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Effective size of two feral domestic cat populations (*Felis catus* L.): effect of the mating system

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A variety of behavioural traits have substantial effects on the gene dynamics and genetic structure of local populations. The mating system is a plastic trait that varies with environmental conditions in the domestic cat (*Felis catus*) allowing an intraspecific comparison of the impact of this feature on genetic characteristics of the population. To assess the potential effect of the heterogeneity of males' contribution to the next generation on variance effective size, we applied the ecological approach of Nunney & Elam (1994) based upon a demo-graphic and behavioural study, and the genetic 'temporal methods' of Waples (1989) and Berthier *et al.* (2002) using microsatellite markers. The two cat populations studied were nearly closed, similar in size and survival parameters, but differed in their mating system. Immigration appeared extremely restricted in both cases due to environmental and social constraints. As expected, the ratio of effective size to census number (N_e/N) was higher in the promiscuous cat population (harmonic mean = 42%) than in the polygynous one (33%), when N_e was calculated from the ecological method. Only the genetic results based on Waples' estimator were consistent with the ecological results, but failed to evidence an effect of the mating system. Results based on the estimation of Berthier *et al.* (2002) were extremely variable, with N_e sometimes exceeding census size. Such low reliability in the genetic results should retain attention for conservation purposes.

Keywords: ecological model, effective population size, *Felis catus*, genetic model, mating system, microsatellites

Introduction

For the purpose of biodiversity conservation it is extremely important to have information about the demographic status of populations and the amount of genetic diversity. Indeed, such information allows pinpointing populations that require attention in conservation plans, and is also essential to define efficient management strategies (Amos & Balmford 2001). However, population/conservation genetics is currently experiencing an explosion of new statistical methods. It is therefore important to evaluate these statistical inference methods using populations of known spatial and temporal behaviour (Basset *et al.* 2001).

Among the critical demographic information the effective population size, N_e , is a parameter of central

importance in population genetics and in conservation management (Frankham 1995; Anthony & Blumstein 2000). The concept of N_e was developed by Wright (1931) to measure the rate of genetic drift and is related directly to the rate of loss of genetic diversity and the rate of increase in inbreeding within a population. It is thus extremely important to estimate N_e in natural populations because a reduction of N_e can influence the dynamics and persistence of populations (Frankham 1995). This quantity represents the number of individuals of an idealized population (all adults reproduce once and at the same age, random mating, equal sex ratio, equal probability for all adults to contribute offspring to the next generation) that will result in the same genetic properties (in terms of random genetic drift) as the observed population of census size N with its own pattern of life-history features. As natural populations can deviate strongly from conditions of this ideal, it is of great importance to assess how changes in life-history

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characteristics of a given population will affect N_e . In particular, theoretical (e.g. Chesser 1991; Nunney 1993; Sugg & Chesser 1994; Anthony & Blumstein 2000; Wedekind 2002) and field studies in mammals (Balloux *et al.* 1998; Pope 1998; Anthony & Blumstein 2000; Garnier *et al.* 2001; Reinhardt & Köhler 2002; see also Wood 1987 and Long *et al.* 1998 in humans) accumulate evidence that gene dynamics and hence effective size are affected substantially by patterns of mating.

The effective population size can be estimated by several approaches, either directly on the basis of life history or breeding system information (termed 'ecological methods' by Nunney & Elam 1994) or indirectly through the analysis of genetic data (Hill 1981; Waples 1989; Pudovkin *et al.* 1996; Berthier *et al.* 2002). The two approaches have been used in natural populations, but interpretation of their results differs noticeably. The ecological approach utilizes detailed information about population functioning and results can be used to predict changes in N_e due to changes in behaviour or in dynamics parameters in the population studied, so that the effect of different conservation strategies on N_e can be evaluated (Nunney & Elam 1994). Unfortunately, the demographic and breeding data necessary to obtain accurate estimates of effective size assume long-term monitoring of populations and are difficult to gather except for few species. Alternatively, genetic data generally require less investment in the field and are potentially available for any species of interest. However, although the genetic approach is easier to apply, it could be mistaken to use it for conservation decisions because it provides no insight into the underlying mechanisms determining N_e (Nunney & Elam 1994): N_e values integrate events such as migration and population subdivision without disentangling their relative importance (Nunney & Elam 1994). Furthermore, many methods have been developed within these two broad approaches that use different information (e.g. social system, generation time or demography for the ecological approach; linkage disequilibrium, heterozygosity excess or temporal changes in allele frequencies for the genetic approach) and rely on different simplifying assumptions. Hence comparison of N_e estimates between species raises problems (Harris & Allendorf 1989), all the more as the quality of the data set may also vary. Rarely, genetic and ecological methods can be tested on one population (e.g. Sugg *et al.* 1996; Dobson *et al.* 1997, in black-tailed prairie dogs *Cynomys ludovicianus*), or more interestingly on several populations within the same species differing by some of life-history characteristics well known to influence N_e .

Our first aim was to estimate the variance effective size of cat populations with contrasted mating systems. The domestic cat populations represent good 'test' populations because the life-history pattern of domestic cats changes greatly according to habitat characteristics, mainly through

the distribution of resources (Liberg *et al.* 2000). Extensive data on demography, social organization and reproductive success of both males and females are available for two cat populations of the same size and survival patterns but differing by their social structure and mating systems. In the first population, males are aggressive and monopolize access to receptive females. As a result, the mating system is polygynous and few males of the population reproduce successfully each year (Say *et al.* 1999). In contrast, in the second population aggressive interactions are much less frequent between males even during the reproductive period. The mating system is promiscuous, with a large number of males of the social group reproducing (Say *et al.* 1999, 2001). Given the crucial role of the breeding system on effective size (Wright 1931, 1938; Caballero 1994), N_e value is likely to be lower in the polygynous population than in the promiscuous one (Anthony & Blumstein 2000).

A second aim of our study was to evaluate the reliability of genetic estimates of N_e . We applied the ecological method of Nunney & Elam (1994) and the genetic methods of Waples (1989) and Berthier *et al.* (2002). The ecological method will serve as a baseline method to evaluate the consistency of the N_e results obtained through the genetic approach. The method of Nunney & Elam (1994) has the advantage of requiring less information about life history than the original equation of Hill (1972, 1979), from which it is derived, while providing a good estimate of N_e (Nunney & Elam 1994; Bouteiller & Perrin 2000). The two genetic methods estimate N_e from temporally spaced samples. The method of Berthier *et al.* (2002) is a new maximum-likelihood method based on the reconstruction of the genealogy of the population's genes. Likelihood-based estimators are generally considered superior to the initial method-of-moments estimators such as that of Waples (1989), in that they are less sensitive to recent departures from migration drift equilibrium and require a lower number of loci (Berthier *et al.* 2002). The violation of the migration drift equilibrium hypothesis is all the more probable when microsatellite data are used. Because the Berthier *et al.* method is just beginning to be utilized by empirical investigators (Hansen *et al.* 2002; Miller & Waits 2003), it is important to multiply examples of application to evaluate its efficiency.

Materials and methods

Species and study area

The domestic cat is a medium-sized slightly dimorphic mammal (males being 20% heavier than females, Pontier *et al.* 1995), with overlapping generations. Females reach sexual maturity at 6–8 months and males at 8–10 months, but first reproduction can be delayed until well after sexual maturity, depending on the ecological characteristics of the population (Say *et al.* 1999).

We studied two cat populations through intensive monitoring based on capture–recapture methods. Cats were trapped using double-door traps, then anaesthetized with an intramuscular injection of ketamine chlorhydrate (Imalgène 1000 15 mg / kg, Rhône Mérieux, Lyon, France) and acepromazine (Vétranquil 5.5% 0.5 mg / kg, Sanofi, Paris, France). The age of the cats was estimated according to Pascal & Castanet’s (1978) method for individuals first trapped at more than 1 year old. It was known precisely for cats living in human houses or for those first trapped as juveniles. A permanent subcutaneous electronic device (transponder Trovan, AEG & Telefunken Electronic) was fitted for the subsequent identification of cats. Fur samples were collected for genetic parentage analysis. Cats were then released at their capture locations. All or almost all individuals were marked according to the population. Regular behavioural observations allow detection of all pregnant females and capture of complete litters. Each captured individual was genotyped for a set of nine microsatellite loci: fca8, fca23, fca43, fca45, fca77, fca78, fca90, fca96 (Menotti-Raymond & O’Brien 1995) and fca37 (Menotti-Raymond, pers. comm.). The number of alleles at each locus varied from five to 14 in the urban population and from six to eight in the rural one (Say *et al.* 1999).

The first cat population studied is a urban feral cat population residing in a hospital park in the centre of Lyon (France; LCR) and has been monitored since 1993. The hospital area is 7.2 ha and is bounded by walls, buildings and high traffic roads. Cats are fed mainly by the hospital staff but also hunt small rodents and birds. The population comprises 25–28 adult males and 25–38 adult females; density of the cats is 972 ± 55 (SD) cats km⁻² depending on the year. Cats form a large multimale / multifemale social group (Say 2000), as in other high-density populations (Natoli & De Vito 1991). Group members usually behave amicably with each other, but are aggressive towards alien cats (Say *et al.* 2001). During the reproductive season, several males can court the receptive females without any aggressive interactions between males (Natoli & De Vito 1991; Say 2000). As a result, a promiscuous mating system is observed with a high rate of multiple paternity (Say *et al.* 1999). Males reproduce as soon as they reach physiological maturity (8 months old; Say *et al.* 1999). Because of the strong environmental constraints, both males and females are strongly philopatric (Devillard *et al.* 2003).

The second cat population, Barisey-la-côte (BAC), is situated in a rural environment in the Northeast of France, and has been monitored since 1991. The village where the cats live is separated from the next cat population by 3–5 km. Cats are fed by their owners but also prey on small mammals and birds. They live alone or in small groups (range: 2–7), mainly on farms. The population comprises 22–28 adult males and 27–39 adult females. Density is 234 ± 63 (SD) cats km⁻². Males are aggressive and monopolize

access to receptive females. The resulting mating system is polygyny, with a very low number of males reproducing successfully each year (Say *et al.* 1999). Furthermore, all the fathers were born in the population studied (Say *et al.* 1999). Age at first reproduction for males is delayed until well after physiological maturity (Liberg 1981; Say *et al.* 1999). Females are philopatric but males can disperse when they reach sexual physiological maturity (Liberg 1981). However, forests where wild cats (*F. silvestris*) and foxes (*Vulpes vulpes*) live can add mortality costs during migration, decreasing the probability of successful male immigration. Cats from BAC have been free from the feline leukaemia virus (FeLV) since the beginning of the monitoring (1991), while the disease is present in the surrounding villages (Xémar, unpublished). FeLV is a common cat disease transmitted easily by direct contact between cats (Jarrett 1985). These results suggest strongly a low level of connection between cat populations in this environment.

The dates of investigation were 1995–98 for LCR, 1992–93 and 1997 for BAC. Both populations were approximately stationary in size and age composition (Say *et al.* 1999). Using capture–mark–recapture methods (Say 2000) the survival rate was shown to be constant over age after sexual maturity and is higher in females (0.73 ± 0.05 in LCR and 0.77 ± 0.06 in BAC) than in males (0.65 ± 0.04 in LCR and 0.62 ± 0.04 in BAC). The genotyping procedure and patterns of paternity have been described in detail elsewhere (Say *et al.* 1999, 2001; Say 2000).

Estimation of N_e

Demographic method. For each of the two populations, N_e was estimated using the Nunney & Elam (1994) equation:

$$N_e = \frac{4r(1-r)NT}{\left[(A_m(1-r) + A_f r) - \left(\frac{2r}{b_f} \right) + (I_{bm}(1-r) + I_{bf}r) + (A_m I_{Am}(1-r) + A_f I_{Af}r) \right]}$$

where N is the number of adults in the population, r is the adult sex ratio, T is the generation time (defined as the average age of parents of each sex), A_i is the mean adult longevity of sex i and b_i the mean fecundity of sex i per season. I_{Ai} and I_{bi} represent the standardized variances in these parameters, i.e. the variance divided by the squared mean. To calculate the generation time of sex i , we used the formulae of Nunney & Elam (1994) for a type 2 survivorship (as adult survival rate is independent of age): $T_i = M_i - 1 + A_p$, where M_i is the estimation of the mean maturation time; A_i is equal to $1/(1 - v_i)$, where v_i is the adult survival rate of the sex i (Table 1). The standardized variance of the mean longevity I_{Ai} is equal to v_i . For each breeding season, we computed the fecundity for the two sexes and their standardized variance, then the effective size.

Table 1 Parameters estimates by sex and population using the ecological approach from Nunney & Elam (1994)

Population	Sex i	Survival rate v_i	Adult Life span A_i	Maturation time M_i	Generation time T_i	Mean generation time T
LCR (urban)	Male	0.65	2.85	1	2.85	3.28
	Female	0.73	3.7	1	3.7	
BAC (rural)	Male	0.62	2.63	2	3.63	3.98
	Female	0.77	4.35	1	4.35	

Genetic method. We applied methods using temporal samples. These are based on the idea that gene frequencies will differ between samples taken at two different times from the same population because of random drift. The amount by which they will differ is inversely proportional to the effective size.

(a) *Waples' (1989) method.* The standardized variance in the allele frequencies change (F_k) for each microsatellite locus was calculated using the following equation (Pollack 1983):

$$F_k = \frac{1}{K-1} \sum_{i=1}^K \frac{(x_i - y_i)^2}{\left(\frac{x_i + y_i}{2}\right)}$$

where K is the number of alleles, and i is the frequency of the respective allele at times x and y , respectively. F_k was then averaged over all loci. The variance effective size was estimated according to Waples (1989):

$$N_e = \frac{t}{2[F_k - 1/(2S_0) - 1/(2S_t) + 1/N]}$$

where t is the number of generations between the two samples: t is computed as the number of years separating the two samples divided by the generation time (mean age of parents at birth weighted by their respective contribution). S_0 and S_t represent sample sizes at time zero and time t , and N represents the adult population census size at time zero. For the rural population, the first sample was taken in 1992 and the second in 1997; for the urban population, samples were taken in 1995 and 1998. We then computed the 95% confidence interval associated with N_e as described by Waples (1989).

(b) *Berthier et al.'s (2002) method.* The method of Berthier *et al.* is a Bayesian coalescent-based method that incorporates two samples from the focal population separated by a given number of generations. For each cat population, we sampled consecutive generations. We took all the adults present in a given year for the first sample. The juveniles born from this pool of adults constituted the second sample. This operation was repeated for each cohort over the

period studied in each population. We specified a prior maximum effective population size at 500, which models our previous knowledge and uncertainty about N_e . The observed distribution of alleles allowed us to obtain the posterior probability function of N_e by a likelihood approach. The model is implemented in TM 3 software (Berthier *et al.* 2002), which computes the maximum-likelihood value as well as the 5% and 95% quantiles of the posterior distribution of N_e . We based our estimates on 50 000 replications.

For all methods, we calculated the harmonic mean of the N_e values over years to take into account fluctuation of the population size in the estimation. Taking the harmonic mean of N_e over years is not completely valid, because the generations overlap. However, the correct average is unknown (Nunney 2002) and in this case any plausible average would lead to the same conclusions. We also reported estimates of the ratio N_e/N , where N is the number of adults.

Results

The variance in reproductive output did not differ between the sexes at LCR (the averaged ratio male/female variance in reproductive success equalled 0.95, Fig. 1), but was 3.1 greater in males than in females at BAC (Fig. 1). The variance in female reproductive success was the same in both populations (8.09 in LCR vs. 8.77 in BAC). Consequently, the two cat populations differed strongly in terms of variance in male reproductive success (Fig. 1).

Ecological method

The sex ratio in the rural population was lower than in the urban one (Table 2). The generation time (mean age of reproductive individuals) was higher in the rural cat population than the urban one.

Fecundity and N_e were computed annually (Table 2). Using the relevant parameter estimates this model yielded $N_e = 18.3$ in BAC, which was approximately 33% of the census population. We obtained $N_e = 23.7$ in LCR, which was equal to approximately 42% of census population size. The polygynous system lowers effective size by approximately 20%.

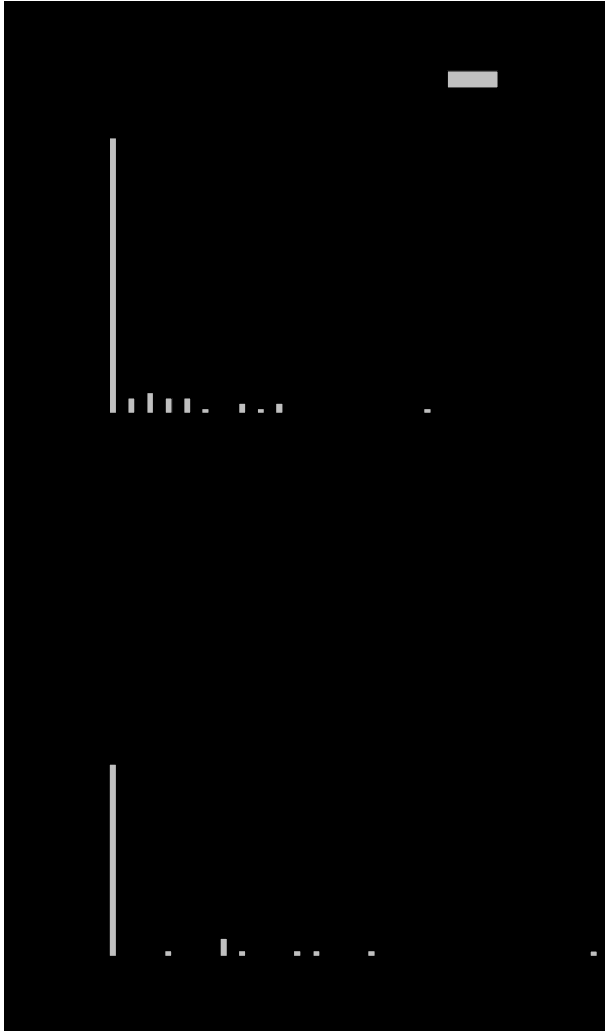


Fig. 1 Observed distribution of annual fecundity among individuals of each sex. The reproductive output is the number of kittens produced per year by each individual.

Genetic method

(a) *Waples' (1989) method.* The generation time was 2.94 in LCR and 3.81 in BAC. The effective sizes were nearly equal for the two populations (Table 3). The ratio of N_e/N can be estimated as approximately 43% in the BAC and approximately 40% in the LCR cat population.

(b) *Berthier et al.'s (2002) method.* We have only one generation separating two samples, $T = 1$. In LCR, the maximum likelihood effective size was equal to 35.6, which is three times larger than the value estimated in BAC ($N_e = 12.0$) (Table 4). The ratio of N_e/N across years was estimated as approximately 22% range (20–24) in BAC and approximately 64% range (30–162) in LCR. The variance was extremely large at LCR, with estimates of effective size sometimes exceeding census sizes.

Discussion

Using Nunney & Elam's (1994) equation, our ranges of estimates of N_e/N (0.33–0.42) for the domestic cat are comparable with those for other Felidae species: 0.42 for the leopard *Panthera pardus* (Spong *et al.* 2000), 0.44 for the cheetah *Acinonyx jubatus* (Kelly 2001), 0.41 for the tiger *Panthera tigris* (Frankham 1995), species which all have nearly the same social organization as the cat in the rural habitat. Empirical values of N_e/N are usually between half and the whole census population size for stable populations (Nunney 1993; Nunney & Elam 1994), but can decrease to 10% of the total population when population size varies from year to year (Frankham 1995). Population sizes being stable over years in the cat populations studied, factors other than population size variation have the potential to decrease the N_e/N (Creel 1998) strongly, such as the variance in reproductive success among males.

Table 2 Summary of the parameters estimates used to calculate the effective size by the Nunney & Elam (1994) method and the ratio N_e/N for the two cat populations (BAC and LCR)

Population	Year	Fecundity (b_i)		Standardized variance of fecundity (I_{b_i})		Number of adults		Sex ratio (r)	Effective size (N_e)	Harmonic mean		
		Female	Male	Female	Male	Female	Male			N_e	N	N_e/N
LCR	1995	1.48	1.19	4.84	4.18	25	31	0.55	19.22			
	1996	1.77	1.92	2.64	1.49	26	24	0.48	23.30			
	1997	2.52	2.5	1.93	1.87	27	26	0.49	24.62			
	1998	1.2	1.65	2.36	2.77	39	29	0.43	29.79	23.65	56	0.42
BAC	1992	1.15	1.94	4.05	10.16	33	18	0.35	14.43			
	1993	1.55	2.45	4.9	3.2	38	22	0.37	25	18.3	55.1	0.33

Table 3 Locus and number of alleles per locus, F_{kj} and F_k , standardized variance in allele frequency change according to Pollack (1983) calculated for each locus and averaged over loci, respectively, generation time, number of generations between samples t , sample size (S_0 , S_t), adult population size (N), estimates of the variance effective size (N_e) and 95% confidence interval (into brackets) and the ratio N_e/N for the two cat populations (BAC and LCR) for the method-of-moment estimator of Waples (1989)

Population	Locus	No. of alleles	F_{kj}	F_k	Generation time	t	S_0	S_t	N	N_e (95%CI)	N_e/N
LCR	fca8	9	0.016								
	fca23	8	0.039								
	fca37	5	0.030								
	fca43	10	0.054	0.030	2.94	1.02	41	36	56	22.57 (14.41–36)	0.40
	fca45	9	0.022								
	fca77	8	0.018								
	fca78	14	0.020								
	fca90	7	0.020								
	fca96	8	0.057								
BAC	fca8	6	0.015								
	fca23	7	0.042								
	fca37	7	0.065								
	fca43	7	0.039								
	fca45	8	0.020	0.053	3.81	1.31	32	18	51	22.13 (10.5–43.4)	0.43
	fca77	6	0.052								
	fca78	7	0.095								
	fca90	6	0.153								
	fca96	7	0.010								

Table 4 Estimates of variance effective population size by the maximum-likelihood estimator of Berthier *et al.* (2002), N_{emax} denotes the prior information about the upper limit of N_e , the maximum likelihood value denotes the N_e (and 95% posterior probability interval) in two cat populations, BAC and LCR, for each study year and averaged

Population	Years	N_{emax}	Max likelihood value	95% posterior probability interval	N	N_e/N
LCR	1995	500	16.83	12.19–39.02	56	0.3
	1996	500	81.22	54.17–447.1	50	1.62
	1997	500	37.66	26.59–205.07	53	0.71
	1998	500	70.75	50.65–455.15	68	1.04
	Harmonic mean			35.58		56
BAC	1992	500	12.01	9.05–21.17	51	0.23
	1993	500	12.19	8.93–20.03	60	0.20
	Harmonic mean			12.1		51.13

As expected (Wright 1938), the demographic estimate of N_e/N is 20% lower in the polygynous cat population, characterized by a higher variance in male reproductive success and delayed age at first reproduction in males than in the promiscuous population, where reproduction is shared more equally among breeders. Contrary to the promiscuous population, only a few males of a given cohort will reach social maturity in the polygynous one, either because of the harassment of resident dominant

males that force some of them to leave the population or because of their low survival rate. Such strong male competition for receptive females leads to a sex-ratio disequilibrium in favour of females that already decreases the effective size. If we compute the breeding sex ratio effective size ($N_e = 4N_m N_f / (N_m + N_f)$), the decrease of N_e is approximately 16% in the rural cat population but only 3% in the urban one, that is characterized by a more even sex-ratio. However, the variance in reproductive success among

males appears to contribute the most to the decrease of N_e . Indeed, using the formula $N_e = (Nb_f T_f - 1) / (b_f T_f + (I_{bf} / T_f) - 1)$ to take the variance in reproductive success into account (Lande & Barrowclough 1987; Creel 1998), the decrease in N_e is 70% and 66% for males and females in LCR, respectively, and 87% and 79% in BAC. Our results thus provide a new example, again showing the importance of the mating system on gene dynamics, and hence on N_e , in mammals (Anthony & Blumstein 2000). To our knowledge, this study also provides the first evidence in favour of a strong effect of the variance in male reproductive success on the N_e/N ratio at the intraspecific level between populations differing essentially according to their mating system. Cat populations close to the ancestral population lifestyle should be studied to complete the overview of the role of mating system on effective size in this species. For example, the cat population of the Kerguelen archipelago, where males are monogamous (Say *et al.* 2002) and dispersal is female-biased at local scale (Devillard *et al.* unpubl.), would provide a good model.

Estimates of N_e from the genetic model of Waples (1989) are in good agreement with the ecological results. The narrow confidence intervals are due probably to the high polymorphism of our microsatellites. However, genetic estimates of N_e/N do not show any difference between the polygynous rural and promiscuous urban cat population. We cannot invoke a different level of successful immigration, because immigration is very low in both populations due to environmental constraints on movements and social constraints on settlement (Devillard *et al.* 2003). A possible explanation might be that the variance in male reproductive success is eroded by euthanasia of kittens by owners in BAC, although this point remains to be verified. Ecological methods are not sensitive to such euthanasia processes, which act at the genetic level.

We were unable to estimate N_e confidently using the Berthier *et al.* (2002) method. Our results show extremely important differences in the estimates of N_e among years (results can vary by as much as 483%) in the urban cat population, in some cases with N_e estimates greater than the census size. While theoretically possible, all empirical studies in mammals conducted until now did not show any case where N_e is greater than the census size (Frankham 1995). The 95% confidence interval of N_e was also very large (see Hansen *et al.* 2002 for similar results with the same sample sizes but with a larger number of generations between samples). Such a large variance may be especially problematic when sample sizes are small, as they often are with endangered species. The reason for the discrepancy between the results from the likelihood-based approach of Berthier *et al.* (2002) and from the moment-based approach of Waples (1989) is unclear; we have no idea about such substantial variability in effective size as determined by the Berthier *et al.* (2002) method in the LCR population.

Simulations from individual-based models are needed to identify precisely the conditions of application of the Berthier *et al.* (2002) method (robustness to violations of underlying assumptions, number of individuals required, number of loci and number of alleles per locus, for better precision and accuracy).

To conclude, combining genetic and ecological approaches in the field whenever possible appears to be a promising route to provide a more complete picture of the population dynamics features acting on N_e (Garrigan *et al.* 2002).

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