

LIVING CLOSE, DOING DIFFERENTLY: SMALL-SCALE ASYNCHRONY IN DEMOGRAPHY OF TWO SPECIES OF SEABIRDS

GIACOMO TAVECCHIA,^{1,2,5} EDUARDO MINGUEZ,³ ANA DE LEÓN,⁴ MAITE LOUZAO,¹ AND DANIEL ORO¹

¹*Institut Mediterrani d'Estudis Avançats (IMEDEA), CSIC-UIB, Miquel Marques 21, Esporles, Mallorca 07190 Spain*

²*Institute of Mathematics, Statistics and Actuarial Science, University of Kent, Canterbury CT2 7NZ United Kingdom*

³*Universidad Miguel Hernández, Avda. de la Universidad s/n, Edif. Torreblanca, Elche, Alicante 03202 Spain*

⁴*Ornithology Group, IBLS, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ United Kingdom*

Abstract. Studies on spatiotemporal pattern of population abundance predict that close populations should exhibit a high level of synchrony, reflected in a parallel time variation of at least one demographic parameter. We tested this prediction for two threatened species of Procellariiformes sharing similar life history traits: the European Storm Petrel (*Hydrobates pelagicus*) and the Balearic Shearwater (*Puffinus mauretanicus*). Within each species, we compared adult survival, proportion of transients (breeders that do not settle), and average productivity at two neighboring colonies. Physical and environmental features (e.g., food availability) of the breeding sites were similar. However, while Balearic Shearwater colonies were free of predators, aerial predators occurred especially in one colony of the European Storm Petrel. Despite this difference, we found similar results for the two species. A high proportion of transient birds was detected in only one colony of each species, ranging between 0.00–0.38 and 0.10–0.63 for the petrels and shearwaters, respectively. This seems to be an emergent feature of spatially structured populations of seabirds, unrelated to colony size or predator pressure, that can have important demographic consequences for local population dynamics and their synchrony. Local survival of resident birds was different at each colony, an unexpected result, especially for predator-free colonies of Balearic Shearwater. Productivity varied between the two colonies of European Storm Petrels, but not between the two colonies of Balearic Shearwaters. We demonstrated that within each species, several demographic parameters were colony specific and sufficiently different to generate short-term asynchronous dynamics. Our findings suggest that, in spatially structured populations, local factors, such as predation or small-scale habitat features, or population factors, such as individual quality or age structure, can generate unexpected asynchrony between neighboring populations.

Key words: *adult survival analysis; Balearic Shearwater; capture-recapture; demography; European Storm Petrel; Hydrobates pelagicus; population synchrony; Procellariiformes; Puffinus mauretanicus; seabirds.*

INTRODUCTION

The degree of synchrony between the different demes of spatially structured populations is an important determinant of their persistence and much attention has been devoted to factors underpinning between-population synchrony (see review in Bjørnstad et al. 1999, Lloyd and May 1999). Moran (1953) showed that the degree of synchrony between two identical systems should equal the degree of correlation between their environments, usually measured by climatic variations (Lande et al. 2003). Empirical evidence of the Moran effect can be found in different taxa (Grenfell et al. 1998; but see Blasius and Stone 2000, Ruetz et al. 2005). In addition to environmental correlation, synchronous

population dynamics also can be induced by parameters such as density-dependent dispersal (Sutcliffe et al. 1996, Paradis et al. 1999). Environmental and dispersal effects are difficult to disentangle (Ranta et al. 1995), but the expected pattern of synchrony is different: although individual dispersal generates a negative correlation between the degree of synchrony and interpopulation distance, climate-induced synchrony is less dependent upon the distance considered (Stenseth et al. 1999). Finally, biotic interactions (such as predator-prey and host-parasitoid systems) also can induce synchrony in population dynamics (Ims and Andreassen 2000, Liebhold et al. 2004a, b).

A general consensus is that the relative roles of climate, dispersal, and predation in shaping synchrony largely depend on the spatial scale and that synchrony is negatively associated with distance (Koenig 1999, Lloyd and May 1999). Climate is the dominant cause of synchrony at a large spatial scale, whereas predation or between-population movements are more likely to act at a medium or small scale (Ranta et al. 1995), depending

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⁵ Address for correspondence: Institut Mediterrani d'Estudis Avançats (IMEDEA), CSIC-UIB, Miquel Marques 21, Esporles, Mallorca 07190 Spain. E-mail: g.tavecchia@uib.es

upon the species dispersal ability (Paradis et al. 1999). Even if these causes act synergistically and are difficult to disentangle, climatic variation and movements generate two implicit predictions regarding synchrony. First, whatever the cause, two neighboring populations should show synchronous dynamics and this should be more evident in species with high dispersal ability (Paradis et al. 1999). Individuals of close populations are more likely to experience the same weather regime, a relatively high exchange probability, and a similar predator pressure, characteristics positively associated with between-population synchrony. Second, the mechanistic explanation of synchronous dynamic is a parallel fluctuation over time between the demographic parameters of the populations (Cattadori et al. 2005). Synchrony measures derived by the analysis of population counts fail to elucidate the mechanisms underlying parallel fluctuations. For this reason, recent studies tend to focus directly on the variation of demographic parameters using detailed information on individual life histories (Lecomte et al. 2004, Cattadori et al. 2005, Frederiksen et al. 2005, Harris et al. 2005, Schaub et al. 2005). Evidence of synchronous dynamics can thus be derived by the time-dependent pattern of demographic parameters, although the parallel fluctuation of one or more of them is a necessary, but not sufficient, condition for synchrony to occur. Moreover this approach is recommended when population abundances are not available or when large sampling errors are associated with them.

We analyzed the synchronous pattern of demographic parameters in two neighboring colonies of two threatened seabirds: the European Storm Petrel (*Hydrobates pelagicus*) and the Balearic Shearwater (*Puffinus mauretanicus*). Despite differences in body mass (average 45 g for Storm Petrels and 500 g for Shearwaters) and foraging niche, the two species share many life history traits: a relative long life span and low fecundity, a cavity-nesting habit and high breeding-site fidelity (Warham 1990, Mínguez and Oro 2003, Oro et al. 2005). The definition and measures of population synchrony are not consistent in the ecological literature (Vik et al. 2004). Here we tested the hypothesis that two colonies in close proximity, sharing the same ecological features, are fluctuating synchronously in time, as predicted by the Moran effect and the generally accepted negative association between distance and synchrony. Because it is notoriously difficult to estimate population abundances for these species, evidence of population synchrony can be achieved only by assessing the parallel time oscillation in least one demographic parameter. The population growth rate of long-lived species is more sensitive to a change in adult survival probability (Lebreton and Clobert 1991), suggesting that parallel oscillations of populations can result from a synchronous change in this parameter. On the other hand, natural selection tends to reduce the temporal variation of the parameter that contributes the most to individual fitness (Gaillard and Yoccoz 2004, Morris and Doak

2004), and observed changes in population growth rate can be driven primarily by a change in fecundity parameters. As a consequence we considered for each species adult survival probability, transient probability (probability of breeding only once) and breeding parameters (hatching success and fledgling success). Numerically, we expect to retain a time effect on one or all of these parameters and to drop the statistical interaction between the “colony” and “time” effects.

To confirm that the dynamics of the study colonies were synchronous, we then estimated the correlation between the colony-specific population growth rates over time (Bjørnstad et al. 1999, Vik et al. 2004), using a matrix population model. We used this approach because an asynchronous fluctuation in demographic parameters is a necessary, but not a sufficient, condition for asynchronous dynamics. This is because the variance of a given demographic parameter is negatively associated with the relative contribution of this parameter to population change, i.e., its sensitivity (Pfister 1998). As a consequence, the variation of a parameter over time does not necessarily result in a change in the population growth rate.

METHODS

Study sites and species

Data for European Storm Petrels were collected during 1993–2002 in two neighboring colonies at Benidorm Island on the western Mediterranean coast of Spain (38°30' N, 0°8' E; Fig. 1). The sites were very close (150 m), but their size varied markedly: one colony, hereafter A_p (the subscripts p and s indicate parameters for Storm Petrels and Balearic Shearwaters, respectively), was a large cave containing an estimated population of more than 200 pairs, while the second colony, B_p , was smaller in size and had an estimated population of about 100 pairs (see also Oro et al. 2005). Despite their proximity, there has been only one record of adult dispersal between the two sites in a 10-year period. The effect of Yellow-legged Gulls *Larus michahellis* preying on adult birds arriving at the sites has apparently increased during the last years, mainly on colony A_p (Oro et al. 2005).

For Balearic Shearwaters, two colonies of the southwestern coast of Mallorca Island (39°31' N, 2°23' E; Fig. 1) were monitored during the period 1997–2004. The sites were 15 km apart, a short distance considering the large foraging range of the species (~40 000 km²; Arcos and Oro 2004). One of the colonies, colony A_s hereafter, had an estimated size of ~200 pairs; the other, B_s , was smaller (~45 pairs) (Oro et al. 2004a). There have been no cases of dispersal recorded during the eight-year period of the study and both colonies were free of predators during the study period.

Adult survival and transient parameters

Adults were captured during the incubation period or just after egg hatching at the nest and were marked using

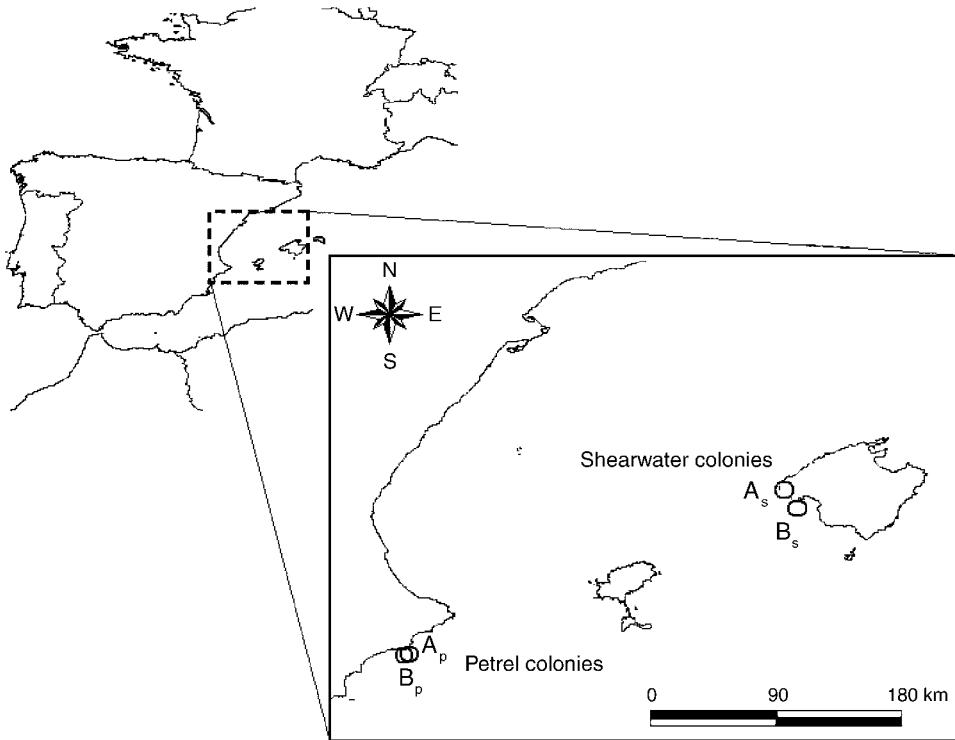


FIG. 1. Colony locations of the European Storm Petrel *Hydrobates pelagicus* (A_p , B_p) and Balearic Shearwater *Puffinus mauretanicus* (A_s , B_s) in the western Mediterranean.

a uniquely coded metal ring (see details in Oro et al. 2004a, 2005). We analyzed the encounter histories of 627 breeding European Storm Petrels and 573 Balearic Shearwaters (474 and 153 in colonies A_p and B_p and 321 and 252 in colonies A_s and B_s , respectively). Adult local survival estimates were obtained by maximum likelihood procedure from individual encounter histories using software MARK version 1.9 (White and Burnham 1999). This approach does not distinguish mortality from permanent emigration, and survival includes an emigration component. Model selection started from the general model assuming a colony-by-year interaction on survival and recapture parameters, noted $\{\phi[(c + t + c.t) p(c + t + c.t)]\}$, where t denoted a year effect, c a colony effect, and $t.c$ denoted their statistical interaction. If populations showed parallel fluctuations in survival probabilities, i.e., synchrony, $t.c$ would not be retained.

We contrasted models with and without temporal variability and the colony-by-time interaction term in order to calculate the fraction of the total temporal deviance explained by a common pattern of variation as in Harris et al. (2005). The goodness of fit of the general model was tested by contingency tables (see Appendix A) using program U_CARE1.4 (Choquet et al. 2000). The goodness-of-fit test sums the results of four sets of contingency tables, traditionally named test3.SR, test3.SM, test2.CT, and test2.CL, built for each time interval (Pollock et al. 1990, Pradel et al. 2005; see Appendix A). Choquet et al. (2005) proposed directional

tests (Z tests) designed to detect systematic deviations from the expected values in the contingency tables of test3.SR and test2.CT. A significant Z value on test3.SR suggests a difference in local survival between newly and already marked birds, an effect known as "transience" (Pradel et al. 1997a). A significant Z value on test2.CT indicates a difference in recapture probability in relation to previous capture, an effect known as "trap dependence" (Pradel 1993; see Appendix A). Both effects were significant in at least one species (see Results). The presence of transients was taken into account by considering extra survival parameters for newly seen individuals, noted ϕ' (Pradel et al. 1997a, Oro et al. 1999, Perret et al. 2003). Note that here transient birds are not erratic or prospecting individuals, but birds that bred at the colony once and were never seen again. The transient probability (noted by τ) can be estimated as

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

where ϕ'_i is the survival rate for newly seen individuals, and ϕ_i that for residents. Confidence intervals for τ can be calculated using the Delta method (Morgan 2000). The trap-dependence effect was corrected for by coding capture histories, as suggested in Pradel (1993) and Pradel et al. (1997b). The remaining extra-binomial variation was taken into account by scaling model deviances by a variance inflator factor, \hat{c} , calculated as

the ratio of the χ^2 goodness of fit to its degrees of freedom (Lebreton et al. 1992).

Breeding parameters

Data on breeding success for the two species were collected by inspecting nests throughout the breeding season. We analyzed the breeding success of 286 nests of European Storm Petrels between 1993 and 2002 (2059 monitored nests in total), and of 136 nests of Balearic Shearwaters between 1997 and 2004 (672 monitored nests in total). We restricted the analysis to active nests only, i.e., where an egg was laid. Nests were followed from the beginning of the laying period until the end of the fledging period. During subsequent visits (an average of five visits per nest and year), we recorded whether the egg hatched and whether the chick survived, i.e., when it reached the fledging age at the end of the breeding season (40 days for European Storm Petrels, 60 days for Balearic Shearwaters). Differentiating egg failure from hatching mortality was simple in the absence of nest predators in all study colonies, and remains of eggs or chicks were easily found in the nest cavities. We first analyzed overall breeding success, i.e., the probability that an egg would produce a fledgling bird. Subsequently, we split breeding success into its two components, namely the hatching success (the probability that an egg will hatch) and the fledging success (the probability that a chick will stay alive until fledging), which in our single-egg study species equated to the number of fledglings per breeding pair. These probabilities were modeled as binomial responses using generalized linear models (software GENSTAT version 7.1; Lawes Agricultural Trust, Rothamsted, UK). Note that the Mayfield method was not applicable here because all nests were monitored from the beginning of the laying phase, and because, in Procellariiformes, the incubation period may vary from nest to nest (Williams et al. 2002).

We investigated which component of breeding success varied the most by measuring the relativized coefficient of variation, CVr, for zero-to-one variables. The CVr is the ratio between the coefficient of variation and its maximum expected value (Morris and Doak 2004). This measure is preferable to the simple coefficient of variation: the variance and the coefficient of variation of zero-to-one variables are truncated because they cannot have high mean and high variance at the same time (Morris and Doak 2004). We used a subsample of 702 nests of European Storm Petrels in which male and females were identified to test whether the heterogeneity in breeding parameters between pairs was significant, considering pair identity as a random effect in a generalized linear mixed model (IRREML [iterated reweighted restricted maximum likelihood] models in GENSTAT version 7.1). Pair identity was not significant; hence, we treated observations from the same pair in consecutive years as independent. For the Balearic Shearwater, data were too sparse to perform a similar analysis and multiple observations of the same pair were

assumed to be independent. We tested the effect of year (t), of the colony (c), and their statistical interaction ($t \cdot c$). As before, if populations were to show parallel fluctuations in breeding parameters, i.e., synchrony, the term $t \cdot c$ would not be significant. To account for model selection uncertainty, model-averaged estimates were presented.

Model selection

Model selection and notation were the same in the analyses of survival and breeding parameters. Once we had accounted for the heterogeneity, we eliminated nonsignificant effects from the general model. Models were compared using Akaike's Information Criterion, AIC (Burnham and Anderson 1998), and were arbitrarily considered equivalent when their values were within 4 points (Burnham and Anderson 1998:123). When this occurred, we retained the most parsimonious model, i.e., the one with the smallest number of parameters. The AIC was denoted as QAIC when an overdispersion parameter was used to scale model deviances, and Δ QAIC was the difference in QAIC between the model tested and the model finally selected. Finally, the AIC was corrected for small sample size (AIC_c) in the adult survival analysis (Burnham and Anderson 1998).

Population modeling

To investigate whether the colony-specific differences were large enough to create asynchronous dynamics, we constructed simple deterministic matrix population models for each colony based on parameter values estimated in the present study. The dominant eigenvalue of matrix A_i^j was taken as the population growth rate between time i and $i + 1$ (see Appendix C; Case 2000, Caswell 2001). Under the hypothesis of synchronous dynamics between the two colonies of each species, we expected a significant correlation between their respective population growth rates. For adults, we used time-specific parameters in the matrices if temporal variability was proved to be significant. Individuals of both species start to reproduce at the age of 3 years (Oro et al. 2004b), but survival estimates for the pre-breeding period are unknown. Hence, for immature birds we assumed the average value of adult survival. The hypothesis of a constant pre-breeding survival equal to the survival of adult birds is likely to be unrealistic, but it is conservative when testing for a correlation between colony-specific population growth rates. A more robust approach to estimating population growth rate using capture-recapture data (Pradel 1996) was not possible in our case because recruitment parameters could not be estimated (only adults were marked). The matrix-based population growth rate does not necessarily reflect the true increase in population size because it does not account for immigration and is based on the unrealistic assumption of a stable age structure. Moreover, our aim was not to model the actual dynamics but to synthesize the demographic information by period for comparison.

TABLE 1. Components of the goodness-of-fit test of the general model assuming year-by-colony-specific parameters at two colonies (A, larger; B, smaller) for each species.

Component	European Storm Petrel						Balearic Shearwater					
	A_p			B_p			A_s			B_s		
	χ^2	df	Z		χ^2	df	Z		χ^2	df	Z	
Test3.SR	29.2	8	2.8	14.7	7	1.1	6.9	6	0.0	31.6	10	2.0
Test3.SM	9.7	8		7.7	6		3.6	5		7.1	6	
Test2.CT	77.1	7	-7.9	7.0	6	-2.0	7.3	5	-1.6	4.9	6	-0.4
Test2.CL	17.3	8		1.2	4		6.1	5		0	1	

Notes: The first two components, test3.SR and test3.SM, test for among-individual homogeneity in survival; test2.CT and test2.CL test for homogeneity in recapture processes (Pollock et al. 1990, Choquet et al. 2005; Appendix A). Z statistics on test3.SR and test2.CT, respectively, are used to test for the presence of transients (animals seen only once) and for a trap-dependence effect (i.e., current capture probability is influenced by previous capture history); see Appendix A. Significant tests are in boldface. For the petrel, colony A_p contained >200 pairs, and colony B_p contained ~100 pairs. For the shearwater, colony A_s contained ~200 pairs, and colony B_s contained ~45 pairs.

In this case, the matrix-based population growth can give an indication of the deterministic growth rate according to the parameters used in the model.

RESULTS

Adult survival parameters

The goodness-of-fit test of the first model $\{\phi(t + c + t.c) p(t + c + t.c)\}$ was significant for both species ($\chi^2 = 163.8$, df = 54, $P < 0.001$ and $\chi^2 = 67.4$, df = 54, $P = 0.017$; Table 1), hence, this first model did not explain the data adequately. This was due to the presence of transients in colonies A_p and B_s , i.e., an excess of newly marked breeders that were never recaptured (Table 1). Moreover, there was an indication that some European Storm Petrels were captured or present more often than others, i.e., a trap-dependence effect (Table 1): we consequently considered specific parameters, noted m , for consecutive recaptures for Storm Petrels (denoted by subscript p). The more general models $\{\phi'_p(t + c + t.c) \phi_p(t + c + t.c) p_p(m + t + c + t.m + c.m + t.c + m.t.c)\}$ ($\chi^2 = 35.98$, df = 26, $P = 0.090$; scale parameter $\hat{c} = 1.53$) and, for shearwaters (subscript s), $\{\phi'_s(t + c + t.c) \phi_s(t + c + t.c) p_s(t + c + t.c)\}$ ($\chi^2 = 28.94$, df = 29, $P = 0.283$; scale

parameter $\hat{c} = 1.06$; Table 1) were used as starting point for the analyses. We began model selection for Storm Petrels by testing the interaction terms in the probability of recapture (models 1–6 in Appendix B). None of these were significant and a trap-dependence effect was significant in colony A_p only (models 2 and 3 in Appendix B). The probability of recapture in colony B_p increased linearly over time (model 6 in Appendix B). A further reduction in the QAIC_c value was obtained by assuming a constant and common adult survival probability for resident birds in A_s and B_s (model 8; Appendix B). In contrast, a time effect on survival of first-seen animals in colony A_p was retained (models 9 and 11; Fig. 2a). The percentage of the variance explained by a colony-by-time interaction was 77% (models 10–12). Although model 8 had a low ΔQAIC_c value, there was evidence that the local adult survival of resident birds changed over colonies when this effect was retested in the presence of a time-varying recapture probability in colony A_s (models 17 and 18), which was dropped in an earlier stage of the model selection. Model averaging of these models yielded survival estimates of 0.781 ± 0.019 (mean \pm SE) and 0.690 ± 0.036 for colony A_p and B_p , respectively. Surprisingly, the colony

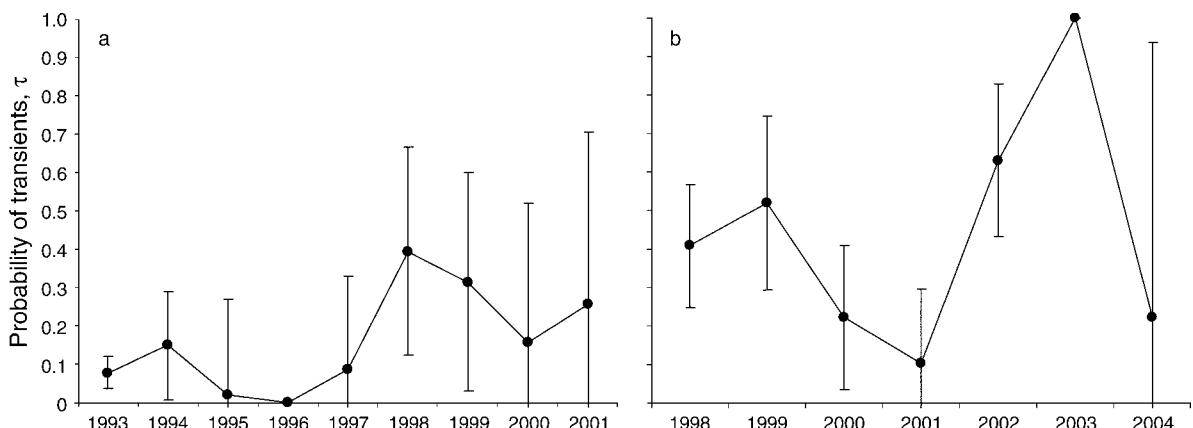


FIG. 2. Mean proportion (and 95% confidence interval) of transients (τ), i.e., breeders that do not settle, for (a) European Storm Petrels and (b) Balearic Shearwaters in colonies A_p and B_s , respectively, with variation over time in both cases.

TABLE 2. QAIC values of models for the estimation of breeding parameters.

Effects	European Storm Petrel success			Balearic Shearwater success		
	Hatching	Fledging	Breeding	Hatching	Fledging	Breeding
$t + c + t.c$	2071.25	961.00	2074.62	689.22	211.90	683.76
$t + c$	2078.25	986.90	2098.92	686.41	206.60	678.23
c	2190.72	1002.40	2199.39	690.35	206.80	679.88
t	2076.25	986.40	2096.92	684.41	204.60	676.23
-	2188.70	1001.90	2197.39	688.43	205.10	677.88
\hat{c}	1.28	1.00	1.30	1.26	1.00	1.31

Notes: Model notation includes t , time; c , colony; $t.c$, interaction between t and c ; and - constant. The overdispersion parameter \hat{c} is used to scale model deviance for each species. Retained models (those within 4 AIC points of the lowest AIC value) are in boldface.

with higher adult survival was the one with higher predation by Yellow-legged Gulls but with a significant lower survival for first-seen birds, i.e., transients.

Results for the Balearic Shearwaters were similar. The first models indicated a significant interaction in the probability of recapture between the colony and time effects (models 19–23 in Appendix B). In particular, recapture probability varied significantly over time in colony A_s but not in colony B_s . When transient and resident birds in colony B_s were assumed to have the same survival, the colony-by-time interaction explained 23% of the spatiotemporal variation in survival and models assuming a common pattern of variation across colonies were rejected (models 24–26, Appendix B). This colony-dependent pattern was caused by the presence of transients in colony B_s . Indeed, resident birds in colony B_s and birds breeding in colony A_s had a similar pattern of variation in survival (model 26), but this pattern was not retained for transient birds (model 27). Again, the retained model (model 27) includes a time-by-colony interaction term due to a variable transience probability, even though the colonies were free of predators. From the model assuming an average value of survival in both colonies (model 30), the survival probability was 0.807

± 0.02 (mean \pm SE) for colony A_s and 0.662 ± 0.04 for resident birds in colony B_s . As for Storm Petrels, adult survival probability of first-seen birds in colony B_s (i.e., transients) was changing with time (Fig. 2b), but in this case the colony with lower adult survival was also the one with transients.

Breeding parameters

The average breeding success was very similar between the two colonies for both species (0.49 and 0.51 for Storm Petrels and 0.62 for the two colonies of Balearic Shearwaters). Despite the similarity of average values, the interaction between colony and year effects was significant for European Storm Petrels ($\Delta\text{QAIC} = 24.3$; Table 2, Fig. 3a): colony B_p had a lower breeding success than colony A_p between 1993 and 1996, but reversing in 1997. The percentage of the total deviance explained by the interaction between year and colony on the breeding success was 26%, but this varied from 16% for the hatching success to 57% for the fledging success. In contrast, the breeding success of the Balearic Shearwater was constant over time and colonies (Table 2, Fig. 3b). For the Storm Petrel, the interaction between year and colony was again significant for hatching and

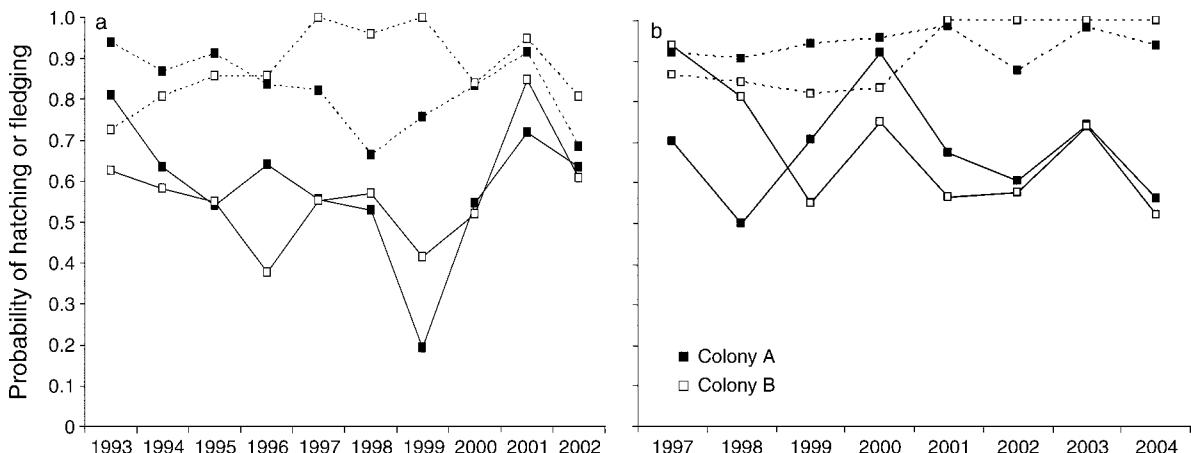


FIG. 3. Changes in hatching (solid lines) and fledging (dashed lines) probabilities according to colony and year for (a) European Storm Petrels and (b) Balearic Shearwaters. Note that fledging probability was conditional to hatching. For the Storm Petrel, colony A had greater values until 1996, but the trend reversed afterward, causing the interaction term between year and colony to be retained during model selection. For the Balearic Shearwater, variations in hatching or breeding success were not significant.

fledging success ($\Delta\text{QAIC} = 7.0$ and 16.3, respectively; Fig. 3a). This effect explained a similar percentage of the total deviance (38%) in both, hatching and fledging success. In larger colonies the hatching success was more variable than the fledging success (Table 3), but these two components showed similar variation in the smaller colonies.

Matrix modeling analysis

The estimated yearly population growth rates of both colonies were not correlated either for European Storm Petrels or for Balearic Shearwaters (Kendall's rank correlation coefficient = 0.11, $P = 0.76$; and Kendall's correlation coefficient = 0.33, $P = 0.38$, respectively). This difference persisted for the Storm Petrel even when transients were not considered.

DISCUSSION

Results suggest that adult survival was mainly time invariant, but, unexpectedly, it was different at each colony of both species. Although the general theory and empirical examples have showed that long-lived birds exhibit constant adult survival (Lebreton 2001, Tavecchia et al. 2001, Weimerskirch 2002), there is recent evidence that this parameter may change steadily in time and space, even at neighboring colonies, influenced by local factors such as food availability or predator density (Cam et al. 2004, Frederiksen et al. 2005). Nevertheless, the colony-specific survival at two adjacent sites found here was difficult to interpret. For Storm Petrels, adult survival was strikingly higher in the colony with higher predation rates (and the only one with a transient effect, probably brought about by predators); for Balearic Shearwaters, this result was even more unexpected because both study colonies were free of predators. The presence of large numbers of transient animals at one colony of each species was an additional emergent feature of the present study; their influence in population dynamics seldom has been described (but see Perret et al. 2003, Cam et al. 2004), and most of the time it has been related to juveniles that disperse from the study site before breeding or to erratic animals that do not breed (e.g., Clark et al. 2004). Furthermore, transients varied stochastically with time (Oro et al. 1999). Again, although increased predation by the Yellow-legged Gull on Storm Petrels could explain the existence of transients (Oro et al. 2005), other unknown factors should drive the same phenomenon in the Balearic Shearwater. Independently of the local causes, a high apparent mortality or permanent emigration of first-seen animals can be demographically significant (Oro et al. 1999, Perret et al. 2003) and strong enough to drive close populations into asynchronous fluctuations.

Breeding parameters of the two species varied significantly over time, although this variation was less pronounced for the Balearic Shearwater. For the European Storm Petrel, the interaction between year and colony was significant for hatching and fledging

TABLE 3. Relativized coefficients of variation, CV_r, of hatching and fledging success.

Colony	European Storm Petrel success		Balearic Shearwater success	
	Hatching	Fledging	Hatching	Fledging
A	0.33	0.25	0.27	0.15
B	0.26	0.28	0.32	0.32

Note: For details on calculation of CV_r, see *Methods*.

success (Fig. 3). This result was unexpected and cannot be related to yearly food availability, which, given the close proximity, must be the same for both colonies. The breeding success in the Balearic Shearwater varied over time but it was constant over time and space. The different pattern between species could be the result of different predation rates, affecting the petrels but not the shearwaters. In the absence of predation, populations sharing the same foraging grounds should show similar breeding parameters (but see Lambrechts et al. 2000, Nel et al. 2002, Genovart et al. 2003). There are two common features in our results that appear to be linked with colony size. First, resident birds in larger colonies have higher local survival than resident birds in small colonies. Second, variation in breeding success occurred mainly because of variation in the probability of hatching. This component of breeding success varies the most in larger colonies, probably due to the greater interindividual variability. Overall, our results showed that, in contrast with general theoretical predictions and empirical examples in many different organisms (Weatherhead et al. 2002, Johnson et al. 2005, Schaub et al. 2005), adjacent populations can exhibit asynchronous dynamics (see also Weimerskirch et al. 1997, Sagar et al. 1999, Frederiksen et al. 2005). The pattern of variation in adult survival, transience probability, and breeding output at each study colony seemed large enough to generate asynchronous dynamics in both species, at least in the short term. This is remarkable, because adult survival in Procellariiformes is nearly time invariant, probably due to environmental canalization of life history traits (see Gaillard and Yoccoz 2004) as natural selection tends to reduce the variability of the parameters that contribute the most to individual fitness (Morris and Doak 2004). The probability of survival of the resident birds was invariant over time in both species. At population level, however, the presence of transients induced a change in survival over time in at least one colony of both species that induces asynchrony. Nevertheless the nonsignificant association between population growth rates should be interpreted with caution due to the several non-estimated parameters (e.g., recruitment, juvenile survival), which were assumed to be the same for both colonies (Appendix C). Moreover, the period of time considered here was relatively short and, in this case, a small number of years with contrasting population trend may be sufficient to disrupt the association between population

growth rates. Our study focused on small-scale processes and we cannot exclude synchrony at larger spatial or temporal scale. Nevertheless, our findings suggest that differences in demographic processes, mediated by local habitat or individual characteristics, can generate unexpected patterns of population synchrony.

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APPENDIX A

Verifying capture–recapture assumptions (*Ecological Archives* E089-006-A1).

APPENDIX B

Modeling survival and encounter probability (*Ecological Archives* E089-006-A2).

APPENDIX C

Species- and colony-specific population matrix models (*Ecological Archives* E089-006-A3).