Ibis (2006), **148**, 146–154

Testing habitat copying in breeding habitat selection in a species adapted to variable environments

DESEADA PAREJO,[1]* DANIEL ORO[2] & ETIENNE DANCHIN[1]

[1]*Laboratoire de Fonctionnement et Évolution des Systèmes Écologiques, CNRS-UMR 7625, Université Pierre et Marie Curie, Bat. A 7eme étage, 7 quai St. Bernard, Case 237, F-75252 Paris Cedex 05, France*

[2]*Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Miquel Marqués 21, 07190 Esporles, Mallorca, Spain*

The habitat copying hypothesis states that animals use the reproductive performance of conspecifics to evaluate habitat quality and choose their future breeding site. We used data from Audouin's Gull *Larus audouinii* (1992–2003), a species adapted to unpredictable environments, to analyse subcolony (as patch) choice within a colony (small spatial scale). We also assessed the suitability of alternative hypotheses to the habitat copying hypothesis. The probability of subcolonies being reoccupied annually increased with their size (as number of nests), which suggests the existence of group adherence effects. Subcolony growth rate was related to its average reproductive success (or patch reproductive success) in the previous year: the higher the reproductive success in a colony, the higher the probability of growth the following year. However, this last result was obtained without considering the effect of colony size on the response variable because colony size is related to it. Therefore, results suggest at the population level that in this system habitat copying might either be one of the strategies used by the species in selecting its breeding habitat, or one of the possible strategies operating alone. The other strategies are group adherence mechanisms, and also the effect of conspecific attraction. At the individual level we failed to find evidence of habitat copying and only the previous success of an individual affected its fidelity to a subcolony. The importance of the lack of environmental predictability in the system is discussed, as predictability is a prerequisite of habitat copying.

In heterogeneous environments, the choice of a breeding site may strongly influence the immediate and lifetime reproductive success of individuals. Habitat heterogeneity thus leads individuals to fitness-enhancing habitat-selection processes (Martin 1993). Such decision-making processes may occur before each reproductive episode (Danchin *et al.* 2001). Highly variable environments lead to a stochastic pattern of dispersal (Switzer 1993, Doligez *et al.* 2003), with each dispersal event being under selection.

To make such settlement choices, animals need information (Wiens 1976, Danchin *et al.* 2001), and may measure all the parameters likely to influence reproductive success, or estimate indices that integrate the effect of all those parameters (Danchin *et al.* 2001). For instance, in many species, breeders rely on their own breeding success (i.e. 'private information' *sensu* Switzer 1997, Taylor 1998) to assess local habitat quality to make dispersal decisions (reviewed in Switzer 1993, 1997, Haas 1998). Several authors have shown that failed breeders are more likely to disperse than successful breeders (e.g. Danchin *et al.* 1998, Doligez *et al.* 1999, Forero *et al.* 1999, Schjørring *et al.* 2000, Serrano *et al.* 2001). Individuals may also use information on conspecifics, either by their presence or abundance (i.e. conspecific attraction; Stamps 2001 and references therein, Serrano *et al.* 2001, Serrano & Tella 2003) or by their reproductive performance (Boulinier & Danchin 1997, Danchin *et al.* 1998, 2001, Doligez *et al.* 2003), as integrative indices of habitat suitability.

The importance of local reproductive success for breeding-habitat selection lies in the fact that it summarizes the effect of a number of environmental factors. The selection of breeding habitat based on conspecific reproductive success has been demonstrated

---

*Corresponding author. Present address: Cátedra de Biología y Etología, Facultad de Veterinaria, Universidad de Extremadura, Cáceres 10071, Spain.
Email: dparejo@unex.es

in a number of avian taxa via correlative approaches (reviewed in Danchin *et al.* 2001, as well as Schjørring *et al.* 1999, 2000, Boulinier *et al.* 2002, Danchin & Cam 2002), or in large-scale experiments (*Ficedula albicollis*, Doligez *et al.* 2002; *Rissa tridactyla*, Boulinier *et al.* 2002). Such a conspecific performance-based strategy has been called 'habitat copying' (Wagner *et al.* 2000, Danchin *et al.* 2001, Wagner & Danchin 2003) and there is also some evidence of interspecific habitat copying (Parejo *et al.* 2005).

The habitat copying hypothesis (HCH) first assumes that the environment is heterogeneous (i.e. patchy; Boulinier & Danchin 1997). Another key parameter in determining the value of information is the extent to which it allows an individual to predict its future fitness in a given patch (Danchin *et al.* 2001), which is linked mainly to environmental predictability. This implies that the information gathered at the end of a breeding season predicts habitat quality in the following year. If this was not the case, the HCH predicts that individuals should not use the local reproductive success as a major source of information in breeding habitat selection because it would not allow individuals to predict their local reproductive expectations (Doligez *et al.* 2003).

In this paper, we are particularly interested in two aspects of habitat copying that have not been studied: the influence of low habitat predictability in the use of local reproductive success in breeding habitat choice (but see Erwin *et al.* 1998 for the assessment of habitat copying in Gull-billed Terns *Sterna nilotica* breeding in unstable habitats), and the importance of the spatial scale at which we test the HCH. We use data from a local Audouin's Gull *Larus audouinii* population. Several biological parameters of this species suggest that it may have been selected to exploit relatively unpredictable environments (Martínez-Abraín *et al.* 2003b). Audouin's Gulls are probably adapted to breed optimally in barrier islands, brackish marshes and coastal dune fields, where the physical conditions at the breeding site may change drastically between successive years. Audouin's Gulls are endemic to the Mediterranean region and show a high turnover (colonization–extinction) rate of local populations (Lambertini 1993, Oro 1998, 2003) suggesting high breeding patch instability. Cam *et al.* (2004) suggest that Audouin's Gulls probably do not use the local reproductive success as a major source of information to select between two colonies that are 80 km apart (the Ebro delta and the Columbretes islands). Here, we analyse subcolony (i.e. patch) choice within the world's largest colony at the Ebro delta (Oro 1998). At this smaller scale, we expect an effect of local (or patch) reproductive success on individual dispersal and settlement decisions. Distances between patches within colonies are very small relative to the distances over which the birds could move (Genovart *et al.* 2003), which renders the gathering of information on the performance of conspecifics much cheaper than at the intercolony scale. Furthermore, different patches within a colony may differ in suitability as a result of local factors such as parasites, predation and height above sea-level. The study colony is spread over 2500 ha of suitable breeding habitat for gulls, which makes it likely that there are variations in habitat suitability within the colony.

If there is some temporal autocorrelation in subcolony quality within the Ebro delta colony, by extrapolating from previous studies (Danchin *et al.* 1998, Doligez *et al.* 1999, Brown *et al.* 2000), we expect:

(1) Patches with the highest breeding success in one year should show the highest probability of being reoccupied in the following year, and, if reoccupied, show the highest rate of increase.

(2) Individual patch fidelity should be affected by patch reproductive success. More specifically, we expect that non-breeders and failed breeders should be more likely to disperse from patches of low quality than from patches of high local reproductive success, whereas successful breeders should prefer not to disperse from patches of low quality because their own previous success there has been high.

Neither of these predictions can result simply from natal philopatry or breeding fidelity: Audouin's Gulls do not start to breed before age 3 years (Oro 1998), although they can visit breeding sites when 2 years old. Thus, an effect of average patch reproductive success (PRS) on local breeding population trends in the following year could only be due to natal philopatry if local population growth rate was associated with the PRS three (or more) years before. By contrast, fidelity of breeders to breeding patches cannot explain a population increase, although it could explain the re-colonization of subcolonies. However, a population increase from one year to the next could be explained by conspecific attraction, either because the most productive patches were also the most crowded ones, or because birds were attracted by conspecifics, independently of their performance. We therefore included population size in analyses in order to distinguish between conspecific attraction-based strategies and PRS-based ones.

METHODS

Data collection and extraction of relevant parameters

We used data from 1992 to 2003 from the Audouin's Gull study colony at the Punta de la Banya (Ebro Delta Natural Park, northeast Spain: 40°37′N, 00°35′E). The site is a flat, sandy saltmarsh on a peninsula connected to the rest of the delta by a narrow 9-km-long sand bar. The breeding area is surrounded by the sea over 90% of its perimeter. The 2500 ha available to breeding gulls are composed of spatially discrete dunes covered by halophilous vegetation. Groups of nests are clearly clumped in subcolonies (see details in Oro *et al.* 1996). These patches seem to differ in the level of predation pressure by Yellow-legged Gulls *Larus cachinnans* (Martínez-Abraín *et al.* 2003a) and by terrestrial predators (Oro *et al.* 1999).

The number of nests in each patch was counted annually during the second week of May, when most pairs had laid, and few broods had hatched, as an estimation of subcolony size (error less than 3%, Oro & Ruxton 2001). In most patches (i.e. subcolonies), we also had a global estimate of the total number of chicks fledged per patch, which allowed us to compute the average PRS in that year. Patches were only used in analyses when all the information was present. Fledglings were ringed with an engraved plastic ring carrying a unique three-digit code (Oro *et al.* 1999), which can be read through a telescope from a distance of up to 150 m. From 1995 to 2003, the breeding performance of some ringed Gulls was recorded during the breeding season (from March to July) as well as the subcolony where they bred. The number of visits to the different patches varied according to patch size (i.e. the number of pairs in each patch) in order to homogenize the effort of reading rings among the subcolonies and thus to limit heterogeneity in resighting probabilities (Pradel *et al.* 1997). We checked all patches for ringed birds every year.

We obtained a total of 41 different breeding individuals coming from 20 different subcolonies for which we knew the individual and group reproductive success, as well as the colony in which it would breed in the following year. Each individual contributes only one variate (one value for year t and $t + 1$ to the analyses). Individual breeding status (failed vs. successful breeding) was estimated only during incubation: individuals that failed to hatch a single egg were considered as failed and any others as successful breeders. Estimation of reproductive success of successful individuals was made by means of direct observation of adults feeding chicks of fledging ages. The number of fledged chicks per focal pair was assumed to be the number of chicks fed when they were around 4 weeks old. Chick age was estimated from plumage characteristics. Individual reproductive success was either defined as a binary (failed vs. succeeded in its breeding attempt) or a continuous variable (number of chicks fledged for those that fledged at least one chick). Similarly, we use two different variables to describe the annual population trend of each patch: (1) the reoccupation probability of patches from year t to year $t + 1$ (0 if a patch occupied in year t is not reoccupied in year $t + 1$; 1 if it is reoccupied); (2) for patches reoccupied in year $t + 1$ the annual growth rate in the number of nesting pairs per patch (computed as the ratio of the numbers of pairs on that patch in two consecutive years, $N[t + 1]/N[t]$).

We considered that birds were faithful to their patch when they bred in successive years in the same subcolony, whereas birds moving from one patch to another between successive years were considered unfaithful. Therefore, patch fidelity was coded as a binary variable.

Several predation events occurred during the study period. They affected most patches over the course of the study. Predators were the European Badger *Meles meles* in 1994 and the Red Fox *Vulpes vulpes* from 1999 onwards. Terrestrial predation at colonies seems strongly to affect both the reproductive parameters and the population dynamics of Audouin's Gulls (Oro *et al.* 1999). Because predation at our colony was either null or important, we accounted for it by including a binary predation variable.

Statistical analyses

We analysed environmental patchiness by testing whether the average reproductive success of pairs varied among patches and/or years (multiway analysis of variance with patch and year as random factors). Because it is difficult to identify what in the PRS is due to the intrinsic habitat quality and to the quality of the individuals, as in Danchin *et al.* (1998), we assume that individuals were distributed randomly among patches relative to individual quality. Under this assumption, the PRS reflects local habitat suitability. However, although this assumption was uncertain, even when high-quality individuals occupied high-quality sites, such an association between individual and habitat quality should still imply that relying on PRS allows individuals to detect the best patches. We thus used the PRS in year *t* as the dependent variable and the year and patch as independent random effects.

Average environmental predictability was analysed by using standardizations of PRS in *t* and *t* + 1 with respect to annual mean as independent and dependent variables, respectively. Because of among-year global variations and among-patch variations for each year, the absolute value of the PRS for a given patch may not reveal fully the value of that PRS relative to the other occupied patches in the same and other years. For instance, an average production of one chick per pair in a patch may be low in very good years, whereas in very poor years it may be the best. Furthermore, patch quality in a given year may differ slightly or greatly. Consequently, we used a standardization of PRS using the deviation from the annual mean for each patch to avoid these problems. We also took into account the effect of predation in subcolony predictability introducing the variable predation in year *t* in the analysis.

We used logistic regression to analyse the role of PRS (conspecific performance-based strategy) and subcolony size (conspecific attraction-based strategy) on patch reoccupation probability. When performing this analysis we used standardized values of PRS and subcolony population size. We performed a linear regression to analyse the role of PRS on the annual multiplication rate per patch using standardized values of PRS and patch annual multiplication rate. Subcolony population size was not included in this last analysis because this variable is related to the dependent variable: the annual multiplication rate is calculated as the ratio between subcolony size in two consecutive years (see above).

We analysed the role of PRS and individual reproductive success (private information) in year *t* on individual breeding patch fidelity from year *t* to year *t* + 1. Individual reproductive success was used first as a binary effect (failed vs. successful individuals: individual reproductive performance), and secondly as an ordered variable (number of fledged chicks per successful pair: individual productivity). We also introduced in this analysis the colony size in year *t* (conspecific attraction) as an independent variable. Standardized values of PRS and subcolony population size were used. Because individuals from the same patch experienced the same environmental conditions, we introduced the patch as a random factor in this analysis to avoid pseudoreplication. We used Generalized Linear Mixed Models (GLMMs; Littell *et al*. 1996) with a logistic link function using SAS (SAS 1999) macro program GLIMMIX (Littell *et al*. 1996).

Standardized values of PRS and subcolony size were correlated (Correlation, $r = 0.3$, $P = 0.001$, $n = 115$) in the population data. Because these two variables were introduced in most of our analyses as independent effects, and collinearity may lead to the misinterpretation of statistical results in regression models (Underwood 1997), we performed several complementary analyses: univariate analyses with each effect separately and two Type I multivariate analyses with one or the other as the first effect. When performing analyses on individual fidelity to subcolonies we used Type III multivariate analyses with standardized values of PRS and of subcolony size as independent variables. This was because the correlation between these two variables was not significant when performed on data from which we had all the necessary information to make these individual analyses (Correlation, $r = 0.16$, $P = 0.30$, $n = 41$).

We use Kolmogorov–Smirnov tests to check the normality of effects, and those variables found not to be normally distributed were transformed. We check the fit of logistic regression models with likelihood-ratio goodness-of-fit tests. The initial models contained the main effects together with all possible interactions, unless stated otherwise. Model selection was carried out by removing, one by one, the effects that were furthest from statistical significance, starting with the highest-order interactions down to the main effects. In the results parameter estimates ± se are shown for significant continuous effects.

RESULTS

Subcolony characteristics

Subcolonies varied from six to 3101 nests; their mean (± sd) size was of 489 (± 534) nests ($n = 115$). Occupation of the different subcolonies varied greatly among years, with a maximum of 23 subcolonies in any one year (Fig. 1). The rates of subcolony extinction and colonization were high (Fig. 1), but abandoned subcolonies were not frequently re-used (only six out of 35 abandoned subcolonies were used later). The total number of subcolonies during the study period was 57.

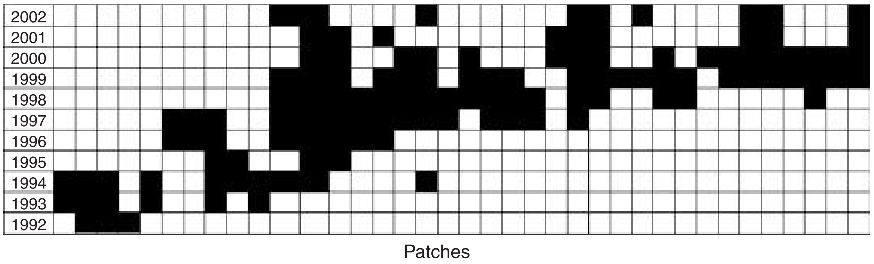

Figure 1. Colonization-extinction dynamics of patches (subcolonies) at the Ebro delta colony. Each column represents a patch during the study period; thus a square represents a patch in a given year. Grey squares indicate occupied patches and white squares unoccupied patches.

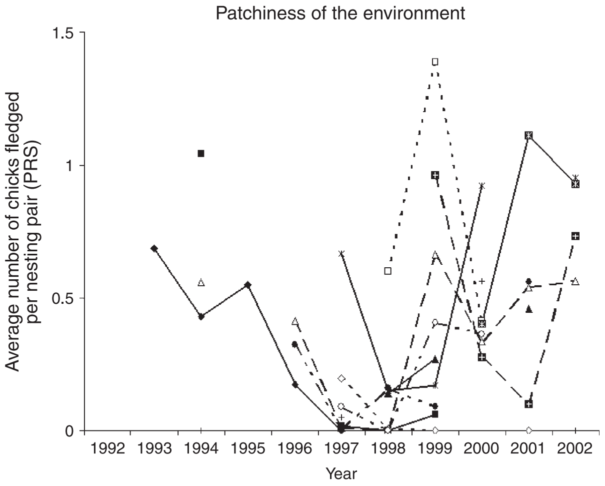

Figure 2. Patchiness of the environment within the Ebro delta colony. Average number of fledged chicks per nest in some of the study subcolonies during the study period. Each subcolony is represented by a different symbol (see text for significance). Relative subcolony reproductive success clearly varies in time.

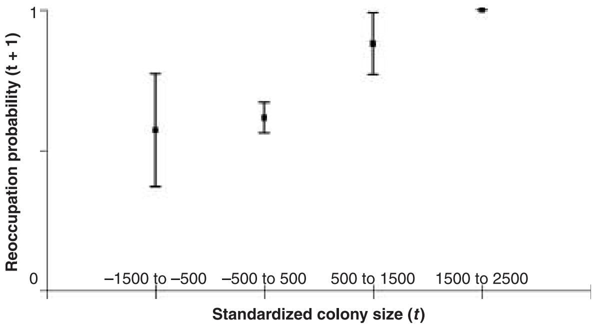

Figure 3. Subcolony reoccupation rate according to its yearly standardized population size: low standardized intervals correspond to the smaller subcolonies.

Environmental patchiness

Patch reproductive success of gulls varied among years (GLM model, $F_{10,51} = 2.53$, $P = 0.015$) and among patches (GLM model, $F_{53,51} = 2.45$, $P = 0.0021$). Although biologically important, the interaction could not be estimated because we only had one line of information per patch-year (with the average reproductive success of that patch-year summarizing the information of that patch) and many patches were abandoned each year (Fig. 1). However, the interaction between year and patch is apparent in Figure 2: a patch that is the best in one year may become very poor some years after (and vice versa). The relative quality of the patches thus varied over years.

Environmental predictability

The relationship found between the standardized PRS(t + 1) and standardized PRS(t) was not significant (GLM model, $F_{1,46} = 0.89$, $P = 0.35$). Predation in year t was not important, either as a main effect (GLM model, $F_{1,46} = 0.03$, $P = 0.86$) or in interaction with the standardized PRS(t) (GLM model, $F_{1,45} = 0.02$, $P = 0.88$). This shows that there is no predictability of subcolony quality.

Population trends

Subcolony reoccupation probability

Patch reoccupation probability in subsequent years was related to standardized colony size (Logistic regression, $\chi^2_{1,94} = 4.75$, $P = 0.03$, Estimate ± se = 0.0011 ± 0.0006), but not related to standardized PRS (Logistic regression, $\chi^2_{1,94} = 2.83$, $P = 0.09$, Estimate ± se = 1.193 ± 0.7439) in year t: larger subcolonies had a higher probability of being reoccupied in the following year (Fig. 3). Type I analyses with standardized subcolony size and PRS on patch reoccupation rate only retained the effect of the standardized subcolony size in both cases (Logistic regression, $\chi^2_{1,94} = 4.75$, $P = 0.03$, Estimate ± se = 0.0011 ± 0.0006). Thus, only colony size was detected as explaining colony reoccupation probability.

Subcolony annual multiplication rate

When including subcolonies that went extinct (lambda = 0), we found that the standardized subcolony multiplication rate was positively related to the standardized PRS in the previous season (GLM model, $F_{1,94} = 3.97$, $P = 0.049$, Estimate ± se = 2.77 ± 1.39). Similarly, the standardized subcolony multiplication rates of reoccupied subcolonies showed a positive relationship with standardized PRS (GLM model, $F_{1,51} = 4.25$, $P = 0.044$, Estimate ± se = 5.38 ± 2.61).

Individual fidelity

The demographic results presented above must reflect individual emigration and settlement decisions. However, we only found a significant effect of individual reproductive performance (i.e. private information) on individual dispersal decisions in the following year (GLMM, $F_{1,40} = 6.15$, $P = 0.0174$). Fidelity to a subcolony was lower in failed (27.3%, $n = 11$) than in successful breeders (60%, $n = 30$). Neither standardized PRS (GLMM, $F_{1,22} = 0.36$, $P = 0.55$), nor standardized colony size (GLMM, $F_{1,23} = 0.66$, $P = 0.42$) or interactions among these variables and individual success (GLMM, $P > 0.20$ for all interactions) affected individual subcolony fidelity significantly. The fidelity of successful individuals was not affected by any of the variables analysed, either as main effects (GLMM, individual productivity in year t: $F_{1,13} = 0.07$, $P = 0.79$; standardized PRS in year t: $F_{1,14} = 0.74$, $P = 0.40$; standardized colony size in year t: $F_{1,15} = 1.40$, $P = 0.25$) or as interactions (GLMM, $P > 0.13$ for all interactions). The patch in which birds bred did not influence these results (GLMM, ns random effect).

DISCUSSION

Spatial and temporal variations within the Ebro delta Audouin's Gull colony only fully satisfied one of the two major assumptions for habitat copying. The environment is patchy, making subcolony selection necessary, whereas subcolony quality is not autocorrelated. Hence, given the lack of predictability in habitat quality, habitat copying should not be the main habitat selection strategy expected on theoretical grounds, and other strategies such as conspecific attraction or random settlement are more probable (Doligez *et al.* 2003).

We found that the reoccupation probability of subcolonies increases with previous population size. This may indicate that the reoccupation of subcolonies in consecutive years needs a minimum stimulus related to the number of breeders in the previous breeding season, i.e. there is some kind of conspecific attraction or group effect in the breeding habitat selection process. This could result from the Allee effect (i.e. positive density dependence at low population sizes; Courchamp *et al.* 1999). In other colonies of this species, patch extinction occurred when the population was decreasing and this was also related to mechanisms of group dispersal (Martínez-Abraín *et al.* 2003b). Furthermore, the average productivity of subcolonies seems not to determine their probability of being reoccupied. Individuals breeding there the previous year may reoccupy the subcolonies and this decision could be based on private information; breeding-patch fidelity could also be acting. The subcolony annual multiplication rate seems to be affected by the previous PRS. This relationship is as predicted by the HCH (annual multiplication rate and PRS being positively correlated). However, there could be other explanations. (i) We cannot discount the possibility of an effect of conspecific attraction because PRS and colony size are positively correlated (see Methods). In that case, Audouin's Gulls could rely on population sizes to evaluate patches and subsequently choose among them. (ii) Breeding site fidelity could be another possible non-exclusive explanation: the success of individuals breeding in patches with high PRS must also be high; we would then expect them to be faithful to their patch. However, population increases in high-quality patches (with high PRS) could not be explained only by this strategy because a population increase requires new recruits, which cannot rely on private information to select a patch. Low population increase from one year to the next could, however, result from the low site fidelity of failed breeders (Oro *et al.* 1999, 2004, Oro & Pradel 2000, Martínez-Abraín *et al.* 2003b).

However, natal philopatry could not explain the relationship between patch annual multiplication rate and the previous PRS. Audouin's Gulls first breed when at least 3 years old. In order to exclude the possibility that offspring produced in one year could affect the demographic trend in their natal subcolony 3 years later, we have tested the effect of PRS on subcolony demographic trends with a 3-year time lag. We failed to find an effect of PRS in year *t*, either on subcolony reoccupation probability from year $t + 2$ to $t + 3$ (Logistic regression, $\chi^2_{121} = 0.23$, $P = 0.63$) or on subcolony multiplication rate from year $t + 2$ to $t + 3$ (Linear regression, $F_{1,21} = 2.14$, $P = 0.16$); our results do not reflect natal philopatry to the natal patch 3 years after the natal year.

At an individual level our results show that, as is generally the case, successful breeders are more patch-faithful than failed breeders, indicating that Audouin's Gulls use private information. We found no evidence that individuals made use of local reproductive success. There are several possible non-exclusive explanations for this. (i) For practical reasons, birds whose broods failed after hatching were excluded from our analyses because we could not detect total failures after hatching, meaning that our samples might be biased. The existence of such biases is supported by the low proportion of failed individuals in our sample (only 11 in 41 birds). Such a bias would not enable us to detect a habitat copying strategy at the individual level. (ii) Because of small sample sizes we might fail to reject the null hypothesis. (iii) Different phenotypes in the population may use different sources of information. As we have no information on natal dispersal, we cannot reject the possibility that to select their first breeding place juveniles rely on different cues from those used by breeders. Such differences in information-use are known to affect the dispersal of Lesser Kestrels *Falco naumanni*, in which species experienced breeders cue mainly on private information whereas juveniles cue on current colony size and the performance of conspecifics from their colony of origin (Serrano *et al*. 2001). Similar differences have been shown between sexes in the Collared Flycatcher *Ficedula albicollis* (Doligez *et al*. 1999). The occurrence of phenotypes using different types of information is also predicted by a theoretical approach to habitat selection (Doligez *et al*. 2003). (iv) In poorly predictable or unpredictable environments, such as those used by gulls, habitat copying is probably one among several more important habitat-selection strategies used in the population. The influence of temporal predictability of the environment on the evolutionary success of using information based on conspecific performance has been stressed in theoretical studies (Boulinier & Danchin 1997, Doligez *et al*. 2003).

Our results at the individual level do not allow us to identify which mechanism of habitat selection is used by Audouin's Gulls for patch choice, and they only allow us to affirm that breeders use private information. Demographic results, instead, seem to point towards either the coexistence of three mechanisms at work (a group effect, a habitat copying strategy and also conspecific attraction) or a scenario in which only one of them operates. Experiments would be required to further this research, but in an endangered species such as this, large-scale experiments, such as those performed in the Kittiwake *Rissa tridactyla* (Boulinier *et al*. 2002) and the Collared Flycatcher (Doligez *et al*. 2002), are not feasible.

Importance of the spatial and temporal scale in testing spatial hypotheses

Previous studies on this metapopulation have analysed mechanisms of dispersal (Oro & Pradel 1999, 2000, Oro *et al*. 1999, 2004, Oro & Ruxton 2001, Genovart *et al*. 2003, Martínez-Abraín *et al*. 2003a, 2003b, Oro 2003, Cam *et al*. 2004). With the exception of Oro and Pradel (2000), which did not test for the spatial variability implicit in the corollaries of the HCH, these studies failed to find evidence for a habitat-copying strategy at a large spatial scale (between colonies separated by an unsuitable spatial matrix). In the present study we report that Audouin's Gulls might be influenced by the performance of conspecifics when choosing a breeding site at a smaller spatial scale, in our case within a large colony. At that scale, we collected data from a significant proportion of the patches within the Ebro delta colony. Animals may use different mechanisms at different scales, and could be physically excluded to prospect different patches at a large geographical scale (Oro & Pradel 1999, Oro & Ruxton 2001). It should be added that as the PRS can only be assessed during a short period just before fledging (Boulinier *et al*. 1996), habitat copying at the intercolony scale may be an unlikely mechanism (Boulinier & Danchin 1997, Oro & Ruxton 2001, Doligez *et al*. 2003).

Habitat copying and environmental stability

In unpredictable environments, habitat copying is counter selected (Doligez *et al*. 2003) because the PRS of conspecifics is not usable. Our results reveal that, within the Ebro delta colony, Audouin's Gulls show little stability in breeding-patch occupation (Fig. 1). Such a high rate of patch abandonment and colonization may itself be an adaptation to unstable environments (Oro & Muntaner 2000, Martínez-Abraín *et al.* 2003a, 2003b). However, in spite of this, and in the absence of statistically measured autocorrelation in patch quality, we suggest that this species may retain the capacity to rely on the PRS of conspecifics under certain situations. This might be advantageous in such a long-lived species because breeding habitat selection occurs several times in a lifetime, and a given individual may face habitats of varying predictability.

We especially thank Emmanuelle Cam for discussion on earlier drafts of the manuscript and also two anonymous referees for useful comments on the manuscript. The analytical work was financially supported by the Picasso programme of integrated actions France–Spain (Dossier 04219NL) and Spain–France (Dossier HF 2001-0147). D.P. was supported by a Postdoctoral Marie Curie Fellowship (contract HPMF-CT-2000-00716) to work at the UPMC in France. Funds were provided also by grants from the Spanish Ministry of Science and Technology (grants ref. BOS2000-0569-C02-02 and BOS2003-01960) and the Ebro Delta Natural Park (Generalitat de Catalunya).

REFERENCES

Boulinier, T. & Danchin, E. 1997. The use of conspecific reproductive success for breeding patch selection in territorial migratory species. *Evol. Ecol.* **11**: 505–517.

Boulinier, T., Danchin, E., Monnat, J.Y., Doutrelant, C. & Cadiou, B. 1996. Timing of prospecting and the value of information in a colonial breeding bird. *J. Avian Biol.* **27**: 252–256.

Boulinier, T., Yoccoz, N.G., McCoy, K.D., Erikstad, E. & Tveraa, T. 2002. Testing the effect of conspecific reproductive success on dispersal and recruitment decisions in a colonial bird: design issues. *J. Appl. Stat.* **29**: 509–520.

Brown, C., Brown, M.B. & Danchin, E. 2000. Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice. *J. Anim. Ecol.* **69**: 133–142.

Cam, E., Oro, D., Pradel, R. & Jimenez, J. 2004. Assessment of hypotheses about dispersal in a long-lived seabird using multistate capture–recapture models. *J. Anim. Ecol.* **73**: 723–736.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. 1999. Inverse density-dependence and the Allee effect. *Trends Ecol. Evol.* **14**: 405–410.

Danchin, E., Boulinier, T. & Massot, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* **79**: 2415–2428.

Danchin, E. & Cam, E. 2002. Can non-breeding be a cost of breeding dispersal? *Behav. Ecol. Sociobiol.* **51**: 153–163.

Danchin, E., Heg, D. & Doligez, B. 2001. Public information and breeding habitat selection. In Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (eds) *Dispersal*: 243–258. Oxford: Oxford University Press.

Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Anim. Behav.* **66**: 973–988.

Doligez, B., Danchin, E. & Clobert, J. 2002. Public information and breeding habitat selection in a wild bird population. *Science* **297**: 1168–1170.

Doligez, B., Danchin, E., Clobert, J. & Gustafsson, L. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *J. Anim. Ecol.* **68**: 1193–1206.

Erwin, R.M., Nichols, J.D., Eyler, T.B. & Stotts, D.B. 1998. Modelling colony size dynamics: the metapopulation of Gull-billed Terns in coastal Virginia. *Auk* **115**: 970–978.

Forero, M.G., Donázar, J.A., Blas, J. & Hiraldo, F. 1999. Causes and consequences of territory change and breeding dispersal distance in the Black Kite. *Ecology* **80**: 1298–1310.

Genovart, M., Oro, D. & Bonhomme, F. 2003. Genetic and morphological differentiation between the two largest breeding colonies of Audouin's Gull *Larus audouinii*. *Ibis* **145**: 448–456.

Haas, C.A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. *Auk* **115**: 929–936.

Lambertini, M. 1993. The ecology and conservation of Audouin's Gull (*Larus audouinii*) at the northern limits of its breeding range. In Monbaillu, X. (eds) *Medmaravis NATO ASI Series*, Vol. G12: 261–272. Berlin: Springer-Verlag.

Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.S. 1996. *SAS System for Mixed Models*. Cary, NC: SAS Institute Inc.

Martin, T.E. 1993. Nest predation and nest sites. New perspectives on old patterns. *Bioscience* **43**: 523–532.

Martínez-Abraín, A., González-Solís, J., Pedrocchi, V., Genovart, M., Abella, J.C., Ruiz, X., Jiménez, J. & Oro, D. 2003a. Kleptoparasitism, disturbance and predation of Yellow-legged Gulls on Audouin's Gulls in three colonies of the western Mediterranean. In Mínguez, E., Oro, D., de Juana, E. & Martínez-Abraín, A. (eds) *Mediterranean Seabirds and Their Conservation*: 89–94.

Martínez-Abraín, A., Oro, D., Forero, M.G. & Conesa, D. 2003b. Temporal and spatial local population dynamics in a long-lived seabird. *Popul. Ecol.* **45**: 133–139.

Oro, D. 1998. Audouin's gull. *Larus audouinii, BWP Update (The Journal of Birds of the Western Palearctic)* **2**: 47–61.

Oro, D. 2003. Managing seabird metapopulations in the Mediterranean: constraints and challenges. In Mínguez, E., Oro, D., de Juana, E. & Martínez-Abraín, A. (eds) *Mediterranean Seabirds and Their Conservation*: 13–22.

Oro, D., Cam, E., Pradel, R. & Martínez-Abraín, A. 2004. Influence of food availability on demography and local population dynamics in a long-lived seabird. *Proc. R. Soc. Lond. B* **271**: 387–396.

Oro, D., Jover, L. & Ruiz, X. 1996. Influence of trawling activity on the breeding ecology of a threatened seabird, Audouin's gull *Larus audouinii*. *Mar. Ecol. – Prog. Ser.* **139**: 19–29.

Oro, D. & Muntaner, J. 2000. La gaviota de Audouin en Cabrera. In Pons, G.X. (ed.) *Las aves del Parque Nacional marítimo-terrestre del archipiélago de Cabrera (Islas Baleares,* *España)*: 95–112. Madrid: GOB, Colecciones Técnicas del Ministerio de Medio Ambiente.

Oro, D. & Pradel, R. 1999. Recruitment of Audouin's Gull to the Ebro Delta colony at metapopulation level in the western Mediterranean. *Mar. Ecol. – Prog. Ser.* **180**: 267–273.

Oro, D. & Pradel, R. 2000. Determinants of local recruitment in a growing colony of Audouin's gull. *J. Anim. Ecol.* **69**: 119–132.

Oro, D., Pradel, R. & Lebreton, J.D. 1999. Food availability and nest predation influence life history traits in Audouin's Gull, *Larus audouinii*. *Oecologia* **118**: 438–445.

Oro, D. & Ruxton, G.D. 2001. The formation and growth of seabird colonies: Audouin's gull as a case study. *J. Anim. Ecol.* **70**: 527–535.

Parejo, D., Danchin, E. & Avilés, J.M. 2005. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? *Behav. Ecol.* **16**: 96–105.

Pradel, R., Hines, J.E., Lebreton, J.D. & Nichols, J.D. 1997. Capture–recapture survival models taking account of transients. *Biometrics* **53**: 88–99.

SAS. 1999. *SAS User's Guide*, Version 8. Cary, NC: SAS Institute.

Schjørring, S., Gregersen, J. & Bregnballe, T. 1999. Prospecting enhances breeding success of first time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. *Anim. Behav.* **57**: 647–654.

Schjørring, S., Gregersen, J. & Bregnballe, T. 2000. Sex difference in criteria determining fidelity towards breeding sites in the great cormorant. *J. Anim. Ecol.* **69**: 214–223.

Serrano, D. & Tella, J.L. 2003. Dispersal within a spatially structured population of lesser kestrel: the role of spatial isolation and conspecific attraction. *J. Anim. Ecol.* **72**: 400–410.

Serrano, D., Tella, J.L., Forero, M.G. & Donázar, J.A. 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *J. Anim. Ecol.* **70**: 568–578.

Stamps, J.A. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. In Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (eds) *Dispersal*: 230–242. Oxford: Oxford University Press.

Switzer, P.V. 1993. Site fidelity in predictable and unpredictable habitats. *Evol. Ecol.* **7**: 533–555.

Switzer, P.V. 1997. Past reproductive success affects future habitat selection. *Behav. Ecol. Sociobiol.* **40**: 307–312.

Taylor, J.B. 1998. *Economics*. Boston: Houghton Mifflin Company.

Underwood, A.J. 1997. *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge: Cambridge University Press.

Wagner, R.H. & Danchin, E. 2003. Conspecific copying: a general mechanism of social aggregation. *Anim. Behav.* **65**: 405–408.

Wagner, R.H., Danchin, E., Boulinier, T. & Helfenstein, F. 2000. Colonies as byproducts of commodity selection. *Behav. Ecol.* **11**: 572–573.

Wiens, J.A. 1976. Population responses to patchy environment. *Annu. Rev. Ecol. Syst.* **7**: 81–20.

Received 27 July 2004; revision accepted 22 September 2005.