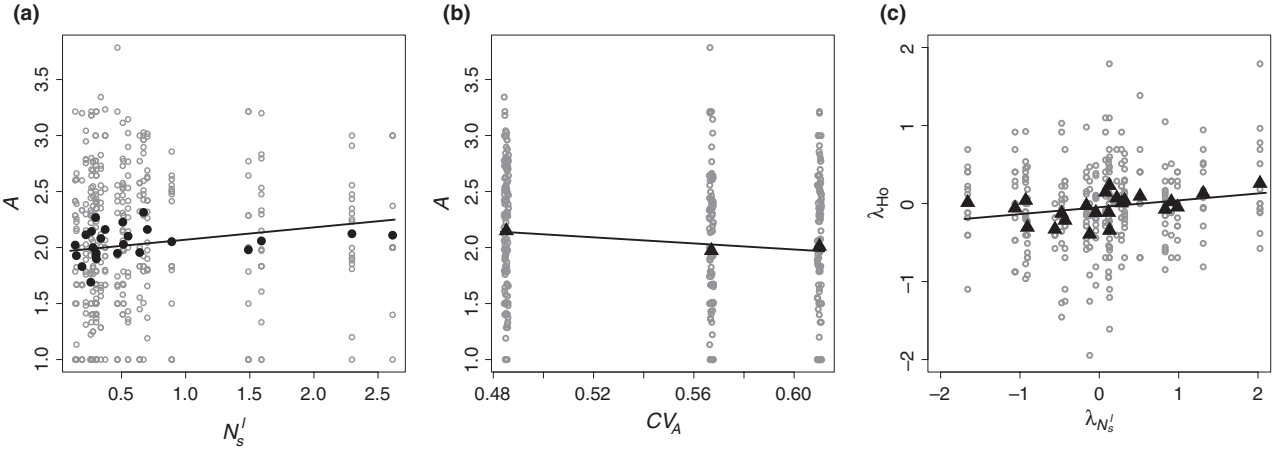

Fig. 3 Effect of (a) the summer local abundance index N_s^I and (b) the coefficient of variation of the summer local abundance index CVa on the allelic richness A and effect of (c) the rate of increase in summer local population abundance index $\lambda_{N_S^I}$ on the rate of increase in observed heterozygosity λ_{H_O}.

putting results in front of theoretical expectations and methodological consequences.

Linking temporal demographic fluctuations and genetic variability at the island scale

The Kerguelen cat population showed marked fluctuations in abundance over time. As these fluctuations are synchronous at all study sites (Santin-Janin 2010), the general pattern of covariation between population abundance and genetic diversity can be initially investigated at the island level. Our analysis failed to detect any significant relation between these fluctuations in abundance and fluctuations in genetic diversity. However, part of the temporal genetic variability from 1 year to another may be attributed to changes in the relative frequencies of individuals originating from the three sites and not to temporal patterns. Pooling samples at the island scale enhances annual sample sizes compared to site-specific annual sample sizes (Table 3). Nonetheless, we acknowledged that some annual sample sizes still remain low (e.g. $n \leq 16$ for 5 years; 2000, 2001, 2002, 2006, 2007, Table 3), probably leading to low statistical power or introducing bias estimates of genetic diversity indices in some years. In addition, pooling samples might also hide the local patterns of covariation between the population abundance index and genetic variability. Finally, averaging genetic variability across loci each year is not satisfactory, just as missing data owing to amplification failure are not uniformly distributed across loci, year and study sites. However, we repeated the analyses with the 8 loci that were typed in more than 97% of individuals, and our results were qualitatively identical (data not shown), i.e. there is no evidence that loci with lower amplification success have caused any bias.

Linking genetic diversity and population abundance at the local scale

Besides being dependent on locus, genetic diversity in a given year depends both on the harmonic mean of local population abundance (for H_E and H_O) and on the coefficient of variation of local population abundance (for A). Both the expected and observed heterozygosities are higher in study sites where cats were less abundant (Table 5). This result does not concur with either theoretical expectations (Crow & Kimura 1970; Frankham *et al.* 2002) or empirical reviews (Frankham 1996). As the harmonic mean of population abundance is a proxy of the intensity of genetic drift (Motro & Thomson 1982), this result leads to the conclusion that genetic diversity is higher when genetic drift is stronger in a given study site. However, as already underlined above, it is difficult to derive some firm interpretations about the relationship between HMa and genetic diversity independently of the effect of CVa on genetic diversity, given that HMa and CVa are partially correlated (Table 1). Indeed, PJDA showed both the highest HMa and the highest CVa during the study period. The negative relationship between the allelic richness and the coefficient of variation CVa of summer local population abundance supports the link between demography and genetic diversity. This result is in agreement with theoretical expectations that state that a succession of large abundance fluctuations is likely to promote loss of alleles (Nei *et al.* 1975; Wright 1978; Motro & Thomson 1982; Whitlock 1992): the more variable in abundance a study site is, the lower its allelic richness. A peculiar association between HMa and CVa has already been proposed to explain a similar and surprising negative correlation between HMa and genetic diversity in red voles (*Myodes rutilus*, Ehrich *et al.* 2009), which impelled the authors to rule out the occurrence of a demo-genetic process in leading to such a result. They indeed suggested that assessing the effect of harmonic mean on genetic diversity indices by comparing populations differing in both amplitude and intensity of population size fluctuations makes no sense. In such a case, it is nearly impossible to disentangle the effects of harmonic mean and population size fluctuations as both factors might have opposite effect on genetic diversity. We believe that our surprising results come from the same reasons as in Ehrich *et al.* (2009): PJDA, PAF and RAT not only differ in harmonic mean of population abundance index but also differ in the intensity and magnitude of population fluctuations as written above. We thus followed the same line of argument, prompted by the fact that among the set of the more parsimonious models for H_O, and H_E (ΔAICc < 2, Table S1, Supporting information), CVa is always an important variable. In addition, A and H_E in a given year and a given site are positively related to the corresponding summer local population abundance (N_s^l), reinforcing the idea that the negative relationship between HMa and genetic diversity is unlikely to be based on demo-genetic processes. We thus concurred with the criticism of Ehrich *et al.* (2009), and we suggested avoiding the use of the harmonic mean as an estimator of long-term population size to study the relationships between demographic fluctuations and heterozygosity in populations characterized by strong multiannual density fluctuations.

Nonetheless, the overall effect of N_s^l on genetic diversity indices appears weak for A and H_E (Fig. 3a) and nonexistent for H_O within each study site, meaning that the number of adults reproducing locally each year had

a moderate impact on the genetic diversity of the offspring produced. Different explanations can be proposed. Minimum population size and growth rate following decline in abundance are the main factors that influence loss of genetic diversity during a mortality event (Nei *et al.* 1975). It may be postulated that the remnant effective population size each year was high enough to prevent significant loss of diversity, as has been hypothesized in previous empirical studies on recent demographic crashes in other animal populations (e.g. Queney *et al.* 2000; Le Gouar *et al.* 2009).

What is thus apparent from the model selection is that it is the rate of change in summer population abundance rather than the summer local population abundance *per se* that perhaps explains best the yearly fluctuations of genetic diversity. The most parsimonious models for A, H_O, λ_{H_E}, λ_{H_O} and λ_A all incorporated $\lambda_{N_S^l}$ (Tables S1 and S2, Supporting information). Despite that the effect of $\lambda_{N_S^l}$ is only significant for λ_{H_O}, all coefficients are positive (Table 5). This is particularly suggestive of higher genetic diversity (mainly for A and H_O) in a given year t or a higher rate of increase in genetic diversity from year t to $t + 1$, when the summer local population abundance increased from year t to $t + 1$. The strength of the positive relationship between λ_{H_O} and $\lambda_{N_S^l}$ is similar whether the local population was growing or decreasing (result not shown). From a theoretical point of view, a greater decrease in genetic diversity is expected with a decreasing population size (Chakraborty & Nei 1977; Hedrick & Miller 1992; Wang & Caballero 1999), whereas an immediate rebound in genetic diversity with a postcrash increase in population size is less expected by these models. Obviously, mutation cannot be considered as a likely explanation, and immigration from adjacent sites appears to be the most likely factor allowing such an association between genetic diversity and population abundance in the growth phases of the demography.

To summarize, changes in population size from year to year are not large enough to durably depauperate genetic variability in the Kerguelen cat population during the study period. In that sense, population abundance fluctuations in the Kerguelen cat population cannot be considered as demographic bottlenecks from a theoretical point of view (Chakraborty & Nei 1977; Hedrick & Miller 1992; Wang & Caballero 1999). Such a pattern of covariation over a short 10-year period, linking population abundance growth rate and genetic diversity would thus probably appear flat if modelled over a long-term historical context. However, our approach allowed us to grasp the pattern of covariation between genetic variability and population abundance at a very fine spatial and temporal scale, i.e. a scale at which behavioural, mating and demographic processes act. We can thus infer the present socio-demographic patterns acting on the population and speculate on a demo-genetic scenario, as evolutionary biologists usually do for demographic history by comparing past and present genetic diversity along a long-term historic scale.

Conclusion: towards a demo-genetic scenario

A peculiarity of the Kerguelen cat population is that variations in population abundance are synchronous at all three studied sites (Santin-Janin 2010). Such synchrony allowed us to infer demographic processes by extrapolating it to the Kerguelen cat population as a whole. When adult cat abundance decreased in a study site from year t to year $t + 1$, abundance in other study sites and also in adjacent unstudied sites (i.e. within a few kilometres) also decreased owing to population synchrony and vice versa. If the abundance of adult cats decreased from one summer to the next, then the genetic diversity of the juveniles produced by these adults also decreased locally between these two summers and vice versa. Once again, the magnitude of these variations in genetic diversity is low but is related to the magnitude of the population abundance index variations. The local cohorts born in year $t + 1$ are thus produced by a restricted number of parents, leading to the lower genetic diversity in this cohort relative to cohorts produced by more abundant adults.

The significant recoveries in adult population abundance in year $t + 2$, commonly observed after a large decrease in population abundance occurring between year t and $t + 1$, can theoretically be attributed both to immigration and to local recruitment, i.e. the product of fecundity and juvenile survival of cats born in $t + 1$. Both immigration and recruitment imply high juvenile survival from $t + 1$ to $t + 2$, which is made possible by low local resource competition (food and shelters) owing to the reduced adult population density. This high juvenile survival implies, in turn, a large local subadult cohort size at the beginning of summer $t + 2$. Density-dependent natal dispersal is common in mammals (Matthysen 2005) and probably relates to the avoidance of local kin competition (Dobson 1982). Reproductive excursion and natal dispersal rates into the focal study sites may increase during summer $t + 2$, thus leading to more genetic exchange between adjacent sites and finally to an increase in heterozygosity of young born in summer $t + 2$, concomitant with an increase in the adult population abundance (see Fauvelot *et al.* 2006; Ortego *et al.* 2007 for similar patterns). In addition, allelic richness might also increase with increasing adult population abundance, as long-distance natal dispersal, i.e. not from other study sites but from

sites more distant than the immediate adjacent sites, is likely to re-introduce alleles that were lost to local populations in the previous decrease. The Kerguelen cat population is indeed assumed to have high genetic structuring between local demes because it has reached carrying capacity within the last 20 years (Pontier *et al*. 2005).

To conclude, in the Kerguelen archipelago, we have demonstrated that yearly fluctuations in feral cat genetic variability were related to yearly fluctuations in population abundance. We acknowledge that it is impossible to disentangle the contributions of recruitment and immigration to the high population abundance growth rate observed during years $t + 1$ and $t + 2$. In addition, the relative importance of local recruitment and immigration is undoubtedly year- and site-specific, possibly buffering the strength of the relationship between the increases in adult population abundance and those of the heterozygosity and allelic richness indices.

In future, information about not only how many animals were lost from 1 year to another but also which animals (e.g. juvenile vs. adults; homozygote vs. heterozygote) were lost will be important (e.g. Kaeuffer *et al*. 2007) to better infer socio-demographic patterns and selective forces acting on this Kerguelen cat population. However, this demo-genetic scenario could be investigated only through dynamical modelling, as data on juvenile survival and reproduction are very difficult to obtain for the feral cat in this sub-Antarctic habitat.

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Data accessibility:

Sample locations, birth years and multilocus microsatellite genotypes are available at DRYAD entry doi:10.5061/dryad.5n4np5df.

Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1 Linking temporal variation in genetic diversity and population abundance at the local and the island scales.

Table S1 Results of model selection for allelic richness (A), expected heterozygosity (H_E), and observed heterozygosity (H_O).

Table S2 Results of model selection for the rate of increase of allelic richness (λ_A), expected heterozygosity (λ_{H_E}), and observed heterozygosity (λ_{H_O}).

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