

Assessment of hypotheses about dispersal in a long-lived seabird using multistate capture–recapture models

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Summary

1. Dispersal contributes to spatio-temporal variation in population size and is a key process in studies of life history evolution and studies with conservation implications. However, dispersal is still one of the major gaps in our knowledge of ecological dynamics. The very large literature on metapopulation dynamics lacks empirical bases on dispersal and relevant behavioural parameters. We used multistate capture–recapture models (data from 1988 to 2001) to address hypotheses about movement probability and habitat selection within a system of two breeding colonies in Audouin's gulls (*Larus audouinii*), an endemic species breeding in the Mediterranean and considered as threatened.

2. Movement probability varied over time, and differed greatly between the colonies.

3. We did not find evidence of an influence of colony size or density of predators on movement probability.

4. In dispersers, our results did not support the hypotheses that movement probability between year t and $t + 1$ was influenced by mean breeding success in the colony of origin (i.e. an indicator of habitat quality) or the destination colony in year t or $t + 1$, or by the ratio of breeding success in these colonies in year t or $t + 1$ (i.e. quality gradient).

5. Overall, movement probability was higher from the smaller colony to the larger, and from the colony with lower breeding success in year t to the more productive one. This provides slight support for two nonexclusive hypotheses about habitat selection (conspecific attraction and conspecific success attraction).

6. Movement probability from the smaller, less productive colony was very high in some years, suggesting that the dynamics of both colonies were strongly influenced by adult dispersal. However, in absolute numbers, more individuals moved from the larger, more productive colony to the smaller one. This suggests that the system may function as a source–sink system.

7. Use of multistate models to re-assess local survival showed that survival was lower in the less productive colony with higher emigration probability. This may reflect genuine differences in mortality between colonies, or more probably differences in permanent emigration from the study area.

Key-words: adult survival, asymmetrical movement, colonies, habitat selection.

Journal of Animal Ecology (2004) **73**, 723–736

Introduction

All population changes result from births, deaths, emigration and immigration. Dispersal contributes to spatio-temporal variation in population size, and is therefore a process to consider in studies with conservation and management implications (e.g. Nichols *et al.* 2000; Cooch, Rockwell & Brault 2001; Hanski 2001; Oro & Ruxton 2001). In addition, dispersal and spatio-temporal variation in local population size and growth rates within metapopulations are components of the selective environment of life history traits (Stearns 1992); they are also relevant to studies of the evolution of life history traits other than dispersal itself (Caswell 1982; Olivieri & Gouyon 1997). Dispersal (and the resulting gene flow) is one of the mechanisms underlying evolution (Barton 2001). However, as emphasized by Hanski (1999) and Bennetts *et al.* (2001), there is a long history of investigation of reproductive parameters and survival probability but dispersal still constitutes one of the major gaps in our knowledge of ecological dynamics. MacDonald & Johnson (2001) pointed out that despite the 'prodigious' number of models of dispersal evolution (Johnson & Gaines 1990), 'there remains an almost complete absence of empirical data on dispersal and other relevant behavioural parameters in recent population extinction studies'. The very large literature on metapopulation dynamics lacks empirical bases (Spendelov *et al.* 1995; Hanski 2001; MacDonald & Johnson 2001).

Until recently, practical difficulties in field studies (e.g. Spindelov *et al.* 1995; Koenig, Van Vuren & Hooge 1996) and limitations of available approaches to statistical inference about movement of individuals among locations were two major obstacles in investigations of dispersal processes (Bennetts *et al.* 2001). Recent development of approaches to estimating movement probability using data from marked animals has considerably increased our ability to address dispersal (e.g. Nichols *et al.* 1992; Clobert 1995; Nichols & Kendall 1995; Nichols 1996; Nichols & Kaiser 1999; Bennetts *et al.* 2001; Williams, Nichols & Conroy 2002). Logistical difficulties still remain substantial: estimation of movement probability within metapopulations requires careful design and the study of marked individuals in several locations simultaneously. In species with high dispersal ability, logistical limitations seldom allow investigators to monitor many locations simultaneously, especially locations far away from the main study area (Koenig *et al.* 1996). As a result, in spite of development of robust approaches to statistical inference about movement in the 1970s (e.g. Arnason 1972, 1973) and implementation of these approaches in flexible software programs in the 1990s (e.g. Brownie *et al.* 1993; Lebreton, Almeras & Pradel 1999; White & Burnham 1999), empirical studies of dispersal among patches using robust approaches to estimating movement probability are still few (but see Hestbeck, Nichols & Malecki 1991; Brownie *et al.* 1993; Spindelov *et al.* 1995; Nisbet & Cam 2002; Senar, Conroy & Boras 2002).

Historically, much of the focus of studies of metapopulation dynamics was on patch occupancy models (e.g. reviewed in Hanski 1999). The proportion of patches occupied depends on patch extinction and colonization probabilities, which depend clearly on dispersal (Hanski 1999; Hanski, Alho & Moilanen 2000). Despite this relationship, as emphasized by Spindelov *et al.* (1995) theories of metapopulation dynamics have produced relatively few predictions about the probability that an individual in a patch moves to another patch (but see Fretwell & Lucas 1970; Pulliam 1988; McPeck & Holt 1992; Holt 1997). Studies of individually marked animals, a powerful approach to direct estimation of movement probability among patches (e.g. Clobert 1995; Nichols & Kendall 1995; Bennetts *et al.* 2001; Hanski 2001) naturally lend themselves to investigations of hypotheses about dispersal (e.g. Spindelov *et al.* 1995). Here we estimated movement between two colonies of Audouin's gulls (*Larus audouinii*), an endemic species breeding in the Mediterranean, and considered as threatened (Oro 1998).

We used multistate capture–recapture models (e.g. Nichols & Kendall 1995) to estimate movement probability. In long-lived species, it is natural to assume that individuals have to make decisions concerning fidelity to their previous breeding site every year. As individuals are likely to experience changes in environmental characteristics throughout life, fixed dispersal strategies (e.g. individual dispersal behaviour being independent of environmental conditions) are unlikely to be favoured by natural selection (e.g. Ronce *et al.* 2001). In mobile long-lived animals dispersing actively, dispersal can be viewed as a 'decision making' problem (i.e. 'to stay or to leave'; e.g. Danchin, Boulinier & Massot 1998; Doligez *et al.* 1999; Brown, Bromberger & Danchin 2000; Murren *et al.* 2001; Serrano *et al.* 2001). It has been hypothesized that decisions are state-specific (i.e. depend on the individual state, such as condition, previous breeding success, breeding habitat and other environmental factors; Mangel & Clark 1988; McNamara & Houston 1996; Danchin *et al.* 1998; Clark & Mangel 2000). Recent syntheses about dispersal highlighted the growing attention the questions of individual plasticity and condition-dependent dispersal are receiving (Danchin, Heg & Doligez 2001; Ims & Hjermann 2001; Ronce *et al.* 2001; Serrano *et al.* 2001; Sutherland, Gill & Norris 2002; Williamson 2002). Our second objective was to assess several hypotheses about factors potentially influencing movement probability between two colonies of Audouin's gulls in the Mediterranean.

In addition, use of multistate capture–recapture models (e.g. Nichols & Kendall 1995) permitted us to refine estimates of survival probability for the study populations. Any study conducted at a single site, or a subset of locations addresses local survival [i.e. (1–true mortality) × fidelity; Nichols *et al.* 1992; Brownie *et al.* 1993; Spindelov *et al.* 1995; Joe & Pollock 2002; Spindelov *et al.* 2002]. Decreased fidelity (i.e. increased probability of permanent emigration out of the study area) will

translate into lower local survival. Results concerning the influence of covariates (e.g. environmental conditions, population size) on local survival may reflect genuine effects on adult mortality, or the confounding influence of permanent emigration (Spendelov *et al.* 1995; Boulinier *et al.* 1997; Nisbet & Cam 2002). Here we used data from two local populations and estimated survival at a larger geographical scale than in earlier studies of the same species (e.g. Oro, Pradel & Lebreton 1999; Oro & Muntaner 2000).

BIOLOGICAL HYPOTHESES

We addressed several hypotheses about movement probability. We followed the approach specified by Nichols & Kendall (1995) and Spendelov *et al.* (1995), and addressed the hypothesis of an influence of year on movement probability, and also the hypothesis that movement probabilities among colonies were equal. When the individual's perspective is considered, the evolution of dispersal can be tackled within the framework of 'habitat selection', the broad scope of which encompasses both the decision of leaving a site and the choice of a new one (Ronce *et al.* 2001). A key question is how individuals make decisions concerning fidelity to the previous breeding site, and if they decide to move, selection of a new one (Danchin *et al.* 2001; Stamps 2001).

One of the main predictions of the 'ideal free habitat selection theory' (the cornerstone of many studies of habitat selection; Fretwell & Lucas 1970) is that natural selection should favour dispersal tactics where moving leads to increased realized fitness (i.e. habitat selection should be shaped by fitness maximization; Holt & Barfield 2001). Fretwell & Lucas (1970) hypothesized that movement between years t and $t + 1$ depends on the relative realized fitness of different locations in year $t + 1$. We might expect individuals in a habitat with lower realized fitness to move to a habitat with higher realized fitness. Densities in the various locations are expected to change as well as realized fitness in each habitat, and eventually realized fitness is equilibrated. Because of the numerous assumptions this theory relies on (e.g. individuals have perfect knowledge of their environment, there is no cost of moving, etc.; Holt & Barfield 2001; Stamps 2001), the scenario leading to the 'ideal free distribution' of individuals in space developed by Fretwell & Lucas (1970) is unlikely to be observed in the wild (Nichols & Kendall 1995). However, the seminal idea that habitat selection is shaped by fitness maximization leads to some specific predictions. In our study area, breeding success (measured by mean fledging success) was highly variable in the two colonies (e.g. Oro *et al.* 1996, 1999; see Results) over the study period, there was no parallelism in temporal variation in local mean success and mean success was never equal in the two colonies. In such a situation, we might expect asymmetrical time-varying movement probability between the colonies.

A dispersal event can be viewed as two consecutive events: the decision regarding fidelity to the previous breeding site and, if individuals disperse, the decision regarding a new breeding site. The hypothesis that fitness maximization shapes habitat selection tactics leads to the question of how individuals can assess fitness prospects in different potential locations. It has been hypothesized that individuals use their own breeding success and the success of conspecifics as cues to assess expected location-specific fitness (Danchin *et al.* 1998; Doligez *et al.* 1999; Brown *et al.* 2000; Serrano *et al.* 2001), and that the decision regarding the location where they will breed in year $t + 1$ is made in year t .

This hypothesis relies on two assumptions: (1) that individuals gather information on breeding success in various potential breeding sites in year t (e.g. through prospecting); (2) breeding success in a given site/year is a good indicator of fitness prospect in this location in the following year (i.e. habitat quality is predictable at the scale of two consecutive years; Danchin *et al.* 1998). If the above assumptions are met, we might expect the probability that individuals leave a location to be negatively correlated with breeding success in the colony of origin (used as a surrogate for realized fitness) in year t . We addressed this hypothesis using ultrastructural models (e.g. Nichols & Kendall 1995; Spendelov *et al.* 1995) where the probability of moving between years t and $t + 1$ is a function of the mean breeding success in the colony of origin in year t . We assessed two variants of this model, one with distinct baseline probabilities of leaving for the two colonies, the other with a common baseline probability of leaving. The former corresponds to a situation where the baseline probability of leaving a colony depends on the colony, the latter to a situation where this baseline probability is similar in all the colonies. We might also expect the probability of moving to a colony to be positively correlated with mean breeding success in that colony in year t . These hypotheses are not mutually exclusive. We addressed the relative importance of mean breeding success in the colony of origin and the destination colony in year t on movement probability in individuals that dispersed between years t and $t + 1$.

Breeding success *per se* may not be sufficient to account for movement. Indeed, fitness cannot be increased by leaving a location (even with low productivity) if there is no other location with higher expected fitness. We might rather expect movement between the two colonies to vary over time and to depend on differences in fitness (i.e. fitness gradient) among locations (Bull, Thompson, & Moore 1987; McPeck & Holt 1992). We used the approach specified by Nichols & Kendall (1995) to investigate the influence of the fitness gradient on movement probability (see Results).

In addition, local mean breeding success in year t may not be a good indicator of fitness prospect in the following year, and individuals may rely on other cues at the beginning of year $t + 1$ to assess local fitness prospect in that year. In this case we might expect local breeding

success in year $t + 1$ to be more important than in year t . Consequently, we considered not only the influence of the fitness gradient or breeding success in each location assessed in year t on movement probability, but also the influence of these factors assessed in year $t + 1$.

We also addressed the influence of colony size (i.e. number of breeding pairs in year t) on movement probability. The ideal free distribution (IFD) (Fretwell & Lucas 1970) relies on the idea that realized suitability varies with the density of conspecifics established in the same location: this theory assumes a negative density-dependent effect. However, density may influence movement probability for other reasons. For example, a limited number of breeding sites may simply prevent individuals from establishing in a location. It has also been hypothesized that there is a positive density-dependent effect in small size colonies (e.g. Stamps 2001). In addition, according to the conspecific attraction hypothesis (Smith & Peacock 1990; Ray *et al.* 1991), in the absence of density-dependence larger colonies are expected to attract more individuals than smaller ones (see also Forbes & Kaiser 1994). One of the colonies in the study area remained much larger than the other throughout the study.

Finally, we investigated the influence of the number of yellow-legged gulls (*L. cachinnans*) established in the same locations as Audouin's gulls on the probability of moving in the latter. Predation on eggs and chicks by yellow-legged gulls influences the overall breeding success in Audouin's gulls, and numbers of yellow-legged gulls are suspected to influence disturbance rate (e.g. Oro 1998; Martínez-Abraín *et al.* 2003a).

Methods

SOME NATURAL HISTORY FEATURES OF AUDOUIN'S GULL

Audouin's gull is a monogamous medium-sized gull species (average weight 570 g) with a modal clutch size of three eggs. The species is a specialist forager preying on clupeoids at night (see details in Oro 1998). The species is an endangered endemic seabird of the Mediterranean region that was considered to be at high risk of extinction in the late 1960s (600–800 pairs, Oro 1998). In 1981, the establishment of a new colony at the Ebro Delta (see below) increased dramatically the total number of breeding pairs, estimated at *c.* 19000 pairs in 1998 (Oro *et al.* 2000).

DATA COLLECTION

Data were collected from 1988 to 2001 in two colonies in the western Mediterranean (Ebro Delta and Columbretes Islands, Fig. 1). The habitat at the Ebro Delta is a flat and sandy peninsula of *c.* 2600 ha. Gulls colonized the peninsula in 1981; they breed in spatially discrete dunes covered by low halophilous vegetation. The peninsula is connected with the mainland only by a long (6 km) and narrow (200 m) sand bar, but terrestrial predators have access to the colony. During the whole breeding season of 1994, a European badger (*Meles meles*) was present at the colony and caused reduced reproductive success in gulls (Oro *et al.* 1999). From 1999 onwards, several foxes (*Vulpes vulpes*) arrived and

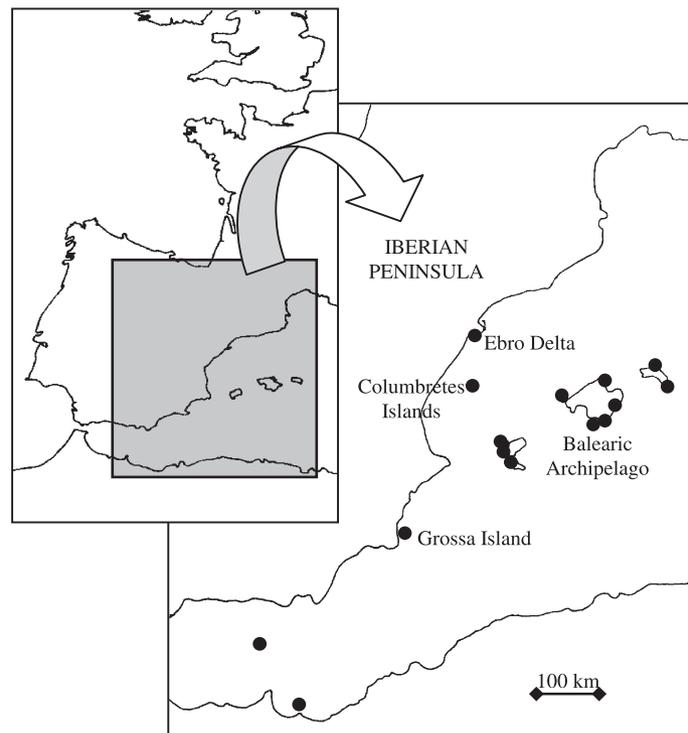


Fig. 1. Map of the western Mediterranean showing the location of most of the Audouin's gull colonies in the region, including those of the study area (the Ebro Delta and the Columbretes Islands). Names of colonies cited in the text are shown here.

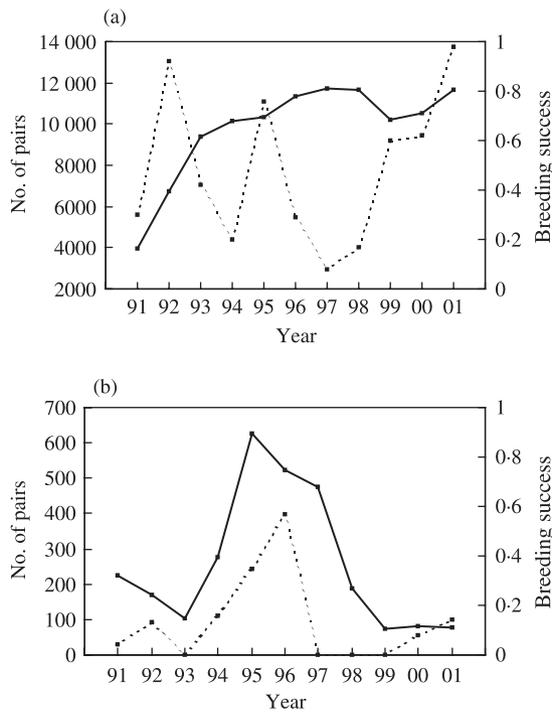


Fig. 2. Breeding numbers (solid lines) and average number of chicks per nest (dashed lines) of Audouin's gulls at the Ebro Delta (a) and the Columbretes Islands (b) used for addressing several biological hypotheses (see Methods for explanation).

were regularly present. Unlike the badger, foxes preyed on adult gulls. The number of corpses found at the colony decreased with time due to fox culling operations (Oro, unpublished data). In contrast, the Columbretes Islands are a group of rocky volcanic islands of 19 ha and located *c.* 57 km off the mainland coast, and are free of terrestrial predators. Gulls colonized the archipelago in 1974 (Martínez-Abraín *et al.* 2003b). The distance between the two colonies is 80 km.

The number of breeding pairs was estimated in every year of the study. Population size was assessed using nest counts, a standard procedure for a ground nesting species such as the Audouin's gull (e.g. Oro & Ruxton 2001; Martínez-Abraín *et al.* 2003b). This approach provides reliable estimates of population size (maximum error: $\pm 3\%$), especially in small colonies (Oro & Ruxton 2001). Breeding numbers fluctuated substantially in the two locations during the study, as well as the average number of chicks per nest. Breeding success was estimated as the average number of chicks at fledging stage per breeding pair (Fig. 2). The number of chicks at fledging stage (*c.* 4 weeks old) was assessed following a standard procedure for the species (e.g. Oro *et al.* 1996), but the approach was different at each colony. We used capture–recapture at the Ebro Delta (Oro *et al.* 1999), and counted fledglings at rafts at the Columbretes islands (Martínez-Abraín *et al.* 2003c).

Individuals were marked as chicks before fledging from 1988 onwards using a plastic band with an engraved three-digit code (e.g. Oro & Pradel 2000). From 1992 to

2001 marked gulls were resighted using a telescope during the breeding season (from March to July), except in 1994 in the Columbretes Islands. Breeding status of birds (breeder or non breeder) was assessed when possible from behavioural observations. Only one resighting per individual and breeding season was retained for analysis. We excluded immature birds (less than 3 years old, the youngest age of first breeding observed in Audouin's gull; Oro *et al.* 1999). We assumed that all observed adult birds were breeders (our objective was to address breeding dispersal). For practical reasons, it was not possible to assess individual breeding status for every bird resighted in colonies.

We recognize that this assumption may have consequences on our results as we may have incorporated some prebreeders, individuals skipping breeding opportunities, prospectors and individuals breeding in other locations into our sample. In this case, if birds breeding in other colonies outside the study area but resighted inside this area have a higher probability of returning to those colonies to breed, the local survival probability estimated in the study area may be underestimated. This bias would result from heterogeneity among individuals in dispersal probability, a 'nuisance' component of local survival. To minimize this bias, we excluded the following birds from the data set: birds with unknown breeding status resighted at the two colonies in the same season, birds resighted at nonbreeding clubs (places attended by nonbreeding birds, both adults and subadults) in a season, birds not resighted within the perimeter of the dunes where they bred previously, and birds with unknown breeding status resighted only once in a season (*c.* 40% of the total resighted birds).

A total of 3385 individuals was retained for analysis from the 28 252 resightings made at the two colonies. We did not consider the influence of age on demographic parameters for practical reasons, mainly because increasing the degree of stratification of the data from the Columbretes Islands seemed unrealistic.

COLONY-SPECIFIC SURVIVAL AND MOVEMENT WITHIN THE STUDY AREA

We used multistate capture–recapture models to estimate colony-specific adult survival and movement probability among colonies (Nichols *et al.* 1992; Clobert 1995; Nichols & Kendall 1995; Spindelov *et al.* 1995; Nichols 1996; Nichols & Kaiser 1999; Williams *et al.* 2002). Analyses were performed using the software program MARK (White & Burnham 1999). We used an information-theoretic approach to model selection (Burnham & Anderson 1998). The biological hypotheses that guided specification of the structure of models were assessed using AICc (Akaike's information criterion adjusted for small sample bias; Burnham & Anderson 1998). Models with the lowest values of AICc were retained as good candidate models (Burnham & Anderson 1998). As AICc values are interpretable only in terms of 'relative value', we relied on AICc weights to select models

(Burnham & Anderson 1998; see examples in Hall, McConnell & Barker 2001; Cooch 2002). Model selection procedures based on information criteria permit consideration of a set of models whose structure reflects specific biological hypotheses that are not necessarily exclusive or alternative. Comparisons among models permitted us to assess these hypotheses, even if the corresponding models are not nested, which precludes use of test statistics such as likelihood ratio tests (Burnham & Anderson 1998). For practical reasons (the very large number of models) we did not consider all the possible models corresponding to simplifications of the general one. We specified and considered a priori biological hypotheses, or hypotheses whose relevance was linked mainly to the need to evaluate the fit of the starting model, and performed model selection in a sequential manner. In the first step we addressed the influence of time on recapture, survival and transition probability and specific hypotheses about trap-dependence and transients (16 different models). In the second step we used the models with the largest support in step 1 to address biological hypotheses about the influence of breeding success on transition probability (22 ultrastructural models; see Results). In addition, we reported only the models whose weights were > 0.01 (after rounding).

Classical capture–recapture models rely on several assumptions regarding independence of individuals and homogeneity of recapture or survival probability among individuals (after accounting for some specific sources of variation) regardless of previous capture history (e.g. Burnham *et al.* 1987; Lebreton *et al.* 1992; Williams *et al.* 2002). Violations of these assumptions may require adjustments to the model structure or correction for overdispersion (e.g. Lebreton *et al.* 1992). Several approaches can be used to assess the fit of the most general model. Some are specific to a given model, e.g. the goodness-of-fit test to the Cormack–Jolly–Seber model based on contingency tables (Burnham *et al.* 1987; Lebreton *et al.* 1992). Others rely on an overdispersion parameter computed by means of bootstrap procedures for any model (White & Burnham 1999). While the latter are more general, they do not allow distinguishing between structural failure and overdispersion. Additionally, their reliability for multistate models is not well established. We used a recently developed goodness-of-fit test to the ‘jolly movement’ model (JMV; Brownie *et al.* 1993) based on contingency tables completed by a likelihood ratio test to assess the fit of the Arnason–Schwarz model (Pradel, Wintrebert & Gimenez 2003). This approach, like the goodness-of-fit test implemented in the software program RELEASE (Burnham *et al.* 1987) for data from a single site, permits the identification of structural failure. After generalizing the Arnason–Schwarz model to account for revealed structural deficiencies, one can compute an estimate of the overdispersion parameter (\hat{c} ; Burnham & Anderson 1998). Burnham & Anderson (1998) recommend using quasi-likelihood in situations where $1 \leq \hat{c} \leq 4$; higher values indicate remaining structural failure of the general model.

Previous survival analyses based on data from the Ebro Delta (Oro *et al.* 1999) and preliminary results obtained using data from the Columbretes Islands (Oro, unpublished data) indicated that one assumption underlying multistate capture–recapture models was not met: the assumption that all simultaneously released individuals have the same probability of being re-observed regardless of whether they were newly marked or they were already marked when captured (e.g. Burnham *et al.* 1987). Furthermore, transients (as opposed to residents) are individuals that leave the study area after first capture and thus have a local survival probability equal to 0 (Pradel *et al.* 1997); the presence of transients in the sample may lead to biased estimates of survival. Our most general model included a distinct parameter accounting for survival of individuals immediately after first capture (i.e. the model accounted for transients). In this model we also accounted for the possibility of trap-dependence on recapture probability (more precisely sighting probability). As above, ignoring such an effect may lead to biased estimates of survival. Incorporating trap-dependence required modification of the data following the approach specified by Pradel (1993) to account for the time elapsed since last capture. We used a separate parameter for the capture at occasion $i + 1$ of animals captured at occasion i . The starting model had the following structure: $S_{i\tau}^1 P_{i\tau m}^1 \Psi_i^{12}, S_{i\tau}^2 P_{i\tau m}^2 \Psi_i^{21}$ where S stands for survival probability, p for recapture probability, and ψ for transition probability. Superscripts 1 and 2 correspond to strata 1 (Ebro Delta) and 2 (Columbretes Islands), respectively. The subscript τ stands for the transient effect. Subscripts t and m stand for ‘time’ (year) and the trap-dependent effect, respectively. Note that survival after first capture was not time-specific in the Columbretes Islands, nor was the recapture probability for captures that took place more than a year after last capture. This constraint was incorporated because of smaller sample sizes in that location (many parameters could not be estimated with more complex models).

Results

The Arnason–Schwarz model did not fit the data ($\chi^2(108) = 545.16, P = 0.00$) and the presence of transients and trap-dependence effects were detected. However, after incorporating the transient and trap-dependent effects, we did not find evidence of structural failure of the general model ($\chi^2(83) = 170.612, \hat{c} = 2.06$). We first assessed a set of hypotheses concerning the presence of transients, trap-dependence and the influence of time on recapture, survival and transition probability (Table 1). For recapture probability, the model with the lowest QAICc value was the model where recapture probability was time-dependent in the Ebro Delta, and there was also a time-specific trap-dependent effect in this location. The influence of time and the trap-dependent effect were additive (Table 1). For recapture probability in the Columbretes Islands, the structure of the general

Table 1. Influence of time on recapture probability P , survival S and transition probability ψ ; evaluation of the trap-dependence and the transient effects

Model name	Parameterization	QAICc	NP	QAICc weight	Model likelihood
M3	$S_{t \rightarrow t}^1, P_{t \rightarrow m}^1, \Psi_t^{12}$	10752.66	64	0.92	1.00
M9	$S_{t \rightarrow t}^2, P_{t \rightarrow m}^2, \Psi_t^{21}$ $S_{t \rightarrow t}^1, P_{t \rightarrow m}^1, \Psi_t^{12}$	10757.79	56	0.07	0.08
M11	$S_{t \rightarrow t}^2, P_{t \rightarrow m}^2, \Psi_t^{21}$ $S_{t \rightarrow t}^1, P_{t \rightarrow m}^1, \Psi_t^{12}$ $S_t^2, P_{t \rightarrow m}^2, \Psi_t^{21}$	10761.70	55	0.01	0.01

QAICc: Akaike's information criterion based on quasi-likelihood and corrected for small sample bias.
NP: number of estimated parameters.

model was retained: there was an influence of time on recapture probability immediately after last capture. None of the other models could be considered as good candidates (Table 1).

We started with the above model to address hypotheses about factors influencing survival probability. In this model survival was time-specific in the Ebro Delta, there was a transient effect in both locations and first-year survival was time-specific in the Columbretes Islands. Recall that lack of time-specificity in subsequent survival in the Columbretes Islands is a constraint we considered at the beginning of the modelling process because of small sample size in later years in this location and estimation problems. We found evidence of a transient effect in both locations (Table 1). The model with the largest support included the influence of time on survival in both locations.

We then addressed the influence of time on movement probability, and set movement probabilities equal. None of these models was retained. The probability that a bird moves to the other location varied among years, and dispersal probability was not balanced (Table 1). Previous survival analyses (Oro *et al.* 1999) provided evidence that the transient effect was greater in 1994, the year a European badger caused reduced breeding success at the Ebro Delta (see also Oro & Pradel 2000). This previous study used an approach not designed to separate formally movement and survival. Here we contrasted movement probability from the Ebro Delta to the Columbretes Islands in 1994 against mean movement probability across all the other years. We did not find evidence that this model performed better in terms of description of the process that gave rise to the data (QAICc = 10773.04, number of parameters = 57).

INFLUENCE OF BREEDING SUCCESS ON MOVEMENT PROBABILITY (ULTRASTRUCTURAL MODELS)

In the next step we investigated the influence of breeding success and colony size on movement probability, based on the model with the largest support above (M3, Table 1). In the first class of models we considered, the probability of moving between times t and $t + 1$ from

location r to location s (with $r \neq s$) was a function of breeding success (BS) in location r at time t (i.e. the location of origin; eqn 1):

$$\Psi_t^{rs} = \frac{e^{(\alpha + \beta \cdot BS_t^r)}}{1 + e^{(\alpha + \beta \cdot BS_t^r)}} \quad \text{eqn 1}$$

Models will be described on the logit scale as follows:

$$\text{logit}(\Psi_t^{rs}) = \ln \left(\frac{\Psi_t^{rs}}{1 - \Psi_t^{rs}} \right) = \alpha + \beta \cdot BS_t^r. \quad \text{eqn 2}$$

Assuming an influence of breeding success in the location of origin on movement probability, we suspected that the probabilities of detecting such a relationship for dispersal from the Ebro Delta to the Columbretes Islands and for movement in the opposite direction were not equal. More precisely, we suspected that detection of an influence of BS in the location of origin on movement probability for movement from the Ebro Delta to the Columbretes Islands was more likely. When individuals leave the Ebro Delta, the first colony they encounter is the Columbretes Islands (south), but this does not hold for individuals leaving the Columbretes Islands. The latter may disperse either to the Ebro Delta (north) or to other colonies located further south. Consequently, we considered situations where this relationship between movement probability and breeding success held only for Ψ_t^{12} or Ψ_t^{21} .

In addition, for different model structures, we built models where the influence of breeding success on the probability of leaving a colony differed among colonies (i.e. there was a different 'baseline' probability of emigrating; eqn 3), or where movement probability depended only on breeding success (eqn 1).

$$\text{logit}(\Psi_t^{rs}) = \alpha_r + \beta \cdot BS_t^r \quad \text{eqn 3}$$

In the above models movement probability varied monotonically as a function of breeding success. We also considered a model where breeding success (mean number of fledglings per pair) was treated as a categorical variable [four classes: (0.00–0.25) (0.26–0.50) (0.51–0.75) (0.76–1.00)].

Lastly, we investigated the influence of breeding success in two consecutive years on movement probability

(i.e. a ‘cumulative’ influence of breeding success, or a ‘memory’ effect of breeding success; eqn 4).

$$\text{logit}(\psi_i^{rs}) = \alpha + \beta_1 \cdot BS_{t-1}^r + \beta_2 \cdot BS_t^r \quad \text{eqn 4}$$

We also addressed the hypothesis that the probability of moving between times t and $t + 1$ from location r to location s (with $r \neq s$) was a function of breeding success in location s at time t (i.e. the destination colony). Individuals may decide to move and establish in a different colony in year $t + 1$ and assess their expected fitness using the realized breeding success in that colony at time t (which implies prospecting in year t ; e.g. Danchin *et al.* 1991; eqn 5).

$$\text{logit}(\psi_i^{rs}) = \alpha + \beta \cdot BS_t^s \quad \text{eqn 5}$$

Alternatively, individuals may be able to assess expected fitness using cues available early during the breeding season in year $t + 1$. To address this hypothesis, we considered models where the probability of moving between time t and $t + 1$ from location r to location s (with $r \neq s$) was a function of breeding success in location s at time $t + 1$ (eqn 6).

$$\text{logit}(\psi_i^{rs}) = \alpha + \beta \cdot BS_{t+1}^s \quad \text{eqn 6}$$

The basis for the following class of models was that individuals may not necessarily leave a location where breeding success was poor if there was no other location where the expected fitness was higher. The probability of moving between times t and $t + 1$ from location r to location s (with $r \neq s$) was a function of the gradient of breeding success between locations s and r at time t (i.e. $\frac{BS_t(\text{destination colony})}{BS_t(\text{location of origin})}$; eqn 7).

$$\text{logit}(\psi_i^{rs}) = \alpha + \beta \cdot \frac{BS_t^s}{BS_t^r} \quad \text{eqn 7}$$

Individuals may also be able to assess expected fitness using other cues at the beginning of breeding season t . Accordingly, we built models where the probability of moving between time t and $t + 1$ from location r to location s (with $r \neq s$) was a function of the gradient of breeding success between locations s and r at time $t + 1$ (i.e. $\frac{BS_t(\text{destination colony})}{BS_t(\text{location of origin})}$; eqn 8).

$$\text{logit}(\psi_i^{rs}) = \alpha + \beta \cdot \frac{BS_{t+1}^s}{BS_{t+1}^r} \quad \text{eqn 8}$$

INFLUENCE OF COLONY SIZE ON MOVEMENT PROBABILITY

With the last class of models we addressed the influence of the size (N) of the colony of origin on movement probability (eqn 9) and the size of the colonies of yellow-legged gulls (eqn 10).

$$\text{logit}(\psi_i^{rs}) = \alpha_r + \beta \cdot N_t^r \quad \text{eqn 9}$$

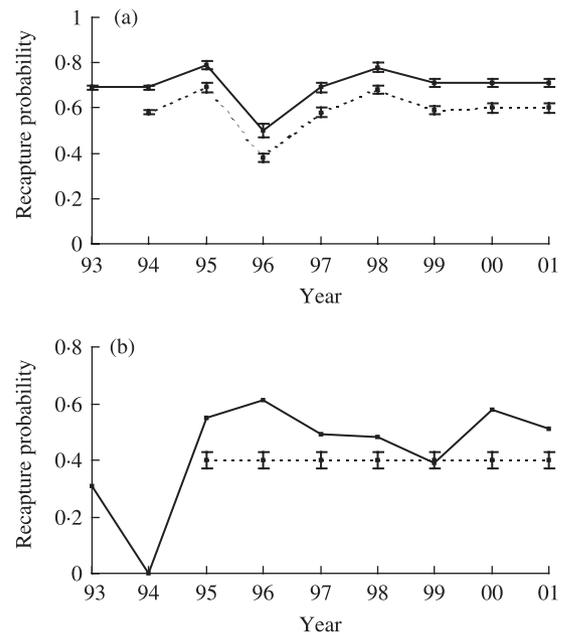


Fig. 3. Estimates (and standard errors) of recapture probability (p_i^r) under model M3 for the Ebro Delta (a) and the Columbretes Islands (b). Solid lines correspond to recapture probability at time t when last capture is at time $t - 1$, while dashed lines correspond to recapture probability when last capture is at time $t - i$ ($i > 1$). Recapture probability at Columbretes in 1994 (p_{94}^{col}) was 0.

$$\text{logit}(\psi_i^{rs}) = \alpha_r + \beta \cdot P_t^r \quad \text{eqn 10}$$

According to the QAICc criterion, in the set including ultrastructural models and model M3, none of the ultrastructural models performed better than model M3 (the AICc weight of model M3 was 1.00 (after rounding); the weight of all the other models was virtually zero).

PARAMETER ESTIMATES

Estimates of recapture probability (Fig. 3) corresponding to model M3 showed that recapture probability was higher at the Ebro Delta Colony than at the Columbretes Islands in most years, probably as a consequence of unequal field effort at the two locations and better field conditions to approach the birds at the Ebro Delta (by car) than at the Columbretes Islands (by foot). In addition, individuals had a higher probability of being sighted in year t if their previous sighting or capture was recent (year $t - 1$). This trap-dependent effect was found in both colonies.

Concerning survival probability (Fig. 4), the transient effect was expressed by a lower survival probability of individuals after their first release. At the Ebro Delta, adult survival changed with time and ranged from 0.98 (SE = 0.01) to 0.88 (SE = 0.01); this lowest value corresponded to the time foxes first entered the colony (1999). Following Cormack (1964), we estimated an average survival for the whole period using the geometric mean of survival estimates: 0.93 (estimated standard error = 0.01, calculated using the delta method; Seber 1982). In addition, we used random effects models to assess ‘true’

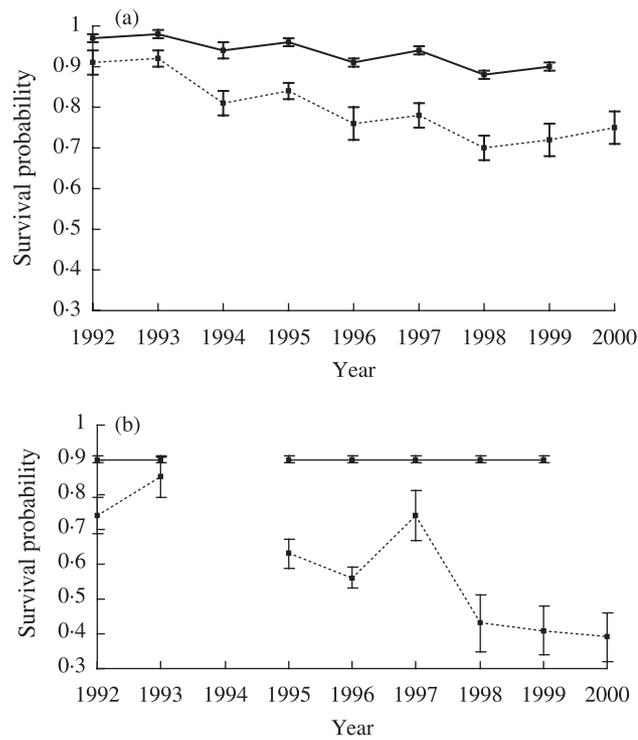


Fig. 4. Estimates of survival probability made under model M3 for the Ebro Delta (a) and the Columbretes Islands (b) Solid lines correspond to survival probability at time t for individuals first observed at time $t - i$ ($i > 1$) (time-dependent at the Ebro Delta and constant at Columbretes), while dashed lines correspond to survival probability for individuals released at time $t - 1$ (i.e. including transients). Survival could not be estimated at Columbretes Islands in 1994.

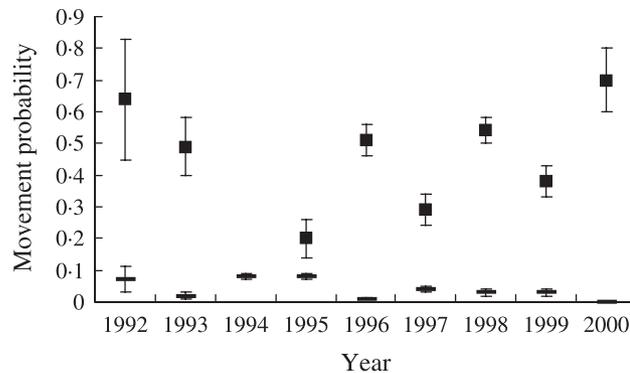


Fig. 5. Estimates (and standard errors) of transition probability (ψ_i^{rs}) under model M3. Square dots are estimates of dispersal from the Columbretes Islands (state 2) to the Ebro Delta (state 1) (ψ_i^{21}); flat dots are estimates of dispersal from the Ebro Delta to Columbretes (ψ_i^{12}). ψ_{94}^{21} was not estimated.

temporal variation in survival vs. sampling variation (e.g. Franklin, Anderson & Burnham 2000; White, Burnham & Anderson 2000; Franklin *et al.* 2002; Loison *et al.* 2002). Shrunken estimates and maximum likelihood (ML) estimates were close except in 1992 (S_{92}^1 ; results not presented here); ML estimates give a reliable idea of genuine temporal variation in survival probability.

We were not able to investigate the influence of time on all survival parameters at the Columbretes Islands, but the mean survival estimate obtained was lower than the mean value at the Delta (0.90, estimated standard error = 0.01). Adult survival at this latter col-

ony was lower than that estimated at the Columbretes Islands only in years that foxes were present at the Ebro Delta (1999 onwards; Fig. 4). Transition probabilities (Fig. 5) differed substantially according to the location of origin: movement probability from the Columbretes Islands ranged from 20% to 70%, whereas movement probability from the Ebro Delta was much lower (1–8%). As above, we used random effects models to assess 'true' temporal variation in movement probability. Shrunken estimates and ML estimates were close in all cases (results not presented here). ML estimates give a reliable idea of genuine temporal variation in transition probability.

Discussion

ASYMMETRIC MOVEMENT PROBABILITY

Our results provided evidence of a substantial difference in movement probability between the Ebro Delta and the Columbretes Islands (see Fig. 5): movement probabilities were much higher from the Columbretes Islands to the Ebro Delta. This supports the results of previous studies conducted at the Ebro Delta that suggested that the dynamics of this colony are influenced strongly by immigration (e.g. Oro & Pradel 1999; Oro & Ruxton 2001). At the same time, the local dynamics at the Columbretes Islands are shaped by emigration to the Ebro Delta (e.g. high movement probability coincided with a substantial decline in breeding numbers; Figs 2 and 5; see also Oro & Pradel 2000), and especially by immigration (Oro *et al.* 2004). Dispersal probabilities from the Ebro Delta are very low but the colony is large. Therefore, this translates into large numbers of individuals dispersing to the Columbretes Islands. We acknowledge the fact that our study system included only two colonies, and that the local dynamics of these local populations were likely to be influenced by movement to and from the other Mediterranean breeding locations (Fig. 1). Even if they do not account for all movement events, our results highlight the importance of dispersal in the spatial dynamics of local populations and metapopulations (Ims & Yoccoz 1997; Johst & Brandl 1997).

A body of elements provide strong evidence that the Ebro Delta is a high-quality location in terms of food resources (especially secondary preys when marine preys are not available), habitat suitability and impact of the predator, the yellow-legged gull (Oro *et al.* 1996; Oro 1998, 1999; Pedrocchi *et al.* 2002; Genovart, Oro & Bonhomme 2003; Martínez-Abraín *et al.* 2003c). During the study, breeding success at the Ebro Delta was significantly higher than at the Columbretes Islands (Mann–Whitney U -test = 14.5, $n = 22$, $P = 0.001$), where complete breeding failure occurred regularly. Results are thus consistent with the hypothesis that individuals select habitat where their fitness prospect is higher (Holt & Barfield 2001).

In addition, movement probability was higher from the smaller colony (the Columbretes Islands) to the larger one (Ebro Delta), which is consistent with the conspecific attraction hypothesis (Smith & Peacock 1990). This is also consistent with the hypothesis proposed by Pulliam (1988) and McPeck & Holt (1992), who considered models 'in which individuals actively select which habitat to occupy and must choose between habitats that can maintain populations without immigration (source habitats) and habitats in which populations can be maintained only by continual immigration (sink habitats). Individuals breeding in source habitats produce more offspring than necessary to replace themselves (fitness > 1), but individuals breeding in sink habitats do not produce enough offspring to replace themselves (fitness < 1)'. In both Pul-

liam's and McPeck & Holt's models, 'large segments of populations in "good" habitats (source habitats or high carrying capacity habitats) will not disperse, while many individuals in "bad" habitats (sink habitats or low carrying-capacity habitats) will disperse each generation'.

However, source–sink dynamics (e.g. Pulliam 1988) and the hypothesis of patch-size-related movement probability (McPeck & Holt 1992) rely on several assumptions, such as demographic and evolutionary equilibrium of the system of local populations and density-dependent fitness. Although this would require thorough investigation, we have no reason to think that density dependence is operating in the Ebro Delta (Oro 1999; Oro & Ruxton 2001), or that the local populations are at demographic equilibrium (Oro & Pradel 2000; Oro & Ruxton 2001; Genovart *et al.* 2003; Oro *et al.* 2004). In the absence of density dependence (Oro 1999), we might expect the larger colony (the Ebro Delta) to attract proportionally more birds from the smaller colony (the Columbretes Islands). Conspecific attraction (i.e. individuals cue on the presence or density of conspecifics to select breeding locations; Forbes & Kaiser 1994; Oro & Pradel 2000; Serrano & Tella 2003) is likely to be much stronger at the Ebro Delta (a colony two orders of magnitude larger than the Columbretes Islands).

INFLUENCE OF COVARIATES ON MOVEMENT PROBABILITY

Our results provided evidence of an increase in dispersal probability when a badger arrived to the Ebro Delta colony and preyed on nests (both eggs and chicks), which resulted in a decrease in breeding success (see also Oro *et al.* 1999). This increase in movement probability was also detected a year later. In contrast, movement probability from the Ebro Delta did not increase when foxes were present (1999 onwards) even though they preyed on breeding adults. Breeding success in those years was very high. Observational data confirmed that foxes did not prey on nests and that predation on adults occurred at night. Surprisingly, we did not record desertion of surrounding nests after a predation event (Oro, unpublished data).

Even though movement probability varied greatly among years, our results did not support any of our a priori hypotheses concerning the influence of covariates on movement probability (e.g. overall breeding success in the colony of origin or colony size in year t). As above, hypotheses based on an influence of habitat characteristics or quality in year t on movement probability between years t and $t + 1$ rely on several assumptions. One of these is that individuals prospect and gain information on the different potential breeding locations. This assumption needs to be evaluated in our study system, and the type of information individuals might gain as well. The Columbretes and the Ebro Delta are 80 km apart, and it is reasonable to think that distance influences negatively the probability that an individual involved in the breeding process in a location visits other colonies at the right time (coinciding with the

'peak' of information quality, i.e. when fledglings are present in colonies; Boulinier *et al.* 1996; Danchin *et al.* 2001). Individuals may not have perfect knowledge of the potential breeding sites and their quality (Oro & Ruxton 2001; Thomas, Baguette & Lewis 2001).

Another assumption has to be met: habitat quality has to be sufficiently predictable from year to year (i.e. if the habitat is of higher quality in year t , the probability that quality will be high in year $t + 1$ is sufficiently high; see Doligez *et al.* 2003 for additional information). Oro & Ruxton (2001) have shown that breeding success in several colonies of Audouin's gull is not auto-correlated over time. However, Doligez *et al.* (2003) have shown that the habitat-copying strategy can be favoured even with very low correlation. In addition, breeding success assessed at the colony level may not be a reliable criterion to assess expected fitness. It is also possible that the scale we used to characterize habitat quality (the overall colony) is not appropriate and that individuals select higher-quality areas within colonies (i.e. subcolonies). Breeding success and other breeding parameters may be distributed heterogeneously within colonies (e.g. Coulson 1968; Genovart *et al.* 2003). In this case hypotheses about habitat selection should be addressed using habitat characteristics described at the right scale, otherwise the relevant movement patterns may be obscured.

In addition, it has been shown that individuals established in habitat of equal quality behave differently according to their own breeding performance, and that age (or experience) influences site fidelity (Danchin *et al.* 1998; Oro *et al.* 1999; Serrano *et al.* 2001). Lack of knowledge of breeding success at the individual level and failure to account for individual experience or individual experience in a given location may have obscured the relationship between overall breeding success and movement probability.

Furthermore, the study area may not be closed; individual decisions in terms of habitat selection may be consistent with various theories about movement of individuals (e.g. Fretwell & Lucas 1970), but failure to account for all movement events (i.e. movement out of the study area was confounded with mortality) may have obscured the influence of relevant covariates such as breeding success or colony size on movement probability. For example, it is difficult to explain why movement probability from the Ebro Delta to the Columbretes Islands remained high a year after the badger was present at the Ebro Delta. If a higher proportion of individuals left the Ebro Delta in 1994 compared to other years as a response to decreased breeding success, and many of them emigrated out of the study area, the response to the specific badger event may not be detectable within the study area. Previous results indicated a strong positive badger effect on the transient parameter (Oro *et al.* 1999). This transient effect may account partly for emigration of individuals with less experience (Oro *et al.* 1999) in the Ebro Delta to colonies located out of the study system.

Lastly, as emphasized earlier, the Columbretes Islands are the first potential breeding location encountered south by individuals leaving the Ebro Delta, and there is no other known potential breeding location further north. On the contrary, individuals leaving the Columbretes Islands may move to several other locations south, but only one north (the Ebro Delta). Our system of two local populations was unlikely to be closed, and some individuals may have dispersed out of the study area, mostly from the Columbretes Islands to the Balearic Islands and Grossa Island (Muntaner 1997; authors' unpublished results). Our estimates of movement probability could reflect a higher probability of missing dispersal events from the Columbretes Islands than from the Ebro Delta and the same bias may hold for survival, which incorporates permanent emigration out of the study area (Nichols *et al.* 1992; Brownie *et al.* 1993; Spindelow *et al.* 1995; Boulinier *et al.* 1997; Joe & Pollock 2002; Nisbet & Cam 2002; Spindelow *et al.* 2002).

PROXIMATE FACTORS AFFECTING ADULT SURVIVAL

Survival was lower at Columbretes Islands than at the Ebro Delta, except for the years during which foxes were present at the Ebro Delta: survival decreased slightly but remained higher than at the Columbretes Islands. In addition, we found evidence of a transient effect in both locations. The transient effect may correspond to the fact that we resighted marked individuals that were not breeders in the location where they were observed. They may be prospectors (such behaviour was recorded in several seagull species; Danchin *et al.* 1991, 1998, 2001; Boulinier *et al.* 1996; Reed *et al.* 1999), either sexually mature non-breeders or individuals that bred elsewhere.

As suggested above, dispersal out of the study area may obscure genuine variation in survival among colonies as well as temporal variation in survival in each location; some data suggest that permanent dispersal from the Columbretes Islands is higher than from the Ebro Delta (authors' unpublished data). It is unclear to us which mortality factor may affect gulls at the Columbretes Islands and not those at the Ebro Delta. For instance, fishing gear, which is an important cause of adult mortality during the breeding season, probably affects birds from both colonies in a similar manner (Oro 1998; Cooper *et al.* 2003). However, higher availability of resources at the Ebro Delta may translate into differences in survival probability. Theory predicts that selection should minimize variation in the demographic parameters to which the population growth rate is more sensitive (Pfister 1998; Sæther & Bakke 2000). In long-lived species, adult survival is expected to be less sensitive to variation in environmental conditions than fecundity (e.g. Stearns 1992). However, recent studies have shown that adult survival in long-lived species may also be sensitive to variation in environmental conditions (Oro *et al.* 1999; Barbraud & Weimerskirch 2001; Jones, Hunter & Robertson 2002; Oro & Furness 2002).

Acknowledgements

We are very grateful to Meritxell Genovart, Albert Bertolero, Alejandro Martínez and wardens of the RN Illes Columbretes for their valuable help with the field work. We thank all the people involved in the ringing programme, especially the technical staff of the RN Illes Columbretes and PN Delta de l'Ebre. We are also grateful to S. J. Dinsmore, Jim Nichols and an anonymous referee for helping us improve the quality of the manuscript. We thank E. Danchin and D. Parejo for their comments on the paper. This study was funded by several agencies and grants: Department Medi Ambient (Generalitat de Catalunya), PN Delta de l'Ebre, CIRIT (Generalitat de Catalunya), Conselleria de Medi Ambient (Generalitat Valenciana), RN Illes Columbretes, grants from the Spanish Ministerio de Ciencia y Tecnología (nos PB91-0271, BOS2000-0569-C02-02, BOS2003-01960 and Integrated Action HF2001-0147), ICONA (Ministerio de Agricultura y Pesca), Life Projects of the EU (nos LIFE96/NAT/E/3118-B4-3200/96/502, LIFE B4-3200/98/447 and LIFE02/NAT/E/8608), and an EU project by Program Quality of Life and Management of Living Resources (no. QLRT-2000-00839). Emmanuelle Cam was supported by the Spanish Ministerio de Educación, Cultura y Deporte (ref. SB2000-0326). Roger Pradel was funded by FBBV and a grant from the University of Illes Balears. Daniel Oro dedicates this work to the memory of Jordi Berraondo, who died during the study.

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Received 21 July 2003; accepted 19 December 2003