Cat impact and management on two Mediterranean sister islands: "the French conservation touch"

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Abstract Feral cats (*Felis catus*) are one of the most damaging introduced species for island species worldwide. While cat control or eradication is handled with increasing efficiency on uninhabited islands, the strong bond with humans, regardless of ownership, makes cat management difficult on inhabited islands. We conducted a cat-removal programme on Port-Cros Island where both the presence of humans and their cats threaten *Puffinus yelkouan*, an endangered Mediterranean endemic species of burrowing petrel. The two largest French-breeding colonies of this procellariid are on the two studied islands: Port-Cros and Le Levant. The cat-removal programme was implemented on Port-Cros, with Le Levant used for comparison. Cat diet studied through scat analysis showed cats to be responsible for killing 162 ± 46 and 21 ± 4 shearwaters per cat and per year on Le Levant and Port-Cros respectively. Bird breeding parameters were monitored during seven years on Port-Cros (before and after cat removal) and three years on Le Levant. By constructing a shearwater population viability model, we calculated that the cat impact on the yelkouan shearwaters threatens the entire population in the long term and justified cat removal. We designed a conservation management plan for Port-Cros where, taking into account human presence, feral cats were live-trapped and domestic cats were sterilised. Following this two year campaign, cat predation of shearwaters ceased, followed by an increase in the shearwater breeding population. Thus, protecting seabirds from cat predation is possible, even on islands where inhabitants are notoriously reticent to any sort of cat removal programme.

Keywords: Feral cat, *Felis catus*, eradication, yelkouan shearwater, *Puffinus yelkouan*, island conservation

INTRODUCTION

The spread of non-indigenous species is considered second only to habitat destruction in harming native communities and considered first to impact island biodiversity (Vitousek *et al.*1995; Williamson 1996; Whittaker and Fernández-Palacios 2007).

Cats (*Felis catus*) were first introduced to islands in the Mediterranean in 9000 BP (Vigne *et al.* 2004; Driscoll *et al.* 2007), and have since been introduced to islands worldwide from the sub Antarctic to the sub Arctic, including the most arid and mesic islands (Ebenhard 1988; Courchamp *et al.* 2003). They are successful invaders of islands because they can survive without access to fresh water, have high fecundity, a high adaptability to novel environments, and have generalist predatory behaviours that allow them to feed on most prey species (Pearre and Maass 1998; Fitzgerald and Turner 2000; Say *et al.* 2002). Cats are one of the most damaging invasive predators on islands (Fitzgerald 1988; Macdonald and Thom 2001) and are responsible, at least in part, for 8% of global bird, mammal and reptile extinctions and a significant threat to almost 10% of critically endangered birds, mammals and reptiles (Medina *et al.* 2011).

Seabirds are often badly affected by cat introduction on islands (Courchamp *et al.* 2003; Blackburn *et al.* 2004; Donlan and Wilcox 2008), particularly petrels and shearwaters, due to their lack of predatory defence and their high vulnerability to adult mortality (Brooke 2004; Le Corre 2008). Different studies have recently shown that several *Puffinus* species, especially those belonging to the Manx shearwater *P. puffinus* worldwide 'complex', are seriously threatened by introduced predators (Mayol-Serra *et al.* 2000; Ainley *et al.* 2001; Cuthbert 2002; Keitt *et al.* 2002; Martínez-Gómez and Jacobsen 2004). The Yelkouan shearwater (*Puffinus yelkouan*) is endemic to the Mediterranean Basin and near threatened and declining (IUCN Red List), with a breeding population possibly not exceeding some thousands of pairs and probably restricted to a few breeding locations, most of which have introduced predators (Bourgeois and Vidal 2008).

Eradicating cats from islands can protect native species from the threat of extinction (Nogales *et al.* 2004) and research on the ecology of insular feral cats can improve the efficacy and prioritization of cat eradications (Fitzgerald 1988; Paltridge *et al.* 1997; Fitzgerald and Turner 2000; Macdonald and Thom 2001).

The Hyères Archipelago has domestic and feral cat populations, and is a major breeding site for Yelkouan shearwater. We studied shearwater population viability in order to conduct relevant feral cat management.

The aims of this study were to: 1) monitor the shearwater populations; 2) study cat diet in relation to the shearwater breeding cycle; 3) evaluate the cat impact on the population viability of shearwaters; and 4) manage cat populations in order to maintain biodiversity on islands.

MATERIALS AND METHODS

Study area

This study was conducted on two islands within the Hyères Archipelago located in the north-western Mediterranean Sea (Fig. 1). Le Levant Island (10.8 km²) has a maximum elevation of 140 m above sea level and is 9.15 km from the mainland. It is a military island for 90% of its area; the remaining 10% is occupied by civilians. Port-Cros Island (6.40 km²) has been protected by National Park status since 1963, has a maximum elevation of 196 m above sea level, and is 15 km from the mainland. The climate is sub-humid, temperate Mediterranean with an average annual rainfall of 582.4 mm and an average annual temperature of 16.5°C (Levant Island Meteorological Office, 1997–2007). The islands are siliceous, Le Levant being mainly covered by the typical shrubs of "maquis" vegetation with sparse sclerophyllous oaks (*Quercus ilex*) and halepo pines (*Pinus halepensis*); Port-Cros being covered by mixed forests of the sclerophyllous oaks and halepo pines.

These islands have long been home to introduced vertebrates including cats for two centuries (Pasqualini 1995), rats (*Rattus rattus*) at least since the Roman period (Ruffino and Vidal 2010), and rabbits (*Oryctolagus cuniculus*). The Mediterranean endemic seabird, yelkouan shearwater is represented on Le Levant by 800-1,300 pairs and on Port-Cros by 140-180 pairs from a world population likely to be fewer than 15,000 pairs (Bourgeois and Vidal 2008).

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Shearwater monitoring

We monitored 100 shearwater burrows on Port-Cros during seven breeding seasons (2003 to 2009) and in 76 burrows during three breeding seasons (2007 to 2009) on Le Levant to record the percentage of occupied burrows and breeding success. Like most seabirds, yelkouan shearwaters have low reproductive output; they start breeding at around 6 years of age, generally first attempts to breed fail, and they produce only one egg per year (e.g., Brooke 1990). They arrive at their breeding sites in late October or early November (Vidal 1985; Zotier 1997), which corresponds to the prospecting period when birds visit the burrows and look for their mate. Egg laying is from mid-March to early April, hatching in May and fledging in July and early August.

A miniature infrared camera on a stiff coaxial cable was "snaked" down each burrow to determine the presence of pairs, eggs or chicks (Bourgeois and Vidal 2007). Burrows were checked nine times during each breeding season: at the end of the pre-laying period, the start, middle and end of the laying and hatching periods, and 15 days before the beginning and at the middle of the fledging period. A last check was done at the end of the breeding season to find possible corpses and confirm chick fledging (Bourgeois 2006). A randomisation test was used to compare the percent of occupied cavities between the first year and the last year of our censuses

Cat diet study

The diet of feral cats was studied through scat analysis (Fitzgerald *et al.* 1991; Bonnaud *et al.* 2007). We opportunistically collected scats on sample paths from October 2002 to August 2004 on Port-Cros and from October 2006 to August 2008 on Le Levant. Scats were collected five times per year: when the shearwaters were prospecting, breeding, hatching, rearing and during their annual exodus. By removing all scats found in the field and excluding very old ones, we assumed that each sampling set represented the cat diet for that period. All scats found were reported on a map with a handheld global positioning system. This sampling allowed us to determine the cat diet during each of the shearwater breeding phases.

Scats were analysed by washing through a 0.5-mm sieve under a stream of hot water and separating all items such as hairs, feathers, bone fragments, teeth, and insect chitin (Nogales *et al.* 1988). Each item was then identified by comparison with reference material. The diet results were given in frequencies of occurrences and numbers of prey. A Pearson χ^2 test for independent samples was used to test the difference of the cat diet on both islands, then randomisation tests were performed to detect differences in cat consumption of each prey thereby allowing comparison of small percentages (PD = observed percentage differences; Manly 1997).

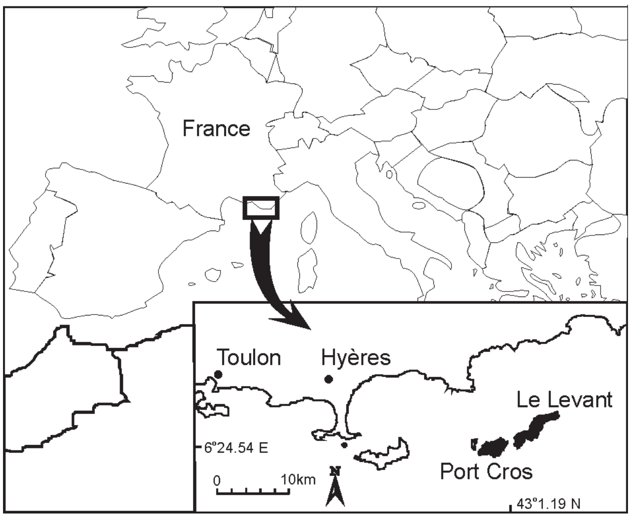

Fig.1 Study site, Hyères archipelago (south east of France). Study conducted on Port-Cros and Le Levant Island.

Cat impact on yelkouan shearwaters

To estimate the magnitude of cat predation on shearwaters, we first calculated the number of shearwaters eaten each year by the cat population. Since no identical parts from two or more shearwaters were found in any one cat scat, each scat were assumed to be of one bird (Keitt *et al.* 2002; Cuthbert 2002; Bonnaud *et al.* 2007). Cats usually defecate once per day (Konecny 1987). Thus, the mean number of the shearwaters per scat is equivalent to the mean number of shearwaters ingested per day and per cat ($NP_{/d}$). The annual mean number of shearwaters killed on Le Levant (NP) by the cat population was calculated as follows:

$NP = NP_{/d} \times 365 \times N_{cat}$ (1)

with N_{cat}: number of cats on the island.

Predation rates were calculated assuming: 1) predation on prospectors (birds looking for a mate and a burrow) (PB) was four times higher than on breeders (birds which were breeders the next year and the current year) (PP); and 2) predation was exerted on prospectors from age 3 (from $N3_P$ to $N6_{+P}$) and on breeders (first breeding assumed at 6 years, (Brook 1990)) ($N6_{+B}$)

$NP = P_B \times (N6_{+B}) + P_P \times (N3_P + N4_P + N5_P + N6_{+P})$ (2)

With $P_P = 4 \times P_B$

And NP = number of shearwaters killed per year.

The impact of cat predation on shearwater population dynamics was assessed by constructing a shearwater demographic population model adapted from Bonnaud *et al.* 2009 (see Appendix for the model structure and implemented parameters). The value of shearwater breeding success without cat predation came from monitoring burrows in Port-Cros colonies during four breeding seasons (2006 to 2009). Cat predation rates were then included in several scenarios depending on cat population estimates and taking into account the higher shearwater population estimates for the both islands (shearwater population of 1) Le Levant Island = 2600 breeders and 2) Port-Cros Island = 360 breeders; Bourgeois and Vidal 2008). The demographic population model was run with ULM (Unified Life Models) mathematical modelling software (Legendre and Clobert 1995) and we conducted Monte Carlo simulations (100 time steps and 1000 trajectories) to account for the uncertainty of several population parameters.

Cat management on Port-Cros Island

Cat presence on Port Cros constituted a threat to the shearwater population which, at 180 pairs, was already small. A cat management programme was started in January 2004. The presence of human inhabitants, and domestic cats meant that the removal of feral cats should be undertaken using only non-lethal methods, i.e. cat living-traps checked each morning and evening. Complete cat eradication was not possible due to the persistence of a small domestic cat population located in the village. The trapping campaign was initially concentrated near the shearwater colonies and then extended along all paths, especially where cat scats were found. A sterilisation campaign was conducted on the domestic cats and all new domestic cats arriving were checked for sterilisation. During and after cat control we collected cat scats during selected phases of the shearwater breeding cycle. We used a Mann-Whitney U test to compare the number of scats found before the beginning of the cat control and after the last feral cat was caught. These scats were analysed only in order to detect shearwater remains.

Table 1 Monitoring of the breeding parameters of the yelkouan shearwater and the percent of occupied nests on Port-Cros and Le Levant Islands.

	Port-Cros Island (360 breeding birds, 100 burrows monitored)							
Year survey	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**mean ± SD**
Occupied burrows	28	32	41	42	39	40	37	37
% occupied burrows	27.7	31.1	39.8	39.6	37.5	38.8	36.6	35.9 ± 4.7
Hatching success*	70.0	85.7	97.4	89.5	73.7	94.7	91.7	86.1 ± 10.5
Fledging success*	92.9	95.8	83.8	85.3	92.9	91.7	100.0	91.8 ± 5.7
Breeding success*	65.0	82.1	81.6	76.3	68.4	86.8	91.7	78.9 ± 9.6
	Le Levant Island (2600 breeding birds, 76 burrows monitored)							
Year survey					**2007**	**2008**	**2009**	**mean ± SD**
Occupied burrows					33	32	30	32
% occupied burrows					46.5	42.1	41.7	43.4 ± 2.7
Hatching success*					93.8	87.1	93.3	91.4 ± 3.7
Fledging success*					76.7	88.9	89.3	84.9 ± 7.2
Breeding success*					71.9	77.4	83.3	77.5 ± 5.7

* Shown as a percentage of the occupied burrows.

Due to the renowned harmful effect of rats on seabirds (e.g., Jones *et al.*, 2008) we tested whether cat control affected rodent numbers. As cats preyed mainly upon rats on this island (Bonnaud *et al.* 2007) a meso-predator release was possible. We set two lines of 30 traps in two different areas of the island and set live traps every 10 meters during four consecutive nights for 19 trapping sessions from December 2004 to August 2008 at three or four months intervals

On Le Levant, other than an awareness campaign about the threat of feral cat presence for island biodiversity, there has been no cat management.

RESULTS

Shearwater monitoring

Shearwater breeding, monitored on Port-Cros from 2003 to 2009 and on Le Levant from 2007 to 2009, showed high breeding parameter values (Table 1). On both islands the percent of occupied nests was low (36% on Port-Cros and 43% on Le Levant). During the study period, nest occupation significantly increased on Port-Cros (PD = -0.149, p = 0.0130) and decreased, but not significantly, on Le Levant. Hatching success increased on Port-Cros and remained stable on Le Levant. Fledging success was high on both islands but slightly higher on Port-Cros where success in the last year sampled reached 100. The overall breeding success increased to reach similar values on both islands.

Cat diet study

We collected and analysed 689 scats on Port Cros and 200 on Le Levant. Cats on both islands preyed mainly upon introduced mammals. Yelkouan shearwater was the most frequent bird found in the scats (Table 2). Other birds (mainly passerines), reptiles and invertebrates were secondary prey. When all prey consumed was considered, significant differences appeared between the cat diets of both islands ($\chi^2 = 314$, $p < 0.001$). The consumption of rabbits (PD = 0.203, $p < 0.001$) and shearwaters (PD = 0.376, $p < 0.001$) were significantly higher on Le Levant than on Port-Cros and consumption of rats (PD = 0.350, $p < 0.001$) and wood mice (*Apodemus sylvaticus*) (PD = 0.322, $p < 0.001$) were significantly lower. More than one mammal per scat was found in scats from Port-Cros, mainly rats and wood mice. Less than one mammal per scat was found in scats from Le Levant, the cat diet being mainly comprised of rabbits and shearwaters.

Regarding cat predation on shearwaters, frequency of occurrence was low on Port-Cros Island (shearwater remains appeared in 5.9% of scats found) compare to that on Le Levant Island (shearwater remains appeared in 44.3% of scats found).

Cat impact on yelkouan shearwaters

The number of shearwaters eaten per cat per year reached 162 ± 46 and 22 ± 4 individuals respectively on Le Levant and Port-Cros. Peaks in predation on shearwaters on both islands were during autumn and winter (October–November and December–February), corresponding to their prospecting period (Fig. 2) and this predation remained high during spring on Le Levant (Fig. 2B).

Table 2 Food categories of the cat diet on Port-Cros and Le Levant Islands expressed as frequency of occurrence and the numbers of prey per scat.

	Port-Cros Island (August 2002 - August 2004)		Le Levant Island (August 2006 - August 2008)	
Food categories	**Frequency of occurrence (%)**	**Number of prey per scat***	**Frequency of occurrence (%)**	**Number of prey per scat**
MAMMALS	91.87	1.57	74.50	0.75
Rattus rattus	77.94	0.95	43.00	0.45
Apodemus sylvaticus	34.69	0.54	2.50	0.03
Oryctolagus cuniculus	6.68	0.09	27.00	0.27
BIRDS	16.69	0.12	51.00	0.51
Puffinus yelkouan	5.81	0.05	43.50	0.44
other-birds	10.89	0.06	7.50	0.08
REPTILES	7.84	0.03	11.50	0.12
INSECTS	11.03	0.05	8.50	0.11

* data only available between August 2003 and August 2004

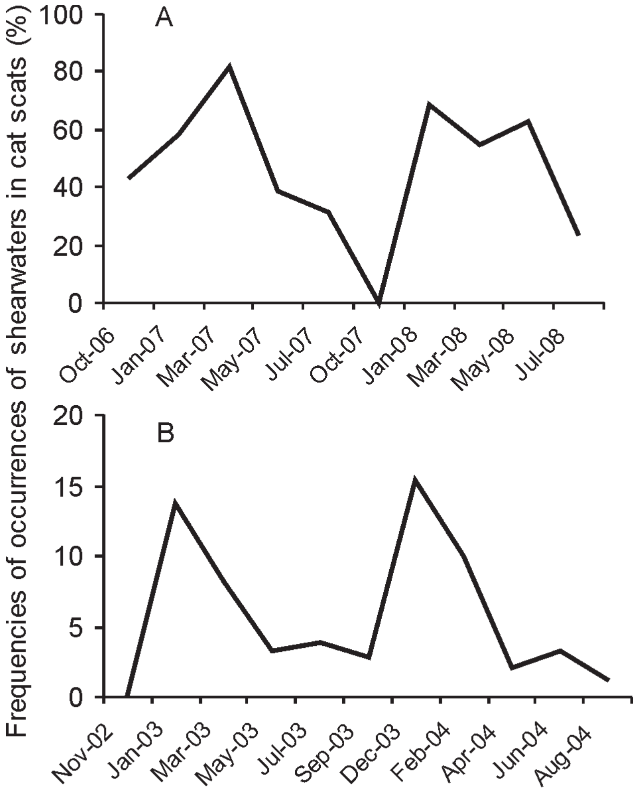

Fig. 2 Frequencies of occurrences of shearwater remains found in cat scats during a 2-year survey on (A) Le Levant Island (B) on Port-Cros Island.

The population of cats on Port-Cros was estimated as 20 based on trapping data during feral cat removal (Bonnaud *et al.* 2010). It was impossible to estimate the cat population of Le Levant but the small number of scats found per sampling period suggested that cat density on this island was lower than on Port-Cros. Thus, we tested three scenarios of 5, 10 and 20 individuals (Table 3). Applying equations (1) and (2) we calculated the number of shearwaters killed per year by cat populations of both islands and the predation rates on breeders and prospectors (Table 3).

The shearwater demographic population models were run using scenarios predicting that: 1) without cat predation the shearwater populations of both islands showed growth rates higher than 1, and 2) with cat predation all scenarios showed decline leading to eventual extinction of the shearwater population.

Cat management on Port-Cros Island

Cat removal started in January 2004, with 28 cats trapped over two years (Table 4). Trapping success progressively decreased, becoming nil by January 2006 despite regular trapping sessions being continued. Subsequently, only neutered domestic cats were seen wandering outside the village and were photographed by cameras placed near paths. No sign of recovery of the cat population was observed. The number of scats found on sampling paths significantly decreased from 0.631 ± 0.119 scats/day before the beginning of cat control to 0.177 ± 0.022 scats/day after the last feral cat was caught ($U = 2$, $p < 0.001$). Between August 2004 and August 2005 only one scat was found (in May) and it contained shearwater remains. Cat scats found after August 2005 were assumed to belong to the few domestic cats wandering around the island but without evidence that they are preying upon shearwaters

Table 4 Numbers of trap nights and cats trapped during the cat management program conducted on Port-Cros Island.

Period	Trap nights	Cats caught
Dec-Feb 04	45	2
Feb-Apr 04	41	4
Apr-Jun 04	89	2
Jun-Aug 04	60	1
Aug-Oct 04	66	3
Oct-Jan 05	190	8
Jan-Mar 05	262	4
Mar-May 05	134	1
May-Aug 05	118	1
Aug-Oct 05	132	0
Oct-Jan 06	617	2
Jan-Mar 06	77	0

Rat trapping success in trap lines varied between seasons and years but remained low during both 1978-1987 (mean: 0.068 ± 0.024 rats caught per trap-night , Granjon and Cheylan 1993) and 2004-2008 (mean: 0.112 ± 0.026 rats caught per trap-night, this study) monitoring periods.

DISCUSSION

Shearwater monitoring

Yelkouan shearwater breeding populations were reduced to a few individuals, especially on Port-Cros, due to predation by cats. Bourgeois and Vidal (2007) and Bourgeois *et al.* (2008b) showed that these breeding habitats are far from saturation. Both have unoccupied burrows within colonies and sites suitable for new colony establishment. Cat predation kills more shearwaters when they are in the prospecting stage of the breeding cycle. As breeders they spend little time on the ground and avoid predation by rapidly entering their burrows (Bourgois *et al.* 2008a). Despite the presence of predators the breeding populations of shearwaters on both islands show high

Table 3 Results of the shearwater demographic models which include cat predation rates according to the size of the cat population on Port-Cros and Le Levant Islands. $Shearwater_{Pop}$: size of the shearwater populations, $N_{shear.killed}$: number of yelkouan shearwater killed per the cat population and per year, Cat_{Pop}: size of the cat populations, PB: cat predation rate on breeding birds, PP: cat predation rate on prospecting birds, λ: growth rate of yelkouan shearwater populations, T_{ext}: predicting time (in years) for yelkouan shearwater population extinction.

	Port-Cros		Le Levant			
$Shearwater_{Pop}$	360		2600			
Cat_{Pop}	0	20	0	5	10	20
$N_{shear. killed}$	0	431 ± 72	0	810 ± 230	1621 ± 460	3241 ± 920
PB	0	0.386 ± 0.065	0	0.101 ± 0.029	0.202 ± 0.057	0.403 ± 0.115
PP	0	1.544 ± 0.260	0	0.404 ± 0.116	0.808 ± 0.228	1.612 ± 0.460
λ	1.0102 ± 0.0000	0.7054 ± 0.0064	1.0101 ± 0.0000	0.8586 ± 0.0001	0.6805 ± 0.0021	0.7331 ± 0.0058
T_{ext} (year)	-	6.3780 ± 0.0185	-	53.6820 ± 0.0649	21.1840 ± 0.0671	6.5830 ± 0.0384

reproductive success (77 to 79% Table 1) when compared to other shearwater and petrel populations (Brooke 1990; Hunter *et al.* 2000; Cuthbert 2002; Dunlop *et al.* 2002; Le Corre *et al.* 2002; Jouventin *et al.* 2003; Igual *et al.* 2007; Rayner *et al.* 2007; Pascal *et al.* 2008). Now that predation is controlled, the settlement of new breeders should increase on Port-Cros.

Cat diet study

Our study supported the common observation that feral cats are highly generalist predators, able to feed on prey ranging from small insects to birds and mammals that weigh more than 500 g (Nogales and Medina 1996; Tidemann *et al.* 1994; Turner and Bateson 2000). However, cats can specialise on what is available and only a few species represented the major part of its diet. Introduced mammals and shearwaters were the prey mainly eaten by cats on these Mediterranean Islands. The differences in cat diet between the two islands are explained by the high frequency of occurrences of rabbits and shearwaters on Le Levant and the high frequencies of occurrences of rats and wood mice on Port-Cros (Bourgeois and Vidal, 2008; Port-Cros National Park pers. comm.). Because rabbits and shearwaters are large prey items, the consumption of one constitutes the required daily food intake per cat (Bonnaud *et al.* 2007). In contrast the consumption of rodents (rats and wood mice) generally requires the cat to prey upon more than one individual and can result in greater diversify in the diet. This indicates that the number of prey items eaten may provide a trophic index which can be used to evaluate cat impact on prey population dynamics.

Cat impact on yelkouan shearwaters

The cat diet studies revealed high cat predation during the prospecting period of the shearwaters and continuing predation throughout the year. Cat predation on the shearwaters reached 162 ± 46 and 22 ± 4 individuals per cat per year respectively on Le Levant and Port-Cros, placing these populations of shearwaters at high risk of local extirpation. These islands have the largest colonies of yelkouan shearwaters in France, being one of the largest in the world (Bourgeois and Vidal 2008).

Mathematical population dynamic models are a useful tool to evaluate the impact of species interactions. Our model predicted annual population growth rates slightly greater than one without cat predation, which was consistent with predictions for populations of other *Puffinus* species: *P. griseus* (1.017, Hamilton and Moller 1995; 1.044, Jones 2002), *P. huttoni* (0.930–1.050, Cuthbert and Davis 2002), *P. opisthomelas* (1.006, Keitt *et al.* 2002), *P. auricularis* (1.001, Martinez- Gómez and Jacobsen 2004) and *P. mauretanicus* (1.007, Oro *et al.* 2004). This suggests that the scenario selected for the yelkouan shearwater can be considered realistic and the model structure suitable. Few studies have taken predation on prospecting birds into account. Prospecting birds are probably more vulnerable to cat predation due to their behaviour: wandering on the ground and calling outside burrows, rather than entering the burrow rapidly after landing (James 1985; Brooke 1990; Ristow 1998; Bourgeois *et al.* 2008a; Bonnaud *et al.* 2009). Even with a small cat population included, the shearwater demographic showed a decrease of the shearwater populations. In some cases, cat predation on prospectors was so high it exceeded the number of prospectors available, indicating immigration from outside these populations. In summary, our results showed that: 1) these shearwater populations cannot survive if they are not supported by immigration; and 2) even if the breeding populations have a high breeding success, these small populations seem to be at a high risk of local extinction due to feral cat predation.

Cat management on Port-Cros Island

Faced by the strong threat exerted by cats on the yelkouan shearwaters, a cat management campaign was conducted on Port-Cros Island. This cat management campaign was, to the best of our knowledge, one of the first conducted in the Mediterranean Basin (Genovesi 2005; Lorvelec and Pascal 2005). It was also one of the few successfully developed using only non-lethal trapping and conserving a domestic population of neutered domestic cats on the island (Nogales *et al.* 2004). Non-lethal trapping proved to be successful in eradicating the feral cat population and rapidly prevented cat predation on native threatened species. No feral cats were observed or trapped on the island during nearly three years following the last feral cat caught in October 2005, despite a reduced but continuous trapping campaign. Feral cat control, which started in 2004, resulted in an increase in numbers of occupied shearwater burrows and breeding pairs, confirming that cat predation, being mainly focused on the prospecting period, probably limits the recruitment of young breeders (Keitt *et al.* 2002; Massaro and Blair 2003; Peck *et al.* 2008). Moreover, due to the high probability of a top-down-regulated ecosystem on Port-Cros, the rat population on this island was carefully monitored during and after cat control (Russell *et al.* 2009). Rat-trapping success values have remained similar to previous values recorded before cat control (Granjon and Cheylan 1993). This suggests that cat control, while diminishing predation pressure on rats, has not led to a significant increase in the rat population size, nor their impact on seabirds.

Implications for conservation

On islands with multiple introduced predators and native prey species, it is commonly suggested that the best solution is the simultaneous eradication of both introduced top- and mesopredators to avoid any risk of mesopredator release effect (Simberloff 2001; Zavaleta *et al.* 2001; Courchamp *et al.* 2003; Blackburn 2008). However, when introduced predators threaten long-lived seabirds, top-predators like cats have larger detrimental effects on their population dynamics than mesopredators (Le Corre 2008; Russell *et al.* 2009). Moreover, top-predator populations are not the only means of regulating mesopredator populations (Blackwell *et al.* 2003). Thus, the eradication of top-predators should be encouraged simultaneously with monitoring the population dynamic of other species that can react to this ecosystem management. Knowing that most of the islands of the Mediterranean basin house feral and domestic cats and native endemic species, this study indicates that even if a complete cat eradication is not feasible, feral cat eradication coupled with the persistence of a neutered domestic cat population can lead to the same results as total eradication (Oppel *et al.* 2011). As intraguild predation involves complex mechanisms and often multiple trophic interactions (top-down or bottom up processes) (Fukami *et al.* 2006; Elmhagen and Rushton 2007; Ritchie and Johnson 2009), each management action should be planned after a full review of the main biotic interactions occurring in the ecosystem considered, so as to optimise native species conservation (Zavaleta *et al.* 2001; Bonnaud *et al.* 2009; Russell *et al.* 2009).

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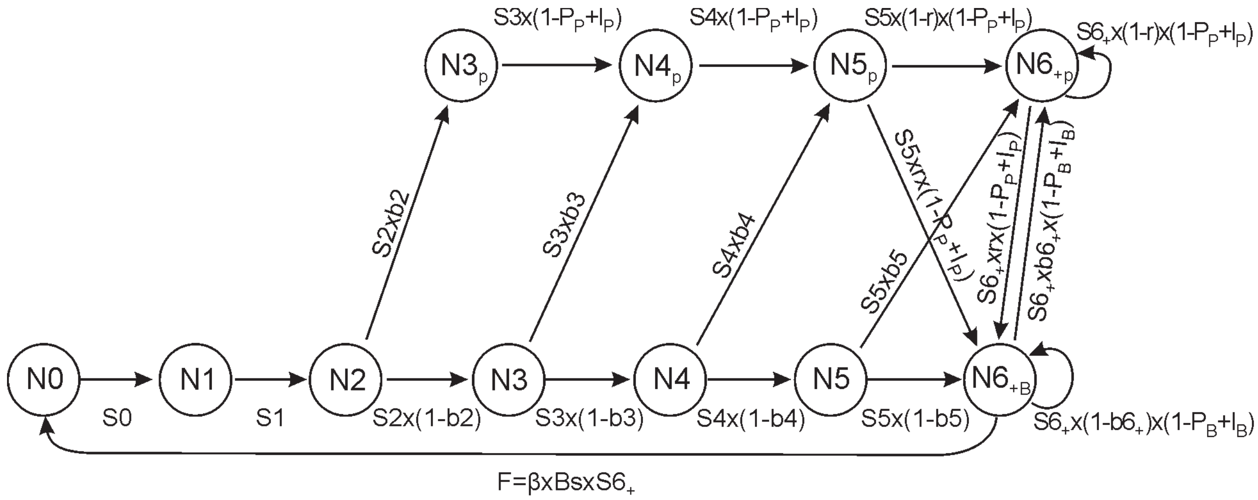
Appendix: Life-cycle representation of the population model for the yelkouan shearwater.

N0 : juvenile age-class (from fledging to age 1); *Nx* : non prospecting sub-adult of age x, Nx_P : prospecting sub-adult of age x, $N6_{+B}$: breeding adult age-class, $N6_{+P}$: prospecting adult age-class, Sx: survival of stage x, bx: percentage of birds of stage x prospecting the colony without breeding, Bs: breeding success, β: sex ratio, F: fecundity, P_B: predation rate on breeding birds, P_P: predation rate on prospecting birds.



Demographic parameters of the Yelkouan shearwater population (based on Bonnaud *et al.* 2009). Standard deviations (s.d.) are given for mean values.

Yelkouan shearwater age-classes	Population proportions with a stable distribution	Shearwater population sizes	
		Port-Cros	Le Levant
N0	0.161	143	1035
N1	0.093	83	598
N2	0.0715	64	460
N3	0.0466	41	300
$N3_P$	0.017	15	109
N4	0.0104	9	67
$N4_P$	0.0479	43	308
N5	0.0014	1	9
$N5_P$	0.0237	21	152
$N6_{+B}$	0.4044	360	2600
$N6_{+P}$	0.1232	110	792

Parameters	Values
S0: survival of stage Juvenile[a]	0.586
S1: survival of stage 1[a]	0.781
S2: survival of stage 2[a]	0.902
S3: survival of stage 3[a]	0.930
S4: survival of stage 4[a]	0.930
S5: survival of stage 5[a]	0.930
S6+: survival of stage 6+[a]	0.930
β: sex ratio[b]	0.5
Bs: breeding success[b]	0.808 ± 0.105
b2: prospecting birds of stage 2[c]	0.267
b3: prospecting birds of stage 3[c]	0.756
b4: prospecting birds of stage 4[c]	0.911
b5: prospecting birds of stage 5[c]	0.978
b6+: prospecting birds of stage 6+[c]	0.261
r: prospecting ads - breed next year[d]	0.96 ± 0.02

Data from: [a] Perrins *et al.* 1973; Brooke, 1990; Hamilton and Moller 1995; Hunter *et al.* 2000; Ainley *et al.* 2001 (*P. puffinus*); Cuthbert *et al.* 2001; Jones 2002 (*Puffinus* sp.), [b] our study, [c]. Bradley *et al.* 1999 (*P. tenuirostris*), [d]Warham 1990