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ORIGINAL ARTICLE

How can the Yelkouan shearwater survive feral cat predation? A meta-population structure as a solution?

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Abstract The Yelkouan shearwater, *Puffinus yelkouan*, is an endangered Mediterranean endemic species of burrowing petrel threatened by feral cats. The life-history parameters of a small population of Yelkouan shearwaters on the Mediterranean island, Port-Cros, were studied in conjunction with the diet of feral cats, to examine the birds' vulnerability to introduced cats. Yelkouan shearwaters were the birds most frequently found in cat scats, with 431 ± 72 birds killed per year, and predation highest during the pre-laying period. A demographic model was created using data for *P. yelkouan* and for closely related shearwater species. Without cat predation, only two of four survival rate scenarios led to a mean growth rate (λ) $\geq$ 1. The model was constrained to have a stable population growth rate and used to predict predation scenarios compatible with the observed population stability, because the population under study has remained stable at around 180 pairs for at least 20 years despite feral cat predation. The results of assuming that the population is closed were inconsistent with the estimated mortalities due to feral cats, while it was possible to reconcile the observed numbers of breeding pairs with the observed mortalities due to cats by assuming that Port-Cros Island is a sink sustained by immigration. This illustrates that small colonies may need to be sustained by larger ones to avoid being driven to extinction. Unfortunately, the absence of a large geographic-scale ringing program makes the precise identification of the origin of the immigrants impossible in this case.

Keywords Demographic models · Endemic seabirds · Introduced predators · Island conservation · Population viability

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Introduction

Due to their low productivity, slow reproductive maturity and a lack of predator defenses, seabirds are known to be highly vulnerable to introduced predators (Moors and Atkinson 1984). For long-lived seabirds, such as petrels and shearwaters, the impact of alien predators is dramatically increased when adult individuals, and not only eggs or chicks, are affected by predation (Warham 1990; Cuthbert et al. 2001). Since its early domestication by humans (Vigne et al. 2004), the cat, *Felis silvestris catus*, has been largely kept as a pet and for rodent control on most island groups worldwide, where it has generally succeeded in establishing feral populations (Long 2003; Nogales et al. 2004). Consequently, this highly adaptable carnivore has become one of the world's most serious threats to island fauna, being responsible for numerous extinctions, extirpations or declines of seabird species world-wide, especially Procellarids (Courchamp et al. 2003; Brooke 2004).

Studies have recently shown that several *Puffinus* populations, 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, *P. yelkouan*, which belongs to this taxonomic group, is strictly endemic to the Mediterranean Basin. This species was long considered to be a Mediterranean subspecies of the globally distributed Manx shearwater (Brooke 1990; Warham 1990), but a taxonomic revision recently elevated the Yelkouan shearwater to the rank of species, distinct from both the Manx shearwater and the Balearic shearwater, *P. mauretanicus* (Bourne et al. 1988; Heidrich et al. 1998; Sangster et al. 2002a, b). Compared with other *Puffinus* species, few studies have dealt with the Yelkouan shearwater, and this species remains probably the least well-known seabird in the Mediterranean in terms of basic distribution, population size and trend. A recent review suggested that the Yelkouan shearwater could be endangered and declining, with a breeding population possibly not exceeding some thousands of pairs and probably restricted to only a few breeding locations, most of which are currently subject to introduced predators (Bourgeois and Vidal 2008). Although it has been clearly established that the Yelkouan shearwater is regularly eaten by feral cats on some Mediterranean islands (Tranchant et al. 2003; Bonnaud et al. 2007), neither the impact nor the temporal patterns of feral cat predation are known. These data are sorely needed (1) to evaluate the degree to which feral cats affect the population dynamics and viability of this species, and (2) to quantify predation to identify when predation occurs and the categories of individuals most subject to cat predation. Moreover, the lack of monitoring during the years preceding and following the studies on the impact of feral cats generally makes it impossible to compare the predictions given by population viability models and field observations of shearwater population dynamics (cats eradicated or not).

In this study, we consider the case of a small Yelkouan shearwater population (140–180 pairs) established on Port-Cros Island, a small Mediterranean island known to hold a stable Yelkouan shearwater population for over 20 years (Vidal 1985; IMEP, unpublished data) despite the continuous presence of and predation by feral cats (Port-Cros National Park, personal communication). This situation is unusual and intriguing because previous studies modelling the impact of feral cats on shearwater population dynamics have generally shown that cat predation, especially on adult birds, leads to shearwater extinction in a very short time (generally only a few decades), even for moderate-sized cat populations and large bird numbers (Ainley et al. 2001; Keitt et al. 2002). Therefore, the long-term persistence of a small shearwater population, despite decades of feral cat presence, constitutes a conservation paradox which, to the best of our knowledge, has never been investigated. While most of the breeding sites of the Yelkouan shearwater also host cat populations, our study site is the only one where the trend of a breeding shearwater population is known. Thus, our study responds to the need to investigate when small populations coexist with introduced predators (Sinclair et al. 1998; Macdonald et al. 1999) and offers a representative and relevant model for other sites.

To understand the persistence of this small Yelkouan shearwater population despite feral cat presence, we analysed the feral cat diet for 2 years to quantify annual predation rates and to determine during what part of their annual cycle shearwaters were killed. Then, we built a deterministic matrix population model incorporating predation data and shearwater life-history parameters. Sensitivity to predation was assessed for the different categories of birds found on colonies. The results of the projection matrix model determined under which parameters and population structure this Yelkouan shearwater population could withstand cat predation.

Materials and methods

Study area and species

This study was conducted on Port-Cros Island (43°00′N, 6°21′E) located in the Mediterranean Sea, off the southeast coast of France. This 640-ha island has been a National Park since 1963.

Two complete and intensive censuses of the Yelkouan shearwater population were carried out on all parts of the island, even the most remote areas, in 1982–1983 (Zotier and Vidal 2004) and 2003–2006 (IMEP, unpublished data), revealing a stable population of 140–180 breeding pairs. Breeding birds nest along the coast, on indented cliffs and under fallen boulders. Colonies are sparse (distributed among 17 sites), with low densities of birds compared with most other Procellarids (Bourgeois and Vidal 2007). Yelkouan shearwaters generally nest in deep natural rock cavities (e.g., among fallen boulders), pre-existing crevices in the rock or burrows they excavate. Bourgeois and Vidal (2007) and Bourgeois et al. (2008b) showed that breeding habitats are far from saturation and that both unoccupied cavities among colonies and sites suitable for colony establishment are available. Yelkouan shearwaters arrive at their breeding sites in late October or early November (Vidal 1985; Zotier 1997). Egg laying is from mid-March to early April, hatching in May and fledging in July and early August. Both adults participate in incubation (shifts of 4 days on average) and chick-rearing (Zotier 1997).

A feral cat population has been established on Port-Cros Island for at least two centuries, due to the establishment of a small village now harboring 40 permanent inhabitants

(Pasqualini 1995). Cat predation on the Yelkouan shearwater has been reported on Port-Cros Island for over 20 years (Vidal 1985; Zotier 1997; Tranchant et al. 2003; P.C.N.P., unpublished data). Until 2004, the National Park administration had not carried out any feral cat control on the island and there was no sign that the cat population had significantly changed during this 20-year period. Cat removal was successfully undertaken from 2004 to 2006.

Population modelling was used to examine how the small shearwater population on Port-Cros Island has succeeded in remaining stable for 20 years despite cat predation. An age- and stage-structured matrix model was built to study the sensitivity of Yelkouan shearwater population growth rate (λ) to four different demographic scenarios based on different survival rates. Since the survival rates of the Yelkouan shearwater are unknown we examined values calculated for closely related species and applied them to a closed population (i.e., with or without predation). The most realistic models (i.e., those resulting in $\lambda \geq 1$) were then modified to incorporate (1) cat predation and (2) cat predation and bird immigration (Table 1).

Cat predation on shearwaters

Feral cat predation was studied through scat analysis (Konecny 1987; Fitzgerald et al. 1991; Clevenger 1995). Scats were collected every 2 months from November 2002 to August 2004 along nearly all the island paths. By removing all scats found in the field and excluding very old ones, we assumed that each sampling set represented the feral cat diet for the two previous months, thus revealing the extent of cat predation on Yelkouan shearwaters for each sampling period (a total of 11 sampling periods during the 2-year study). This sampling allowed us to relate cat predation patterns with the shearwater breeding phases for two complete annual cycles. We calculated the mean number of Yelkouan shearwaters killed by cats annually based on cat diet analysis under the assumption that all remains of shearwaters found in a scat belonged to a single bird. This assumption was made because no identical remains from two or more Yelkouan shearwaters were found in the same scat ($n = 689$) and because even if a cat eats 50% of a Yelkouan shearwater weight (432 g), leaving behind wings, feathers and head (Cuthbert 2002; Keitt et al. 2002), this prey supplies it with enough food for 1 day (mean daily biomass consumed by a Port-Cros feral cat = 201 g; Bonnaud et al. 2007). Since cats usually defecate once per day (Konecy 1987), the Yelkouan shearwater mean number per scat is equivalent to the Yelkouan shearwater mean number ingested per day and per cat ($NP_{/d}$). The annual mean number of Yelkouan shearwater killed on Port-Cros Island (NP) by the feral cat population was calculated as:

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

with N_{cat} = number of cats on the island

Three categories of birds are found in shearwater colonies: breeding adults, prospecting birds (non-breeders that visit colonies coming from inside or outside the breeding colony) and chicks (Warham 1990). The latter category was considered to be shielded from cat predation, being protected by deep and narrow burrows (Bourgeois and Vidal 2007). Therefore, predation risk was evaluated for breeding and prospecting birds. The behaviour of breeding shearwaters differs from that of prospecting shearwaters when in colonies. Breeding birds coo and call from burrows simultaneously with their mate, enter one burrow and stay inside, or land close to the burrow entrance, whereas prospecting birds individually call from the air, outside burrows or on the ground, enter and leave several burrows, wander outside burrows, and land and rapidly fly far away from burrows (Storey 1984; James 1985; Brooke 1990; Bretagnolle et al. 1998; Ristow 1998). We expected a difference in predation risk between the two bird categories due to each group's particular ground behaviour, and predation risk was assumed to be proportional to the time spent outside burrows, i.e., a priori greater for the prospecting birds than for breeding birds. Thus, ground behaviour of birds outside burrows was monitored for nine nights just before the new moon during the incubation period, with nocturnal vision binoculars. These

Table 1 Summary of the analyses of Yelkouan shearwater, *Puffinus yelkouan*, population models

Case	Parameters		
	Common among scenarios	Scenario specific	Calculated within the model
1. Closed population[a]	β, Bs, b2–b6$_+$, r	S0–S6$_+$	λ
2. With theoretical predation (P_{theo}) but no immigration	β, Bs, b2–b6$_+$, r, I (=0)	S0–S6$_+$	P_{theo}[b]
3. With observed predation (P_{obsv}) and immigration	β, Bs, b2–b6$_+$, r, P_{obsv}	S0–S6$_+$	I[b]

[a] Only scenarios for which $\lambda \geq 1$ were considered further

[b] Calculated so that $\lambda \sim 1$

observations were combined with the results from a 5-year burrow monitoring and bird ringing study (2002–2007; Bourgeois et al. 2008a), which permitted us to identify precisely each occupied burrow and to be sure that each bird entering a burrow was a breeder. Thus, we distinguished the two categories of birds and timed how long each category stayed on open ground.

Population modelling and cat impact

The ULM (Unified Life Models) mathematical modelling software (Legendre and Clobert 1995) was used to estimate Yelkouan shearwater population viability, and we conducted Monte Carlo simulations to account for the uncertainty of several population parameters. The Yelkouan shearwater has never been the subject of a long-term population study, so we assumed that it first returns to the colony at age 3 and first breeds at age 6, as found for the closely related Manx and Balearic shearwaters (Brooke 1990; Oro et al. 2004). This is a reasonable assumption because procellarids are known to have very homogeneous life history traits, within a given genus. Thus, a stage-based, post-breeding population matrix model (Caswell 2001) was constructed with 11 age classes (Fig. 1): 1 juvenile age-class (N0, from fledging to age 1), 5 sub-adult age-classes (N1–N5, ages 1–5) which had not returned to the colony, 3 prospecting sub-adult age classes which had already returned to the colony ($N3_P$–$N5_P$, ages 3–5), 1 prospecting adult age-class ($N6_{+P}$, ≥6 years old) and 1 breeding adult age-class ($N6_{+B}$, ≥6 years old). Size (Ni), survival rate (Si) of each age-class (i = 0 to 6_+), percentage of birds prospecting the colony without breeding (bi), percentage of birds prospecting the colony and breeding the following year (r), sex ratio (β) and breeding success (Bs) were model parameters.

The model only considers females. The number of breeders (≥6 years old, $N6_{+B}$) was assumed to be 180 because this is the highest census estimate and led to the most realistic population structure (Fig. 2). We constructed four annual survival scenarios based on information for closely related and well-studied species, i.e., the Manx and Balearic shearwaters. The "pessimistic" scenario was based on the survival rate estimates for the Balearic shearwater (Oro et al. 2004), and the "medium" scenario on mean survival rates for the Manx shearwater (Ainley et al. 2001). The last two scenarios, "optimistic" and "optimal", were based on the overall mean and the mean of maximum survival rates for adult *Puffinus* shearwaters (Perrins et al. 1973; Hamilton and Moller 1995; Hunter et al. 2000; Cuthbert et al. 2001; Jones 2002). The survival rates for fledglings and ages 1–5 were calculated using the method of Ainley et al. (2001) to achieve to a total survival of 0.333 between fledging and the age of 6 years.

Very few studies have taken the role of prospecting birds visiting colonies in population dynamics into account, although it is commonly accepted that fifty percent of

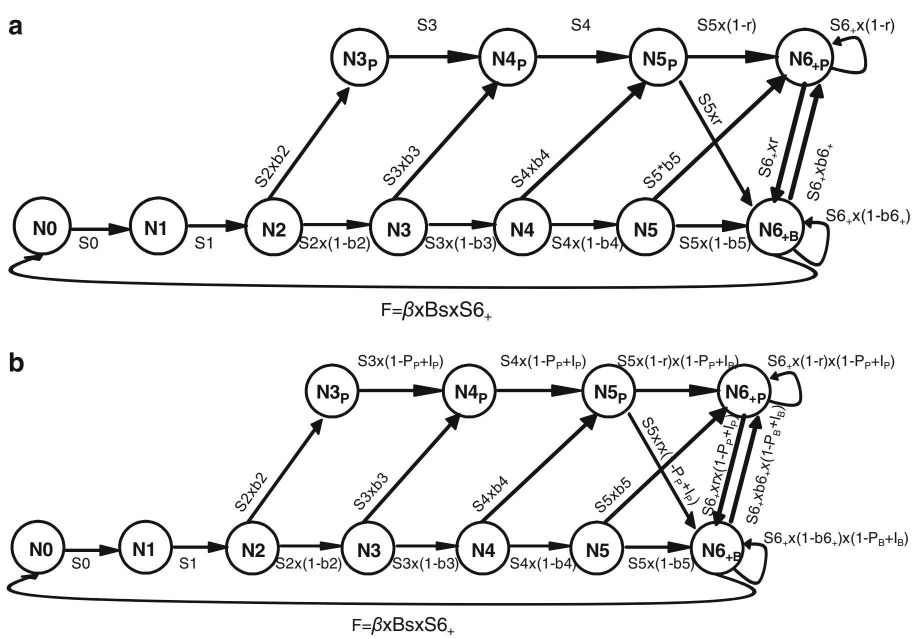


Fig. 1 Life-cycle representation of the population model for the Yelkouan shearwater, *Puffinus yelkouan*. **a** Closed population without cat predation; **b** open population with cat predation and bird immigration. N0, Juvenile age-class (from fledging to age 1); Nx, non-prospecting sub-adult of age 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; I_B, immigration rate of breeding birds; I_P, immigration rate of prospecting birds

shearwaters visiting islands are prospecting birds (Warham 1990; Ristow 1998). We used the values observed for the short-tailed shearwater *P. tenuirostris* (Bradley et al. 1999), to estimate percentages of sub-adult birds which will prospect the colony the following year (bi) (Table 2). The percentage of prospecting adult birds that will breed the following year (r) was estimated at 0.96 ± 0.02, because birds rarely skip two successive years (Warham 1990).

We modelled adult (≥6 years old) breeding fecundity (F) as the product of sex ratio at birth (assumed to be balanced) (β) and breeding success (Bs, fledglings/laying eggs). To measure Yelkouan shearwater breeding success without cat predation, we used the results from the monitoring of cavities occupied by bird pairs on Port-Cros Island during three consecutive breeding seasons (2004–2007), after the removal of most cats from this island (after October 2004, number of scats reduced by 80% and remains of shearwaters were only found in 2 scats). A miniature infrared camera on a stiff coaxial was "snaked" down each cavity to determine the presence of eggs or chicks. Cavities were checked nine times during each breeding season (end of the pre-laying period, start, middle and end of the laying and hatching periods, 15 days before the beginning and at mid-fledging period). A last check was conducted at the end of the breeding season with a view to finding corpses to confirm fledging survival rate.

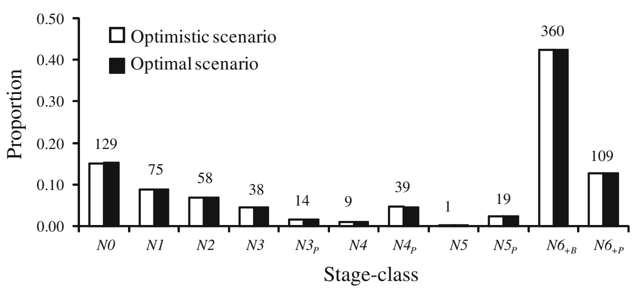


Fig. 2 Yelkouan shearwater stage-class proportions for a population stable at 180 breeding pairs and without cat predation. The number of individuals per stage-class are indicated above the bars

Predation rates were modelled separately for prospecting (P_P) and breeding birds (P_B) because of the differences in their ground behaviour and consequently in their vulnerability to predation. We determined the maximum number of predated shearwaters (NP_{Btheo} and NP_{Ptheo}, respectively, for breeding and prospecting birds) that a closed population can theoretically tolerate without declining (Table 1) because the studied population has remained stable over the last 20 years. However, observed number of shearwaters preyed on annually by cats (NP_{Bobsv} and NP_{Pobsv}, respectively, for breeding and prospecting birds) was substantially higher than this (see "Results"). The model was therefore modified to incorporate immigration of both breeders and prospecting birds (Table 1). The difference between observed mortality due to cats and NP_{Bobsv} and NP_{Pobsv} gave the number of immigrant breeders (NI_B) and prospecting birds (NI_P) that were needed annually for population stability, and hence the immigration rates for breeders (I_B) and prospecting birds (I_P):

$$I_B = (NP_{Bobsv} - NP_{Btheo})/N6_{+B}, \quad NI_B = NP_{Bobsv} - NP_{Btheo} \tag{2a}$$

$$I_P = (NP_{Pobsv} - NP_{Ptheo})/(N3_P + N4_P + N5_P + N6_{+P}), \quad NI_P = NP_{Pobsv} - NP_{Ptheo} \tag{2b}$$

Table 2 Demographic parameters and their sources used for the two scenarios for which $\lambda > 1$ in the absence of cat predation and immigration

Parameters	Scenarios	
	Optimistic	Optimal
S0: survival of juvenile[a] stage	0.586	0.605
S1: survival of stage 1[a]	0.781	0.806
S2: survival of stage 2[a]	0.902	0.922
S3: survival of stage 3[a]	0.930	0.960
S4: survival of stage 4[a]	0.930	0.960
S5: survival of stage 5[a]	0.930	0.960
$S6_+$: survival of stage 6+[a]	0.930	0.960
β: sex ratio[b]	0.5	
Bs: breeding success[b]	0.728 ± 0.079	
b2: fraction of stage 2 birds which prospect[c]	0.267	
b3: fraction of stage 3 birds which prospect[c]	0.756	
b4: fraction of stage 4 birds which prospect[c]	0.911	
b5: fraction of stage 5 birds which prospect[c]	0.978	
$b6_+$: fraction of stage 6+ birds which prospect[c]	0.261	
r: prospecting adults which will breed in the next year[d]	0.960 ± 0.020	

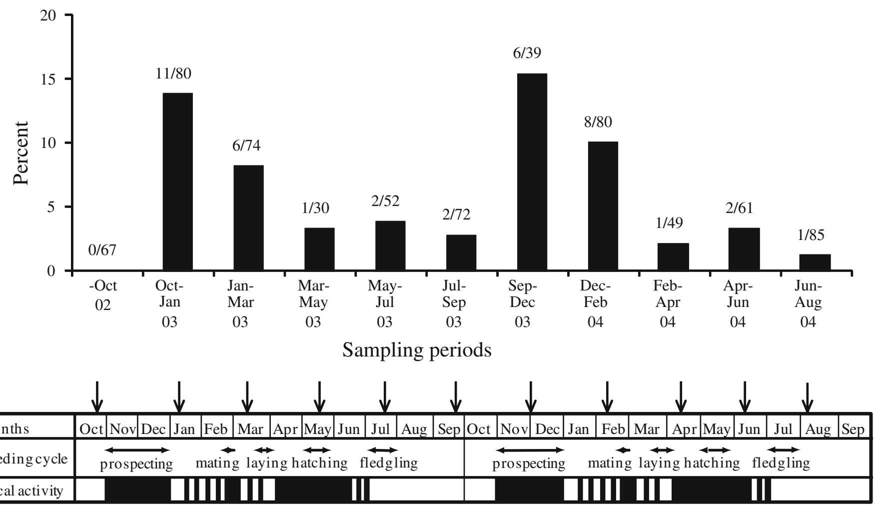
[a] Data from Perrins et al. (1973); Brooke (1990); Hamilton and Moller (1995); Hunter et al. (2000); Ainley et al. (2001) (*P. puffinus*); Cuthbert et al. (2001); Jones (2002) (*Puffinus* sp.)

[b] Our study

[c] Bradley et al. (1999) (*P. tenuirostris*)

[d] Warham (1990)

Fig. 3 Predation pattern (percent frequency) by feral cats on the Yelkouan shearwater on Port-Cros Island (August 2002–August 2004) according to the different phases of the Yelkouan shearwater breeding cycle



Results

Cat predation on shearwaters

During the 2 years of sampling, 689 scats were collected on all parts of the island (303 and 386 scats during the first and second breeding cycles, respectively). Almost all cat scats (92%) contained mammal remains (introduced rats and rabbits). Birds occurred in 16.7%, reptiles in 7.8%, and insects in 11.0% of scats. The Yelkouan shearwater was the most frequently encountered bird species in the feral cat diet (Bonnaud et al. 2007). Yelkouan shearwater remains were present in 5.9 ± 0.99% of cat scats (6.6% in the first year and 5.2% in the second year). Feral cats preyed on shearwaters throughout the year, but with a clear peak of predation every year from October to February, which corresponds to the Yelkouan shearwater pre-laying stage (Fig. 3). The frequency of Yelkouan shearwater remains in cat scats reached 15% during this peak of predation and 75% of the scats, which contained Yelkouan shearwater remains, were found during this period. The mean number of Yelkouan shearwaters ingested per day and per cat ($NP_{/d}$) was 0.059 ± 0.0099. Cat population figures were obtained from a removal programme conducted after this cat diet analysis (Keitt et al. 2002). Twenty-eight feral cats were removed during the 2-year trapping programme, of which 8 were under 1 year old. Thus, we considered the cat population to be 20 individuals before cat control. Applying Eq. 1 gave the number of Yelkouan shearwaters preyed on by cats annually, NP = 431 ± 72 individuals.

Prospecting birds were found to stay on the ground outside burrows four times as long as breeding birds (12.70 ± 6.75 vs 3.33 ± 1.76 min, respectively, Fig. 4). Thus, predation risk for a prospecting bird was considered four times as high as for a breeding bird ($P_P = 4 \times P_B$).

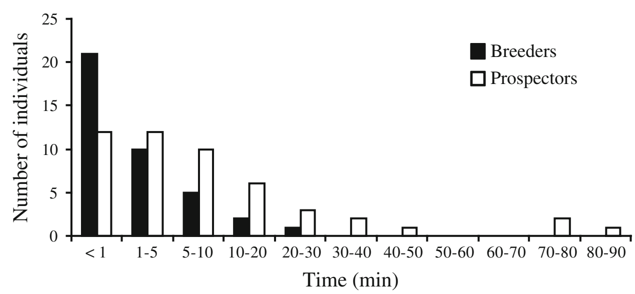


Fig. 4 Time spent outside burrows and on the ground by prospector and breeder Yelkouan shearwaters

Population modelling and cat impact

Breeding success was 0.728 ± 0.079 during the three studied breeding seasons after cats were removed (2004–2007). Without predation, the four survival rate scenarios led to a growth rate (λ) of 0.8681 ± 0.0001, 0.9869 ± 0.0001, 1.0045 ± 0.0001, and 1.0364 ± 0.0001, respectively. The "pessimistic" and "medium" scenarios predicted population extinction in 45 and ca. 450 years, while the "optimistic" and "optimal" scenarios predicted an increase in population size (Table 3, case 1). Thus, only the "optimistic" and "optimal" scenarios were realistic for this shearwater population (a growth rate slightly higher than 1 with no predation, e.g., Jones 2002).

Stable stage distributions calculated for the "optimistic" and "optimal" scenarios were nearly identical (Fig. 2). The number of Yelkouan shearwaters preyed on per year (NP) under the assumption that breeding ($N6_{+B}$) and prospecting ($N3_P$ to $N6_{+P}$) birds are subject to feral cat predation is $NP = P_B \times (N6_{+B}) + P_P \times (N3_P + N4_P + N5_P + N6_{+P})$ where $P_P = 4 \times P_B$. The maximum (theoretical) predation rate that this population can tolerate [0.003 and 0.024 on the breeding population (P_{Btheo}) and 0.012 and 0.096 on the

Table 3 Predation and immigration rates (and corresponding numbers of shearwaters, NP and NI, respectively), population growth rates (λ) predicted by models based on the two most realistic demographic scenarios ("optimistic" and "optimal") for three cases: (1) with neither predation nor immigration, (2) with theoretical predation but no immigration, and (3) with observed predation and immigration. When possible ±SE is indicated

Case	Bird status	Scenario									
		Optimistic					Optimal				
		Predation		Immigration		λ	Predation		Immigration		λ
		Rate	NP	Rate	NI		Rate	NP	Rate	NI	
1	Breeders	0	0	0	0	1.0045 ± 0.0001	0	0	0	0	1.0364 ± 0.0001
	Prospectors	0	0	0	0		0	0	0	0	
2	Breeders	0.003	1	0	0	1.0002 ± 0.0001	0.024	9	0	0	1.0003 ± 0.0001
	Prospectors	0.012	2	0	0		0.096	17	0	0	
3	Breeders	0.398 ± 0.067	143 ± 24	0.394 ± 0.067	142 ± 24	0.9912 ± 0.0017	0.398 ± 0.067	143 ± 24	0.372 ± 0.067	134 ± 24	0.9903 ± 0.0018
	Prospectors	1.592 ± 0.268	288 ± 49	1.580 ± 0.268	286 ± 49		1.592 ± 0.268	288 ± 49	1.497 ± 0.268	271 ± 49	

prospecting population (P_{Ptheo}), respectively, for the "optimistic" and the "optimal" scenarios; Table 3] were calculated so that $\lambda = 1$. These predation rates correspond to 1 and 9 breeding birds (NP_{Btheo}) and 2 and 17 prospecting birds (NP_{Ptheo}) preyed on per year for the entire population (males and females), respectively, for the two scenarios (Table 3, case 2). These predation rates are much smaller than the estimate of annual morality due to cat predation.

The number of Yelkouan shearwaters preyed on annually estimated from the feral cat diet (NP = 431 ± 72 birds killed per year) implies an observed cat predation rate of 0.398 ± 0.067 for the breeding population (P_{Bobsv}) and 1.592 ± 0.268 for the prospecting population (P_{Pobsv}), once allowance is made for immigration (Table 3, case 3). These observed cat predation rates correspond to 143 ± 24 breeding birds (NP_{Bobsv}) and 288 ± 49 prospecting birds (NP_{Pobsv}) annually. The corresponding number of animals immigrating to Port-Cros Island are 142 ± 24 and 134 ± 24 immigrant breeding birds (NI_B) and 286 ± 49 and 271 ± 49 immigrant prospecting birds (NI_P) per year, respectively, for the "optimistic" and the "optimal" scenarios, leading to immigration rates of 0.394 ± 0.067 and 0.372 ± 0.067 for the breeding population (I_B) and 1.580 ± 0.276 and 1.497 ± 0.268 for the prospecting population (I_P).

Discussion

Cat predation on shearwaters

Yelkouan shearwater was the dominant bird species in the feral cat diet and this secondary prey provided a substantial energy supply for cats (Bonnaud et al. 2007). As Port-Cros is a small island and cats can have large home ranges (the distance between shearwater colonies and scats containing shearwater remains exceeded 1 km), all cats are able to access Yelkouan shearwater colonies. Shearwater remains in cat scats were found throughout the year, but most frequently during late autumn and early winter. Thus, most shearwaters were preyed on during their pre-breeding period when they are most active vocally and are most detectable, and when colonies are most fully occupied, especially by prospecting birds, which are probably easier to catch (Brooke 1990; Ristow 1998). The higher shearwater availability to cats during this period is exacerbated by the lesser availability of the cats' primary prey (rats and rabbits) (Bonnaud et al. 2007). The rate of predation on shearwaters was lower during the post-breeding exodus (early August to late October), when most birds have left the colony. Finally, the fact that patterns of cat predation intensity were strongly correlated with the shearwater breeding cycle underlines the need for studies of predator impact to be conducted over at least one complete year, to avoid biassing the estimation of predation rates.

The observed predation pattern seemed to be the same between years, which indicates that the observed situation was neither exceptional nor due to chance. Yelkouan shearwater remains were present in 5.9% of feral cat scats, which was fairly low considering other shearwater studies (Jones 1977; Keitt et al. 2002; Martínez-Gómez and Jacobsen 2004). However, this predation rate resulted in a very large number of killed individuals (431 ± 72 shearwaters per year) given the number of breeding pairs on Port-Cros Island. Both breeding and prospecting birds were predated and we found that prospecting birds were four times more vulnerable to cat predation.

Very few studies have taken predation on prospecting birds into account, although according to Imbert et al. (2003) cats mainly affect petrel populations by killing prospecting and pair-forming breeders. The mortality of breeders has both short- and long-term effects on the population dynamics of petrels. The short-term effect is an immediate decrease in breeding success due to the inability of petrels to incubate and feed chicks when one of the pair has died, and the long-term effect is a decrease in future recruitment. Prospecting bird survival is also considered important in "buffering" a population against the impact of environmental variation on population growth (Jones 2002).

Population modelling and cat impact

The "pessimistic" and "medium" survival rate scenarios correspond to growth rates <1, and thus predicted that the studied population should be driven to extinction even without any cat predation. The 20-year persistence of the population suggested that the survival rates that underlie these scenarios are probably under-estimates for this population. In contrast, the other two survival rate scenarios corresponded to annual population growth rates slightly greater than 1, 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 scenarios selected for the Yelkouan shearwater can be considered realistic and the model structure suitable, and that this species should be very sensitive to predation on adults (Cuthbert et al. 2001).

When we forced stability without immigration, it predicted that only very few birds would be killed each year. This implies that the shearwater population on Port-Cros Island cannot survive given the predation rates estimated from the feral cat diet study. Consequently, the number of prospecting birds must be much higher than that implied if the Yelkouan shearwater population of Port-Cros Island is a closed population. Rather, this population needs to be sustained by immigration of prospecting birds from other colonies. Immigration of prospectors and breeders (i.e., arrival of new birds in the colony, not natal fledglings) has been demonstrated to have an important impact on the population dynamics and viability of the sooty shearwater *P. griseus* (Hamilton and Moller 1995; Jones 2002). Immigration has been estimated for an unusually small *P. tenuirostris* population in Tasmania (Serventy and Curry 1984; Bradley et al. 1991); 45% of the breeders in this population are natal recruits while external immigrants represented 122% of the total number of natal prospecting sub-adults (Hunter et al. 2000). The immigration rate required to supplement the local population (breeders and natal prospectors) was under 0.80 for our *P. yelkouan* population, indicating that this hypothesised process is plausible and realistic, especially in the absence of alternative hypotheses to explain the stability of this small and preyed upon population.

Some of the world's largest Yelkouan shearwater colonies, especially Le Levant Island (800–1,300 pairs), Sardinia (5,000–12,000 pairs) and Malta (1,400–1,560 pairs) (Bourgeois and Vidal 2008) are found in the north-western Mediterranean, in the vicinity of Port-Cros Island. These populations are potential sources of large numbers of immigrant birds. Unfortunately, the origin of birds re-stocking the Port-Cros population remains unknown in the absence of long-term and large-scale ringing programmes and population monitoring on most of these breeding sites. Genetic studies could possibly help clarify how the different Mediterranean populations interact, and to determine the geographic origin of non-natal recruits (e.g., Manel et al. 2005), even though recent studies on seabirds have shown that dispersal can homogenise genetic differentiations (e.g., Friesen et al. 2007). The combination of molecular, morphometric or biogeochemical markers may be a promising way to improve geographic analysis (Gómez-Díaz and González-Solís 2007). The high immigration rate predicted by our study indicates a quite unusual population structure and functioning, since seabird species, especially procellarids, are generally considered to show strong philopatry and site fidelity (Austin et al. 1994; Bried and Jouventin 2002). From a conservation perspective, this underlines the need to consider shearwater population management on a scale broader than the colony itself, and to identify and conserve the large source populations able to rescue smaller satellite colonies.

However, we cannot rule out the possibility that this apparent stability is temporary, hiding a critical situation.

Small populations are much more vulnerable to the negative effects of demographic stochasticity, environmental catastrophes and inbreeding depression, especially when top predator populations (cats) are themselves dependent on the fluctuating dynamics of exotic primary prey (rodents) (Jones 2002, 2003). Despite immigration, small populations have been shown to be very sensitive to predation due to inverse density-dependent predation (Cuthbert 2002; Jones 2002; our study). Removal has been proved to be a powerful tool for solving the problem of feral cats, and has already been applied on several islands (Nogales et al. 2004) with conclusive effects on endangered shearwater populations (Keitt and Tershy 2003). The removal of cats from Port-Cros undertaken in 2004, coupled with annual shearwater population monitoring (IMEP, unpublished data), should enable us to compare the dynamics observed in the field with predictions given by the different models.

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