

# Modelling demography and extinction risk in the endangered Balearic shearwater

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## Abstract

Several demographic parameters of Balearic shearwater (*Puffinus mauretanicus*) were estimated and used to model extinction probabilities for the species, which is an endemic seabird confined to a Mediterranean archipelago. Adult survival was analyzed through capture–recapture models at two colonies free of adult predators during 1997–2002. Extinction probabilities for the world breeding population were modelled using Monte Carlo simulations of population trajectories, introducing stochasticity both demographic and environmental. Adult survival estimate (0.780, SE = 0.020, 95% Confidence Intervals: 0.739–0.816) was unusually low for a Procellariiform, suggesting that sources of mortality other than predators (e.g. fishing gears) also occur. A deterministic model showed a declining trend for the world breeding population ( $\lambda = 0.952$ ), and significantly less than 1. Population viability analysis showed that in the presence of environmental and demographic stochasticities, mean extinction time for the world population was estimated at 40.4 years (SE = 0.2), and mean growth rate showed a 7.4% decrease per year. Demographic stochasticity played a more important role than environmental stochasticity in population growth rate.

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## 1. Introduction

The Balearic shearwater (*Puffinus mauretanicus* Lowe; family Procellariidae) is one of the rarest seabirds in the world. Recent studies have shown that birds breeding at the Balearic archipelago (western Mediterranean) are genetically and morphologically distinct from the Levantine shearwaters *P. yelkouan*, and is now considered a different species, rather than a subspecies or a race (Austin, 1996; Mayol, 1997; Heidrich et al., 1998, 2000). This has implied a very small breeding distribution, and together with a dramatic decline in the estimated numbers (world breeding population is estimated at less than 2000 pairs), has lead researchers to consider the species as threatened (Arcos and Oro, in press). Although several studies have recently analyzed several

features of the ecology of the species (e.g. Aguilar, 2000; Arcos et al., 2000; Arcos and Oro, 2002), demographic information is sparse. Some data have been recorded on hatching and breeding success although sample sizes were always small (e.g. Aguilar, 1992, 1993, 1997). It is also known that some factors are negatively affecting the population dynamics of Balearic shearwaters and other seabird species breeding at the same region (Mayol, 1986; Cooper et al., in press). Even though human predation and loss of suitable habitat were probably the main causes of heavy decline and local extinction of most of these species up to recent decades (Mayol, 1986; Aguilar, 1997; Alcover, 2000; Mayol et al., 2000), other factors such as predation by alien terrestrial mammals (both rats and carnivores) or mortality at fishing gears have been proposed to be now the main threat (Aguilar, 2000; Mayol et al., 2000; Belda and Sánchez, 2001). However, very little is known about the impact of these factors on the population dynamics of Balearic shearwaters (Arcos and Oro, in press). Thus, a detailed demographic study is crucial to assess population

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viability and conservation implications for this rare species (Lebreton and Clobert, 1991; Caswell, 2001).

In this study, we estimated for the first time adult survival of Balearic shearwaters. Owing that all Procellariiformes are long-lived organisms (e.g. Croxall and Rothery, 1991; Russell, 1999) adult survival is the demographic parameter suspected to have the greatest impact on population growth rate. We used this estimation and other life history traits to perform a population viability analysis and to assess the risk of extinction and expected lifetime for the total world population.

## 2. Methods

### 2.1. Study area

The study was conducted during 1997–2002 at two colonies located in Mallorca (western Mediterranean). One colony (Sa Cella) was located in a big cave at the foot of a vertical sea cliff on Mallorca Island and was accessible only from the sea. The other colony was spread in several small caves on a calcareous rocky islet (Conills de Malgrats) south of Mallorca. While the first cave is free of carnivores and rats, Black rats (*Rattus rattus*) are present in the second colony. Rats are known to predate on Procellariiformes, especially on eggs and chicks, and even on adults (e.g. Warham, 1990). Nevertheless, several eradication campaigns have been carried out at Conills colony, and density of rats is probably low, which in turn may determine low or even absence of predation (Amengual and Aguilar, 1998; Aguilar, 2000). Moreover, Balearic shearwaters are sufficiently large to be safe against rats, and have not found indications of rat predation on eggs or chicks at Conills colony during the study (43 nests monitored, see later). The two colonies are legally protected and no human impact on the colonies has been recorded in the past decade. Breeding pairs were estimated at ca. 170–210 at the big cave and 40–50 at the islet (own data).

Body mass of Balearic shearwaters is ca. 500 g, and males are slightly larger than females (Genovart et al., in press). Females lay a single egg at a nest site (a burrow, a crevice or directly on bare ground) during February–March, and incubation lasts ca. 50 days. Chick rearing period extends for ca. 65–70 days (own data).

### 2.2. Data collection and demographic analysis

Nests were marked and breeding success (as percentage of fledglings by eggs laid) was estimated at the two colonies during 2001–2002. Only nests where the whole breeding cycle was monitored were considered. Productivity was constant between years and colonies (Table 1; three-dimensional contingency table,  $\chi^2 = 3.43$ , d.f. = 4,  $P > 0.05$ ).

Table 1

Fecundity of Balearic shearwaters at the two study colonies during 2001–2002, expressed as the proportion of nesting attempts (pairs laying an egg) that produced a fledgling ( $n$  showed the number of nests monitored)

Year	Sa Cella	$n$	Conills	$n$	Total	$n$
2001	0.62	107	0.48	23	0.59	130
2002	0.59	91	0.75	20	0.62	111
Total	0.61	198	0.60	43	0.61	241

A ringing programme on chicks and adults has been carried out since 1981 at several colonies. In total, 880 adults and 1092 chicks have been caught and ringed. However, the limited number of recaptures in most of these years and colonies precluded a complete analysis of the data. Only data from the two study colonies during 1997–2002, when the number of recaptures was sufficiently large, was consequently used. Birds were trapped by hand at the caves mostly at night when individuals visit the colonies. During 1997–1999 we took into account all the individuals trapped at holes and crevices (i.e. potential nest sites) only during the breeding season (from early March to late June), although some of them could be non-breeding individuals (either immatures or adults; see later). We added data from 2000–2002, but only for those individuals recorded as breeders (incubating an egg or with a chick), since this information was systematically recorded during this period. Birds were marked with monel rings with a unique code and the code was recorded when the birds were caught in subsequent years.

#### 2.2.1. Survival estimates by capture–recapture modelling

Capture–recapture modelling was applied to the data set to estimate survival. Models rely on the assumption that all marked individuals have the same survival probability, regardless of whether they were marked at the sample occasion immediately before the current resighting (e.g. Burnham et al., 1987; reviewed in Williams et al., 2002). Nevertheless, several sources of heterogeneity in survival probability among individuals violate this assumption: one of these sources is the presence of transients. Since birds caught during the period 1997–1999 could include some non-breeders (see earlier), we took into account the potential bias of this effect for these years. Transients are individuals that leave the study area after first capture and thus have a subsequent local survival probability equal to 0 (Pradel et al., 1997). The presence of transients in the marked sample may bias estimation of survival. Comparisons between models including a residency parameter ( $1 - \tau < 1$  (not all the individuals in the sample are residents) or equal to 1 (the marked sample includes residents only) addresses the presence of transients in the study colonies (Hines, 1996). Importantly, the presence

of transients indicates emigration out of the study area or in our case, occurrence of animals simply visiting the caves, but not able to breed (see earlier). This parameter can have a biological meaning such as dispersal probability (e.g. Oro et al., 1999) but in our study the only matter of interest is birds that are breeders (i.e. the estimation of adult survival). However, as usual, we cannot tell to what extent the local survival probability of individuals resighted several times reflects true survival (i.e. it may also incorporate permanent emigration out of the study area). Thus, local adult survival estimation cannot distinguish mortality from permanent emigration. Nevertheless, we assumed that this bias was small in our species since breeding dispersal is probably a very uncommon phenomenon as recorded for other Procellariiformes (e.g. Warham, 1990; Aguilar, 2000).

We started with the Cormack-Jolly-Seber (CJS) model ( $\phi_{t,c}, p_{t,c}$ ), where  $\phi$  is the local survival rate and  $p$  is the recapture probability (e.g. Pollock et al., 1990; Lebreton et al., 1992). This model had time-specific ( $t$ ) parameters for each colony ( $c$ ), and can be considered the general model for departure (see details in Lebreton et al., 1992). For model selection and assessment of the biological hypotheses guiding model development (Burnham and Anderson, 1998), it is critical that the general model fit the data (Lebreton et al., 1992). Consequently, we first assessed the fit of the general model using the program U-Care (Choquet et al., 2000). The program provides insight into possible violations of the assumptions underlying the CJS model (see Burnham et al., 1987; Pradel et al., 1997). Two tests are used to assess whether these assumptions are met in our CJS initial model: TEST2 and TEST3. TEST2 deals with capture heterogeneity, and check whether some individuals can have different recapture probabilities than others. TEST3 tests the assumption that all marked individuals alive at ( $t$ ) have the same probability of surviving to ( $t+1$ ), and test specifically the presence of transients (or non-breeders in our case). Analyses were performed using program MARK (White and Burnham, 1999). Model notation followed Lebreton et al. (1992). A model including two factors and their interaction was described using an asterisk. Additive models were described using a “+” symbol instead, while “.” indicated that the parameter was constant with time. The biological hypotheses underlying the structure of models were assessed using AICc (Akaike Information Criterion corrected by the quasi-likelihood parameter  $c$ , see White and Burnham, 1999). Models with the lowest values of AICc were retained as good candidate models (Lebreton et al., 1992; Anderson and Burnham, 1999). Models with differences in AICc values lower than 4 were considered as “equivalent” (i.e. data were insufficient to lead to definitive conclusions concerning the process that gave rise to the data; Anderson et al., 1994; Burnham et al., 1995). To account for the model selection uncertainty,

we estimated model parameters by the model averaging procedure, which considers the relative importance of each fitted model (Burnham and Anderson, 1998).

We finally partitioned the variance of the apparent survival rates into sampling variance and process variance using random effects models, since a large sampling variance makes difficult the identification of the biological processes underlying the variability in survival (e.g. Burnham and White, 2002).

### 2.2.2. Population viability modelling

Population viability analysis and risk of extinction of the world breeding population were assessed by population modelling. As initial value in our models, we took the highest of the available estimates of the world breeding population up-to-date: 2000 breeding females (Arcos and Oro, in press). As a first step, we modelled the life-cycle of the population based on its life-history traits. The life-cycle graph corresponded to a prebreeding census (Fig. 1; Caswell, 2001). Demographic parameters were not sex-dependent. The parameters were  $s_a$ , adult survival (or survival of breeders, from the age of 3 years, see Section 3);  $s_0$ , juvenile survival;  $s_1$ , survival rates for immatures;  $a$ , age at first breeding; and  $\varepsilon$ , fertility. Fertility comprised  $\beta$ , or proportion of breeders, probability of taking a sabbatical year  $k$  (see below) and productivity or breeding success  $P$  (see earlier for methods). No information was available on immature survival of Balearic shearwaters. Data on survival other than adult age classes in seabirds are sparse, since immature birds do not normally visit the breeding sites and their survival cannot be easily estimated (e.g. Nichols et al., 1990; Lebreton, 2001). Thus, we arbitrarily set a progressive decrease of 5% in survival rate for the immature age classes starting from the adult survival estimate calculated by capture–recapture modelling. This can be considered an optimistic procedure since in seabirds, immature and subadult survival is much lower than adult estimates (e.g. Harris et al., 1994; Spendelov et al., 2002). Moreover, only two age classes

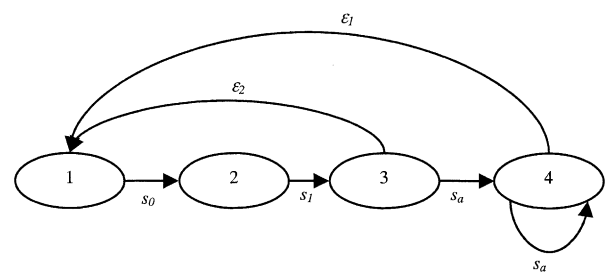


Fig. 1. Life-cycle representation of the population model. Stage 1 is juvenile birds of age one, stage 2 is immature birds of age two, stage 3 is breeders of age three, and stage 4 is breeders of older ages;  $s_i$  are survival for each age class  $i$  (juvenile, immature and adult); fertility  $\varepsilon$  is different for stage 3 ( $\varepsilon_1$ ) than for stage 4 ( $\varepsilon_2$ ) because proportion of breeders ( $\beta$ ) was different between the two stages (see Section 2 for explanations).

were considered immature since birds start to breed at 3 years old (see later). Uncertainty affected also other parameters such as age at first breeding and proportion of breeders. Although ca. 1100 chicks were ringed at several colonies during 1986–2001, very few birds were recovered as breeding adults, and age-specific probabilities of breeding (e.g. Lebreton et al., 1990) could not be estimated. However, 20 of those chicks were first recorded breeding at the study colonies at a mean age of 7.2 years (S.D.=3.6), 30% starting at the youngest age of 3 years (Fig. 2). Distribution was probably biased by several factors (small sample size, detection probabilities, numbers of birds marked per cohort, lack of recaptures for many years), but we could set a minimum age of first breeding at 3 years. We also set an optimistic approach of 70% proportion of breeders ( $\beta$ ) for 3 years age class and 100% for older age classes (see Fig. 1). Even though many Procellariiformes take sub-battical years (e.g. Warham, 1990), the probability of skip breeding in Balearic shearwaters was also uncertain. We obtained a sample of 16 nests where at least data from three consecutive years were recorded. After eliminating data of first and last years when no breeding was recorded (the first case could be a first no-breeding occupation of a nest site and the second case could indicate a definitive abandon of the nest), we estimated the probability that a nest site was unoccupied given that it was occupied in the previous year at 0.213 (SE=0.060). Assuming no movement among nest sites (own observations), an occupied nest site may become unoccupied in the following year if either (a) both birds survived and they skip breeding or (b) at least one of the adults died. The probability ( $k$ ) of an occupied burrow becoming unoccupied could thus be written as:

$$k = p(s_3^2) + (1 - s_3^2), \quad (1)$$

where  $s_3$  is adult survival and  $p$  the probability of skipping for breeders, which can thus be estimated by:

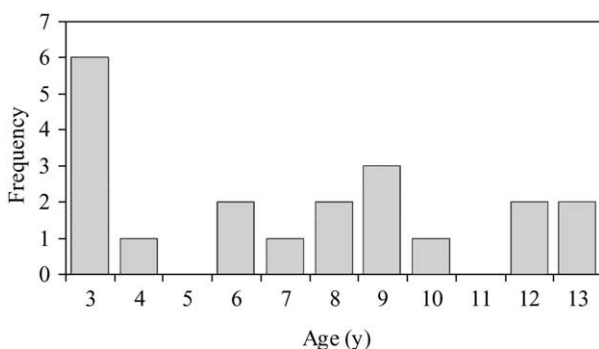


Fig. 2. Age of first detected breeding of Balearic shearwaters ringed and recaptured at the study colonies. Due to several constraints the bars do not necessarily show the true age of first reproduction (see Section 2).

$$p = \frac{k - 1}{s_3^2} + 1 \quad (2)$$

A standard error for this estimate  $p$  obtained by the delta method, is

$$SE(p) = (1 - p) \sqrt{\left(\frac{SE(k)}{k - 1}\right)^2 + \left(\frac{2s_3 SE(s_3)}{s_3^2}\right)^2} \quad (3)$$

These equations gave estimates of  $k$  of 0.261 (SE=0.063).

Two sets of simulations were carried out: deterministic and stochastic. Deterministic age-structured matrix models were used to test the null hypothesis that the population was stable or increasing, that is  $H_0: \lambda \geq 1$ , where  $\lambda$  is the population growth rate (Caswell, 2001). Estimated population growth rate  $\hat{\lambda}$  was calculated from the deterministic matrix. The standard error  $SE(\hat{\lambda})$  was calculated from the variances of the matrix entries using the series approximation method (Caswell, 2001). The null hypothesis was tested by computing the statistic test  $z$ :

$$z = \frac{1 - \hat{\lambda}}{SE(\hat{\lambda})},$$

which under  $H_0$  has a normal distribution with mean 0 and variance 1.

The simple structure of the deterministic model allowed us to assess the relative importance of basic demographic parameters without stretching beyond the limits of the available data. Even though some parameters (such as age at first reproduction) had an unknown degree of uncertainty, recent studies indicate that additional age structure in matrix models has little influence on either population growth rate or perturbation analyses (Heppell et al., 2000; Caswell, 2001; Yearsley and Fletcher, 2002; Yearsley et al., 2003).

Simulation by stochastic models were used to investigate extinction probabilities. Three different scenarios were considered for modelling extinction probabilities: (a) only with demographic stochasticity, (b) only with environmental stochasticity, and (c) with stochasticity both demographic and environmental. Input parameters of the models were randomly selected from uniform distributions between the upper and lower 95% confidence limits for each demographic parameter. Probabilistic distributions of demographic parameters were applied to add demographic stochasticity, which assigned population sizes to integer values. The same demographic parameters were assigned to males and females, and sex ratio was assumed to be balanced. We calculated the numbers of breeders  $np$  using the binomial distribution  $B(u, \beta)$ , with  $u$  the minimum number of males and females and  $\beta$  the proportion of breeders. For environmental stochasticity, each demographic



parameter  $x$  was obtained from a normal distribution with a mean value and its standard deviation estimated in the field during the study. This stochasticity allowed the parameters to oscillate between bad and good values and environmental effects either negative or positive were thus simulated. We did not consider density dependence in population models (e.g. Yearsley et al., 2003) since population growth rate was negative in all cases (see Section 3). Finally, to assess the relative importance of both stochasticities we performed two simulations on extinction probabilities, one with only demographic stochasticity and the other with only environmental stochasticity.

From matrix models, we estimated growth-rate sensitivity and elasticity to demographic parameters  $x_i$  (Caswell, 2001). Monte Carlo simulations were used to draw population trajectories (1000 runs) over time (100 years) and to estimate extinction probabilities, which were computed as the number of extinct trajectories over the total number of trajectories.

### 3. Results

A total of 374 adults (281 at Sa Cella and 93 at Conills) were caught at least once during 1997–2002 (Table 2). Program U-Care showed that the CJS model ( $\phi_{t,c}, p_{t,c}$ ) fitted our data (TEST2 + TEST3:  $\chi^2 = 24.715$ , d.f. = 23,  $P = 0.365$ ). TEST3 showed that there was no transient effect at Sa Cella colony, whereas it could exist such effect at Conills colony (TEST3:  $\chi^2 = 3.9217$ , d.f. = 4,  $P = 0.417$ ; and  $\chi^2 = 8.2951$ , d.f. = 4,  $P = 0.081$  respectively). We interpreted this result as emigration of birds new to the Conills colony in the first years probably as a consequence of capturing visitors (i.e. non-breeding individuals) among breeders. The CJS model

denoted as ( $\phi_{t,c}, p_{t,c}$ ) (see notation in Lebreton et al., 1992) was used as a starting point for model selection with MARK, although additional models (denoted [ $\tau_{c2}, \phi, p$ ]) were constructed to take into account the transient effects on Conills colony (noted as  $c2$ ). The finally selected model (Model 2: [ $\phi(\cdot), p(c^*t)$ ]) indicated that survival was constant and estimated at 0.780 (SE = 0.020, 95% CI: 0.739–0.816; Table 3). Modelling did not show any change in adult survival between the two colonies (Models 4 and 8). Models with a transient effect on Conills colony (e.g. Models 3, 5 or 7) were either retained as good models. Recapture probability estimates under the selected model ranged between 0.158 (SE = 0.052) and 0.881 (SE = 0.058) at Sa Cella colony and 0.669 (SE = 0.082) and 0.769 (SE = 0.093) at Conills colony (Fig. 3). Effort of recapture (indicated by  $ef$  in the models, see Table 3), measured as number of days spent at each colony each year, did not influence recapture probabilities, neither as linear association (Model 12) nor as quadratic effect (Model 13). Random effects models were not well ranked suggesting that sampling variance was small with respect to process variance (Models 14 and 15). The weighted average of adult survival estimate was 0.772 (SE = 0.026, 95% CI: 0.711–0.823), showing that the estimate given by our finally selected model was robust and reliable.

Using the demographic parameters estimated or set in our study (see Table 4), the results of the deterministic population model showed a declining trend ( $\lambda = 0.952$ ),

Table 2  
Capture–recapture data for Balearic shearwater ringed and recaptured between 1997 and 2002 at the two study colonies of Mallorca Island: Conills Island and Sa Cella cave

	Released	Newly marked	Year next recaptured					Never recaptured
			1998	1999	2000	2001	2002	
<i>Conills</i>								
1997	28	16	4	2	0	0	6	
1998	27	11	16	2	0	0	9	
1999	44	24		24	5	2	13	
2000	47	19			25	6	16	
2001	38	8				21	17	
<i>Sa Cella</i>								
1997	69	8	7	6	3	3	42	
1998	71	63	16	16	10	6	23	
1999	52	29		15	17	2	18	
2000	56	18			33	7	16	
2001	130	67				89	39	

Table 3  
Capture–mark–recapture models and their AICc (Akaike Information Criterion corrected by the quasi-likelihood parameter  $c$ ) to estimate adult survival of Balearic shearwaters

Model	AICc	$\Delta$ AICc	Par	Deviance
1: $\phi(c^*t), p(c^*t)$	1178.932	6.62	18	87.802
2: $\phi(\cdot), p(c^*t)$	<b>1172.317</b>	<b>0.00</b>	<b>11</b>	<b>95.967</b>
3: $\&tau;(c2^*t), \phi(\cdot), p(c^*t)$	1175.607	3.29	12	95.011
4: $\phi(c), p(c^*t)$	1174.400	2.08	12	95.962
5: $\&tau;(c2), \phi(\cdot), p(c^*t)$	1174.405	2.09	12	95.966
6: $\phi(t), p(c^*t)$	1177.767	5.45	14	95.129
7: $\&tau;(c2^*t), \phi(\cdot), p(c^*t)$	1178.006	5.69	16	91.138
8: $\phi(c), p(t)$	1214.235	41.92	7	146.163
9: $\phi(\cdot), p(c)$	1260.147	87.83	3	200.234
10: $\phi(c), p(c)$	1260.166	87.85	4	198.225
11: $\phi(c), p(\cdot)$	1271.611	99.29	3	211.698
12: $\phi(\cdot), p(c^*ef)$	1254.664	82.35	5	190.686
13: $\phi(\cdot), p(c^*ef^2)$	1253.462	81.14	7	185.384
14: $\phi(\cdot), p(c^*t)^\xi$	1909.156	736.84	21.0	893.424
15: $\phi(\cdot), p(c^*ef)^\xi$	1595.122	422.81	15.5	1591.136

Models are ranked according to deviance values. The  $\Delta$ AICc column corresponds to the difference between the AICc of each model and the AICc of the selected model, which is in bold.  $\phi$  is the apparent survival,  $p$  the recapture probabilities,  $\tau$  the transient probability,  $t$  stands for the year effect,  $c$  for the colony effect ( $c2$  indicates Conills colony) and  $ef$  for the recapture effort, measured in days of field work by breeding season;  $\xi$  shows the random effects models. The number appearing before model notation is used in the text to refer to different models (see Section 3).

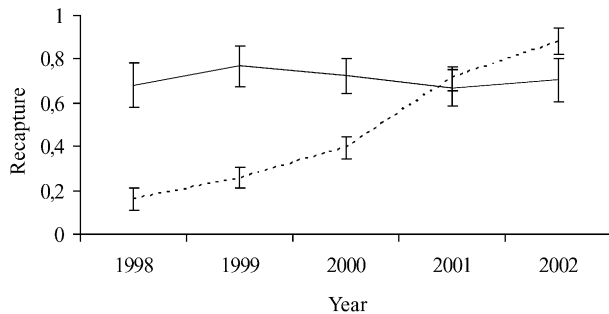


Fig. 3. Recapture probabilities (and Standard Error, SE) of Balearic shearwaters during the study: solid line shows the recaptures at Conilys colony and dashed lines recaptures at Sa Cella colony.

Table 4

Estimate and 95% confidence intervals (CI) for demographic parameters used in the population models

	Estimate	95% CI
Adult survival	0.78	[0.74–0.82]
Juvenile survival	0.70	[0.63–0.78]
Immature survival	0.74	[0.66–0.81]
Breeding success	0.59	[0.51–0.67]
Probability of skipping	0.26	[0.14–0.38]

and population growth rate was significantly less than 1 ( $z = 2.17$ ,  $P < 0.01$ ). The growth rate was most sensitive to changes in adult survival, whereas the other parameters had a similar low impact on  $\lambda$  (Fig. 4). Monte Carlo simulations showed that population trajectories decreased rapidly with time (Fig. 5), at the same rate but inversely than extinction probabilities (Table 5). Demographic stochasticity played a more important role than environmental stochasticity in population growth rate (Table 5). With both stochasticities considered together, mean extinction time was computed at 40.4 years (SE = 0.2), and mean growth rate showed a 7.41% decrease per year (Table 5). When adult survival was set to a higher value (0.90) more normal for *Puffinus* species

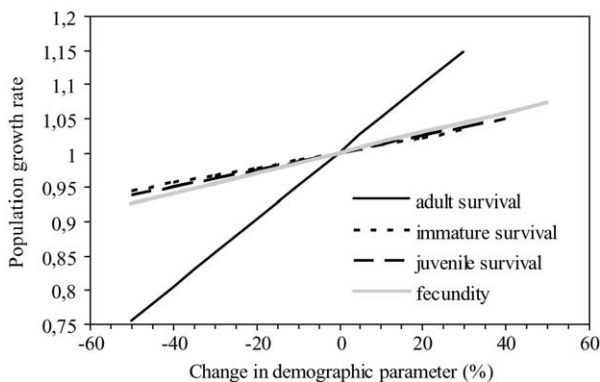


Fig. 4. Sensitivity of the population growth rate ( $\lambda$ ) to changes in the various demographic parameters of the deterministic model for Balearic shearwaters. Lines are truncated at the right when parameters attained their maximum values (for instance, adult survival because a 28% increase resulted in 100% survival).

(e.g. Perrins et al., 1973; Warham, 1990), the mean trajectory increased slowly ( $\lambda = 1.0067$ , SE = 0.001; Fig. 5) and none of the population trajectories went extinct ( $z = 6.70$ ,  $P < 0.001$ ).

#### 4. Discussion

Results shown in our study confirm that a general decline is probably occurring for the whole population of Balearic shearwaters (Arcos and Oro, in press). In Cabrera Island, 60% of the colonies have disappeared in the last few decades (Aguilar, 2000), while a recent survey in Formentera Island (where ca. 50% of the world population breeds) did not record any breeder in all the 30 suitable breeds (where remains of ancient breeding were found) visited in a single cliff (SEO, unpublished data). The lack of a reliable estimate of population size for the total world breeding population of Balearic shearwaters is one of the main problems when any population modelling is carried out. Even though numbers of Balearic shearwaters were underestimated (which could be the case especially for the non-breeding population) time to extinction would be simply delayed (Wissel and Zschke, 1994). The degree of uncertainty is important for the reliability of population modelling (Hunter et al., 2000; Caswell, 2001; Brook, 2000; Williams et al., 2002). However, population growth rates and probabilities of extinction are independent of initial population sizes above a numeric threshold for which demographic stochasticity does not play a crucial role (Wissel and Zschke, 1994). In our study reliability of extinction probabilities and growth rates are probably high because the most sensitive parameter to population growth rate in the species, adult survival, was estimated with a narrow confidence interval, which suggests that predictions of the models were sufficiently accurate (Brook, 2000; Hunter et al., 2000). When breeding numbers are difficult to estimate as is the case for many Procellariiformes (Gilbert et al., 1998; Heaney et al., 2002), estimation of demographic parameters and their use in population modelling are crucial to assess trends and to elaborate a conservation diagnose of endangered species (Bibby, 1994; Beissinger and Westphal, 1998; Russell, 1999; Caswell, 2001). Moreover, the simulations included the different values of demographic parameter estimates, so the best case scenarios were also considered. However, more years of monitoring would provide more robust data on the effects of age on breeding (e.g. Hunter et al., 2000) or on other parameters with a degree of uncertainty. Incorporating more data would also yield more robust survival estimates or would identified some environmental (climate, food) or individual (sex, age) features influencing survival (e.g. Tavecchia et al., 2001; Weimerskirch, 2002). Large data sets have allowed researchers to refute

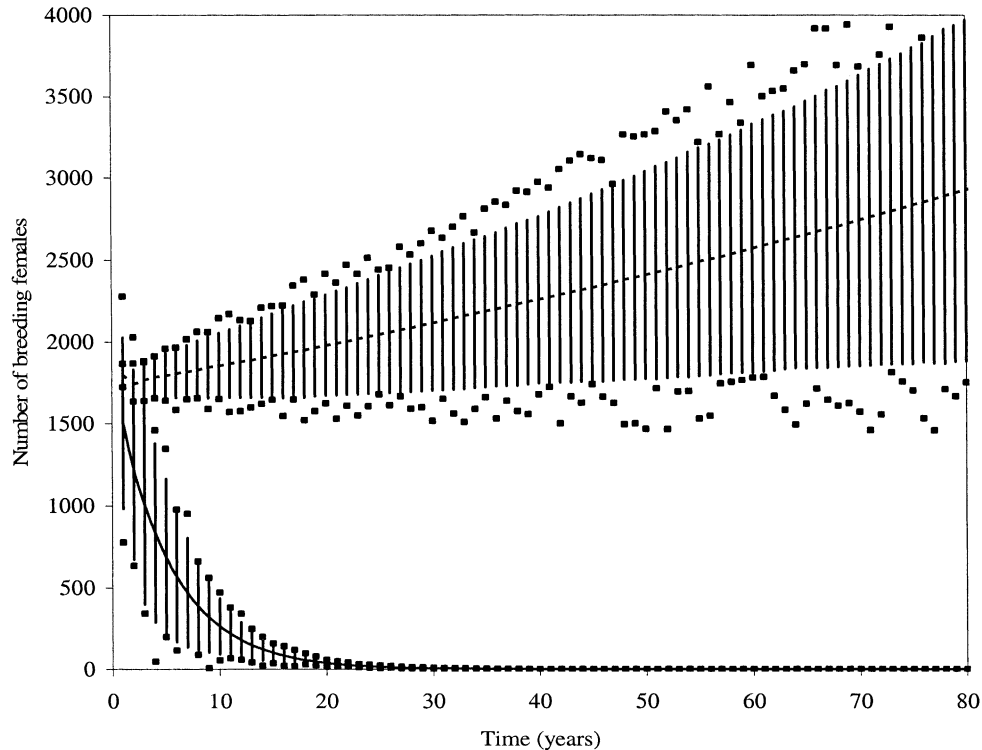


Fig. 5. Simulated Monte Carlo population trajectories of Balearic shearwaters for the whole population. Solid line shows the mean trajectory with estimated adult survival at the study colonies, and dashed line with a theoretical adult survival for the species of 0.90. Bars represent two times the standard deviation ( $2\sigma$ ) of the mean, and dots the maximum and minimum population value for each time step.

Table 5

Extinction probabilities for Balearic shearwater population simulations under the three scenarios considered: demographic and environmental stochasticity together, only demographic stochasticity, and only environmental stochasticity [population growth rate  $\lambda$  (and standard error in parentheses) is shown for the three scenarios]

Year of simulation	Extinction probabilities		
	Environmental and demographic	Only demographic stochasticity	Only environmental stochasticity
10	0.0000	0.0000	0.0000
20	0.0000	0.0000	0.0000
30	0.0150	0.0000	0.0000
40	0.5610	0.0000	0.0000
50	0.9520	0.0200	0.0000
60	0.9980	0.3750	0.0000
70	1.0000	0.8150	0.0000
80	1.0000	0.9720	0.0250
90	1.0000	0.9950	0.1020
100	1.0000	0.9990	0.1524
$\lambda$	0.926 (0.001)	0.949 (0.001)	0.974 (0.0035)

the general thought that adult survival in seabirds was constant, and several studies have shown that survival can vary with time and with environmental factors especially during catastrophic events (e.g. climatic and oceanographic anomalies) or with human activities (e.g. industrial fisheries, oil spills; see revision in Weimerskirch, 2002).

Results also suggest that the main conservation concern for Balearic shearwaters is adult survival, which is unusually low for a Procellariiform (e.g. Warham, 1990; Hamer et al., 2002; Weimerskirch, 2002). This demographic parameter should thus be managed to avert extinction, as is found in most long lived endangered species (e.g. Basse et al., 1997; Owens and Bennett, 2000). Other demographic parameters such as productivity or skipping breeding seemed normal for a shearwater, although age of first reproduction (3 years) was younger than in most Procellariiformes. The most likely sources of adult mortality are also the main conservation concern for most seabirds throughout the world: at breeding sites, alien carnivores, and at feeding grounds, by-catch on fishing gears (mainly long lines) (Weimerskirch et al., 1997; Brothers et al., 1999; Tasker et al., 2000; Gilman, 2001). Predators are probably the cause of historical extinction of Balearic shearwaters on the main islands (e.g. Alcover, 2000) and are nowadays affecting large colonies such as those at Formentera Island (Aguilar, 1997). The main predators are feral cats (Aguilar, 2000; Mayol et al., 2000), a problem that affects many faunas at oceanic islands, where most recent extinctions have occurred (e.g. Bloomer and Bester, 1992; Bibby, 1994; Huyser et al., 2000; Risbey et al., 2000; Keitt et al., 2002). It is important to note that adult survival in our study was estimated in two colonies free of carnivores, and thus mortality was probably

resulting from at-sea factors, and more likely fishing gears. Mortality of Balearic shearwaters in long lines at the western Mediterranean is already suspected (Belda and Sánchez, 2001; Cooper et al., in press), but its impact is still unknown. Nothing is either known about this threat during migration and at wintering quarters, in regions where fisheries are important (e.g. south-western North Atlantic, western Africa), nor about other factors such as oil spills or drops in food availability that affect other shearwaters (Brichetti et al., 2000; Baduini et al., 2001; Lovvorn et al., 2001). Demographic stochasticity seems to play an important role in population dynamics of Balearic shearwaters (see Table 5), and more important than environmental stochasticity (Caswell, 2000, 2001). Factors increasing adult mortality of Balearic shearwaters are probably also affecting other vulnerable seabird species breeding in the Mediterranean and wintering in the Atlantic Ocean, such as Levantine *P. yelkouan* and Cory's shearwaters *Calonectris diomedea*, European storm petrels *Hydrobates pelagicus* or Audouin's gull *Larus audouinii*.

Balearic shearwater is not yet among the list of European most threatened birds (Gallo-Orsi, 2001). Political and administrative acceptance of taxonomic and conservation status by international conservation agencies is first needed to implement an effective action plan for the species. Population viability analysis performed in our study showed that probabilities of extinction are extremely high. Extinction time estimated here classified the species as critically endangered by IUCN (International Union for Conservation of the Nature) criteria, the highest category for a species non extinct in the wild. Urgent management measures (such as control of predators and reduction of mortality at fishing gears) and more years of monitoring to identify other threats are needed to ensure the conservation of Balearic shearwaters and in turn of other seabird species endemic of the Mediterranean region.

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### References

- Aguilar, J.S., 1992. Resum de l'atlas d'ocells marins de les Balears, 1991. Anuari Ornitologic Balear 7, 17–28.
- Aguilar, J.S., 1993. Seguiment de la població reproductora de *Puffinus yelkouan mauretanicus* al Parc Nacional de Cabrera, 1993. Anuari Ornitologic Balear 8, 51–53.
- Aguilar, J.S., 1997. Biología y conservación de la pardela balear *Puffinus mauretanicus*. Documents Tècnics de Conservació. Conselleria de Medi Ambient, Ordenació del Territori i Litoral (Govern Balear), Palma de Mallorca.
- Aguilar, J.S., 2000. La población de Pardela Balear (*Puffinus mauritanicus*) en el Parque Nacional del archipiélago de Cabrera. In: Pons, G.X. (Ed.), Las aves del Parque Nacional marítimo-terrestre del archipiélago de Cabrera (Islas Baleares, España). GOB-Ministerio de Medio Ambiente, Madrid, pp. 33–44.
- Alcover, J.A., 2000. Vertebrate evolution and extinction on western and central Mediterranean Islands. *Tropics* 10, 103–123.
- Amengual, J.F., Aguilar, J.S., 1998. The impact of the black rat *Rattus rattus* on the reproduction of Cory's shearwaters *Calonectris diomedea* in the Cabrera National Park, Balearic Islands, Spain. In: Association "Les amis des oiseaux", Medmaravis (Ed.), Ecologie des oiseaux marins et gestion intégrée du littoral en Méditerranée. Arcs Editions, Radès, pp. 94–121.
- Anderson, D.R., Burnham, K.P., White, C.G., 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75, 1780–1793.
- Anderson, D.R., Burnham, K.P., 1999. Understanding information criteria for selection among capture-recapture or ring-recovery models. *Bird Study* 46, 14–21.
- Arcos, J.M., Massutí, E., Abelló, P., Oro, D., 2000. Fish associated with floating drifting objects as a feeding resource for Balearic Shearwaters *Puffinus mauretanicus* during the breeding season. *Ornis Fennica* 77, 177–182.
- Arcos, J.M., Oro, D., 2002. Significance of fisheries discards for a threatened Mediterranean seabird, the Balearic shearwater *Puffinus mauretanicus*. *Marine Ecology Progress Series* 239, 209–220.
- Arcos, J.M., Oro, D. Pardela Balear *Puffinus mauretanicus*. In: Madroño, A., Martí, R. (Eds.), Libro Rojo de las Aves de España. SEO/BirdLife and Ministerio de Medio Ambiente, Madrid (in press).
- Austin, J.J., 1996. Molecular phylogenetics of *Puffinus* Shearwaters: preliminary evidence from mitochondrial cytochrome b gene sequences. *Molecular Phylogenetics and Evolution* 6, 77–88.
- Baduini, C.L., Lovvorn, J.R., Hunt Jr., G.L., 2001. Determining the body condition of short-tailed shearwaters: implications for migratory flight ranges and starvation events. *Marine Ecology Progress Series* 222, 265–277.
- Basse, B., Wake, G.C., McLennan, J.A., 1997. Predation thresholds for survival of endangered species. *IMA Journal of Mathematics Applied in Medicine and Biology* 14, 241–250.
- Beissinger, S.R., Westphal, M.I., 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62, 821–841.
- Belda, E.J., Sánchez, A., 2001. Seabird mortality on longline fisheries in the western Mediterranean: factors affecting bycatch and proposed mitigating measures. *Biological Conservation* 98, 357–363.
- Bibby, C.J., 1994. Recent past and future extinctions in birds. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 344, 35–40.
- Bloomer, J.P., Bester, M.N., 1992. Control of feral cats on sub-Antarctic Marion Island, Indian Ocean. *Biological Conservation* 60, 211–219.
- Brichetti, P., Foscolo, U., Boano, G., 2000. Does El Niño affect survival rate of Mediterranean populations of Cory's Shearwater? *Waterbirds* 23, 147–154.



- Brook, B.W., 2000. Pessimistic and optimistic bias in population viability analysis. *Conservation Biology* 14, 564–566.
- Brothers, N., Cooper, J., Lokkeborg, S., 1999. The Incidental Catch of Seabirds by Longline Fisheries: Worldwide Review and Technical Guidelines for Mitigation (unpublished report). FAO Fisheries Circular, Rome.
- Burnham, K.P., Anderson, D.R., White, G.C., 1995. Selection among open population capture-recapture models when capture probabilities are heterogeneous. *Journal of Applied Statistics* 22, 611–624.
- Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference, a Practical Information-Theoretic Approach. Springer-Verlag, New York.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., Pollock, K.H., 1987. Design and Analysis Methods for Fish Survival Experiments based on Release-recapture. American Fisheries Society, Bethesda.
- Burnham, K.P., White, G.C., 2002. Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics* 29, 245–264.
- Caswell, H., 2000. Prospective and retrospective perturbation analysis: their roles in conservation biology. *Ecology* 81, 619–627.
- Caswell, H., 2001. Matrix Population Models. Sinauer Associates, Sunderland, USA.
- Choquet, R., Reboulet, A.-M., Pradel, R., Lebreton, J.-D., 2000. U-CARE (Utilities- CApture-REcapture) User's Guide. CEFE-CNRS, Montpellier. Available: <ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR/u-care/>.
- Cooper, J., Baccetti, N., Belda, E.J., Borg, J.J., Oro, D., Papaconstantinou, C., Sánchez, A. Seabird mortality from longline fishing in the Mediterranean Sea and Macaronesian waters: a review and a way forward. *Scientia Marina* (in press).
- Croxall, J.P., Rothery, P., 1991. Population regulation of seabirds: implications of their demography for conservation. In: Perrins, C.M., Lebreton, J.-D., Hiron, G.J.M. (Eds.), *Bird Population Studies, Relevance to Conservation and Management*. Oxford University Press, Oxford, pp. 272–296.
- Gallo-Orsi, U., 2001. Saving Europe's Most Threatened Birds: Progress in Implementing European Species Action Plans (unpublished report). BirdLife International, Wageningen.
- Genovart, M., McMinn, M., Bowler, D., 2003. A discriminant function for predicting sex in the Balearic Shearwater. *Waterbirds* 26, 72–76.
- Gilbert, G., Gibbons, D.W., Evans, J., 1998. *Bird Monitoring Methods*. RSPB, Sandy.
- Gilman, E., 2001. Integrated management to address the incidental mortality of seabirds in longline fisheries. *Aquatic Conservation* 11, 391–414.
- Hamer, K.C., Schreiber, E.A., Burger, J., 2002. Breeding biology, life histories, and life history-environment interactions in seabirds. In: Schreiber, E.A., Burger, J. (Eds.), *Biology of Marine Birds*. CRC Press, Boca Raton, pp. 217–261.
- Harris, M.P., Buckland, S.T., Russell, S.M., Wanless, S., 1994. Post fledging survival to breeding age of Shags *Phalacrocorax aristotelis* in relation to year, date of fledging and brood size. *Journal of Avian Biology* 25, 268–274.
- Heaney, V., Ratcliffe, N., Brown, A., Robinson, P.J., Lock, L., 2002. The status and distribution of European Storm-petrels *Hydrobates pelagicus* and Manx Shearwaters *Puffinus puffinus* on the isles of Scilly. *Atlantic Seabirds* 4, 1–16.
- Heidrich, P., Amengual, J.F., Wink, M., 1998. Phylogenetic relationships in Mediterranean and North Atlantic shearwaters (Aves: Procellariidae) based on nucleotide sequences of mtDNA. *Biochemical Systematics and Ecology* 26, 145–170.
- Heidrich, P., Amengual, J.F., Ristow, D., Wink, M., 2000. Phylogenetic relationships among Procellariiformes based on nucleotide sequences, with special consideration of the Mediterranean and North Atlantic Shearwaters. In: Yésou, P., Sultana, J. (Eds.), *Monitoring and Conservation of Birds, Mammals and Sea Turtles of the Mediterranean and Black Seas*. Environment Protection Department, Malta, pp. 159–175.
- Heppell, S.S., Caswell, H., Crowder, L.B., 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* 81, 654–665.
- Hines, J.E., 1996. TMSURVIV User's Manual. Pages National Biological Survey, Patuxent Wildlife Research Center, Laurel.
- Hunter, C.M., Moller, H., Fletcher, D., 2000. Parameter uncertainty and sensitivity analysis of a population model: setting research priorities for shearwaters. *Ecological Modelling* 134, 299–323.
- Huysen, O.A.W., Ryan, P.G., Cooper, J., 2000. Changes in population size, habitat use and breeding biology of Lesser Shearwaters (*Chionis minor*) at Marion Island: impacts of cats, mice and climate change? *Biological Conservation* 92, 299–310.
- Keitt, B.S., Wilcox, C., Tershy, B.R., Croll, D.A., Donlan, C.J., 2002. The effect of feral cats on the population viability of black-vented shearwaters (*Puffinus opisthomelas*) on Natividad Island, Mexico. *Animal Conservation* 5, 217–223.
- Lebreton, J.-D., 2001. The use of bird rings in the study of survival. *Ardea* 89, 85–100.
- Lebreton, J.-D., Hemery, G., Clobert, J., Coquillart, H., 1990. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations. I. Transversal models. *Biometrics* 46, 609–622.
- Lebreton, J.-D., Clobert, J., 1991. Bird population dynamics, management, and conservation: the role of mathematical modelling. In: Perrins, C.M., Lebreton, J.-D., Hiron, G.J.M. (Eds.), *Bird Population Studies, Relevance to Conservation and Management*. Oxford University Press, Oxford, pp. 105–125.
- Lebreton, J.-D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypothesis using marked animals: a unified approach with case studies. *Ecological Monographs* 62, 67–118.
- Lovvorn, R.J., Baduini, C.L., Hunt Jr., G.L., 2001. Modeling underwater visual and filter feeding by planktivorous shearwaters in unusual sea conditions. *Ecology* 82, 2342–2356.
- Mayol, J., 1986. Human impact on seabirds in the Balearic Islands. In: Medmaravis, Monbaillu, X. (Eds.), *Mediterranean Marine Avifauna: Population Studies and Conservation*. Springer-Verlag, Berlin, pp. 379–396.
- Mayol, J., 1997. Specific identity of the Balearic Shearwater *Puffinus mauretanicus* (Lowe 1951). *Anuari Ornitológic Balear* 12, 3–11.
- Mayol, J., Aguilar, J.S., Yésou, P., 2000. The Balearic Shearwater *Puffinus mauretanicus*: status and threats. In: Yésou, P., Sultana, J. (Eds.), *Monitoring and Conservation of Birds, Mammals and Sea Turtles of the Mediterranean and Black Seas*. Environment Protection Department, Malta, pp. 24–37.
- Nichols, J.D., Spindel, J.A., Hines, J.E., 1990. Capture-recapture estimation of prebreeding survival rate for birds exhibiting delayed maturation. *Journal of Field Ornithology* 61, 347–354.
- Oro, D., Pradel, R., Lebreton, J.-D., 1999. The effects of nest predation and food availability on life history traits in Audouin's gull. *Oecologia* 118, 438–445.
- Owens, I.P.F., Bennett, P.M., 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Science* 97, 12144–12148.
- Perrins, C.M., Harris, M.P., Britton, C.K., 1973. Survival of Manx shearwaters *Puffinus puffinus*. *Ibis* 115, 535–548.
- Pollock, K.H., Nichols, J.D., Brownie, C., Hines, J.E., 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107.
- Pradel, R., Hines, J.E., Lebreton, J.-D., Nichols, J.D., 1997. Capture-recapture survival models taking account of transients. *Biometrics* 53, 88–99.
- Risbey, D.A., Calver, M.C., Short, J., Bradley, J.S., Wright, I.W., 2000. The impact of cats and foxes on the small vertebrate fauna of

- Heirisson Prong, Western Australia. II. A field experiment. *Wildlife Research* 27, 223–235.
- Russell, R.W., 1999. Comparative demography and life history tactics of seabirds: implications for conservation and marine monitoring. In: Musick, J.A. (Ed.), *Life in the Slow Lane: Ecology and Conservation of Long-lived Marine Animals*. American Fisheries Society, Bethesda, pp. 51–76.
- Spendelov, J.A., Nichols, J.D., Hines, J.E., Lebreton, J.-D., Pradel, R., 2002. Modelling postfledging survival and age-specific breeding probabilities in species with delayed maturity: a case study of Roseate Terns at Falkner Island, Connecticut. *Journal of Applied Statistics* 29, 385–405.
- Tasker, M.L., Camphuysen, C.J., Cooper, J., Garthe, S., Montevecchi, W.A., Blaber, S.J.M., 2000. The impacts of fishing on marine birds. *ICES Journal of Marine Science* 57, 531–547.
- Tavecchia, G., Pradel, R., Boy, V., Johnson, A.R., Cézilly, F., 2001. Sex- and age-related variation in survival and the cost of first reproduction in Greater Flamingos. *Ecology* 82, 165–174.
- Warham, J., 1990. *The Petrels. Their Ecology and Breeding Systems*. Academic Press, London, UK.
- Weimerskirch, H., Brothers, N., Jouventin, P., 1997. Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam Albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. *Biological Conservation* 79, 257–270.
- Weimerskirch, H., 2002. Seabird demography and its relationship with the marine environment. In: Schreiber, E.A., Burger, J. (Eds.), *Biology of Marine Birds*. CRC Press, Boca Raton, pp. 115–135.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, 120–139.
- Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. *Monitoring and Management of Animal Populations*. Academic Press, San Diego.
- Wissel, Ch., Zaszke, S.H., 1994. Stochastic birth and death processes describing minimum viable populations. *Ecological Modelling* 76, 193–201.
- Yearsley, J.M., Fletcher, D., 2002. Equivalence relationships between stage-structured population models. *Mathematical Biosciences* 179, 131–143.
- Yearsley, J.M., Fletcher, D., Hunter, C., 2003. Sensitivity analysis of equilibrium population size in a density-dependent model for short-tailed Shearwaters. *Ecological Modelling* 163, 1–11.