

Estimating predation on breeding European storm-petrels (*Hydrobates pelagicus*) by yellow-legged gulls (*Larus michahellis*)

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Abstract

Several hypotheses about changes in adult survival of European storm-petrels *Hydrobates pelagicus* and predation by yellow-legged gulls *Larus michahellis* at Benidorm Island (western Mediterranean) during 1993–2003 were assessed. Two approaches were used: analysis of pellets containing remains of predated petrels from two caves, and multistate capture–recapture models using recaptures of breeders together with recoveries only from one of these caves. These models were used to estimate separately adult storm-petrel survival and a minimum probability of being killed by gulls. At least 11–14% of the storm-petrels killed had been ringed as breeders. Local adult survival varied greatly among years, from 0.701 (SE = 0.095) to extremely high values (0.951, SE = 0.031) for such a small species (0.833 on average for the whole period). Nevertheless, it was not possible to assess whether this variation was influenced by inter-annual differences in gull predation. The peak of predation occurred in June, when maximum numbers of prospecting petrels visit the colonies. Predation was much higher at the cave that received stronger illumination from Benidorm city. Minimum predation probabilities estimated from capture–recapture varied with time from 0.022 (SE = 0.011) to 0.040 (SE = 0.016), and increased significantly after the powering of light received from the city in 1997. In these years, predation by yellow-legged gulls accounted for a large percentage of mortality of storm-petrels at Benidorm Island (up to 33%). Both methodological approaches confirmed that predation was carried out by specialist gulls, and that neither the size of the gull colony nor its food availability influenced predation on petrels. Management might reduce predation rate by removing gulls that nest in the caves, since these individuals tend to kill most storm-petrels.

Key words: predation, *Hydrobates pelagicus*, *Larus michahellis*, Benidorm, breeding

INTRODUCTION

Predation of storm-petrels by large seabirds has typically been studied in sub-polar regions at colonies where large numbers of both species breed, and high predation rates are described (Furness, 1981; Phillips, Thompson & Hamer, 1999; Stenhouse & Montevecchi, 1999; Stenhouse, Robertson & Montevecchi, 2000). There is little information, however, about the extent of predation in small populations at lower latitudes.

The European storm-petrel *Hydrobates pelagicus* breeds along the European Atlantic coast and throughout the Mediterranean Sea, where the subspecies *H. p. melitensis* has been described (Hémery & D'Elbee, 1985; Bretagnolle, 1992; Bretagnolle & Zotier, 1998). This subspecies is legally protected in Spain, and considered a conservation priority (Minguez, 2003).

Yellow-legged gulls *Larus michahellis* have shown a pronounced population increase over the past few decades (Vidal, Maedail & Taton, 1998), mostly owing to the availability of abundant and predictable food sources from rubbish dumps and from commercial fisheries discards in the western Mediterranean (Oro, Bosch & Ruiz, 1995; Bosch *et al.*, 2000; Martínez-Abraín, Maestre & Oro, 2002). Like many other large gull species, yellow-legged gulls may also cause breeding failures and mortality of other smaller seabirds, owing to increased predation (Oro & Martínez-Vilalta, 1994; Hernández-Matías & Ruiz, 2003; Martínez-Abraín, Gonzalez-Solis *et al.*, 2003). This is especially true during periods when local trawling fisheries are closed and discards are unavailable (Oro & Martínez-Vilalta, 1994).

At their breeding colonies, most storm-petrels avoid excessive predation by gulls by being strictly nocturnal (Watanuki, 1986; Huntington, Butler & Mauck, 1996). Bright moonlight tends to reduce night-time activity over land (Watanuki, 1986; Warham, 1990; Mougeot &

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Bretagnolle, 2000), and ambient light levels affect the number of birds coming ashore (Klomp & Furness, 1992). Since moonlight affects the number of birds coming to land, and, therefore, the rate of predation, strong light from close human sources is also expected to affect predation rates, either by allowing gulls to hunt storm-petrels at night or by reducing storm-petrel activity (Nelson, 1989).

Most storm-petrel individuals visiting colonies at night are prospecting non-breeders and pre-breeders (Fowler, Okill & Marshall, 1982; Warham, 1990, 1996). If a large proportion of attacks is directed at non-breeders, the impact on storm-petrel population dynamics will be lower than would otherwise be expected (Phillips *et al.*, 1999). Unfortunately, it is almost impossible to distinguish whether storm-petrel remains in pellets are from breeding or non-breeding petrels, unless the pellets contain rings of known breeders.

An understanding of the impact of predation by gulls on smaller seabirds in the Mediterranean may become important if gull numbers continue to increase or if food from human sources such as refuse dumps and fishing discards decreases following new environmental policies. Anthropogenic changes to the environment that may affect predation are: (1) alterations in food availability to gulls or other large predatory seabirds, such as a reduction in discard availability (Oro & Martínez-Vilalta, 1994; Oro & Furness, 2002; Furness, 2003); (2) changes in light conditions, in nocturnal prey species.

In this paper the predation rates of yellow-legged gulls on European storm-petrels in a small island colony located close to a large coastal city is estimated. Different a priori hypotheses were tested: for instance, whether predation rate by gulls has increased since 1997 when a new light installation in the city greatly increased the illumination at the colony. A potential additive effect of predation was also tested after 2000, when a trawling moratorium was established and gulls were probably forced to switch to secondary prey resources. Whether predation increased with the number of breeding gulls in the colony was also tested, as it has been suggested that the two variables can be positively associated (Oro, Genovart *et al.*, 1996; Martínez-Abraín, Gonzalez-Solis *et al.*, 2003). For most of the hypotheses tested, two methodological approaches were used: (1) an analysis of the number of gull pellets found; (2) modelling capture–recapture histories of ringed breeders. Multistate survival models mixing two different types of competing events were used: live recaptures (breeders monitored at nests over the years) and dead recoveries (rings found in gull pellets). These models are frequently based on Markov chains (Lebreton, Almeras & Pradel, 1999; Lebreton & Pradel, 2002) and allowed us to estimate separately the competing sources of mortality of European storm-petrels. With live recaptures, local adult survival and then mortality (for a number of ecological factors) that occurred between breeding seasons were estimated. For recoveries, the minimum probability of being killed by a gull in a season was estimated, provided that the detection probability of pellets was less than one.

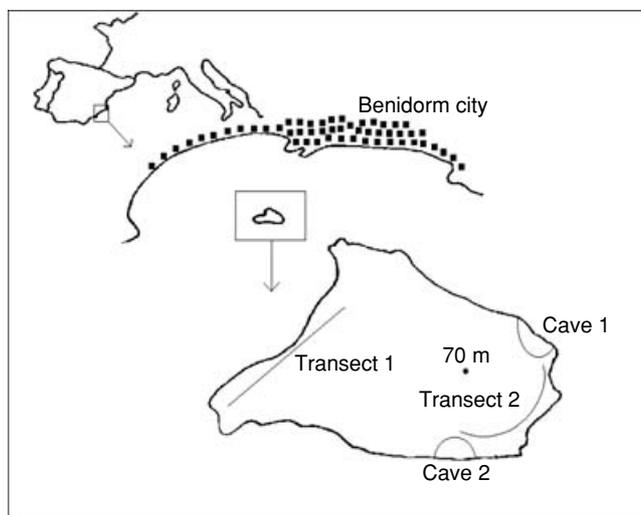


Fig. 1. Benidorm Island, showing position of the caves, where most storm-petrels *Hydrobates pelagicus* breed, and transects, where pellets were collected.

METHODS

This study was carried out on Benidorm Island, a Special Protection Area for the conservation of the European storm-petrel, in the western Mediterranean coast of Spain ($38^{\circ}30'N$, $0^{\circ}08'E$). This 6.5-ha island is 3 km offshore from Benidorm city, one of the most visited tourist destinations in Europe. European storm-petrels breed all round the island, but concentrate in two high-density colonies inside caves (Fig. 1) where they nest under boulders and in crevices. The breeding population of storm-petrels on the island has been estimated at > 400 pairs (Mínguez, 1994). One of the colonies (cave 1) contains > 200 breeding pairs. This cave faces north, and receives direct light from the city at night. The other colony (cave 2) houses *c.* 100 breeding pairs and faces east, i.e. away from the city. The caves are *c.* 150 m apart, and 3–4 m a.s.l. A seasonal trawling moratorium is established in this region to allow the fish populations to recover from overfishing. Since 2000 the moratorium has operated during May, and is coincident with the chick rearing period for yellow-legged gulls. During the rest of the year local fisheries operate from Monday to Friday and rest during the weekend.

Since 1993, 2368 European storm-petrels have been ringed on Benidorm Island, caught at nests and in mist-nets, and *c.* 50 nests have been checked annually. At each nest, both members of the pair and the chick were checked for ringing.

Gulls nest both in the caves and on open ground on top of the island. Predation was studied by exhaustive collection of gull pellets, which contain regurgitated, indigestible food items. Pellets have been collected opportunistically since 1994 and following specific field protocols since 2000. Both caves were checked for pellets. Pellets were also collected along 2 transects of 150 m. One transect ran along the western side of the island, where a large number of gulls roost (transect 1), and the other between

Table 1. Basic information of predation of *Hydrobates pelagicus* by *Larus michahellis* in 2000 and 2002 in Benidorm Island

| Year | 2000 | 2002 |
|---------------------------------------|------------|------------|
| No. of pellets found | – | 240 |
| No. of tibias in pellets | 229 | 239 |
| Estimated no. of total petrels killed | 115 | 120 |
| Estimated no. of fledglings killed | – | 11 (9.2%) |
| No. of ringed individuals killed | 31 | 30 |
| No. of ringed as breeders | 13 (11.3%) | 17 (14.2%) |
| Yellow-legged gull breeding pairs | 361 | 463 |

both caves (transect 2). Regurgitations are assumed to be indicative of the capture location (but see Stenhouse & Montevecchi, 1999), i.e. pellets found in 1 cave were assumed to indicate birds killed in that cave. This is supported by the fact that all rings found in pellets in a cave belonged to a bird ringed in that cave, never in the other. To estimate the minimum number of storm-petrels killed, the number of tibia in each pellet were counted. Rings are easily recovered from pellets as they remain on the tibia. Feathers in each pellet were also carefully checked to identify chicks or fledglings, according to their new plumage and, especially, based on the presence of down (Harris, 1974). The number of petrels killed per day was estimated as a predation rate index. The effects of colony, date and moon phase on daily predation rate on storm-petrel were estimated without correcting for the probability of finding a pellet with a ring. This approach allowed us to use all the information available, although it could be more biased (underestimated in our case, see e.g. Boulinier *et al.*, 1997) than the capture–recapture method (see below).

The breeding population of yellow-legged gulls on Benidorm Island was > 400 pairs in 2002 (Table 1). The island is also used as a roost, and the number of gulls increases considerably at night. Fifty gull nests were checked weekly during the 2000 breeding season to estimate laying dates. These territories were inspected for pellets containing storm-petrels. Pairs were considered ‘specialist’ when > 2 pellets containing bird remains were found in their territories.

At Benidorm Island, European storm-petrels return to land only during darkness (Mínguez, 1996). To obtain a nocturnal activity index of petrels, and compare it between caves, petrel activity was measured weekly from June to August 2002. Observations of flying birds were made from inside caves, 2.5 h after sunset. For 2 min repeated 3 times (6 min of observation in each colony), all birds passing a 5 × 15 cm rectangle, sited 20 cm from observer eyes were counted. No additional artificial light was needed as the birds were silhouetted against the residual light. Furthermore, artificial lights are known to disturb storm-petrel activity (Mínguez, 1996). Measurements were only made at this hour to minimize disturbance and to avoid affecting gull behaviour. Measurements were made as consecutively as possible to compare activity in the two caves.

The phase of the moon was scored as new (0), crescent and wane (1), and full (2). Light intensity was also

Table 2. Combined parameterization of the multistate model for European storm-petrels *Hydrobates pelagicus* with a mixture of live recaptures and dead recoveries. The non-stochastic matrix Φ shows the two states of the model, alive and newly dead, and their probabilities from time t to $t+1$. Parameter β is the by-product of m_i and q_i (see text for explanations). The two transitions from the state newly dead are fixed to 0 in our model. The column vector P of state-specific capture probabilities is composed by p (the recapture probability of the state alive) and the recapture probability of the state newly dead, which in our study is fixed to 1

$$\begin{array}{l} \text{Alive} \\ \text{Newly dead} \end{array} \begin{bmatrix} \phi & \beta \\ 0 & 0 \end{bmatrix} \begin{bmatrix} p \\ 1 \end{bmatrix}$$

measured in the middle of the entrance of the caves with a digital photometer, set vertically c. 1 m above floor level to record light coming from outside the caves.

Capture–recapture analysis

For the capture–recapture analysis, only storm-petrels monitored during 1993–2003 as breeders in the nests were considered. Birds caught in mist-nets were removed from the analysis to avoid adding individuals of unknown breeding status, and thus deviances from the more general Cormack–Jolly–Seber model, such as the transient effect (Pradel, Hines *et al.*, 1997). Birds were caught at the end of the incubation period to minimize nest desertion owing to disturbance. A total of 476 breeders were marked in nests at cave 1 at least once and used in the analysis. Insufficient data from cave 2 precluded a similar capture–recapture analysis. To limit heterogeneity in recapture probabilities (Pradel, Hines *et al.*, 1997; Prévot-Julliard, Lebreton & Pradel, 1998), the effort of recapture was distributed uniformly through the colony and all the nests were checked for ringed birds in all years.

Captures were used to build the capture–recapture histories. At the same time, recoveries of breeders from gull pellets were incorporated in the capture–recapture histories with a different code to distinguish between a live recapture and a recovery. To estimate separately adult survival and the probability of being caught by a yellow-legged gull, multistate capture–recapture models were built. These models constitute a natural framework for mixtures of information (such as recoveries and recaptures) in individual history data (Lebreton, Almeras *et al.*, 1999; Joe & Pollock, 2002; Lebreton & Pradel, 2002). Live recapture and dead recoveries are particular multistate models. The combined parameterization (see Lebreton, Almeras *et al.*, 1999) of a mixed recapture–recovery model was used as a 2 states model as is shown in Table 2. The matrix of combined survival-transition probabilities from t to $t+1$ estimated adult local survival probability (denoted ϕ) and the transition parameter (denoted here as β), which is the by-product of m_i (the probability of being killed by yellow-legged gulls at time i) and q_i (the probability of recovering a ring in a pellet at time i). Thus there were only 2 parameters in the column vector of capture probabilities, with P being the recapture probability and fixing to 1 the capture probability of the

state newly dead (see Table 2 and Lebreton, Almeras *et al.*, 1999). Since m_i and q_i were not separately identifiable parameters, β equated to the minimum probability of being killed by a gull. For instance, imagine an actual probability of being killed by a gull of 0.15: when q_i approached 0, i.e. when very few rings in pellets were found, gave a value of $\hat{\beta}$ far from 0.15, but there was still a minimum predation probability. Opposite, when q_i approaches 1 (when all rings were hypothetically found) then the value of $\hat{\beta}$ approaches m_i , which would be the actual probability of being killed by a gull (0.15 in our example). Following our field observations, it was assumed that no pellets produced in time t_i were found in time $t > i$. Thus, the addition of recoveries was considered suitable in our study, because of these data, the date of death is important. To calculate the minimum probability of being killed by a gull relative to the fact of being dead for a number of causes (predation by gulls plus others unknown), the formula $\hat{\beta}_i/1 - \hat{\phi}_i$ was used.

Data were analysed as in classical capture–recapture methods (Lebreton, Burnham *et al.*, 1992). First, the goodness-of-fit of the more general multistate model was analysed (see Pradel, Wintrebert & Gimenez, 2003), here the conditional Arnason–Schwarz (CAS) model using the software U-Care (Choquet *et al.*, 2003a). Testing the fit of the more general model is actually a critical issue for further testing and model selection (Lebreton, Almeras *et al.*, 1999). The global test for the fit of the CAS model was highly significant ($\chi^2 = 205.5$, d.f. = 52, $P < 0.001$). The component tests within TEST 3GSR ($\chi^2 = 27.5$, d.f. = 9, $P < 0.001$) and TEST MITEC ($\chi^2 = 138.7$, d.f. = 17, $P < 0.001$) showed respectively that a strong effects of both transients and trap dependence (immediate trap-effect on capture only) occurred. The main transient effects were detected after 1997 when the lights of the city were more powerful and illuminated the cave, probably increasing the rate of desertion after manipulation. These years accounted for most of the chi-square value of TEST 3GSR ($\chi^2 = 17.8$, d.f. = 3, $P < 0.001$). To avoid modelling transient, which had little biological meaning here, it was decided to suppress the first capture in the capture–recapture histories (Pradel, Hines *et al.*, 1997) rather than starting with different parameters for the first year survival. By doing this, TEST 3GSR was no longer significant ($\chi^2 = 13.4$, d.f. = 8, $P = 0.098$) although we still had a strong trap-dependence effect (TEST MITEC: $\chi^2 = 94.5$, d.f. = 12, $P < 0.001$). The fact that trap-dependence persisted after suppressing the first capture suggested that trap-dependence was not concentrated only in the first capture occasion. After suppressing the successive first captures, the trap-effect actually persisted heavily (all TESTS MITEC highly significant). Different sources of trap-dependence can occur in our study: 1 is genuine trap-dependence, when animals are handled and some change in behaviour can alter the subsequent capture. In our study, trap-shyness (resulting from changing of nest after first manipulation) would be more expected than trap-happiness. This is not true, since tests suggested the existence of trap-happiness. Another source of trap-dependence effect would occur if some study nests were

more prone to be checked for breeding adults than others, generating heterogeneity of capture, a non-genuine form of trap-dependence, although nests with difficult access were not marked either monitored. Sabbatical years (years with skipping breeding), a behaviour commonly recorded in Procellariiformes, could also generate some trap-dependence. If the chances of taking a sabbatical years increases with age (in our study in the time elapsed since first capture), this could generate the ‘age’ effect recorded here on recapture probabilities. Thus, it was decided to start with 2 families of models as reference models: models with immediate trap-dependence on recapture probabilities (p_{m^*t}), and models with recapture probabilities varying with the time elapsed since first capture (p_a). In models with trap-dependence on recapture probability varying over time (p_{m^*t}), no parameter is separately identifiable (Pradel, 1993; Gimenez, Choquet & Lebreton, 2003). Thus, these models were used with caution as they could not provide reliable parameter estimates owing to identifiability problems. Nevertheless, the more general model was still suitable as a reference model for the rest of models with no problems of identifiability. To ensure the identifiability of parameters of the most parsimonious model, the deviance profile of several parameters (using M-SURGE software) was drawn to assess their potential redundancy. By using U-Care software (for details see Choquet *et al.*, 2003a) capture–recapture histories were thus split into multiple pieces (see Pradel, 1993) to implement the trap-dependence model, in which a further cause of variability in capture probability results from a Markovian dependence on previous capture.

The second step thus started from 2 modified multistate models that accounted for trap-dependence: $(\phi_t, \beta_t, p_{m^*t})$ (Pradel, 1993), and (ϕ_t, β_t, p_a) , from which additional models were constructed. These models were fitted by the maximum likelihood method using the program M-SURGE (Choquet *et al.*, 2003b), which allows for a combined parameterization of survival and transition.

Models were then constrained by ecological hypotheses based on factors that, in our view, could affect survival or recapture probabilities (see above and Table 3). The possibility that effort (measured as the number of pellets collected every year) influenced recapture probabilities was tested. Model selection was assessed using Akaike’s Information Criterion (AIC) (see Burnham & Anderson, 1998).

RESULTS

Analysis of pellets from Benidorm Island in 2000 and 2002 indicated, as estimated by the number of tibias, that 115 and 120 storm-petrels were eaten by gulls, respectively (Table 1). In 2002, the number of pellets found was 239: 167 (70%) in cave 1; 36 (15%) in cave 2; 4 (2%) in transect 1 and 32 (13%) in transect 2. Most pellets were found in cave 1 ($\chi^2 = 266.9$, d.f. = 3, $P < 0.001$; Fig. 2).

Of the 50 territories of gulls checked, remains of storm-petrels were found in 11, and only five of these gull pairs were considered ‘specialist’ (with more than one pellet found). Two of them were inside cave 1, one inside cave 2,

Table 3. Summary of the main different multistate models (ϕ_t , β_t , p_{m^*t}) built with M-SURGE applied to estimate local survival probability ϕ , transition probability β (or minimum predation probability) and recapture probability P . General rules for description are: *, interaction between effects; +, additive effects

| Model notation | Biological hypothesis |
|-------------------------------------|---|
| Modelling ϕ | |
| ϕ_t | Survival is time dependent |
| ϕ | Constant survival |
| ϕ_F | Constant survival, which decreased linearly since the establishment of the fishing trawling moratorium |
| Modelling β | |
| β_t | Minimum predation probability is time dependent |
| β | Constant minimum predation probability |
| β_e | Minimum predation probability is dependent on effort of recapture (total no. of pellets found) |
| β_g | Minimum predation probability is dependent on the number of breeding gulls |
| β_f | Minimum predation probability is dependent on the establishment of the fishing trawling moratorium |
| β_l | Two levels of minimum predation probability before and after the increase of light power at Benidorm city |
| β_L | Constant minimum predation, which increased linearly since the increase of light power at Benidorm city |
| β_F | Constant minimum predation, which increased linearly since the establishment of the fishing trawling moratorium |
| Modelling P | |
| p_a | Recapture varied with time elapsed since first capture (age effect) |
| p_A | Recapture varied with time elapsed since first capture as a linear trend |
| p_{m^*t} | Immediate trap-dependence in recapture |
| $p_{m^{+mt}}$ | Constant capture whether the animal was not captured at the preceding occasion, time-dependent otherwise |
| p_m | Two levels of capture probability whether the animal was captured at the last occasion |

and two on transect 2. The mean number of pellets found around a nest was 7 (range 3–10). All pellets found around gull territories coincided with the breeding season of gulls, i.e. from March to June. In cave 2, no more pellets were found after breeding gulls left the cave.

In 2002, the median hatching date of yellow-legged gulls was 28 April ($n = 28$). Storm-petrels began visiting their colonies in early April and remained until September, so they were ‘available’ throughout the entire chick-rearing period of gulls, and afterwards. Median laying date of storm-petrels was 2 June ($n = 136$; Fig. 2). The number of pellets found differed between months ($\chi^2 = 74.7$, d.f. = 5, $P < 0.001$), with the highest number of pellets collected in June (Fig. 2). This was just after storm-petrel laying, and the month when the activity of storm-petrels was also highest. The number of pellets found each month was higher in cave 1 than in the rest of the study areas (April: $\chi^2 = 8.0$; d.f. = 1, $P = 0.005$; May: $\chi^2 = 86.7$;

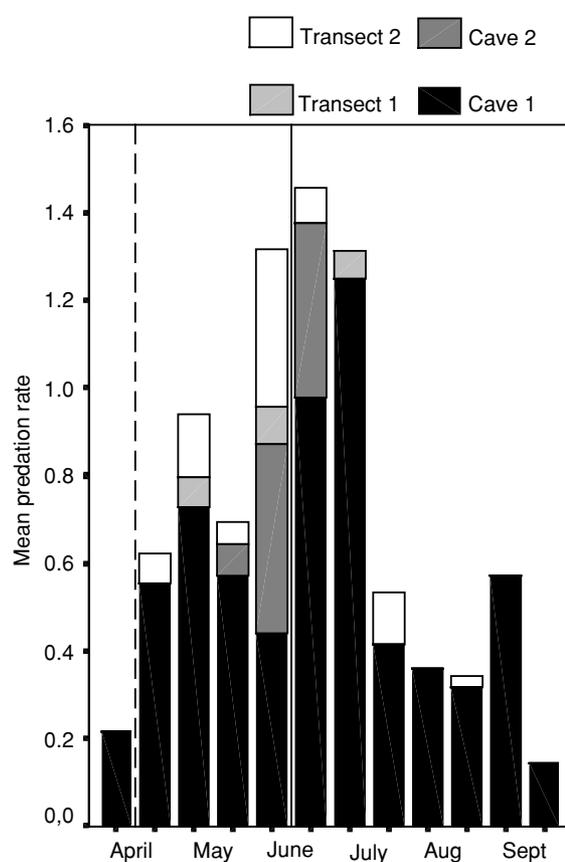


Fig. 2. Mean predation rate (no. of individuals/day) fortnightly in 2002 in the four areas of study. Lines, median laying date of yellow-legged gulls *Larus michahellis* (discontinuous) and European storm-petrels *Hydrobates pelagicus* (continuous) at Benidorm Island.

d.f. = 3, $P < 0.001$; June: $\chi^2 = 40.9$; d.f. = 3, $P < 0.001$; July: $\chi^2 = 79.5$; d.f. = 3, $P = 0.001$; August: $\chi^2 = 5.3$; d.f. = 1, $P = 0.021$; September: $\chi^2 = 12.5$; d.f. = 1, $P < 0.001$). In May, when the trawler moratorium occurred, the total number of pellets found was higher than in April, but lower than in June ($\chi^2 = 32.0$; d.f. = 2, $P < 0.001$). There was no difference in predation rate between Mondays (after weekend fishery stop) and Fridays (paired t -test: $t = -0.8$, $n = 12$, $P = 0.44$) from June to August 2002. Thus, there was no effect of fishery closure on predation by yellow-legged gulls.

Cave 1 was significantly more illuminated than cave 2 (0.11 ± 0.01 vs 0.04 ± 0.04 ; paired t -test: $n = 12$, $t = 5.78$, $P < 0.001$), and light was also less variable in cave 1 (Levene test: $n = 24$, $F = 10.55$, $P = 0.004$) probably because cave 1 receives regular illumination from the city. There was no relationship between mean predation rate and moon phase, controlling by date (ANCOVA: $F_{2,36} = 0.41$, $P = 0.67$; Date: $F_{1,36} = 4.97$, $P = 0.03$). From April to September, predation rate was higher in cave 1 than in cave 2 (0.57 ± 0.44 , $n = 36$ vs 0.08 ± 0.27 , $n = 36$), but it did not depend on moon phase (Table 4).

Activity indices varied with date and did not differ between the two caves. They were not related to residual

Table 4. Result of generalized linear model analysis of the effects of cave, date and phase of the moon on daily predation rate on European storm-petrel *Hydrobates pelagicus* on Benidorm Island from April to September 2002 ($n = 72$)

| | d.f. | F | P |
|--------------------------|------|--------|-------|
| Date | 1 | 3.728 | 0.058 |
| Cave | 1 | 31.572 | 0.000 |
| Moon phase | 2 | 0.007 | 0.993 |
| Moon phase \times cave | 2 | 0.389 | 0.679 |

Table 5. Result of generalized linear model analysis of the effects of place, date and ambient illumination on daily predation rate on European storm-petrel *Hydrobates pelagicus* on Benidorm Island from June to August 2002 ($n = 24$)

| | d.f. | F | P |
|--------------|------|--------|-------|
| Illumination | 1 | 0.055 | 0.817 |
| Date | 1 | 17.540 | 0.000 |
| Cave | 1 | 0.004 | 0.949 |

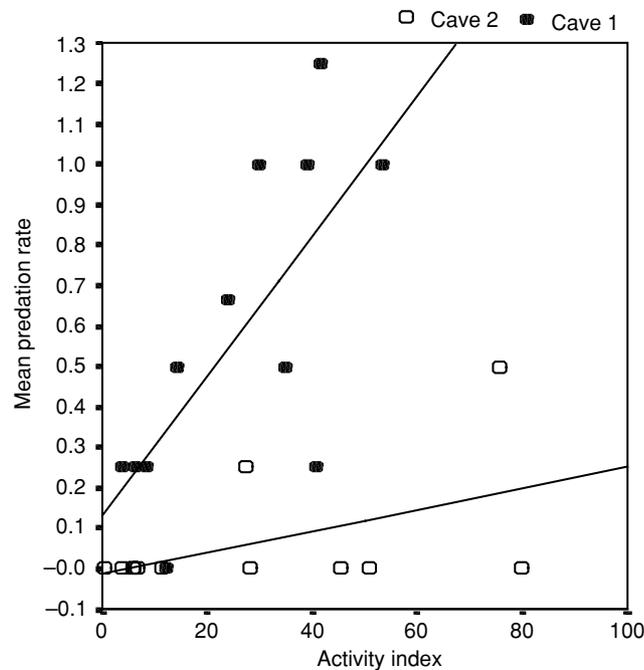


Fig. 3. Daily predation rate (no. of individuals/day) in 2002 and nocturnal activity index of storm-petrels *Hydrobates pelagicus* in the two caves at Benidorm Island.

light at night in front of each cave (Table 5). There was, however, a significant relationship between predation in both caves and the activity index of petrels (ANCOVA: $F_{1,24} = 22.7$, $P < 0.001$; activity index: $F_{1,24} = 6.4$, $P = 0.019$; Fig. 3).

Capture–recapture analysis

The capture–recapture models with an age structure on recapture probabilities (ϕ , β , p_a) showed much lower AIC than models with an immediate trap-effect only

Table 6. Modelling survival, minimum predation probability and recapture of European storm-petrels *Hydrobates pelagicus* breeding at Benidorm Island. For each model, the Akaike Information Criterion (AIC), the Δ AIC (i.e. the difference in AIC between the model in question and the selected model), the number of estimable parameters (np), and the deviance are given. Models were ranked by their AIC. Bold, general models considered (see Methods). Model notation is according to Lebreton *et al.* (1992, 1999) and Pradel (1993)

| Model | np | Deviance | AIC | Δ AIC |
|---|-----------|----------------|----------------|--------------|
| ϕ_t, β_{e+t}, p_A | 14 | 1803.81 | 1831.81 | 0 |
| ϕ_t, β_{e+F}, p_a | 21 | 1791.94 | 1833.94 | 2.13 |
| ϕ_t, β_e, p_a | 20 | 1793.96 | 1833.96 | 2.15 |
| ϕ_t, β_e, p_A | 13 | 1809.03 | 1835.03 | 3.22 |
| ϕ_t, β_t, p_A | 20 | 1796.95 | 1836.94 | 5.13 |
| ϕ_t, β_{e+L}, p_A | 6 | 1825.45 | 1837.45 | 5.64 |
| ϕ_F, β_e, p_a | 13 | 1812.64 | 1838.64 | 6.83 |
| ϕ_t, β_t, p_a | 27 | 1786.59 | 1840.59 | 8.78 |
| ϕ, β_t, p_A | 12 | 1819.54 | 1843.54 | 11.73 |
| ϕ_t, β_l, p_A | 4 | 1836.82 | 1844.82 | 13.01 |
| ϕ_F, β_{e+F}, p_a | 14 | 1817.28 | 1845.28 | 13.47 |
| ϕ_t, β, p_A | 12 | 1824.24 | 1848.24 | 16.43 |
| ϕ_t, β_F, p_a | 20 | 1808.86 | 1848.86 | 17.05 |
| ϕ_t, β_{e+F}, p_A | 14 | 1822.01 | 1850.01 | 18.2 |
| ϕ_t, β_e, p_m | 13 | 1831.61 | 1857.61 | 25.8 |
| $\phi_t, \beta_e, p_{m+m^*t}$ | 20 | 1817.97 | 1857.97 | 26.16 |
| ϕ_F, β_e, p_m | 6 | 1847.31 | 1859.31 | 27.5 |
| $\phi_t, \beta_e, p_{m^*t}$ | 28 | 1803.85 | 1859.85 | 28.04 |
| ϕ_t, β_t, p_m | 20 | 1821.03 | 1861.03 | 29.22 |
| $\phi_t, \beta_t, p_{m^*t}$ | 35 | 1796.15 | 1866.15 | 34.34 |
| ϕ_F, β_e, p_{m+t} | 14 | 1838.50 | 1866.50 | 34.69 |
| ϕ_t, β_t, p_{m+t} | 27 | 1815.78 | 1869.78 | 37.97 |
| ϕ_t, β, p_m | 12 | 1860.27 | 1884.27 | 52.46 |
| ϕ, β, p_m | 4 | 1880.46 | 1888.46 | 56.65 |
| ϕ, β, p_{m^*t} | 19 | 1850.85 | 1888.85 | 57.04 |
| ϕ_t, β_g, p_m | 12 | 1877.32 | 1901.32 | 69.51 |
| $\phi_t, \beta_g, p_{m^*t}$ | 27 | 1850.22 | 1904.22 | 72.41 |

(ϕ, β, p_{m^*t}) (see Table 6). Most models with survival varying with time worked better than models with constant survival or with survival decreasing after the establishment of the trawling moratorium (Table 6), suggesting that other environmental factors during or out of the breeding season were influencing the time variation in survival. The four best models were statistically equivalent (Table 6), but second and third models had problems with identifiability of some parameters. The final selected model was the first model (ϕ_t, β_{e+t}, p_A) with the lowest AIC and with no problems of parameter redundancy. This model showed: (1) a great time variation in local adult survival, from 0.701 (SE = 0.095) to 0.951 (SE = 0.031) (Fig. 4a); (2) a positive (and significant) influence of effort at collecting pellets on the minimum predation probability, with an additive positive (and also significant) effect of increased illumination on this probability, which also varied with time but much less than survival, from 0.022 (SE = 0.011) to 0.040 (SE = 0.016); (3) a significant and negative trend for recapture probability (Fig. 4b). Deviance profile of parameters of this model showed that they were all separately identifiable. Although survival varied with time, it was not possible to assess whether

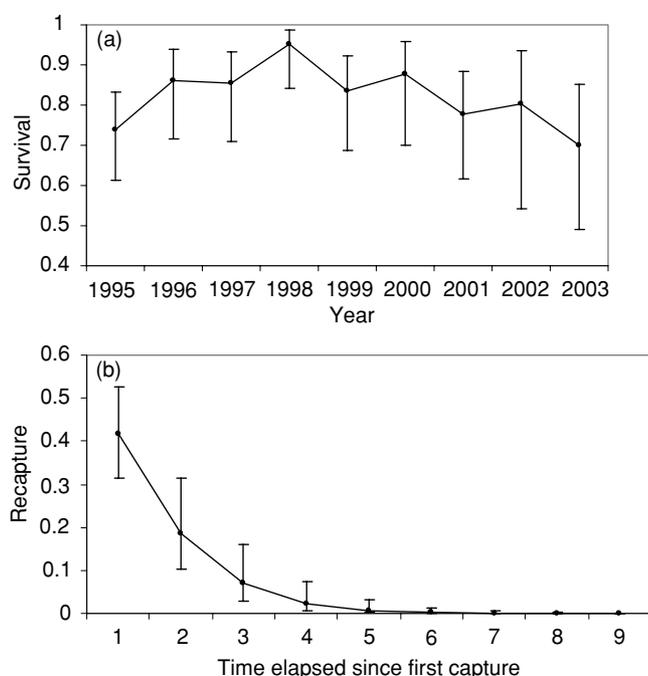


Fig. 4. Yearly estimates of local adult survival (a) and recapture (b) probabilities of European storm-petrels *Hydrobates pelagicus* breeding at Benidorm Island under the final selected model (ϕ_t , β_{e+t} , p_A ; see text). (b) Recapture probabilities as time elapsed since first capture. Errors bars, 95% CI.

this variation was influenced by inter-annual differences in gull predation. An average survival estimate for the whole period was calculated using the geometric mean of survival estimates following Cormack (1964): 0.833, with a SE of 0.042 calculated through the delta method (Seber, 1982). Minimum predation probabilities were not influenced by the size of the colony of yellow-legged gulls nor by the establishment of a trawling moratorium since 2000 (Table 6). From the final selected model (ϕ_t , β_{e+t} , p_A), the minimum probabilities of being killed by a gull relative to the fact of being dead for a number of causes was estimated, and varied between 0.075 (when pellets were collected opportunistically and the city lights were not in use) and 0.329 (when effort at collecting pellets was the highest (following a field protocol) and the city lights were already in use).

DISCUSSION

Results from the analysis of pellets suggest that predation was relatively constant at Benidorm Island. Capture–recapture modelling showed a time variation in the minimum predation probability of being killed by a gull, but this time variation could be the result of varying efforts each year when collecting pellets. Predation seems to be largely related to seasonality of storm-petrels, rather than that of gulls. The peak of predation occurred in June,

just after storm-petrels laid their eggs, and when most prospectors visit the colonies (pers. obs.).

Analysis of both pellets and capture–recapture agreed about the lack of a relationship between predation and fishery activity or abundance of gulls. These results seem to indicate that only certain gulls take storm-petrels, probably those that breed near storm-petrel colonies. The existence of specialist individuals has been shown in a number of studies on gulls (Hario, 1994; Finney *et al.*, 2001; Guillemette & Brousseau, 2001; Martínez-Abraín, Gonzalez-Solis *et al.*, 2003).

The petrel colony inside cave 1 showed a higher predation rate and during more months than that of cave 2. Cave 1 was significantly more illuminated than cave 2, probably making it easier for gulls to capture flying storm-petrels. In fact, in the past few years, storm-petrels have shown a preference for cave 2 (i.e. a higher occupancy rate of nest boxes at this site; De León & Mínguez, 2003). Capture–recapture modelling did not allow for a comparison of minimum predation probabilities between caves, but the final selected model showed a significant increase of these probabilities at cave 1 after the city lights were in use. Lack of a relationship between storm-petrel activity and the phase of the moon may indicate that light from Benidorm city affects storm-petrel activity around the whole island.

Although storm-petrels are the smallest seabirds, their life-history traits are characteristic of long-lived species (Russell, 1999; Weimerskirch, 2002). Thus, they should be highly sensitive to any change in adult survival, whereas other demographic parameters, such as survival of immatures, recruitment, and fecundity, should have a lower impact on population dynamics. Estimates of adult survival varied with time, although it was not possible to identify factors influencing this variability. Survival values seemed normal for a species of the Hydrobatidae family (Warham, 1990; Russell, 1999; Hamer, Schreiber & Burger, 2002; Weimerskirch, 2002), especially as survival was estimated in cave 1, where predation rates by gulls were highest. More years of monitoring would allow us to assess whether predation by yellow-legged gulls is responsible (at least partially) for the changes recorded in adult survival through variation in the ecological conditions for gulls (e.g. food availability, change in the number of specialists) or changes in urban light conditions. Other factors may also influence survival of storm-petrels breeding in Benidorm, such as predation by other predatory birds, food supply or ecological features, at both breeding and wintering areas (Mínguez, 2003). Recently, it has been shown that adult survival in several species of seabirds is more sensitive to environmental conditions than previously thought (Bricchetti, Foscolo & Boano, 2000; Jones, Hunter & Robertson, 2002; Oro & Furness, 2002). In our study, 9% of storm-petrels predated were fledglings. All of them were found in September when most storm-petrels fledge. Fledglings may be at their most vulnerable to predators at the time of departure, and are probably easy prey. Storm-petrel mortality owing to gull predation at colonies has been frequently considered to involve largely non-breeding storm-petrels (Morse &

Buccheister, 1977; Huntington *et al.*, 1996; Adam & Booth, 1999). Nevertheless, at least 11–14% of storm-petrels killed in this study were breeders, which is a minimum estimate because there is no information about the status of non-ringed birds, although many may be breeders. Stenhouse & Montevecchi (1999) studying Leach's storm-petrels *Oceanodroma leucorhoa* suggested that, owing to the late arrival of prospectors in NW Atlantic colonies, predation by gulls may be directed at breeding storm-petrels and have little effect on non-breeders. As a relatively large proportion of birds killed at Benidorm were breeders, the impact on storm-petrel population dynamics could be considerably higher than would otherwise be expected (Phillips *et al.*, 1999). On the other hand, predation of small petrels by large gulls should be a common phenomenon in evolutionary terms (adult petrel survival was actually normal in our study for such a species), although environmental changes of human origin (such as the increase in light conditions) may alter this relationship. In conclusion, predation should be carefully monitored. Any trend toward a higher intensity of predation would probably have considerable influence on small populations of storm-petrels. Our capture–recapture modelling suggested that in some years at least 33% of mortality was caused by gulls. Management may reduce predation rate by removing gulls that nest in the caves, because these individuals tend to kill most storm-petrels. This method could be applied only after careful identification of specialist predators had been carried out (Guillemette & Brousseau, 2001), and it is more ethical, easier and cheaper than large-scale culling.

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REFERENCES

- Adam, R. G. & Booth, C. M. (1999). Storm petrel *Hydrobates pelagicus* rings in great black-backed gull *Larus marinus* pellets. *Ringing Migr.* **19**: 298.
- Bosch, M., Oro, D., Cantos, F. J. & Zabala, M. (2000). Short term effects of culling on the ecology and population dynamics of a yellow-legged gull colony. *J. appl. Ecol.* **37**: 369–385.
- Boulinier, T., Sorci, G., Clobert, J. & Danchin, E. (1997). An experimental study of the costs of reproduction in the Kittiwake *Rissa tridactyla*: comment. *Ecology* **78**: 1284–1287.
- Bretagnolle, V. (1992). Variation géographique des vocalisations de pétrels ouest-paléarctiques et suggestions taxonomiques. *Alauda* **60**: 251–252.
- Bretagnolle, V. & Zotier, R. (1998). Levels of endemism in Mediterranean Procellariiformes: evidences from morphometrics, behaviour and genetics. In *Ecologie des oiseaux marins et gestion intégrée du littoral en Méditerranée*: 10–30. Medmaravis & Association 'Les Amis des Oiseaux' (Eds). Tunis: Arcs Editions.
- Brichetti, P., Foscolo, U. & Boano, G. (2000). Does El Niño affect survival rate of Mediterranean populations of Cory's shearwater? *Waterbirds* **23**: 147–154.
- Burnham, K. P. & Anderson, D. R. (1998). *Model selection and interference, a practical information-theoretic approach*. New York: Springer-Verlag.
- Choquet, R., Reboulet, A. M., Pradel, R., Gimenez, O. & Lebreton, J. D. (2003a). *U-Care user's guide, version 2.0*. Mimeographed document. Montpellier: CEFE/CNRS. ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR/U-CARE.
- Choquet, R., Reboulet, A. M., Pradel, R., Gimenez, O. & Lebreton, J. D. (2003b). *User's manual for M-SURGE 1.0*. Mimeographed document. Montpellier: CEFE/CNRS. ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR/M-SURGE.
- Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika* **51**: 429–438.
- De León, A. & Mínguez, E. (2003). Occupancy rates and nesting success of European storm-petrels breeding inside artificial nest-boxes. *Sci. Mar.* **67**(Suppl. 2): 109–112.
- Finney, S. K., Wanless, S., Harris, M. P. & Monaghan, P. (2001). The impact of gulls on puffin reproductive performance: an experimental test of two management strategies. *Biol. Conserv.* **98**: 159–165.
- Fowler, J. A., Okill, J. D. & Marshall, B. (1982). A retrap analysis of storm petrels tape-lured in Shetland. *Ringing Migr.* **4**: 1–7.
- Furness, R. W. (1981). The impact of predation by great skuas *Catharacta skua* on other seabird populations at a Shetland colony. *Ibis* **123**: 534–539.
- Furness, R. W. (2003). Impacts of fisheries on seabird communities. *Sci. Mar.* **67**(Suppl. 2): 33–45.
- Gimenez, O., Choquet, R. & Lebreton, J.-D. (2003). Parameter redundancy in multistate capture–recapture models. *Biom. J.* **45**: 704–722.
- Guillemette, M. & Brousseau, P. (2001). Does culling predatory gulls enhance the productivity of breeding common terns? *J. appl. Ecol.* **38**: 1–8.
- Hamer, K. C., Schreiber, E. A. & Burger, J. (2002). Breeding biology, life histories, and life history–environment interactions in seabirds. In *Biology of marine birds*: 217–261. Schreiber, E. A. & Burger, J. (Eds). Boca Raton: CRC Press.
- Hario, M. (1994). Reproductive performance of the nominate lesser black-backed gull under the pressure of herring gull predation. *Ornis Fenn.* **71**: 1–10.
- Harris, S. W. (1974). Status, chronology, and ecology of nesting storm-petrels in northwestern California. *Condor* **76**: 249–261.
- Hémery, G. & D'Elbee, E. (1985). Discrimination morphologique des populations Atlantique et Méditerranéenne de pétrel tempête *Hydrobates pelagicus*. In *Oiseaux marins nicheurs du Midi et de la Corse*: 63–67. Thibault, J. C., Guyot, I. & Cheylan, G. (Eds). Aix-en-Provence: du CROP.
- Hernández-Matías, A. & Ruiz, X. (2003). Predation on common tern eggs by the yellow-legged gull at the Ebro Delta. *Sci. Mar.* **67**(Suppl. 2): 95–101.
- Huntington, C. E., Butler, R. G. & Mauck, R. A. (1996). Leach's Storm-petrel, *Oceanodroma leucorhoa*. In *Birds of North America*: 1–32. Poole, A. & Gill, F. (Eds). Philadelphia, PA: BNA.
- Joe, M. & Pollock, K. H. (2002). Separation of survival and movement rates in multistate tag-return and capture recapture

- models. In *Statistical analysis of data from marked bird populations*. Morgan, B. J. T. & Thomson, D. L. (Eds). *J. appl. Stat.* **29**: 373–384.
- Jones, I. L., Hunter, F. M. & Robertson, G. J. (2002). Annual adult survival of Least auklets (Aves, Alcidae) varies with large-scale climatic conditions of the North Pacific Ocean. *Oecologia (Berl.)* **133**: 38–44.
- Klomp, N. I. & Furness, R. W. (1992). Patterns of chick feeding in Cory's shearwaters and the associations with ambient light. *Waterbirds* **15**: 95–102.
- Lebreton, J.-D., Almeras, T. & Pradel, R. (1999). Competing events, mixtures of information and multistrata recapture models. *Bird Study* **46**: 39–46.
- 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. *Ecol. Monogr.* **62**: 67–118.
- Lebreton, J.-D. & Pradel, R. (2002). Multistate recapture models: modelling incomplete individual histories. *J. appl. Stat.* **29**: 353–369.
- Martínez-Abraín, A., Gonzalez-Solís, J., Pedrocchi, V., Genovart, M., Abella, J. C., Ruiz, X., Jiménez, J. & Oro, D. (2003). Kleptoparasitism, disturbance and predation of yellow-legged gulls on Audouin's gulls in three colonies of the western Mediterranean. *Sci. Mar.* **67**(Suppl. 2): 89–94.
- Martínez-Abraín, A., Maestre, R. & Oro, D. (2002). Demersal trawling waste as a food source for western Mediterranean seabirds during the summer. *ICES J. mar. Sci.* **59**: 529–537.
- Mínguez, E. (1994). Censo, cronología de puesta y éxito reproductor del paño común (*Hydrobates pelagicus*) en la Isla de Benidorm (Alicante E de España). *Ardeola* **41**: 3–11.
- Mínguez, E. (1996). Nesting feeding strategy of the British storm-petrel *Hydrobates pelagicus* in a Mediterranean colony. *J. Zool. (Lond.)* **239**: 633–643.
- Mínguez, E. (2004). Paño Europeo *Hydrobates pelagicus*. In *Libro Rojo de las Aves de España*: 55–57. Madroño, A., Gonzalez, C. & Atienza, J. C. (Eds). Madrid: SEO/BirdLife & Ministerio de Medio Ambiente.
- Morse, D. H. & Buccheister C. W. (1977). Age and survival of breeding Leach's storm-petrels in Maine. *Bird-Banding* **48**: 341–349.
- Mougeot, F. & Bretagnolle, V. (2000). Predation risk and moonlight avoidance in nocturnal seabirds. *J. avian Biol.* **31**: 376–386.
- Nelson, D. A. (1989). Gull predation on Cassin's auklet varies with the lunar cycle. *Auk* **106**: 495–497.
- Oro, D., Bosch, M. & Ruiz, X. (1995). Effects of a trawling moratorium on the breeding success of the yellow-legged gull *Larus cachinnans*. *Ibis* **137**: 547–549.
- Oro, D. & Furness, R. W. (2002). Influences of food availability and predation on survival of kittiwakes. *Ecology* **83**: 2516–2528.
- Oro, D., Genovart, X., Ruiz, X., Jiménez, J. & García-Gans, J. (1996). Differences in diet, population increase and breeding performance between two colonies of Audouin's gulls *Larus audouinii* during breeding seasons affected by a trawling moratorium. *J. avian Biol.* **27**: 245–251.
- Oro, D. & Martínez-Vilalta, A. (1994). Factors affecting kleptoparasitism and predation rates upon a colony of Audouin's gull (*Larus audouinii*) by yellow-legged gulls (*Larus cachinnans*) in Spain. *Waterbirds* **17**: 35–41.
- Phillips, R. A., Thompson, D. R. & Hamer, K. C. (1999). The impact of great skua predation on seabird populations at St Kilda: a bioenergetics model. *J. appl. Ecol.* **36**: 218–232.
- Pradel, R. (1993). Flexibility in survival analysis from recapture data: handling trap-dependence. In *Marked individuals in the study of bird populations*: 29–37. Lebreton, J.-D. & North, P. M. (Eds). Basel, Switzerland: Birkhäuser Verlag.
- Pradel, R., Hines, J. E., Lebreton, J.-D. & Nichols, J. D. (1997). Capture–recapture survival models taking account of transients. *Biometrics* **53**: 88–99.
- Pradel, R., Wintrebert, C. M. A. & Gimenez, O. (2003). A proposal for a goodness-of-fit test to the Arnason–Schwarz multisite capture–recapture model. *Biometrics* **59**: 43–53.
- Prévot-Julliard, A. C., Lebreton, J.-D. & Pradel, R. (1998). Re-evaluation of the adult survival of a long-lived bird species, the black-headed gull (*Larus ridibundus*) in presence of recapture heterogeneity. *Auk* **115**: 85–95.
- Russell, R. W. (1999). Comparative demography and life history tactics of seabirds: implications for conservation and marine monitoring. In *Life in the slow lane: ecology and conservation of long-lived marine animals*: 51–76. Musick, J. A. (Ed.). Bethesda, MD: American Fisheries Society.
- Seber, G. A. F. (1982). *The estimation of animal abundance and related parameters*. New York: Macmillan.
- Stenhouse, I. J. & Montevecchi, W. A. (1999). Indirect effects of the availability of capelin and fishery discards: gull predation on breeding storm-petrels. *Mar. Ecol. Prog. Ser.* **184**: 303–307.
- Stenhouse, I. J., Robertson, G. J. & Montevecchi, W. A. (2000). Herring gull *Larus argentatus* predation on Leach's storm-petrels *Oceanodroma leucorhoa* breeding on Great Island, Newfoundland. *Atl. Seabirds* **2**: 35–44.
- Vidal, E., Maedail, F. & Tatoni, T. (1998). Is the yellow-legged gull a superabundant bird species in the Mediterranean? Impact on fauna and flora, conservation measures and research priorities. *Biodivers. Conserv.* **7**: 1013–1026.
- Warham, J. (1990). *The petrels. Their ecology and breeding systems*. London: Academic Press.
- Warham, J. (1996). *The behaviour, population biology and physiology of the petrels*. London: Academic Press.
- Watanuki, Y. (1986). Moonlight avoidance behavior in Leach's storm-petrels as a defense against slaty-backed gulls. *Auk* **103**: 14–22.
- Weimerskirch, H. (2002). Seabird demography and its relationship with the marine environment. In Schreiber, E. A. & Burger, J. (Eds). *Biology of marine birds*: 115–135. CRC Press, Boca Raton.