Is the Yelkouan shearwater *Puffinus yelkouan* threatened by low adult survival probabilities?

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ABSTRACT

Many seabird species are experiencing population declines, with key factors being high adult mortality caused by fishery by-catch and predation by introduced predators on nesting islands. In the Mediterranean, both of these pressures are intensive and widespread. We studied the adult survival of an endemic Mediterranean seabird, the Yelkouan shearwater (*Puffinus yelkouan*), between 1969–1994 and 2007–2010 in Malta and between 2004–2010 in France using mark–recapture methods. Mean annual survival probabilities for breeding adults were below 0.9 for all colonies and periods. Between 1969–1994, annual survival for adults of unknown breeding status was on average 0.74 (95% confidence interval: 0.69–0.80) in Malta, possibly as a result of various human disturbances (including illegal shooting), light pollution and fisheries by-catch. Over the period 2004–2010, we found strong support for variation in adult survival probabilities between breeders and non-breeders, and islands with and without introduced predators in France. Survival probabilities for non-breeders (0.95, 0.81–1.0) appeared to be higher than for breeders (0.82, 0.70–0.94), but were imprecise partly due to low recapture probabilities. In Malta, we found evidence for heterogeneity in survival probabilities between two unknown groups (probably breeders and non-breeders), and seasonal variation in survival probability. Birds were more likely to survive the period including the peak breeding season than an equally long period during which they roam widely at sea. Although annual adult survival probability was still low (0.85, 0.58–1.0), colony protection measures appear to have reduced mortality at nesting cliffs. A population model indicated that colonies in France and Malta would currently require continuous immigration of 5–12 pairs per year to maintain stable populations. Our estimates of adult survival probabilities over the past four decades are consistent with overall population declines. Threats to Yelkouan shearwaters require immediate management actions to avoid ongoing population declines in the western Mediterranean.

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1. Introduction

Population declines of many seabird species worldwide are being caused by low adult survival probabilities (Hunter et al., 2000; Cuthbert et al., 2001; Wanless et al., 2009). Two of the main drivers of low adult survival probabilities in seabirds are accidental by-catch in fisheries (Tuck et al., 2001; Baker and Wise, 2005; Žydelis et al., 2009), and predation by introduced predators on nesting grounds (Cuthbert, 2002; Keitt et al., 2002; Jones et al., 2008). The Mediterranean Sea is surrounded by densely populated nations, and fishing intensity and other human pressures on the marine ecosystem are generally high (Farrugio et al., 1993; Belda and Sánchez, 2001; Cooper et al., 2003; Halpern et al., 2008). In addition, human disturbance of most seabird nesting islands has led to a long history of introductions of mammalian predators (Martin et al., 2000; Ruffino et al., 2008; Traveset et al., 2009). As a consequence, two pelagic seabird species (Balearic *Puffinus mauretanicus* and Yelkouan *Puffinus yelkouan* shearwaters) breeding only in the Mediterranean basin have suffered population declines and are of conservation concern (Oro et al., 2004; Bourgeois and Vidal, 2008).

Both species originally belonged to the Manx shearwater *P. puffinus* superspecies, and were elevated to species status by

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recent taxonomic revision using ecological, morphological and genetic traits (Heidrich et al., 1998; Sangster et al., 2002; Brooke, 2004). The Balearic shearwater has received much attention in the past decade because of its critical conservation status (Oro et al., 2004; Louzao et al., 2006a; Louzao et al., 2006b; Genovart et al., 2007; Tavecchia et al., 2008; Navarro et al., 2009). In contrast, relatively little information exists on the demography and conservation status of the Yelkouan shearwater, with recent work focusing on a small portion of its breeding range (Bourgeois and Vidal, 2007, 2008; Bourgeois et al., 2008b; Ruffino et al., 2008; Bonnaud et al., 2009).

The Yelkouan shearwater is restricted to the Mediterranean basin and the Black Sea, and its breeding range extends from the Marseille Islands (France) to Bulgarian islands in the Black Sea (Bourgeois and Vidal, 2008), with hybridisation between Balearic and Yelkouan shearwaters occurring farther west on the Spanish island of Minorca (Genovart et al., 2007; Curé et al., 2010). As with many seabird species, only vague population estimates exist. The best available estimates are based on surveys at 17 of 40 known breeding colonies, and give a range of 6000–9500 breeding pairs for the global population of Yelkouan shearwaters (Bourgeois and Vidal, 2008). Colonies that have been monitored over time suggest that the species may be declining (Bourgeois and Vidal, 2008), but neither the magnitude nor the potential causes of these range-wide declines have been studied.

Yelkouan shearwaters can suffer substantial predation pressure by introduced mammalian predators on breeding grounds (Bourgeois et al., 2008b; Bonnaud et al., 2009). Furthermore, by-catch in long-line fisheries has likely reduced adult survival as is suspected for the closely related Balearic shearwater (Belda and Sánchez, 2001; Cooper et al., 2003; Oro et al., 2004), and other forms of human interference (e.g. light pollution, wind turbines) may also have negative effects (Le Corre et al., 2002; Montevecchi, 2006; Cruz-Delgado et al., 2010). In Malta, the indiscriminate shooting of all birds including Yelkouan shearwaters is a serious threat that persists despite considerable conservation efforts to halt these illegal activities (Magnin, 1986; Raine and Temuge, 2009; Borg et al., 2010). Due to spatial variation in these known or suspected mortality factors, Yelkouan shearwater survival probabilities may vary over relatively small spatial scales (Tavecchia et al., 2008). Information on adult survival probabilities from several colonies is therefore urgently needed to assess the population status of the Yelkouan shearwater.

In this study, we used ringing data from two important breeding sites to estimate adult survival probabilities of Yelkouan shearwaters over two periods. In Malta, ringing efforts between 1969 and 1994 provided valuable historical data. More recently, intensive ringing efforts in Malta and the Hyères archipelago in France provided data to estimate adult survival probabilities between 2004 and 2010. We used these estimates to update an existing population model for the species (Bonnaud et al., 2009), and assessed whether French and Maltese breeding colonies are viable or function as population sinks. We used this information to make recommendations for the conservation of Yelkouan shearwaters.

2. Material and methods

2.1. Study species phenology

Yelkouan shearwaters live at sea between August and September each year. In October, birds begin arriving at the colony and carry out pre-laying visits to potential nest sites until February (Borg et al., 2002). The single egg is usually laid in mid March (Bourgeois et al., 2008a), and the incubation period spans about 50 days (Vidal, 1985). Eggs begin hatching in late April or early May, and young fledge between late June and early August. Colonies are therefore active between October and the end of July in the following year (Borg et al., 2002; Bourgeois et al., 2008a). The age of recruitment is unknown for Yelkouan shearwaters. We assumed that Yelkouan shearwaters are similar to related species (Manx and Balearic shearwaters), and that prospectors return to colonies at the age of 3 years and start breeding at the age of 6 years (Brooke, 1990; Oro et al., 2004; Bonnaud et al., 2009).

2.2. Ringing and monitoring effort in France

In France, we studied Yelkouan shearwaters in four colonies located on Port-Cros (43°00′ N, 6°23′ E) and Porquerolles (43°00′ N, 6°12′ E) islands in the Hyères archipelago. Port-Cros (640 ha) and Porquerolles (1250 ha) islands are nature reserves managed by the Port-Cros National Park, hosting an estimated 210–270 pairs of Yelkouan shearwater. The shearwaters nest along the coast on indented cliffs and fallen boulders with varying degrees of vegetation, offering rock cavities/crevices and excavated burrows for nesting (Bourgeois and Vidal, 2007; Bourgeois et al., 2008b). Feral cats strongly affected Yelkouan shearwater populations by preying upon adults (Bonnaud et al., 2007; Bonnaud et al., 2009). A conservation project launched in 2004 and completed in 2005 reduced cat predation to zero on Port-Cros (Bonnaud et al., 2010), but cats remain on Porquerolles. Black rats are present on both islands and may affect breeding success, but no adult predation by rats has been observed (Ruffino et al., 2008).

Access to the colonies was difficult due to dense vegetation, unstable, siliceous substrate and steep slopes. Birds were captured and ringed in the study colonies from 2004 to 2010. We captured birds by hand at their breeding sites when they entered their cavities or when they landed on the ground at night. Breeding sites were visited monthly from February to June during slightly moon-lit nights, avoiding the laying period when the birds are more sensitive to disturbance. We ringed birds with uniquely numbered metal rings from the French National Museum of Natural History. We distinguished breeders and non-breeders by combining behavioural observations at the colony during capture with data from breeding monitoring: 'non-breeders' did not enter nest-cavities, but remained on the ground outside nest-cavities, whereas 'breeders' rapidly entered nest-cavities after landing. Cavities that were entered by 'breeders' were occupied during nest monitoring (Bourgeois et al., 2008a).

2.3. Ringing and monitoring effort in Malta

The study site in Malta was located at Rdum tal-Madonna (35°59′ N, 14°22′ E), a rocky section of coastline with tall cliffs along the north-east coast of Malta. The geological formation at this site is composed of coralline limestone of Oligo-Miocene age, with cliffs penetrated by caves, crevices and fissures and associated gravel slopes, ideal breeding habitat for Yelkouan shearwaters (Bourgeois and Vidal, 2007). The site is listed as a Special Protection Area for Yelkouan and Cory's *Calonectris diomedea* shearwaters, with the Yelkouan shearwater population estimated to be 398 to 602 breeding pairs (Borg et al., 2010). From 2006 through 2010, targeted conservation measures were carried out to improve breeding and survival conditions for Yelkouan shearwaters. Conservation activities included control of invasive mammals (black rats *Rattus rattus*, brown rats *R. norvegicus*), reduction of human disturbance (shooting, nest robbing, ferreting, climbing, garbage disposal) and minimisation of nocturnal boat traffic near nesting cliffs (Borg et al., 2010).

The breeding colony of Yelkouan shearwaters at Rdum tal-Madonna in Malta was discovered in 1969, and we conducted studies at two distinct cliff ledges and a natural rock cave at the base of the

cliffs. From 1969 to 1994, birds were captured and ringed at a ledge offering crevices, fissures, rabbit burrows and a shallow cave to breeding shearwaters (hereafter referred to as site RM02). In 1996, part of this cliff-face collapsed and the entire ledge became inaccessible. Fieldwork at this site was therefore discontinued after 1994. Two annual visits were made to the colony between March and June. During these visits, adult birds were captured using loose netting placed in front of nest cavities or by hand or noose within nest cavities. We ringed all captured birds with uniquely numbered metal rings provided by the Valletta Ringing Scheme run by BirdLife Malta.

From 2007 to 2010, we captured and ringed birds at a natural rock cave and another cliff ledge approximately 350 m from site RM02. The rock cave (hereafter RM03) was located just above sea level and provided several crevices among boulders for nesting shearwaters. The cliff ledge (hereafter RM04) provided a good vantage point for mist netting and was situated <100 m from site RM03. Given their proximity, RM03 and RM04 were considered to have equal adult survival rates, but due to different accessibility, the recapture probabilities of shearwaters were assumed to differ between these two sites.

We visited sites RM03 and RM04 weekly during the early stages of the breeding season (from October to March). Between the end of May and the beginning of July, we visited the sites every second night to ensure that the majority of individuals present in the colony were ringed. Adult birds returning to or departing from the colony were caught at night by hand or using mist nets.

While birds captured at their burrow entrances could reliably be identified as breeders, the breeding status of some birds caught in Malta could not be determined. Thus, both our historic and recent period datasets likely included a mixture of breeders and non-breeders. We considered a mixture model (Pledger et al., 2003) to accommodate this source of uncertainty in our data (see Section 2.6).

2.4. Goodness-of-fit testing and model selection

We used capture–mark–recapture models to estimate adult survival probabilities from ringing and recapture data. For each survival analysis, we first performed goodness-of-fit tests in Program U-CARE v. 2.3.2 (Choquet et al., 2009). We used specific tests for transience (Test 3.Sr) and trap-dependence (Test 2.CT). If these tests indicated significant lack of fit, we included an effect of transience on survival probabilities (Pradel et al., 1997) and an effect of trap-dependence on recapture probabilities (Pradel, 1993), respectively. In addition to these tests, we estimated the variance inflation factor $\hat{c}$ as the quadratic χ^2 statistic divided by its degrees of freedom from the overall goodness-of-fit test. $\hat{c}$ provides an omnibus measure of heterogeneity in recapture and survival probabilities, including heterogeneity due to trap-dependence and transience (Choquet et al., 2009).

Due to differences in study design, we used different model structures for analysis of datasets from France and Malta (see Sections 2.5 and 2.6). For each analysis we used an information-theoretic approach to select models and calculate relative weights of evidence for each model (Burnham and Anderson, 2002). When $\hat{c} \leqslant 1$, we based model selection on AIC_c; we adjusted for overdispersion and ranked models according to $QAIC_c$ if $\hat{c}$ exceeded 1.0 (Burnham and Anderson, 2002). For the estimation of survival and recapture probabilities we used model-averaging to account for model selection uncertainty if there was support for more than one model in our candidate model set. In those model sets including mixture- and non-mixture-type models, model-averaging was restricted to just one of these model subsets. We compared estimated survival probabilities between different countries and periods using Z-tests.

2.5. Survival analysis in France

In France, we used each year as a distinct encounter occasion to estimate annual survival probabilities, and did not consider estimating monthly recapture probabilities during the same year due to sparse data which precluded use of the robust design (Kendall et al., 1997). After visually inspecting frequency histograms of the temporal distribution of monitoring effort, we confirmed that the temporal distribution of effort was similar among years and that the length of the encounter occasion (5 months) would not bias our estimates of survival probabilities (Smith and Anderson, 1987).

Because breeders and non-breeders may have different survival probabilities, and birds can change from the state 'breeder' to the state 'non-breeder' or vice versa between years, we used multi-state, open population capture–mark–recapture models to estimate annual survival (Φ), recapture (p) and state transition probabilities (ψ) for breeders and non-breeders. We fitted these models in program MARK 6.0 (White and Burnham, 1999) via the RMark interface version 1.9.6 (Laake and Rexstad, 2008) in program R 2.12.1 (R Development Core Team, 2010).

We constructed four candidate models representing biologically plausible scenarios of variation in adult survival rates. We hypothesised that survival could either vary by island (Tavecchia et al., 2008), by breeding status of the captured individual (Townsend and Anderson, 2007) or by both of these factors. We also constructed a model that held survival probability constant for birds on both islands and in both breeding states. Multi-state models can suffer from parameter non-identifiability, and other problems, when models are overparameterized relative to available data (Schaub et al., 2004; Bailey et al., 2010). Because the combined population of Yelkouan shearwaters on Port-Cros and Porquerolles is only ~500 birds, and these are difficult to capture, it was not possible to specify fully time-dependent models to examine temporal variation in adult survival (Schaub et al., 2004; Bailey et al., 2010; Lindberg, 2011). We used additive models because there was insufficient data to explore interactions between factors.

Given differing susceptibilities to capture, it was unrealistic to assume that recapture probability was similar for breeders and non-breeders (Sanz-Aguilar et al., 2010). We therefore included state-dependent recapture probability in all our candidate models. We further explored variation in recapture probabilities between islands, and among each year in our study period, as sampling effort varied over time and between islands. Thus, there were three candidate models explaining variation in recapture probability. These were combined with all four models exploring variation in survival probability, leading to 12 models in our candidate model set for this analysis.

2.6. Survival analysis in Malta

We estimated adult annual survival probabilities separately for the two periods 1969–1994 and 2007–2010 in Malta. The direct comparison of survival probabilities between those two periods was confounded by location within the Maltese colony, because the historically studied cliff site collapsed in 1996. However, there is little reason to assume that adult survival probabilities would systematically differ between two sections of the same colony that are <500 m apart, thus adult survival probabilities for the two sections of the colony that we studied on Malta should represent the same population.

Because it was logistically unfeasible to determine breeder status for all birds in Malta we did not have the data required to specify a multi-state model. In place of this model structure, we estimated adult survival probability with single-state, open population capture–mark–recapture models with and without a

two-part mixture in program MARK 6.0 (White and Burnham, 1999; Pledger et al., 2003). Our mixture models included probabilities of being in one of two groups at each site (RM02, RM03, RM04) and different survival and recapture probabilities for each group. *A priori*, we suspected that the mixture models would detect differences in probabilities between breeders and non-breeders in our Malta datasets. We used simulated annealing in program MARK to estimate parameters in our mixture models. To avoid reporting estimates based on local minima, we re-ran each mixture model multiple times using different starting values.

For the historic period (1969–1994), we first assessed the performance of two models with either constant or fully time-structured recapture probability while maintaining survival probability constant. Based on effect sizes and model selection uncertainty, recapture effects supported in this part of our analysis were then used in our analysis of survival probabilities. We considered *a priori* that annual survival could vary either by year or decade (1969–1980, 1980–1990, 1990–1994), that transient individuals may have been present, and that breeders and non-breeders might have different survival probabilities. Because many survival parameters were non-estimable in a fully time-structured model due to sparse data, we devised two simplifications and assessed these along with the decadal structure: a half-decadal time structure, and a time structure pooling periods with sparse data and estimating annual variation for periods with sufficient data (hybrid model). The half-decadal time structure divided each decade in half, thus examining variation in survival for multi-year periods starting with 1969–1975 and ending with 1990–1994. Data were particularly sparse over two periods in the dataset, 1969–75 and 1990–94. In the hybrid model, we estimated a survival probability for each of those periods, and unique parameters for each year in between.

We explored each of the three time structures (decadal, half-decadal, hybrid) in models with and without interactions between transience and time effects. Two sets of nine competing models, identical except one set included the two-part mixture allowing breeders and non-breeders to have different survival and recapture probabilities, were assessed in this analysis.

For the period 2007–2010 we utilised the information from increased monitoring efforts at the two sites RM03 and RM04 between January and July to estimate adult survival probability during the breeding and non-breeding season (a period consisting of 6–8 months) as a function of monthly recapture probabilities over the breeding period. By estimating monthly survival over the breeding period we were able to assess evidence for mortality at breeding sites over the 2007–2010 period. We considered three effects *a priori* that were likely to influence our recapture probabilities: site, trap-dependence and month. We suspected trap-dependence over months within the breeding period, a unique aspect of this dataset. To identify the most parsimonious recapture model, we first fitted five candidate models including all possible combinations of site and month; all of these models included the trap effect (see Section 3.4). We incorporated a two-part mixture into the top two models from this assessment. Recapture effects supported in this part of our analysis were then used in our analysis of survival probabilities in the same way as for the historic period.

We hypothesised that adult survival could be either constant, vary by year, and/or vary between two periods; January–June (which includes the peak breeding period) and July–December (which includes the period between breeding seasons when the birds roam widely at sea). We considered all possible combinations of seasonal and annual variation (4 models), and all of these models included a transience effect (see Section 3.4). Interactions could not be evaluated due to sparse data. Lastly, we incorporated a two-part mixture into each of the four survival models. A total of 15 candidate models were assessed in this analysis.

To calculate an average annual survival probability from estimated seasonal survival probabilities, we multiplied monthly survival probabilities from the breeding period by survival over the non-breeding interval and used the delta method to estimate standard errors (Powell, 2007). We compared mean survival probability between the two periods on Malta by means of a Z-test as the two periods were independent. Z-tests and standard error estimation were performed in R 2.12.1 using the add-on packages 'PASWR' and 'msm', respectively.

2.7. Population modelling and population growth rate

Because adult survival probabilities are key determinants of population growth rates in long-lived seabirds (Croxall and Rothery, 1991; Weimerskirch, 2002; Doherty et al., 2004), we assessed the population growth rate (λ) of Yelkouan shearwaters using our mean annual survival estimates in a stochastic population model. The model contained the following demographic parameters: (1) reproductive output (fledglings per breeding pair per year); (2) annual survival probability of birds between fledging and age one year; (3) immature survival (survival between age 1 and 6 years); (4) breeding adult survival (survival of breeding birds age $\geqslant$ 6 years); (5) non-breeding adult survival (survival of non-breeding birds age $\geqslant$ 6 years); and (6) breeding propensity (proportion of recruited birds breeding per year). A more detailed description of the population model can be found in Bonnaud et al. (2009). In this analysis we replaced the previously used survival probability of 0.93 for breeders and non-breeders with empirical estimates from our study.

We used the survival probabilities estimated for birds in France and Malta (between 2007–2010) in two separate population models to estimate current population growth rates for these sites. Population models were constructed using ULM (Unified Life Models) mathematical modelling software (Legendre and Clobert, 1995) with Monte Carlo simulations to account for the uncertainty of population parameter estimates (Bonnaud et al., 2009). We used estimates of the size of breeding populations in France (Bourgeois and Vidal, 2008) and in Malta (Borg et al., 2010) in 1000 Monte Carlo simulations of population trajectories over 100 years. We present the mean and standard error of the population growth rate across all simulations.

Because the Yelkouan shearwater population on the Hyères archipelago has been stable for the past 20 years (Bonnaud et al., 2009), we used the estimated population growth rate to assess the number of breeding pairs that would be present in France after 10 years. We then calculated the difference between that number and the present population size to estimate the number of immigrants required to maintain a stable population given the empirically estimated adult survival rates. We performed a similar calculation for the colony in Malta. Because the population estimates for both locations are surrounded by considerable uncertainty, we performed these calculations for both the minimum and maximum estimate of population size and present the results as ranges for each location.

3. Results

3.1. Number of shearwaters captured

We ringed 692 Yelkouan shearwaters in Malta between 1969 and 2009, and 238 in France from 2004 to 2009. In Malta, only 41% of all ringed shearwaters were captured more than once (119 at RM03 and RM04, and 166 at RM02). In France, about 72% (171) of all ringed shearwaters were captured more than once.

3.2. Adult survival in France

Goodness-of-fit tests indicated that there was a significant transience effect (test 3G.Sr, $\chi_9^2 = 28.361$, $P = 0.001$), presumably because Yelkouan shearwaters exhibit strong site tenacity and recaptures were only possible for birds returning to the same nesting site. We therefore included an effect of transience in each model. We found evidence of overdispersion ($\hat{c} = 1.69$), and consequently based model selection on $QAIC_c$.

There was considerable model selection uncertainty, with three models receiving similar support given the data. These top models included differences in survival probability between breeders and non-breeders, and two of the these models included differences between islands (Table 1). Due to strong support for models including an effect of breeding status on survival probability, model-averaged mean survival probabilities differed for non-breeders and breeders on both islands (Table 2). According to two of the top models, birds on Port-Cros were 1.6 times more likely to survive than birds on Porquerolles, where cats remain as predators (Table 2). Model-averaged mean annual survival probabilities for both islands combined were 0.95 (95% confidence intervals: 0.81–1.0) for non-breeders and 0.82 (0.70–0.94) for breeders.

Model-averaged recapture probabilities were <0.42 for non-breeders in all years, but were >0.43 for breeders in all years and on both islands (Table 2). Transition probabilities between breeding states were low, with model-averaged transition probability from breeder to non-breeder estimated as 0.089 (±0.04 s.e.) and from non-breeder to breeder as 0.108 (±0.04).

3.3. Adult survival in Malta 1969–1994

The goodness-of-fit tests indicated no significant lack of fit (global test, $\chi_{64}^2 = 59.86$, $P = 0.62$) and no overdispersion ($\hat{c} = 0.991$).

Nonetheless, test 3.Sr indicated statistically significant evidence of transience in the dataset (standardised log-odds ratio statistic = 2.01, $P = 0.044$), and we therefore included transience as an effect in all candidate models.

There was very strong support for annually varying recapture probability (Table 3), and we included this effect in all models exploring variation in survival probability. The most parsimonious model for the period 1969–1994 included only a transience effect on survival and annually varying recapture probability, and received almost exclusive support given the data (Table 3). The only other model receiving some support was the constant survival and time-dependent recapture model. Models including a two-part mixture acquired no support. Model-averaged estimates from models excluding the mixture indicated low annual survival probability for Malta in historic times (Table 2). The most supported model indicated that newly-marked birds were 2.3 times more likely to leave the study area (i.e., not 'survive') than residents.

Model-averaged recapture probabilities from models excluding the mixture were very low and ranged from 0.05 (±0.03 s.e.) to 0.63 (±0.21) with a mean across all years of 0.23 (95% CI 0.10–0.42).

3.4. Adult survival in Malta 2007–2010

The goodness-of-fit tests indicated that there was a significant effect of transient birds (test 3.Sr, standardised log-odds ratio statistic LOR = 2.886, $P = 0.003$ for RM04, and LOR = 3.561, $P < 0.001$ for RM03). A significant effect of trap-dependence was present at site RM03 (test 2.CT, LOR = −3.139, $P = 0.002$), but not at RM04 (LOR = −0.576, $P = 0.56$). To accommodate these results, we incorporated effects of transience and trap-dependence on survival and recapture probabilities for both sites. Given results of test 2.CT, we also compared a model with trap-dependence fitted to only RM03

Table 1

Comparison of multi-state mark–recapture models used to estimate annual adult survival (Φ), recapture (p) and transition (ψ) probabilities of Yelkouan shearwaters on two islands off south-eastern France between 2004 and 2010. k indicates the number of estimable parameters and $\omega QAIC_c$ the relative weight of evidence for each model. Model notation follows Lebreton et al. (1992) with (·) indicating no variation in the parameter, (time) indicating that a parameter varies among years, and (breeder) and (island) indicating that parameters vary with breeding status and island, respectively. Multiple effects were entered additively into models (indicated by '+'). All models included separate transition probabilities for breeders and non-breeders (ψ (breeder), omitted in table) and effects to account for transience (Pradel et al., 1997).

Model	k	$\Delta QAIC_c$	$\omega QAIC_c$	Evidence ratio	QDeviance
Φ(transience + island + breeder) p(breeder)	8	0.00	0.29	1.00	1156.72
Φ(transience + breeder) p(breeder)	7	0.38	0.24	0.83	1160.86
Φ(transience + island + breeder) p(breeder + island)	9	0.78	0.19	0.68	1154.52
Φ(transience + breeder) p(breeder + island)	8	2.37	0.09	0.31	1160.73
Φ(transience) p(breeder)	6	3.31	0.05	0.19	1169.28
Φ(transience + island) p(breeder)	7	3.83	0.04	0.15	1166.67
Φ(transience + island + breeder) p(breeder + time)	13	4.75	0.03	0.09	1147.02
Φ(transience + island) p(breeder + island)	8	5.07	0.02	0.08	1165.28
Φ(transience + breeder) p(breeder + time)	12	5.20	0.02	0.07	1151.35
Φ(transience) p(breeder + island)	7	5.37	0.02	0.07	1169.28
Φ(transience) p(breeder + time)	11	8.58	0.00	0.01	1160.62
Φ(transience + island) p(breeder + time)	12	9.11	0.00	0.01	1157.94

Table 2

Model-averaged estimates of adult annual survival (Φ) and recapture (p) probabilities from resident Yelkouan shearwaters at a colony in north-eastern Malta between 1969 and 1994 (site RM02) and 2007–2010 (sites RM03/RM04), and on two islands in the Hyères archipelago, France from 2004–2010. s.e. = standard error of the estimate, calculated using the delta method if model estimates had to be multiplied or averaged.

Country	Group	Site	Mean Φ	s.e.	Mean p	Min p	Max p
France	Breeder	Porquerolles	0.793	0.070	0.602	0.438	0.751
France	Breeder	Port-Cros	0.851	0.053	0.581	0.440	0.719
France	Non-breeder	Porquerolles	0.947	0.081	0.233	0.121	0.414
France	Non-breeder	Port-Cros	0.961	0.063	0.218	0.107	0.406
Malta	Mixture 2[a]	RM03/RM04	0.848	0.134	0.450	0.067	0.929
Malta	Mixture 1[b]	RM03/RM04	1.000	0.006	0.156	0.011	0.672
Malta	Unknown	RM02	0.741	0.028	0.229	0.046	0.633

[a] Possibly breeders, mixture 2 from a two-part mixture model (see text for details).
[b] Possibly non-breeders, mixture 1 from a two-part mixture model (see text for details).

Table 3

Comparison of single state, open population, mark–recapture models used to estimate annual adult survival (Φ) and recapture (p) probabilities of Yelkouan shearwaters at a colony in north-eastern Malta (RM02) between 1969 and 1994. Model notation as in Table 1, with '×' indicating multiplicative effects; 'transience' indicates an effect to account for permanent emigration after initial capture (Pradel et al., 1997). Due to data sparseness a fully time-structured model with annually varying survival probabilities was not possible, and 'decade', 'half-decade' and 'hybrid' indicate increasingly fine-grained temporal variation in survival probability (see text for details). Mixture models mentioned in the text acquired no support and are not shown.

Model	k	ΔAIC_c	ωAIC_c	Evidence ratio	Deviance
Φ(transience) p(time)	22	0.00	0.89	1.00	357.63
Φ(·) p(time)	21	4.46	0.10	0.11	364.29
Φ(transience + decade) p(time)	24	10.51	0.01	0.01	363.74
Φ(transience + half-decade) p(time)	26	11.93	0.00	0.00	360.72
Φ(transience + hybrid) p(time)	34	12.50	0.00	0.00	343.15
Φ(transience × decade) p(time)	26	14.14	0.00	0.00	362.93
Φ(transience × half-decade) p(time)	30	14.60	0.00	0.00	354.39
Φ(transience × hybrid) p(time)	41	18.93	0.00	0.00	333.18
Φ(·) p(·)	2	30.07	0.00	0.00	429.79

(Table 4). Consistent with tests 2.CT and 3.Sr, the omnibus test of heterogeneity indicated overdispersion ($\hat{c}$ = 1.86).

The two most parsimonious models for this period, which acquired >99% of the QAIC$_c$ weight, were mixture models including seasonally varying survival probability and an effect of transience, and recapture probability varying between seasons, sites and between initial and subsequent recapture events (trap-dependence; Table 4). None of the non-mixture-type models were supported. The model-averaged probability of being in mixture one was 0.62 (±0.22 s.e.) and 0.44 (±0.12) at RM04 and RM03, respectively. Estimates of survival for residents in mixtures one and two were similar to estimates for non-breeders and breeders in France (Table 2), respectively, suggesting that the mixture approach may have accounted for heterogeneity in recapture and survival probabilities that were a function of breeder state. Model-averaged survival probabilities for the second mixture group (possibly 'breeders') were 0.999 (±0.008) from January to June, and 0.849 (±0.080) from July to December.

Annual survival of the first mixture group (possibly 'non-breeders') was significantly higher than annual survival of breeders in France ($z = -2.79$, $P = 0.005$) and birds in Malta between 1969–1994 ($z = 9.04$, $P < 0.001$). Due to large standard errors, statistical significance tests concluded that the recent annual survival probability of the second mixture group (possibly 'breeders') was not significantly higher than during the 1970–1990s ($z = 0.78$, $P = 0.43$). Nonetheless, differences in point estimates were substantial and biologically relevant (Table 2). There were no significant differences between annual survival estimates for either breeders or non-breeders between France and Malta (all $P > 0.5$, see Table 2). We did not assess differences in survival among years and locations for newly-marked birds as these estimates were confounded by permanent emigration.

Model-averaged recapture probabilities were highly variable among time and between sites, and generally lower for mixture group 1 than mixture group 2. For the first group, recapture probabilities ranged from 0.024 (±0.005 s.e.) to 0.34 (±0.09) at site RM03, and from 0.01 (±0.007) to 0.09 (±0.11) at site RM04; for the second mixture group, estimates ranged from 0.15 (±0.11) to 0.93 (±0.10) at site RM03, and from 0.07 (±0.04) to 0.67 (±0.11) at site RM04.

3.5. Population growth rates

The stochastic population model using recruitment and breeding parameters from our study populations (Bourgeois and Vidal, 2007; Bonnaud et al., 2009), and the adult survival probabilities estimated here, indicated that population growth rate in France would theoretically be 0.940 (±0.0001). The mean predicted time to extinction was between 96 and 97 years for population sizes of 210–270 pairs, respectively. Hence, the French population would experience population declines of 6.0% per year, but because monitoring indicates that the population has remained stable over the past 20 years, we assumed that immigrants compensated for the loss of breeding adults (Bonnaud et al., 2009). Given a current population size of 210–270 pairs, an average of 9–12 breeding pairs would have to immigrate to and start breeding on the Hyères archipelago every year to maintain a stable population.

In Malta, we used the survival estimates from the two-part mixture models to estimate λ. We first estimated λ with our empirical estimates from the two mixture groups, and assumed that these two groups reflected breeders and non-breeders, respectively. Because mixture group 1 had an unrealistic high survival probability (Table 2), and we did not know whether the two unknown mixture groups actually reflected breeders and non-breeders, we also estimated λ using the non-breeder survival probability from France instead of the estimate of mixture group 1. These two approaches yielded λ of 0.985 (±0.0002) and 0.972 (±0.0003), respectively. The mean predicted time to extinction was >100 years for population sizes of 398–602 pairs with either approach. The Rdumtal-Madonna colony with its current size of 398–602 breeding

Table 4

Comparison of two-part mixture, single state, open population mark–recapture models used to estimate monthly adult survival (Φ) and recapture (p) probabilities of Yelkouan shearwaters at a colony in north-eastern Malta (RM03/RM04) between 2007 and 2010. Model notation as in Tables 1 and 3; 'season' indicates variation in survival and recapture probabilities at the seasonal scale (breeding season = January–June, non-breeding season = July–December); 'transience' indicates an effect to account for permanent emigration after initial capture (Pradel et al., 1997), 'trap' indicates models accounting for trap-dependence in recapture probability (Pradel, 1993). Non-mixture-type models mentioned in the text acquired no support and are not shown.

Model	k	$\Delta QAIC_c$	$\omega QAIC_c$	Evidence ratio	QDeviance
Φ(transience + season) p(site + trap + time)	29	0.00	0.50	1.00	1875.33
Φ(transience + season + year) p(site + trap + time)	31	0.03	0.50	0.99	1870.91
Φ(transience) p(site + trap + time)	28	20.70	0.00	0.00	1898.25
Φ(·) p(site + trap + time)	27	22.01	0.00	0.00	1901.77
Φ(·) p(site + trap[a] + time)	27	24.29	0.00	0.00	1904.05
Φ(transience + year) p(site + trap + time)	30	24.63	0.00	0.00	1897.74

[a] Trap-dependence effect only at RM03.

pairs would require an annual influx between 5–12 breeding pairs to remain stable.

4. Discussion

Adult survival probability for breeding Yelkouan shearwaters across the western Mediterranean is currently too low to maintain stable populations. Annual survival probabilities <0.90 are generally considered unsustainable for shearwater populations (Croxall and Rothery, 1991; Hunter et al., 2000; Weimerskirch, 2002) and we found mean adult survival probabilities above this threshold only for non-breeders in France, and an unknown mixture group which may reflect non-breeders in Malta (Table 2).

Between the 1970–1990s, survival probability for adults nesting in Malta was as low as survival probabilities of the critically endangered and declining population of Balearic shearwaters (Oro et al., 2004). More recent survival probabilities appear to have benefited from ongoing conservation efforts to increase site-specific protection of shearwaters by controlling introduced mammals and various other factors related to human disturbance, such as illegal shooting, and light and noise pollution (Bonnaud et al., 2010; Borg et al., 2010). However, these efforts directed at breeding grounds may not be sufficient, because neither in Malta nor on the French islands in the Port-Cros National Park have annual survival probabilities of breeding Yelkouan shearwaters increased to a level that would sustain stable populations. Immigration of birds may explain why some of these populations have not declined (Bonnaud et al., 2009, 2010).

4.1. Potential causes for low adult survival probabilities

Bird shooting in Malta remains pervasive, and both legal and illegal shooting activities have affected many bird populations in Malta for decades (Magnin, 1986; Raine, 2007; Raine and Temuge, 2009). Yelkouan shearwaters in Malta have historically suffered from this illegal shooting activity, and consistent with the killing of birds near nesting cliffs our study found that survival was extremely low between 1969 and 1994. Other forms of human disturbance at nesting cliffs, light pollution, and mortality in the expanding long-line fishery in the Mediterranean Sea (Belda and Sánchez, 2001; Cooper et al., 2003; Dimech et al., 2008) may also have contributed to high mortality over this period. Despite improvements at nesting sites on land since the 1970–1990s, our recent (2007–2010) estimates of annual adult survival probability suggest that the population of Yelkouan shearwaters in Malta may persist only due to immigration. Our estimates of extremely high survival over the breeding period in Malta suggest that most of the mortality in recent years occurred outside the breeding season. This finding is consistent with current management efforts to reduce direct mortality at the nesting cliff (Borg et al., 2010), and it implicates mortality at sea as the greatest current threat to the population in Malta.

In France, the removal of feral cats as predators of shearwaters on one of the islands resulted in only a small increase of mean annual survival probability of breeders. In addition, annual survival of breeders on the now predator-free Port-Cros Island (0.85) remains below what is needed to maintain a stable population. Thus, as for the colonies in Malta, it is likely that the greatest threat to the persistence of the Yelkouan shearwater colonies in France is human-caused mortality at sea.

Patterns in our estimates of survival, which implicate fishing mortality as a critical source of mortality for Yelkouan shearwaters, are consistent with the presumed cause of low adult survival probabilities in the Balearic shearwater (Oro et al., 2004; Tavecchia et al., 2008). These inferences are limited given that data on fishing

effort remain unavailable for the Mediterranean (Lleonart and Maynou, 2003; Franquesa et al., 2008) and there are no data on seabird by-catch rates from industrial fisheries in the region. Artisanal long-line and bottom-line fisheries in Malta appear to kill very few Yelkouan Shearwaters (Darmanin et al., 2010), but Darmanin et al. (2010) were not able to assess by-catch in other types of artisanal fisheries or industrial fishing fleets in international waters. Because we found strong support for particularly low survival during the period when Yelkouan shearwaters move across the Mediterranean and Black Seas and are not vulnerable to land-based disturbances, it is likely that fishery by-catch is an ongoing threat to Yelkouan shearwaters.

Given the sensitivity of population stability to changes in adult survival, eradication of mammals as significant predators at nesting colonies remains an important priority for the conservation of seabirds (Nogales et al., 2004; Wanless et al., 2009). Feral cats were eradicated from Port-Cros Island in 2005, but they remain on Porquerolles Island. Our results suggest that adult survival probabilities might have been slightly higher on Port-Cros than on Porquerolles Island. This albeit small increase indicates that cat removal may have had a positive effect on adult survival, consistent with existing knowledge from other species (Keitt and Tershy, 2003; Martínez-Gómez and Jacobsen, 2004).

The Yelkouan shearwater population on Port-Cros increased following feral cat eradication, implying that cat eradication may have led to higher recruitment in addition to a modest increase in adult survival (Bonnaud et al., 2010). However, our population model indicated a declining population ($\lambda = 0.94$) for the two French islands combined. A constant annual immigration of >9–12 breeding pairs is necessary to explain population growth on Port-Cros Island (Bonnaud et al., 2010). Too little information exists on other Yelkouan shearwater colonies in the north-western Mediterranean Sea to assess sources of immigrants. Likely sources include nearby colonies on Le Levant Island (Hyères archipelago, France; 800–1300 pairs) and along the north-western Italian coast (Bourgeois and Vidal, 2008).

4.2. Shortcomings of the sampling design and analysis

Because our survival estimates for Yelkouan shearwaters predict an ongoing decline of the species, it is prudent to closely examine potential factors that could have introduced bias and affected our estimates. One profound difficulty in mark–recapture studies of nocturnal and burrow-nesting seabirds like Yelkouan shearwaters is that capture is logistically challenging and the number of birds that can be repeatedly captured is therefore limited (Sanz-Aguilar et al., 2010). To accommodate this limitation, sampling can be extended to several months, as in this study, but this approach risks introducing heterogeneity in recapture probabilities. If recapture probabilities over the sampling period are heterogeneous, survival probabilities can be biased. One source of heterogeneity in recapture probabilities is mortality over the sampling interval. Especially during 1969–1994, some Yelkouan shearwaters were deliberately killed by humans at breeding colonies in Malta. Nonetheless, such bias is likely to be small if the temporal distribution of capture effort is similar among years (Smith and Anderson, 1987), and recapture probability is >0.2 (O'Brien et al., 2005), two criteria that were reasonably met by our data.

Recapture probability was markedly lower for non-breeders than for breeders in France, and the survival estimates of this group were therefore very imprecise. In Malta, we found a pattern for survival and recapture probabilities similar to France between the two unknown mixture groups, and we therefore cautiously interpreted these groups as breeders and non-breeders. Non-breeders are believed to be more vulnerable to predation by terrestrial predators (Bonnaud et al., 2009) because non-breeders remain

on the ground outside burrows approximately four times as long as breeders, which enter nesting burrows shortly after landing (Bourgeois et al., 2008a). Our survival estimates suggest a reverse pattern, although the estimated survival probabilities for non-breeders appear biologically unrealistic (Table 2). Nonetheless, the direction of the difference in survival probability would be consistent with a cost-of-breeding hypothesis. Additional research will be necessary to interpret this unexpected result.

In summary, capture methods and intrinsic heterogeneity in catchability can affect survival estimates (Crespin et al., 2008; Vögeli et al., 2008). However, despite fundamentally different capture, sampling, and analytical designs, our recent annual adult survival probabilities were very similar for breeders in France and Malta. Variation in survival estimates from long-term seabird monitoring programmes is more likely to stem from underlying biological variation among sites or periods than from capture methods when sources of heterogeneity, including transience and trap-dependence, are accounted for (Sanz-Aguilar et al., 2010). While we recognise that some of our survival estimates are surrounded by considerable uncertainty, we are confident that our general conclusion that adult survival probabilities are too low to maintain stable populations are not artefacts of sampling designs or capture methods.

4.3. Implications for conservation

Despite lack of precision for some survival probabilities, our estimates are consistent with the hypothesis that low adult survival probability may have caused population declines that led to the disappearance of known breeding colonies from several French and Italian islands in the 1980s and 1990s (Bourgeois and Vidal, 2008). These findings confirm the concerns of an earlier plea to list the Yelkouan shearwater as a threatened species both in EU directives and on the IUCN Red List (Bourgeois and Vidal, 2008), where it is currently listed as 'Near Threatened'.

In order to improve the conservation status of the species, we recommend that the threat of fishery by-catch of Yelkouan shearwaters be addressed. On-going efforts to remove introduced predatory mammals from islands, and to reduce human disturbance, such as direct persecution on Malta, should be continued and expanded to additional colonies. Additional threats including light pollution, habitat loss and the development of offshore wind farms should be monitored. The conservation projects at the Rdum-tal-Madonna colony in Malta and on Port-Cros Island in France indicate that even focused land-based conservation action to minimise the effects of invasive species and human disturbance at nesting colonies may not sufficiently improve adult survival probabilities if mortality occurs predominantly elsewhere. Measures that reduce accidental by-catch of Yelkouan shearwaters and other seabirds in commercial fishing operations in the Mediterranean and Black seas would likely yield large conservation benefits. Such measures have been widely implemented in fisheries around the world (Løkkeborg, 2003; Gilman et al., 2005; Cox et al., 2007), and it is now up to policymakers to implement and enforce such measures for commercial fisheries in the Mediterranean and Black seas.

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