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ORIGINAL ARTICLE

# Recapture processes and biological inference in monitoring burrow-nesting seabirds

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**Abstract** Capture–mark–recapture methods are used widely for monitoring and diagnosis of bird populations as they permit robust estimates of population abundance and demographic parameters (e.g. survival) to be obtained from incomplete records of individual life histories. The statistical analysis of these data relies on the important assumption that individuals of the same local populations (i.e. colony) have the same parameters (the homogeneity assumption). We used data from six medium- to long-term monitoring schemes of local Mediterranean populations of the European Storm Petrel *Hydrobates pelagicus* to empirically show that the level of individual heterogeneity and the consequent bias in the parameter of interest depend on the recapture methodology, which has important consequences for the experimental design. We found that the recapture probability varied over time and among methodologies. The study design had a strong influence on the proportion of transients caught (i.e. individuals not recaptured after marking); however, the survival probability estimate for resident birds was fairly similar across the studies. The differences found in survival seem to depend on the biological variability between sites (e.g. predation pressure), and not on the recapture methods.

**Keywords** Capture–recapture analysis · Monitoring scheme · Procellariiformes · Survival probability · Transients

## Introduction

Medium- to long-term bird monitoring schemes aim to provide valuable information on demographic parameters for species or population diagnosis (Spina et al. 1993;

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Gregory et al. 2005; Nichols and Williams 2006). In natural populations accurate estimates are difficult to obtain due to sampling errors in counts and incomplete data on individual life histories (Williams et al. 2002; Sutherland 2006). Consequently, the most common methods for estimating population parameters are based on a statistical framework that accommodates detection failure, e.g. 'distance-sampling' (Buckland et al. 1993) or 'capture–mark–recapture' techniques (Seber 1962; Williams et al. 2002). In capture–mark–recapture methods, the recapture probability, i.e. the probability of capturing or detecting an individual known to be in the population, is often considered a nuisance parameter estimated simply to obtain unbiased measurements of the survival probability or population abundance. However, variations and heterogeneity in the recapture probability reflect changes in the sampling effort as well as real biological processes (see, for example, Clobert et al. 1994; Viallefont et al. 1995; Crespin et al. 2008). In addition, recapture processes might be more complex than expected (Pradel et al. 1997; Crespin et al. 2008), and undetected sources of variation in the recapture probability can still bias the estimates (Pledger and Efford 1998; Kendall 1999; Kendall et al. 2004). As different field protocols might lead to different types of biases, it is important to evaluate which method is most appropriate for estimating the parameter of interest.

We used data from six different medium- to long-term monitoring projects of the European Storm Petrel *Hydrobates pelagicus melitensis* to investigate the effects of sampling effort and sampling methodology on the demographic inferences. The European Storm Petrel is a small burrow-nesting seabird (average body mass of 28 g; Warham 1990) of the Mediterranean basin. Due to the human introduction of predators on the large islands, the species is now confined to islets (Thibault et al. 1996; Martin et al. 2000; de León et al. 2006) and is considered to be locally vulnerable (Mínguez 2004). Storm Petrels are pelagic and only return to land at night to breed or to prospect for potential breeding colonies (Watanuki 1986; Warham 1990). Their activity pattern coupled with the burrow-nesting habit (Scott 1970; Ramos et al. 1997; Ratcliffe et al. 1998) makes Storm Petrel populations difficult to monitor with nest or individual counts (Mitchell and Newton 2004). Exhaustive counts of breeding birds or burrows are in most cases impossible and the population abundance estimates usually vary greatly, even for a single colony (Ambagis 2004 and references therein). This is also a problem for other species with a similar life history and breeding habits, such as other petrels and shearwaters. More accurate insights into the population dynamics of these species can be obtained by analysing of the life histories of individually marked birds (Oro et al. 2004; Tavecchia et al. 2008; Sanz-Aguilar et al. 2008, 2009b). Individual-based data are normally collected by capturing incubating petrels in their nests or using mist-nets placed near the breeding colonies (Hemery 1980; Furness and Baillie 1981; Sydeman et al. 1998; Amengual et al. 1999; Lo Valvo and Massa 2000; Sanz-Aguilar et al. 2008). These data can be used to estimate several demographic parameters, providing that certain critical assumptions are maintained (Seber 1962; Lebreton et al. 1992). For example, if individuals do not have the same detectability and/or survival, the population abundance estimates derived from capture–recapture models may be biased (Link 2003; Schwarz and Arnason 2006).

In order to investigate the potential and limitations of alternative protocols we (1) gathered capture–recapture data from six Storm Petrel breeding locations in the Mediterranean basin and verified whether they met the basic assumptions of capture–recapture analysis, (2) modelled recapture processes, (3) estimated the annual survival probability and the proportion of transient birds, and (4) evaluated the differences between colonies in relation to the monitoring protocols and objectives.

## Methods

### Individual data and monitoring schemes

We used information from five independent monitoring schemes of six Storm Petrel colonies in the Mediterranean basin (Fig. 1). All the schemes aimed to collect data for population diagnosis, including estimates of the average survival probability and population abundance over time, and provide information for management actions. The schemes, however, varied in duration, methods and sample size according to the location, the number of people involved and the financial support (Appendix 1: Table 5). Due to these differences in the time and duration of the studies, each dataset has been treated separately using the same analytical procedure. For the sake of simplicity, we shall refer to the locations using abbreviations of their names. Hence, the two colonies on Benidorm Island (eastern Spain) are denoted 'B1' and 'B2', respectively; the colony on Marettimo Island (Italy) is denoted 'MA' and the colonies on Hormigas, Palomas (south-eastern Spain) and Na Plana (Cabrera Archipelago, eastern Spain), 'HO', 'PA' and 'NP', respectively (Fig. 1). We outline below the relevant features of the six datasets and refer readers to Appendix 1 for a more detailed description of each monitoring protocol. In the three local populations located inside accessible caves (B1, B2 and MA), breeding adults were captured on their nest once per breeding season, mainly during the end of the incubation period or when attending recently hatched chicks, in order to minimise disturbance (Blackmer et al. 2004) (Table 1). In addition, in colonies B1 and B2, nests were monitored during the

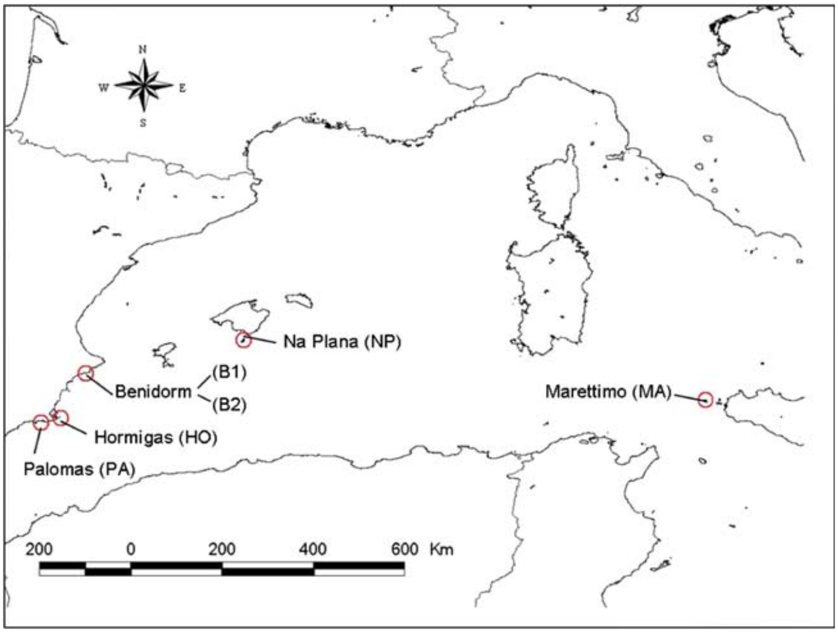

**Fig. 1** Location of the study areas: caves 1 (B1) and 2 (B2) in Benidorm Island (Alicante, Spain), Marettimo Island (MA) (Italy), Hormigas Island (HO) and Palomas Island (PA) (Murcia, Spain), and Na Plana Island (NP) (Cabrera Archipelago, Mallorca, Spain)

**Table 1** Characteristics of Storm Petrel *Hydrobates pelagicus melitensis* monitoring schemes at five islands of the Mediterranean basin

| Colony (notation) | Colony area (ha) | Years of monitoring | Methodology | Breeding status | Month of most captures | Approximate number of breeding pairs[a] |
|---|---|---|---|---|---|---|
| Benidorm (Alicante, Spain) (B1) | 6.5 | 1993–2006 | Nest monitoring | Breeders | June | 200–300 |
| Benidorm (Alicante, Spain) (B2) | 6.5 | 1994–2006 | Nest monitoring | Breeders | June | 100–150 |
| Marettimo (Sicily, Italy) (MA) | 1,200 | 1991–1994; 1996; 1998–2006 | Nest monitoring | Breeders | July | 2,000 |
| Hormigas (Murcia, Spain) (HO) | 0.7 | 1996–1997; 1999–2000; 2004–2006 | Mist-netting | Unknown | July | 250–350 |
| Palomas (Murcia, Spain) (PA) | 1.2 | 1996–2000; 2004–2006 | Mist-netting | Unknown | July | 300–500 |
| Na Plana (Cabrera, Spain) (NP) | 5.6 | 1994–1998 | Mist-netting + tape-lures | Unknown | August | 200–300 |

[a] Note that this information is an estimate based on the field researchers' experience

entire breeding season to estimate breeding success (Sanz-Aguilar et al. 2008, 2009b). In these two colonies, an experimental culling program of the specialist Yellow-legged Gull *Larus michahellis* that preys on petrels has been carried out since 2004 (Sanz-Aguilar et al. 2009a). We thus considered two periods, one before and one after the culling program, as survival greatly improved after the removal of the specialist predators (Sanz-Aguilar et al. 2009a). At the other locations (HO, PA and NP), petrels were caught at night using mist-nets (Table 1). The breeding status of mist-netted birds was unknown because there is no obvious criterion to distinguish breeders and non-breeders captured in this way (Furness and Baillie 1981). In colony NP, petrels were lured into nets using a playback of their vocalisations, which is a method commonly employed to increase the number of captures (Table 1). The birds were captured in different months, and in three datasets at least one year of data was missing (Table 1 and Appendix 1: Table 5 ).

In summary, individual encounter histories came from six locations where birds were captured using one of three possible methods: on their nest (3 programs), in mist-nets without tape-lure (2 programs) and in mist-nets combined with acoustic lures to attract birds (1 program).

## Statistical analysis

Individual data collected in the six monitoring programs were analysed using capture–recapture techniques to estimate local survival, recapture probabilities (Lebreton et al. 1992) and the proportion of transient birds, i.e. birds seen only at marking (Pradel et al. 1997). Although some birds were recaptured more than once within a recapture occasion, data were too sparse to use a robust design approach (Kendall and Nichols 1995; Kendall et al. 1997) and therefore data within the same breeding season were pooled to obtain a single capture–recapture occasion per year. For each dataset, the capture–recapture analysis began by testing the goodness-of-fit to the Cormark-Jolly-Seber model (CJS), which assumes full time variation of the recapture and survival parameters (Lebreton et al. 1992). Under the assumption that individuals share the same parameters, i.e. the homogeneity assumption, the distribution of encounter histories can be written as a combination of the probability to survive the interval $[i, i+1]$, denoted as $\phi_i$, and the probability that an individual known to be alive is caught, or seen, at $i$, denoted as $p_i$ (Lebreton et al. 1992). Testing the goodness-of-fit to the CJS model assesses whether data meet the homogeneity assumption regardless of individual past and present history. The goodness-of-fit test is based on contingency tables built for each recapture occasion and was calculated using the U-CARE 2.2.2 program (Choquet et al. 2005). It includes a specific test for the presence of transient birds, called the 'Test 3.SR', which compares whether the survival probability of newly marked birds differs from the survival of birds caught on previous occasions (see Appendix I in Tavecchia et al. 2008). If important, this effect can be accommodated by including specific parameters for the first survival after marking (Pradel et al. 1997). Survival soon after marking is then a weighted average between the survival of transient birds, equal to zero by definition, and the survival of resident birds. Pradel et al. (1997) have shown that the proportion of transients, $\tau_i$, in the population can be calculated as the relative difference between survival during the first year after marking, here denoted as $\phi'$, and the subsequent survival, here denoted as $\phi$, so that:

$$\tau_i = 1 - \frac{\phi_i'}{\phi_i}$$

Confidence intervals for $\tau$ can be calculated using the Delta method (Morgan 2000). The goodness-of-fit test also includes a specific test, called 'Test 2.CT', to verify whether some birds are captured more often than others, an effect denoted as "trap-dependence" (Pradel 1993). The trap-dependence effect can be corrected by re-coding capture histories and including an additional parameter in the recapture probability (see more details in Pradel 1993). Additional lack of fit can be taken into account by scaling model deviances using a scale parameter, classically denoted as $\hat{c}$, as in logistic linear regressions (Crawley 1993). This parameter is calculated as the goodness-of-fit statistic on its degree of freedom (Lebreton et al. 1992). As a general procedure, we began by modelling the probability of recapture by testing the full effect of time, a linear constraint (only in colony B2; see Tavecchia et al. 2008), and the influence of the recapture effort (i.e. number of capture occasions per year), and included, when necessary, the trap-dependence effect, denoted as '$m$'. We then modelled the survival probability as a function of time, age after marking (i.e. the 'transient' effect), and their statistical interaction. In addition, we considered two periods for colonies B1 and B2: one from 1993 to 2003 with high predation pressure, and a second period from 2004 to 2006 with low predation pressure (Sanz-Aguilar et al. 2009a). Models were built and fit to the data using the M-SURGE program (Choquet et al. 2004, 2006). Model selection was based on Akaike's Information Criterion adjusted for the effective sample size and overdispersion (QAICc) calculated as $\mathrm{QAIC}_c = \frac{\mathrm{dev}}{\hat{c}} + 2 * \mathrm{np}$, where dev is the model deviance, $\hat{c}$ the variance inflation factor, and np the number of separately identifiable parameters in the model (Burnham and Anderson 2002). In addition, for each model $j$, we calculated the Akaike weights, $w_j$, as an index of its relative plausibility (Burnham and Anderson 2002). For each location, the time-dependent estimates were obtained by model averaging in which each model contributed to the final estimate according to its Akaike weight (Burnham and Anderson 2002). We compared site-dependent survival and transient probabilities by means of a $Z$ test (Zar 1984), as estimates across datasets were independent.

## Results

Although we found that the datasets had some similarities, the models with the highest Akaike weights differed at each location due to site-specific differences in selective pressures, sample methodology and sample size. The model selection is described fully in Appendix 2 and summarised in Table 3; here, we outline the most relevant differences or similarities. The goodness-of-fit test revealed a significant difference in survival between newly marked and already marked, i.e. resident, birds in all datasets (Table 2). We also found a significant trap-dependence effect in colonies B1 and MA, but not in the other datasets (Table 2). We began by building time-dependent models that accommodate the transient effect by including two apparent age classes in the survival probabilities (Pradel et al. 1997) and the trap-dependence effect in colonies B1 and MA. The remaining heterogeneity was accounted for by scaling the model deviances using a variance inflation factor, $\hat{c}$, specific for each dataset (Table 2). Recapture probabilities varied over time in all locations, but not as a function of the recapture effort (Appendix 2). The recapture probability was highest in colonies B1 and B2 where nests were monitored throughout the breeding season, although adults were caught only once. Despite a similar

**Table 2** Goodness-of-fit tests of the Cormack-Jolly Seber model (CJS), including time- and colony-dependent parameters for birds at the colonies of Benidorm Island (B1 and B2), Marettimo (MA), Hormigas (HO), Palomas (PA), and Na Plana (NP)

| Colony | B1 | | B2 | | MA | | HO | | PA | | NP | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Goodness-of-fit components | $\chi^2$ | *df* | $\chi^2$ | *df* | $\chi^2$ | *df* | $\chi^2$ | *df* | $\chi^2$ | *df* | $\chi^2$ | *df* |
| 'CJS Model'total | **85.16** | **43** | **57.25** | **38** | **101.64** | **68** | **28.71** | **10** | **48.18** | **16** | **26.51** | **6** |
| 3.SR transient effect | **40.88** | **12** | **22.31** | **11** | **40.55** | **11** | **27.09** | **4** | **29.92** | **6** | **23.73** | **3** |
| 3.SM | 8.29 | 12 | 16.81 | 10 | 20.11 | 21 | 0.89 | 2 | **12.36** | **3** | 1.30 | 1 |
| 2.CT trap-dependence effect | **28.01** | **11** | 10.59 | 10 | **22.63** | **9** | 0.73 | 2 | 5.43 | 4 | 1.48 | 2 |
| 2.CL | 7.97 | 8 | 7.54 | 7 | 18.35 | 27 | 0.00 | 2 | 0.48 | 3 | 0.00 | 1 |
| 'Model with transients' | 44.28 | 31 | 34.94 | 27 | 61.09 | 57 | 1.62 | 6 | 18.26 | 10 | 2.78 | 4 |
| $\hat{c}$-'Model with transients' | 1.43 | | 1.29 | | 1.07 | | 1 | | 1.83 | | 1 | |
| 'Model with transients and trap-dependence' | 16.27 | 20 | | | 38.46 | 48 | | | | | | |
| $\hat{c}$-'Model with transients and trap-dependence' | 1 | | | | 1 | | | | | | | |

Tests 3.SR and 3.Sm are the survival rate tests and Tests 2.ct and 2.CL are the capture rate tests. Significant chi-square statistics ($P < 0.05$) are in bold

**Table 3** Summary of model selection (including models with the highest Akaike weights) for local survival (denoted $\phi'$ and $\phi$ for transient and resident birds, respectively) and recapture probabilities (denoted *P*) based on capture–recapture data of European Storm Petrels in the colonies of Benidorm (B1 and B2), Marettimo (MA), Hormigas (HO), Palomas (PA), and Na Plana (NP)

| Model number–colony notation | Recapture | Survival | np | dev | QAICc | *w* |
|---|---|---|---|---|---|---|
| 4–B1 | $P_{t+m}$ | $\phi'_t + \phi_t$ | 28 | 2,733.36 | 2,789.36 | 0.40 |
| 10–B2 | $P_T$ | $\phi'_{cull} + \phi_{cull}$ | 6 | 906.68 | 714.86 | 0.64 |
| 5–MA | $P_{t+m}$ | $\phi'_t * \phi$ | 28 | 3,536.06 | 3,592.06 | 0.94 |
| 6–HO | $P_t$ | $\phi' * \phi_t$ | 14 | 1,308.98 | 1,336.98 | 0.70 |
| 7–PA | $P_t$ | $\phi' * \phi$ | 9 | 1,381.20 | 772.75 | 0.81 |
| 7–NP | $P_t$ | $\phi' * \phi$ | 6 | 634.06 | 646.06 | 0.57 |

See more details in Appendix 2: Table 6

*np* Number of parameters in the model, *dev* deviance, *QAICc* Akaike's information criterion adjusted for small sample size (c) and overdispersion (Q), *w* Akaike weights, *t* time effect, *T* linear trend in time, *m* trap dependence effect, *cull* effect of gull culling (two periods were considered, one from 1993 to 2003 and one from 2004 to 2006)

+ indicates parallel variation, i.e. the additive effect, * indicates interaction terms

methodology, in MA the probability of recapture was low, probably due to the fact that the colony was visited only once per season. The recapture probability using mist-nets was high in HO, but low in the other two colonies (PA and NP), even when animals were lured using recorded calls. The survival probability generally varied over time for resident and/or transient birds, with the exception of birds from colonies PA and NP where the survival probability was constant (Table 3 and Appendix 2). The average survival probability of resident birds ranged between 0.7 and 0.9 (Fig. 2). The lowest value was found for birds from colonies B1 and B2 during the period in which predation by gulls was high (Fig. 2, Table 4). Except in colony HO, the proportion of transients was higher in the datasets from mist-net studies (Fig. 3, Table 4). The highest value, 0.68 (0.06 SE), was found at NP, where birds were captured using mist-nets in combination with tape-lures (Fig. 3). This value, however, is not significantly different from the

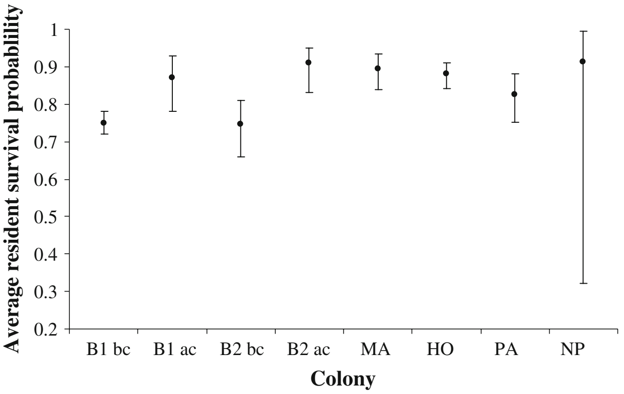

**Fig. 2** Average Storm Petrel resident survival probabilities during the study periods in colonies B1 and B2 (Benidorm), MA (Marettimo), HO (Hormigas), PA (Palomas), and NP (Na Plana) obtained from models (8–B1, 10–B2, 7–MA, 7–HO, 7–PA and 7–NP; Appendix 2: Table 6). Note that in the Benidorm colonies we considered two periods: before and after specialist Yellow-legged Gulls were culled, denoted *bc* and *ac*, respectively

**Table 4** Comparison of the estimates (*Z* test) of the average resident survival and the average transient proportions (from models 8–B1, 9–B1, 10–B2, 7–MA, 7–HO, 7–PA and 7–NP; Appendix 2: Table 6) in the colonies B1 and B2 (Benidorm), MA (Marettimo), HO (Hormigas), PA (Palomas), and NP (Na Plana)

| | Average resident survival probabilities | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | MA | B1 bc | B1 ac | B2 bc | B2 ac | PA | HO | NP |
| Average transient proportions | | | | | | | | |
| MA | | **2.42** | 0.55 | **2.71** | 0.38 | 1.70 | 0.51 | 0.02 |
| B1 bc | 0.15 | | * | 0.08 | **5.06** | **2.21** | **6.55** | 0.16 |
| B1 ac | 0.43 | * | | 1.94 | 0.80 | 0.84 | 0.25 | 0.04 |
| B2 bc | 1.01 | 0.80 | 1.14 | | * | 1.34 | **2.55** | 0.17 |
| B2 ac | 1.18 | 0.74 | 1.27 | * | | 1.87 | 0.84 | 0.00 |
| PA | **4.56** | **3.99** | **4.43** | **2.77** | **3.58** | | 1.45 | 0.09 |
| HO | **2.19** | 1.65 | **2.15** | 0.53 | 1.05 | **2.61** | | 0.03 |
| NP | **9.73** | **7.48** | **8.47** | **4.92** | **7.12** | 1.40 | **5.29** | |

In the Benidorm colonies, we considered the average estimates for the periods before (*bc*) and after (*ac*) predator removal. Note the estimates of these two periods within the same colony cannot be compared by *Z* test as they are not independent. In this case, the statistical significance can be deduced by model QAICc values (Appendix 2). Significant effects ($P < 0.05$) are in bold

* Not independent estimates

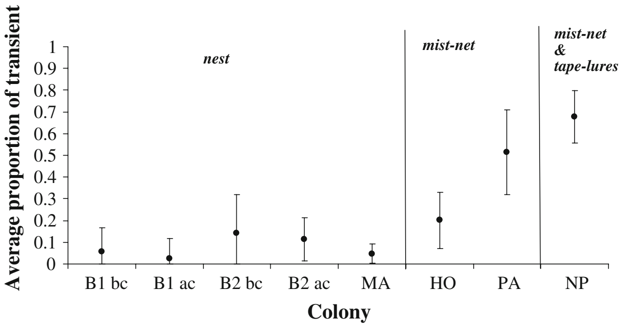

**Fig. 3** Estimated average proportion of transients in the studied colonies, B1 and B2 (Benidorm), MA (Marettimo), HO (Hormigas), PA (Palomas), and NP (Na Plana), obtained by models without time effects (models 8–B1, 10–B2, 7–MA, 7–HO, 7–PA and 7–NP; Appendix 2: Table 6). In the Benidorm colonies we considered two periods: before and after specialist Yellow-legged Gulls were culled, denoted *bc* and *ac*, respectively

one for colony PA (Table 4). Due to temporal gaps in capture–recapture data, the time-dependent estimates of the survival probabilities cannot be estimated separately in several cases, which prevent a full comparison of the time-dependent survival estimates across the studies.

## Discussion

Methods for obtaining robust estimates of demographic parameters from individual-based data rely on the important assumption that all marked individuals have the same survival and detection probabilities, which is called the homogeneity assumption (Lebreton et al. 1992; Williams et al. 2002). In capture–mark–recapture studies, a given capture methodology can increase the level of heterogeneity across individuals, which has important consequences for the estimate of the parameter of interest.

### Site- and method-specific differences in recapture probability

A first result was that the recapture probability was different across studies and over time. Interestingly, the temporal variability was not associated with the measure of the recapture effort, i.e. the number of days of capture per year. The recapture probability was generally higher when birds were captured on their nest, except for colony MA due to the lateness of the single visit (Appendix 1: Table 5, Appendix 2: Fig. 4). A late visit generally resulted in only a small number of adults being captured because they tend to leave the nest (during the day) a few days after the chicks hatch (Mínguez and Oro 2003). In colonies where petrels were captured using mist-nets, the yearly variation in the recapture probabilities may also correspond to the seasonal changes in the proportion of non-breeding prospectors, food availability, weather conditions and the moon phase (Scott 1970; Furness and Baillie 1981; Watanuki 1986; Boulinier and Lemel 1996; Mougeot and Bretagnolle 2000). Indeed, differences can sometimes be recorded even in as short a time as two consecutive nights (personal observation). Bad and mild wind conditions can substantially alter mist-net efficiency and therefore influence recapture probability if the number of capture sessions per year is low. This was not evident in our data, as recapture did not covary with the effort. Recapture probability did not increase when tape lures were used. This was probably because the majority of birds attracted by the playback were prospectors that were never recaptured (Okill and Bolton 2005). As a consequence, although the absolute number of birds captured with lures may be high, the number of recaptures is similar to the one obtained in studies without lures. In studies in which individuals were caught on their nests, we found the recapture probability to be heterogeneous, an effect known as trap-dependence. This is probably because some breeders are more easily captured than others, depending on their nest location or accessibility, or because some individuals may settle in a less accessible site following a breeding failure, death of previous partner or human disturbance (Blackmer et al. 2004; Crespin et al. 2008). Recapture heterogeneity across individuals, whether in survival or recapture, makes it difficult to obtain a reliable estimation of population size. Pledger and Efford (1998) proposed a method for obtaining unbiased estimates of population size that includes recapture heterogeneity into the capture–recapture models; however, Link (2003) has recently demonstrated that there are still some difficulties with this method. This limitation has to be taken into account when planning the protocol methodology of a monitoring study.

## Survival probability and the proportion of transients

An important result was that average estimates of the survival probability of resident birds, i.e. individuals that were recaptured at least once, were similar regardless of the capture methodology or site. On Benidorm Island (colonies B1 and B2) estimates were lower before the removal of the specialist Yellow-legged Gulls (Oro et al. 2005; Sanz-Aguilar et al. 2009a). The removal of these predators substantially increased the estimates to values comparable with those of colonies where the predation level is thought to be lower. At the NP colony, where petrels were captured using mist-nets in combination with acoustic lures, the resident survival estimate had a large confidence interval, probably due to the large proportion of transient individuals in the dataset and the relatively short duration of the monitoring program. The average resident survival estimates provided here are consistent with the values found for the Atlantic colonies of the subspecies *pelagicus*: 0.85–0.91 on Biarritz (south-western France, Hemery 1980) and 0.87 in Eilean Hoan (northern UK; Insley et al. 2002). Zuberogoitia et al. (2007) found a lower survival value (0.76) in Aketx (northern Spain), but this value, and the value found by Insley et al. (2002), may include an unknown proportion of transient birds with a survival equal to 0 by definition.

We found that a substantial proportion of the birds captured were 'transient' individuals, i.e. individuals never seen again after marking (Pradel et al. 1997). The proportion of transient birds, however, was higher in datasets from mist-net studies, and increased when birds were lured into the nets using a playback device, which suggests that a high proportion of non-breeding prospectors may be susceptible to being captured with this method, as already pointed out in previous studies (Furness and Baillie 1981; Podolsky and Kress 1989). Okill and Bolton (2005) found that the prospector fraction of the Storm Petrel's population is composed of young birds aged between 2 and 5 years. Studies on other long-lived birds have shown that the survival probability is generally lower among the youngest age classes (Tavecchia et al. 2001; Ratcliffe et al. 2002). Consequently, studies in which a higher proportion of prospectors are captured should have a high level of heterogeneity in survival. The transient proportion, however, can also vary across studies despite a similar methodology due to site-specific differences in predation pressure, intrinsic individual quality (Tavecchia et al. 2008; Sanz-Aguilar et al. 2008) and colony attractiveness linked to colony size (Brown et al. 1990; Oro and Pradel 2000). We found, for example, that on the small islet of HO, which hosts a smaller Storm Petrel colony than the larger island of PA, the transient proportion was lower despite birds being captured in mist-nests at both sites. In colonies B1 and B2, the transient proportions were slightly lower after the experimental removal of predators. The presence of transients can be accommodated in models for estimating survival probability; however, this presence cannot be accommodated in models for estimating population size because in these models individual heterogeneity in survival and/or recapture impairs the estimates (Kendall et al. 2004). In some cases, the population of resident birds could be estimated by correcting the population abundance estimate by subtracting the transient proportion. However, the number obtained might not be informative because only a small portion of the real population of breeders is generally caught in their nests or in mist-nets, as it is difficult, if not impossible, to cover the entire colony with nets.

## Monitoring scheme and biological inferences

We have illustrated the similarities and differences derived from different recapture methods for monitoring populations of a burrow-nesting seabird. In particular, we have shown how recapture processes influence the level of heterogeneity among individuals and ultimately the estimation and precision of the demographic parameters. Our results suggest that monitoring schemes for Storm Petrels should be designed in relation to the target parameter and the precision desired. First, it is important to assure continuity over relatively long periods of time. Gaps in capture–mark–recapture data can be easily accommodated in the capture–recapture models, but they generate problems of parameter identifiability and therefore biological inference. Although this may seem trivial advice, three out of the six long-term schemes analysed here had at least one gap in the capture–recapture time series (Appendix 1), which may be the case for many studies whose results have not been published. Second, goodness-of-fit tests should be carried out before data are analysed in order to determine the potential survival or recapture heterogeneity and to incorporate these effects into the models (Lebreton et al. 1992). Third, the recapture probability can be maximised by choosing the right period, site and number of visits to the colony. In our case, recapture probability was extremely low in some years and for some datasets. As a rule of thumb, a recapture probability less than 10% results in imprecise survival estimates due to the covariation between these two parameters (Hargrove and Borland 1994). It may be desirable to visit the colony on similar dates over the years and, if nests cannot be followed, to place mist-nets within the colony rather than outside. Estimates of resident survival can be obtained by repeated captures of individuals at their nest or in mist-nets, providing the structure of the capture–recapture model includes specific parameters for transient birds and, in specific cases, accommodates recapture heterogeneity. When possible, capturing breeding petrels in their nests and limiting the manipulation time to marking is preferable. Indeed, besides a higher recapture rate, it is also possible to collect more information on demographic parameters, such as breeding success or the occupancy rate, which can be used as a proxy of population abundance (Sanz-Aguilar et al. 2008). However, in the majority of Storm Petrel colonies, nests are inaccessible to researchers and the use of mist-nets may be the only approach available for estimating survival (Mitchell and Newton 2004). Note that the use of mist-nets, especially with the support of playback calls, results in a higher number of captures, but it also increases the proportion of transient birds in the dataset. Therefore, survival estimates for resident birds are usually less precise and population abundance estimates are impossible to obtain. We recommend restricting the use of acoustic lures to specific studies (i.e. movements or age-structure of wandering prospectors). For the Storm Petrel, none of the capture methodologies allowed informative estimates of colony or population size to be obtained. Their population trends can be more successful monitored by investigating variations in survival probabilities of resident birds (the most important predictor of population growth rate in long-lived species; see Saether and Bakke 2000), rather than by wide, imprecise estimates of population size (Tavecchia et al. 2008).

## Zusammenfassung

Fang-Wiederfangmethoden und biologische Schlussfolgerungen beim Monitoring von in Höhlen brütenden Seevögeln

Fang-Wiederfangmethoden werden sehr häufig für ein Monitoring und zur Diagnose von Vogelpopulationen verwendet, weil sie zuverlässige Schätzwerte zu Populationsgrößen und demographischen Parametern (z.B. Überlebensrate) aus unvollständig erfassten Lebensgeschichten von Individuen liefern. Die statistische Auswertung dieser Daten beruht auf der grundlegenden Annahme, dass Individuen derselben lokalen Populationen (d.h. einer Kolonie) die gleichen Eigenschaften besitzen (Homogenitäts-Annahme). Um empirisch zu zeigen, dass das Niveau der individuellen Heterogenität und der daraus resultierende Fehler im jeweils betrachteten Parameter von der Wiederfangmethodik abhängt, woraus sich entscheidende Konsequenzen für das Experimentdesign ergeben, verwendeten wir die Daten von sechs mittel- bis langfristigen Monitoring-Programmen von lokalen mediterranen Populationen der Sturmschwalbe *Hydrobates pelagicus*. Wir fanden heraus, dass die Wiederfang-Wahrscheinlichkeit über die Zeit und zwischen den Fangwiederfangmethoden variierte. Das Experimentdesign hatte einen starken Einfluss auf den Anteil an gefangenen Durchzüglern (d.h. Individuen, die nach der Markierung nicht wieder gefangen wurden); die Abschätzung der Überlebenswahrscheinlichkeit der residenten Vögel viel jedoch zwischen den unterschiedlichen Studien ziemlich ähnlich aus. Die festgestellten Unterschiede in der Überlebensrate scheinen von der Varianz in den biologisch relevanten Parametern zwischen den Kolonien abzuhängen (z. B. Prädationsdruck) und nicht von den Wiederfangmethoden.

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## Appendix 1

### Storm Petrel monitoring schemes on five Mediterranean islands

*Benidorm Island (colonies B1 and B2)*—The first two datasets come from Benidorm Island (Alicante, Spain; Fig. 1) where petrels concentrate in two natural caves, hereafter denoted as cave B1 and B2, about 150 m apart, with approximately 200 and 100 breeding pairs, respectively. Most nests found inside the two caves are accessible to researchers and a program began in 1993 with the aim of monitoring breeding birds in the two caves (from 1994 in cave B2, see also Sanz-Aguilar et al. 2008, 2009b). In 1996, a number of artificial nest-boxes were installed inside the two caves to investigate if colony sizes were constrained by nest availability. The boxes were mainly occupied in cave B2, although it appears that the number of available nests is not a

**Table 5** Number of days of capture and Storm Petrels marked and recaptured per year at the study sites

| Colony (notation) | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Number of days of capture* | | | | | | | | | | | | | | | | | |
| Benidorm (Alicante, Spain) (B1) | | | 20 | 38 | 13 | 14 | 7 | 9 | 10 | 16 | 4 | 20 | 4 | 8 | 14 | 19 | 196 |
| Benidorm (Alicante, Spain) (B2) | | | | 16 | 8 | 6 | 4 | 4 | 7 | 8 | 5 | 14 | 4 | 10 | 15 | 17 | 118 |
| Marettimo (Sicily, Italy) (MA) | 1 | 1 | 1 | 2 | | 1 | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 15 |
| Hormigas (Murcia, Spain) (HO) | | | | | | 1 | 2 | | 2 | 2 | | | | 2 | 4 | 2 | 15 |
| Palomas (Murcia, Spain) (PA) | | | | | | 3 | 4 | 2 | 7 | 3 | | | | 1 | 2 | 2 | 24 |
| Na Plana (Cabrera, Spain) (NP) | | | | 3 | 5 | 11 | 10 | 4 | | | | | | | | | 32 |
| *Number of birds captured* | | | | | | | | | | | | | | | | | |
| Benidorm (Alicante, Spain) (B1) | | | 169 | 224 | 136 | 124 | 113 | 127 | 109 | 99 | 78 | 67 | 49 | 63 | 139 | 173 | 1670 |
| Benidorm (Alicante, Spain) (B2) | | | | 52 | 30 | 20 | 9 | 12 | 31 | 19 | 53 | 51 | 58 | 78 | 115 | 144 | 672 |
| Marettimo (Sicily, Italy) (MA) | 21 | 106 | 134 | 252 | | 292 | | 62 | 235 | 91 | 119 | 159 | 96 | 147 | 53 | 122 | 1889 |
| Hormigas (Murcia, Spain) (HO) | | | | | | 32 | 70 | | 10 | 314 | | | | 157 | 300 | 156 | 1039 |
| Palomas (Murcia, Spain) (PA) | | | | | | 65 | 212 | 28 | 139 | 437 | | | | 125 | 174 | 317 | 1497 |
| Na Plana (Cabrera, Spain) (NP) | | | | 45 | 154 | 279 | 345 | 24 | | | | | | | | | 845 |
| *Proportion of already marked birds among the captures* | | | | | | | | | | | | | | | | | |
| Benidorm (Alicante, Spain) (B1) | | | 0 | 0.57 | 0.79 | 0.77 | 0.76 | 0.78 | 0.76 | 0.77 | 0.79 | 0.67 | 0.84 | 0.60 | 0.50 | 0.66 | 0.63 |
| Benidorm (Alicante, Spain) (B2) | | | | 0 | 0.47 | 0.70 | 0.67 | 0.75 | 0.45 | 0.74 | 0.30 | 0.67 | 0.69 | 0.60 | 0.60 | 0.68 | 0.56 |
| Marettimo (Sicily, Italy) (MA) | 0 | 0 | 0.11 | 0.10 | | 0.18 | | 0.39 | 0.35 | 0.34 | 0.39 | 0.34 | 0.41 | 0.29 | 0.41 | 0.38 | 0.25 |
| Hormigas (Murcia, Spain) (HO) | | | | | | 0 | 0 | | 0.40 | 0.23 | | | | 0.18 | 0.44 | 0.61 | 0.32 |
| Palomas (Murcia, Spain) (PA) | | | | | | 0 | 0.04 | 0.14 | 0.09 | 0.10 | | | | 0.11 | 0.19 | 0.26 | 0.13 |
| Na Plana (Cabrera, Spain) (NP) | | | | 0 | 0.01 | 0.10 | 0.20 | 0.46 | | | | | | | | | 0.13 |
| *Month of capture (number of days of capture per month)* | | | | | | | | | | | | | | | | | |
| Benidorm (Alicante, Spain) (B1) | | | 4 (1)<br>5 (7)<br>6 (8)<br>7 (2)<br>8 (2) | 4 (3)<br>5 (17)<br>6 (14)<br>7 (3)<br>8 (1) | 5 (5)<br>6 (7)<br>7 (1) | 6 (9)<br>7 (5) | 5 (2)<br>6 (5) | 6 (5)<br>7 (1)<br>8 (3) | 5 (1)<br>6 (7)<br>7 (2) | 6 (15)<br>7 (1) | 5 (1)<br>6 (3) | 6 (16)<br>7 (4) | 6 (4) | 6 (4)<br>7 (4) | 6 (10)<br>7 (4) | 5 (5)<br>6 (12)<br>7 (2) | 4 (4)<br>5 (38)<br>6 (119)<br>7 (29)<br>8 (6) |
| Benidorm (Alicante, Spain) (B2) | | | | 5 (2)<br>6 (10)<br>7 (4) | 5 (3)<br>6 (4)<br>7 (1) | 6 (6) | 6 (4) | 6 (4) | 6 (5)<br>7 (2) | 6 (7)<br>7 (1) | 6 (5) | 6 (10)<br>7 (4) | 6 (4) | 6 (5)<br>7 (4)<br>8 (1) | 5 (2)<br>6 (8)<br>7 (5) | 5 (5)<br>6 (12) | 5 (12)<br>6 (84)<br>7 (21)<br>8 (1) |
| Marettimo (Sicily, Italy) (MA) | 8 (1) | 8 (1) | 8 (1) | 7 (1)<br>8 (1) | | 7 (1) | | 8 (1) | 7 (1) | 7 (1) | 7 (1) | 7 (1) | 7 (1) | 7 (1) | 7 (1) | 7 (1) | 7 (10)<br>8 (5) |

**Table 5** continued

| Colony (notation) | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hormigas (Murcia, Spain) (HO) | | | | | | 7 (1) | 7 (2) | | 7 (1)<br>8 (1) | 4 (1)<br>7 (1) | | | | 4 (1)<br>7 (1) | 4 (1)<br>5 (1)<br>6 (1)<br>7 (1) | 6 (1) | 4 (3)<br>5 (1)<br>6 (2)<br>7 (7)<br>8 (1) |
| Palomas (Murcia, Spain) (PA) | | | | | | 6 (2)<br>7 (1) | 6 (1)<br>7 (2)<br>8 (1) | 6 (1)<br>7 (1) | 4 (1)<br>5 (1)<br>7 (3)<br>8 (2) | 5 (1)<br>7 (1)<br>8 (1) | | | | 7 (1) | 4 (1)<br>5 (1) | 5 (1)<br>7 (1) | 4 (2)<br>5 (4)<br>6 (4)<br>7 (10)<br>8 (4) |
| Na Plana (Cabrera, Spain) (NP) | | | | 8(3) | 6(1)<br>7(2)<br>8(2) | 6 (3)<br>7 (3)<br>8 (5) | 7 (6)<br>8 (4) | 7 (1)<br>8 (3) | | | | | | | | | 6 (4)<br>7 (12)<br>8 (17) |

limiting factor in the larger colony (de León and Mínguez 2003). There is evidence that predation pressure by the Yellow-legged Gull *Larus michahellis* reduced petrel survival probabilities (Oro et al. 2005; Sanz-Aguilar et al. 2009a). In 2004, an evidence-based culling program of specialist gulls was implemented in order to reduce the level of predation (Sanz-Aguilar et al. 2009a). In both colonies, breeding birds were caught annually at their nest generally during the end of the incubation period (June). Nests were monitored several times during the incubation period in order to catch both members of the pair and verify their breeding success (Table 5).

*Marettimo Island (colony MA)*: At the colony on Marettimo Island (Egadi Archipelago, Sicily, Italy; Fig. 1) marking and recapture of birds was conducted annually from 1991 to 2006, with the exception of 1995 (Lo Valvo and Massa 2000). The colony was visited once a year as it is difficult to access (Table 5) and breeding adults were marked or recaptured during incubation or as they were attending recently hatched chicks (July–August). In 1997, a late visit to the colony resulted in only chicks being ringed and hence no recaptures of adults are available for that year. The colony is located inside a large cave with approximately 2,000 breeding pairs.

*Hormigas (colony HO) and Palomas (colony PA) Islands*: On Hormigas (D) and Palomas (E) Islands (Murcia, Spain; Fig. 1) petrels breed inside generally small inaccessible caves, small crevices over the island and also, on Hormigas, on human structures. A regular mist-netting program began in 1996 on the two islands. Capture sessions were between April and August but the capture effort varied among years depending on sea conditions, so that between-session intervals are, in some cases, larger than a year (Table 5). The number of nets varied between sessions but the most common configurations were 3 mist-nets measuring 36–50 m at Palomas and 6–7 mist-nets measuring 84–100 m at Hormigas. The mist-nets were usually placed on fixed points. Sampling was carried out between 1 h before sunset and 1 h after sunrise, and therefore encompassed the entire activity period of the Storm Petrels in the colony. Data records until 2004 were obtained form ANSE files and from 2005 onwards from the Ringing Office.

*Na Plana island (colony NP)*: The last dataset came from the monitoring program on Na Plana Island (Cabrera Archipelago, Balearic Islands, Spain; Fig. 1). Here, most of the Storm Petrels nest on the island's coast in often unidentified or inaccessible caves and crevices (Amengual et al. 1999). From 1994 to 1998, an intensive mist-netting program was carried out during summer (June–September). Birds were captured during dark moon nights and were lured into nets by petrel vocalisations played on a portable tape recorder installed between two nets of 20 m combined length from 2200 to 0500 hours.

## Appendix 2

See Table 6 and Fig. 4.

**Table 6** Modelling local survival (denoted as $\phi'$ and $\phi$ for transient and resident birds, respectively) and recapture probabilities (denoted as $P$) based on capture–recapture data from European Storm Petrels at the colonies of Benidorm (B1 and B2), Marettimo (MA), Hormigas (HO), Palomas (PA), and Na Plana (NP)

| Model–colony notation | Recapture | Survival | np | dev | QAICc | ΔQAICc | *w* |
|---|---|---|---|---|---|---|---|
| 1–B1 | $P_{t+m}$ | $\phi'_t * \phi_t$ | 38 | 2,714.21 | 2,790.21 | 0.85 | 0.26 |
| 2–B1 | $P_{+m}$ | $\phi'_t * \phi_t$ | 27 | 2,762.90 | 2,816.90 | 27.54 | 0 |
| 3–B1 | $P_{effort+m}$ | $\phi'_t * \phi_t$ | 28 | 2,758.26 | 2,814.26 | 24.90 | 0 |
| **4–B1** | $\boldsymbol{P_{t+m}}$ | $\boldsymbol{\phi'_t + \phi_t}$ | **28** | **2,733.36** | **2,789.36** | **0** | **0.40** |
| 5–B1 | $P_{t+m}$ | $\phi'_t * \phi$ | 28 | 2,738.28 | 2,794.28 | 4.92 | 0.03 |
| 6–B1 | $P_{t+m}$ | $\phi' * \phi_t$ | 27 | 2,755.46 | 2,809.46 | 20.09 | 0 |
| 7–B1 | $P_{t+m}$ | $\phi' * \phi$ | 16 | 2,780.61 | 2,812.61 | 23.25 | 0 |
| 8–B1 | $P_{t+m}$ | $\phi'_t * \phi_{cull}$ | 29 | 2,731.94 | 2,789.94 | 0.58 | 0.30 |
| 9–B1 | $P_{t+m}$ | $\phi_{cull}' * \phi_{cull}$ | 18 | 2,773.06 | 2,809.06 | 19.69 | 0 |
| 1–B2 | $P_t$ | $\phi'_t * \phi_t$ | 34 | 865.55 | 738.97 | 24.11 | 0 |
| 2–B2 | $P_T$ | $\phi'_t * \phi_t$ | 25 | 874.88 | 728.21 | 13.35 | 0 |
| 3–B2 | $P$ | $\phi'_t * \phi_t$ | 24 | 909.79 | 753.26 | 38.40 | 0 |
| 4–B2 | $P_{effort}$ | $\phi'_t * \phi_t$ | 25 | 903.18 | 750.14 | 35.28 | 0 |
| 5–B2 | $P_T$ | $\phi'_t + \phi_t$ | 15 | 889.33 | 719.41 | 4.55 | 0.07 |
| 6–B2 | $P_T$ | $\phi'_t * \phi$ | 15 | 903.86 | 730.67 | 15.81 | 0 |
| 7–B2 | $P_T$ | $\phi' * \phi_t$ | 14 | 892.05 | 719.52 | 4.66 | 0.06 |
| 8–B2 | $P_T$ | $\phi' * \phi$ | 4 | 928.38 | 727.67 | 12.81 | 0 |
| 9–B2 | $P_T$ | $\phi' * \phi_{cull}$ | 5 | 911.92 | 716.91 | 2.05 | 0.23 |
| **10–B2** | $\boldsymbol{P_T}$ | $\boldsymbol{\phi_{cull}' * \phi_{cull}}$ | **6** | **906.68** | **714.86** | **0** | **0.64** |
| 1–MA | $P_{t+m}$ | $\phi'_t * \phi_t$ | 37 | 3,526.28 | 3,600.28 | 8.23 | 0.02 |
| 2–MA | $P_{+m}$ | $\phi'_t * \phi_t$ | 26 | 3,622.41 | 3,674.41 | 82.35 | 0 |
| 3–MA | $P_{effort+m}$ | $\phi'_t * \phi_t$ | 31 | 3,665.78 | 3,727.78 | 135.72 | 0 |
| 4–MA | $P_{t+m}$ | $\phi'_t + \phi_t$ | 30 | 3,538.20 | 3,598.20 | 6.14 | 0.04 |
| **5–MA** | $\boldsymbol{P_{t+m}}$ | $\boldsymbol{\phi'_t * \phi}$ | **28** | **3,536.06** | **3,592.06** | **0** | **0.94** |
| 6–MA | $P_{t+m}$ | $\phi' * \phi_t$ | 26 | 3,580.03 | 3,632.03 | 39.97 | 0 |
| 7–MA | $P_{t+m}$ | $\phi' * \phi$ | 16 | 3,590.08 | 3,622.08 | 30.02 | 0 |
| 1–HO | $P_t$ | $\phi'_t * \phi_t$ | 15 | 1,308.92 | 1,338.92 | 1.94 | 0.27 |
| 2–HO | $P$ | $\phi'_t * \phi_t$ | 12 | 1,506.11 | 1,530.11 | 193.14 | 0 |
| 3–HO | $P_{effort}$ | $\phi'_t * \phi_t$ | 13 | 1,453.66 | 1,479.66 | 142.69 | 0 |
| 4–HO | $P_t$ | $\phi'_t + \phi_t$ | 13 | 1,317.42 | 1,343.42 | 6.44 | 0.03 |
| 5–HO | $P_t$ | $\phi'_t * \phi$ | 14 | 1,326.63 | 1,354.63 | 17.65 | 0 |
| **6–HO** | $\boldsymbol{P_t}$ | $\boldsymbol{\phi' * \phi_t}$ | **14** | **1,308.98** | **1,336.98** | **0** | **0.70** |
| 7–HO | $P_t$ | $\phi' * \phi$ | 8 | 1,359.72 | 1,375.72 | 38.74 | 0 |
| 1–PA | $P_t$ | $\phi'_t * \phi_t$ | 19 | 1,359.82 | 781.07 | 8.32 | 0.01 |
| 2–PA | $P$ | $\phi'_t * \phi_t$ | 14 | 1,411.28 | 799.19 | 26.44 | 0 |
| 3–PA | $P_{effort}$ | $\phi'_t * \phi_t$ | 16 | 1,409.93 | 802.45 | 29.7 | 0 |
| 4–PA | $P_t$ | $\phi'_t + \phi_t$ | 16 | 1,364.99 | 777.9 | 5.14 | 0.06 |
| 5–PA | $P_t$ | $\phi'_t * \phi$ | 15 | 1,366.82 | 776.9 | 4.14 | 0.10 |
| 6–PA | $P_t$ | $\phi' * \phi_t$ | 15 | 1,374.81 | 781.26 | 8.51 | 0.01 |
| **7–PA** | $\boldsymbol{P_t}$ | $\boldsymbol{\phi' * \phi}$ | **9** | **1,381.2** | **772.75** | **0** | **0.81** |
| 1–NP | $P_t$ | $\phi'_t * \phi_t$ | 10 | 630.21 | 650.21 | 4.15 | 0.07 |
| 2–NP | $P$ | $\phi'_t * \phi_t$ | 8 | 645.32 | 661.32 | 15.26 | 0 |
| 3–NP | $P_{effort}$ | $\phi'_t * \phi_t$ | 9 | 634.77 | 652.77 | 6.71 | 0.02 |

**Table 6** continued

| Model–colony notation | Recapture | Survival | np | dev | QAICc | ΔQAICc | *w* |
|---|---|---|---|---|---|---|---|
| 4–NP | $P_{t}$ | $\phi'_{t} + \phi_{t}$ | 9 | 631.17 | 649.17 | 3.11 | 0.12 |
| 5–NP | $P_{t}$ | $\phi'_{t} * \phi$ | 9 | 630.94 | 648.94 | 2.88 | 0.13 |
| 6–NP | $P_{t}$ | $\phi' * \phi_{t}$ | 8 | 633.75 | 649.75 | 3.69 | 0.09 |
| **7–NP** | $\boldsymbol{P_{t}}$ | $\boldsymbol{\phi' * \phi}$ | **6** | **634.06** | **646.06** | **0** | **0.57** |

The best model (highest QAICc weight) is shown in bold text

*np* Number of parameters in the model, *dev* deviance, *QAICc* Akaike's information criterion adjusted for small sample size (c) and overdispersion (Q), Δ*QAICc* the difference in QAICc between the current and the model with the lowest QAICc, *w* Akaike weights, *t* time effect, *T* linear trend in time, *effort* recapture effort (number of capture occasions per year), *m* trap dependence effect, *cull* effect of gull culling (two parameters, one for the period 1993–2003 and one for 2004–2006)

+ indicates parallel variation, i.e. the additive effect, * indicates interaction terms

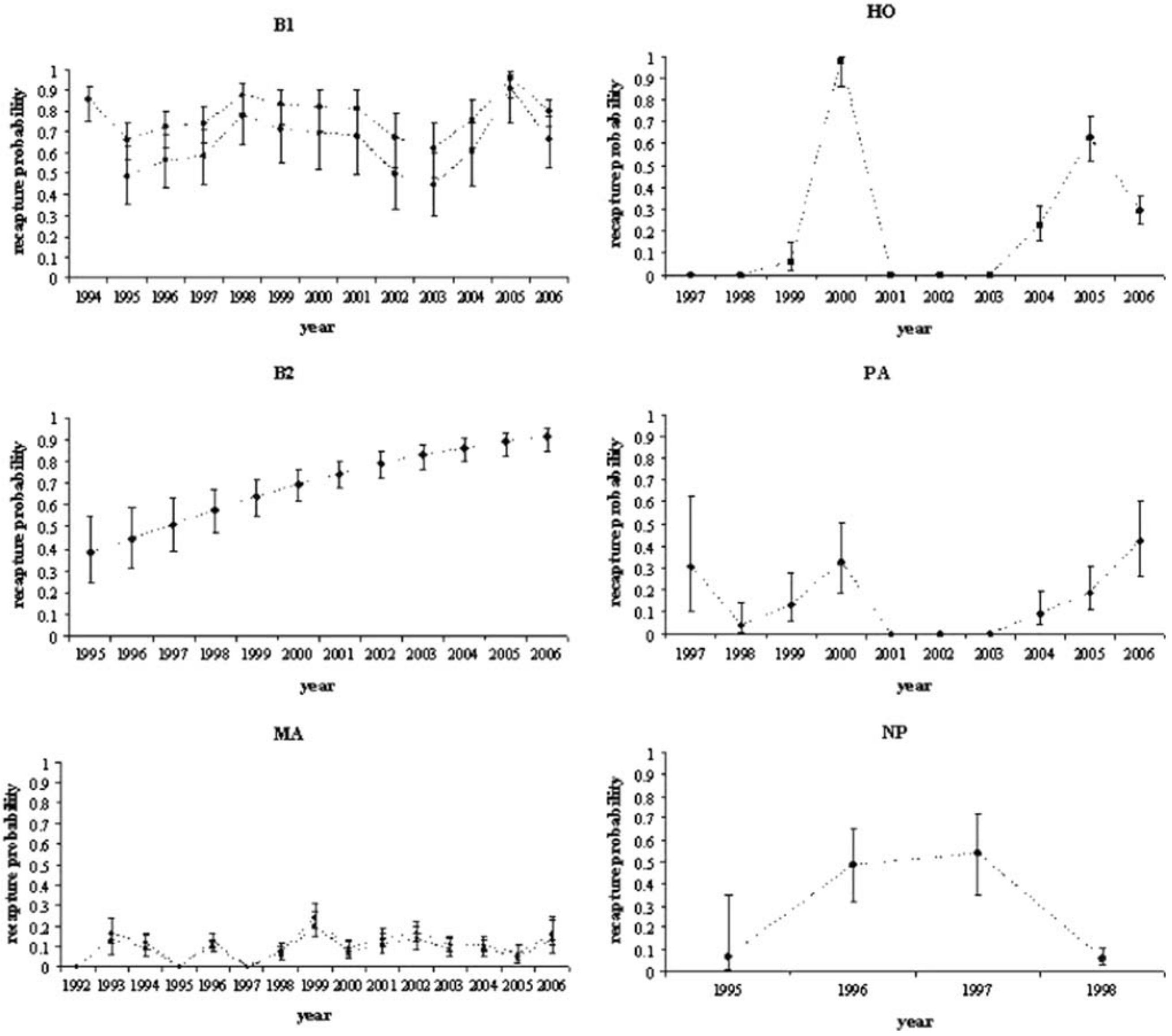

**Fig. 4** Model averaged estimates of recapture probabilities during the study periods at colonies B1(cave 1, Benidorm), B2 (cave 2, Benidorm), MA (Marettimo), HO (Hormigas), PA (Palomas) and NP (Na Plana). Note that at B1 and MA there are two recapture probabilities. The *upper line* for B1 is for trap-happy individuals and the *lower line* at MA is for trap-shy individuals, the other *lines* are for the rest of the birds

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