

# The formation and growth of seabird colonies: Audouin's gull as a case study

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## Summary

1. Simulations of a stochastic, individual-based predictive model were used to investigate the ecological processes relating to the formation and growth of colonies (local populations) of Audouin's Gull (*Larus audouinii* Payraudeau). A colony was established in 1981 at the Ebro Delta (in the north-western Mediterranean) and since then, the colony has grown dramatically at an average rate of 44% per year, such that by 1997 it held 65% of the total world population of this species.
2. Our model shows that the observed growth in the colony cannot be explained without large-scale immigration of individuals into the colony. Although immigration occurred in most of the years throughout the study, years with an absence of immigration and even with net emigration from the colony also occurred.
3. The most likely source of immigrants was the colony on the Chafarinas Islands (655 km southwards from the Ebro Delta), which has been the largest known colony excluding the Delta in every year since 1981. However, immigrants from other neighbouring colonies apart from the Chafarinas, and even from other colonies beyond the western Mediterranean metapopulation were presumably also involved.
4. Immigration from other colonies is likely to be driven by temporal heterogeneity in the relative quality of the different colonies, combined with individuals dispersing to search for and select the most suitable breeding place, in order to increase their fitness. However, breeding success at the Ebro Delta colony was not autocorrelated from one year to the next, suggesting that the predictability of the environment was low.
5. Predictability was also low in other colonies within the metapopulation, independently of their size or relative quality. Results suggest that the presence of conspecifics (rather than local reproductive success) may be more important for immigrants in breeding site selection.
6. Colonization of the Ebro Delta was probably facilitated by the effective protection of the site against human disturbances, which produced a new, empty, high quality site for prospecting gulls. This may be considered a stochastic and density independent event, of a type that may have been a much more important influence on seabird colony formation than has been appreciated.

*Key-words:* colony growth, dispersal, immigration, metapopulation, *Larus audouinii*.

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## Introduction

Much recent consideration has been devoted to the ecological processes involved and the evolutionary

function of coloniality in socially breeding birds (e.g. Brown, Stutchbury & Walsh 1990; Brown & Bomberger Brown 1996; Danchin & Wagner 1997; Rolland, Danchin & de Fraipont 1998; Brown, Bomberger Brown & Danchin 2000), and in colonial seabirds in particular (Kharitonov & Siegel-Causey 1988; Clode 1993; Buckley 1997; Danchin, Boulinier & Massot 1998). However, there has been little empirical

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**1** data relating to the formation and growth of colonies (Ollason & Dunnet 1983; Porter & Coulson 1987; Coulson & Nève de Mévergnies 1992). It is known that colonization of an empty patch and its subsequent growth implies immigration of individuals from existing local populations within a metapopulation (Ims & Yoccoz 1997; Hanski 1998). As such, immigration is an exogenous component of local population dynamics, and immigrants may enter the colony as first breeders (natal dispersal) or as individuals that previously bred in another colony (breeding dispersal). Different theoretical models have pointed out the importance of dispersal to population and metapopulation dynamics, focusing on its importance for both the recolonization of extinct patches (e.g. Hanski 1998) and for fluctuations of local populations (e.g. Johst & Brandl 1997). Thus, comprehension of the ecological and evolutionary mechanisms underlying the immigration process is crucial, if we are to understand how colonies are formed and how they grow. Immigration relies on a process of individual decisions at both departure and settlement, with immigrants trying to select the most suitable place to breed. At departure level, dispersal may be triggered by economic thresholds, conflict over resources or inbreeding avoidance (Hansson 1991). Once dispersed, immigrants must select a site to breed, and may assess the quality of the different patches using environmental cues, such as the presence of conspecifics (social attraction) or their reproductive success (e.g. Reed & Dobson 1993; Brown & Rannala 1995; Boulinier & Danchin 1997; Danchin *et al.* 1998; Brown *et al.* 2000). Much less attention has been dedicated to the process of habitat selection for the first immigrants settling at a previously empty patch (Smith & Peacock 1990). While several factors operating at these patches (such as suitable environmental conditions for breeding or low interspecific competition) have been recognized to influence colonization probabilities positively (e.g. Brooke, Lockwood & Moulton 1995; Grant & Grant 1995), little is known about the process of breeding habitat selection by colonizers. Since colonizers cannot rely on information from the presence or reproductive success of conspecifics, such pioneering may be a risky strategy (Smith & Peacock 1990; Forbes & Kaiser 1994; Mönkkönen *et al.* 1999).

Here we study the formation and growth of a colony of Audouin's gull *Larus audouinii* at the Ebro Delta (north-western Mediterranean), and the ecological processes involved. To our knowledge, this colonization is unique among studies of population or metapopulation dynamics of social and long-lived birds. The species was considered threatened by extinction, and first estimated numbers gave very low world population sizes during the 1960s and 1970s (800 and 2000 breeding pairs, respectively, see de Juana & Varela 1993). Since 1981, when the first colonizers settled at the Ebro Delta, the colony has grown dramatically at an average growth rate of 44% per year, and in 1997 it concentrated more than 60% of the total world population of the species, estimated at 18 000 breeding pairs (Oro 1998).

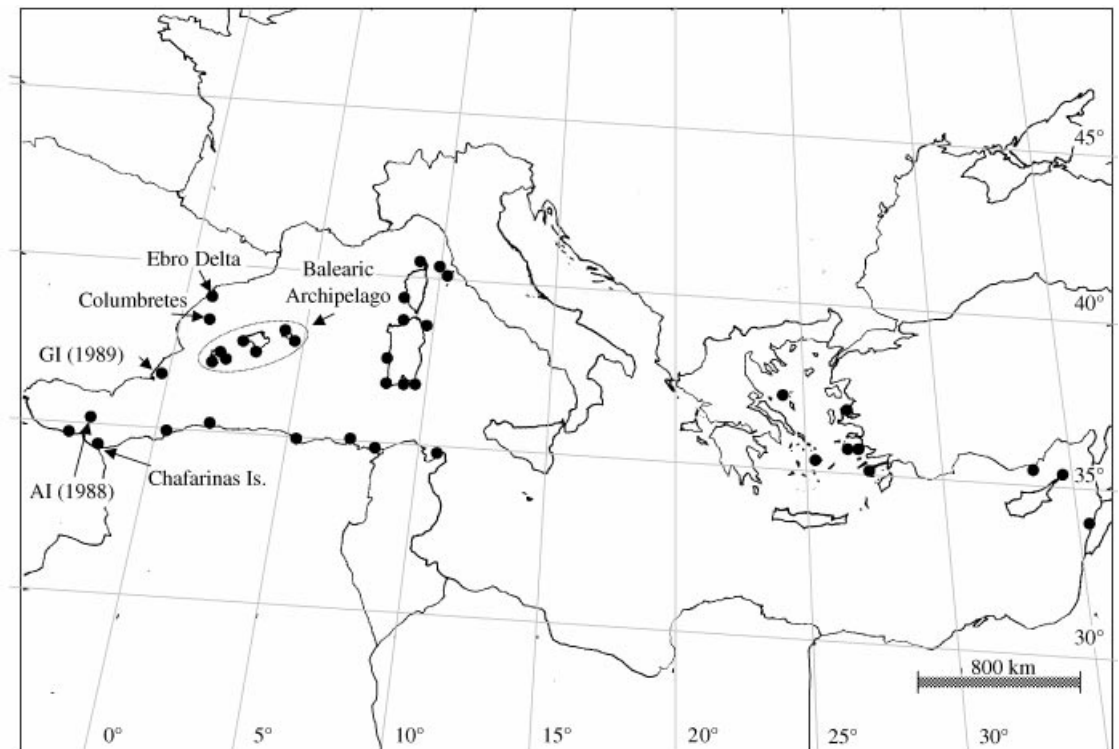
There has been controversy over whether this extreme colony growth has happened entirely through internal production, or whether immigration has been involved. It has been suggested that some immigration occurred during the first years (Ruiz *et al.* 1996), and that the Chafarinas Islands colony, which has always been the largest known colony excluding the Ebro Delta in every year since 1981, was the source of these immigrants (de Juana & Varela 1993). Several studies show that natal recruits do not always sustain a local population, and that immigration can play an important role in population growth rates (e.g. Ollason & Dunnet 1983; Porter & Coulson 1987; Ainley, Ribic & Wood 1990; Danchin & Monnat 1992; Morais, Santos & Vicente 1998). The first aim of the present study is to estimate the net number of breeding females migrating into the colony each year, using a mathematical model utilizing demographic parameters estimated at the Ebro Delta. These parameters are well studied in the colony, which allows us to make predictions about the size of internal production. At the same time, the size of neighbouring colonies through the study period within the western Mediterranean metapopulation has been estimated (e.g. Oro 1998; Oro & Pradel 1999), which allows us to make predictions about where the migrants came from. Comparison between the predictions of this model and estimates of colony size allow us to assess the net rate of immigration to or from the colony in each year. The hypothesis that conspecific reproductive success is the environmental cue used by immigrants to recruit to the Ebro Delta is also assessed (see Danchin *et al.* 1998 and references therein). To do this, the two assumptions of the hypothesis are tested: first, that reproductive success for a given year was different among colonies (i.e. patchiness of the environment); and second, that reproductive success in a given colony was predictable from one year to the next (Boulinier & Danchin 1997; Danchin *et al.* 1998).

## Methods

### STUDY AREA AND ESTIMATION OF COLONY SIZE

The study was conducted at the Punta de la Banya (Ebro Delta Natural Park, NE Spain: 40°37'N, 00°35'E) (see Fig. 1). The site is a flat sandy salt marsh on a peninsula connected to the rest of the Delta by a narrow 9 km long sand bar (see details in Oro & Pradel 2000).

Since the establishment of the colony in 1981, the number of nests has been counted each year, in order to estimate colony size. Censuses were carried out during 1–4 days (depending on the size of the whole colony) in the second week of May, when most pairs had laid, but few broods had hatched (see Ruiz *et al.* 1996 and references therein). During the periods 1981–83, 1988–89 and 1992–97, the number of nests was counted by a team of four to 12 people (depending on the size and shape of both the whole colony and the subcolonies),



**Fig. 1.** Map of the western Mediterranean region showing the location of the Audouin's gull colonies existing in 1981 when the Ebro Delta colony was established. Only the names of large colonies are shown. The two sites colonized in this region after the colonization of the Ebro Delta (Grossa Island -GI- and Alborán Island -AI-) are also shown together with the year of establishment (see text).

moving in a line back and forth throughout the dunes or the dikes. Counting efficiency was assessed by marking counted nests with a coloured small bead dropped into the nest; immediately after the count, an observer searched the area previously counted by the team and recorded the number of marked and unmarked nests. During the periods 1984–87 and 1990–91, counts of nests were performed counting incubating adults from a distance using a telescope. Counting efficiency with this method had previously been assessed by comparison with the other assessment technique. Census error varied depending on the size of the whole colony or sub-colony, the location of the sub-colonies, and the number of people involved in the census, and the method used (Ruiz *et al.* 1996), see Appendix.

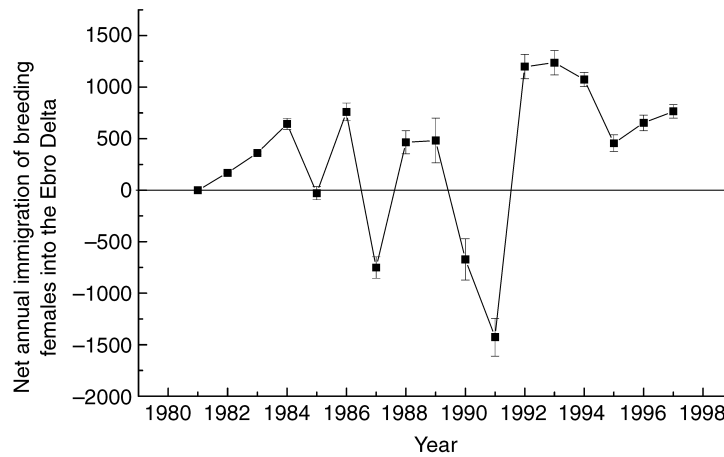
#### THE MODEL

We constructed an individual-based model. The probability of each individual surviving from year to year, the age it matures, and the breeding success of that individual in each subsequent year until its death are all determined by stochastic selection from probability distributions. By comparing the predicted number of females that originate from the Ebro Delta breeding each year with the counted number breeding, we can estimate the net number of emigrants or immigrants each year. The predictive model starts in 1981 when 36 females bred (Oro 1998). Each of these females produces a number

of fledglings drawn stochastically (independently for each female) from the empirically derived probability distribution given in the Appendix.

We are only interested in female chicks, and assume a balanced sex ratio (Genovart 1999), sex of each chick being determined stochastically. Chicks join the breeding population at either age 4, 4 or 5 years (Oro & Pradel 2000). Annual survival rate for juveniles is 79% in the first year, and 88% thereafter (Oro 1998). Thus, each chick has a 61% chance of surviving to age 3. Of these individuals, 84% begin breeding that year (Oro & Pradel 2000). Of the remainder, 95% of those that survive another year join the breeding population at age 4, the remainder becoming sexually mature at age 5, provided that they survive another winter (Oro & Pradel 2000).

The number of breeding females in the current year can come from three sources: birds that bred in the colony in the last year returning, chicks born in the Delta becoming sexually mature, and migrants. Each female that bred the previous year has a 91% chance of survival (Oro *et al.* 1999). The number of new recruits is determined as above. For each year, we also have a measured estimate of the total number of breeding females, subject to a measurement error (see Appendix). Hence, we stochastically obtain a prediction for the actual number of breeding females that year, and subtract the predicted numbers of new recruits and survivors from the previous year, to obtain an estimate



**Fig. 2.** Estimated number, obtained from the model, of breeding females migrating to the Delta each year. Since the model contains several stochastic factors, we ran 100 realizations of the model, and plot the median and 5 and 95%-iles for each year.

of the number of breeding females that immigrated into the colony.

The estimated total number of breeding females is used to generate the number of chicks born that year, as the model moves forward to the next year. The only alteration was introduced between 1994 and 1995, because a terrestrial predator entered the colony, decreasing the probability of adult local survival to 81% (Oro *et al.* 1999; Oro & Pradel 2000). Because the model has several stochastic elements, different runs of the model for the same parameter values can produce different results. Hence, we perform 100 realizations of the model and quote the median values, along with 5% and 95% percentiles. For all but the first 3 years, population sizes are sufficiently large that stochastic effects tend to cancel, and between-run variation is small. Certainly, variation was sufficiently small that we can safely attribute differences between model predictions and measured population sizes to migration rather than being simply an artefact of the stochastic nature of the model, especially since each measured population size was generally comfortably outwith the range of model predictions for that year.

The Chafarinas Islands model is identical to that of the Ebro Delta, except that the estimates of the population size are different (see Table 2 in Appendix) and there was no unusually high breeding dispersal between years 1994 and 1995. Counting error was assumed to be equal than that of the Ebro Delta (see Appendix). Two sets of simulations were generated: in one, fledgling production was equivalent to that of a good year (1992) at the Ebro Delta; in the other, it was equivalent to a poor year (1994).

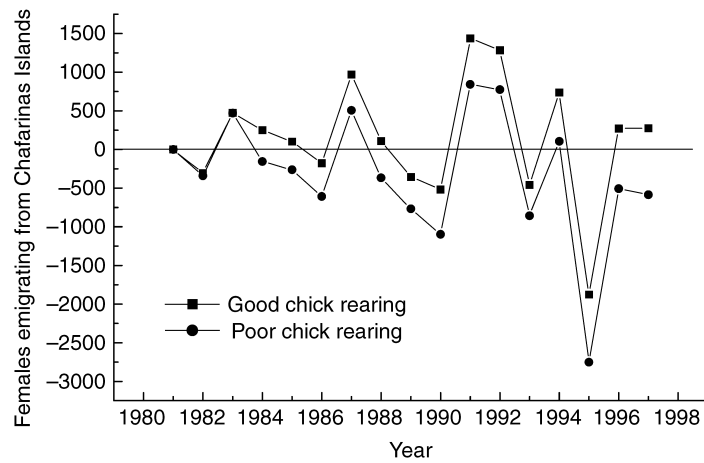
#### TESTING ASSUMPTIONS OF THE CONSPECIFIC BREEDING SUCCESS HYPOTHESIS

The two assumptions of the conspecific breeding success hypothesis (see Introduction) were tested using the number of chicks fledged per pair as a measure

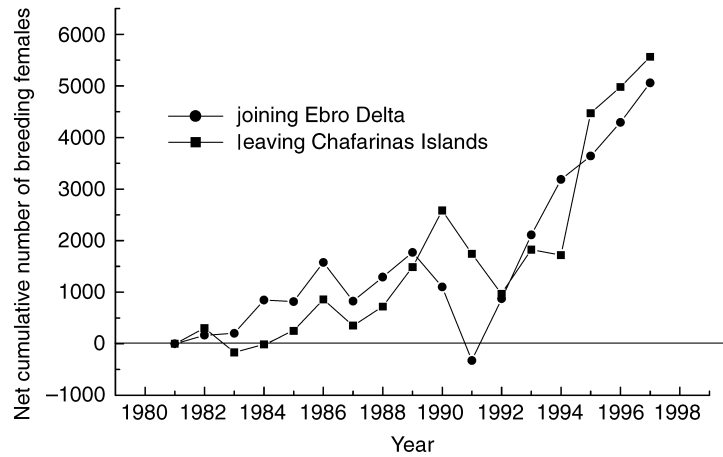
of reproductive success at four colonies: Ebro Delta (during 1991–97), Columbretes Islands (during 1987–97), Chafarinas Islands (during 1993–97) and Grossa Island (during 1993–97), using data from Oro *et al.* (1996), Ruiz *et al.* (1996); Oro (1998) and D. Oro (unpublished results). To assess the differences in reproductive success among colonies in different years, we used a non-parametric block analysis of variance (i.e. Friedman test) only for the period 1993–97, when data was available for the four colonies.

#### Results

Predictions of the model (Fig. 2) show that, if our model is an accurate reflection of the dynamics at the Ebro Delta colony, then the observed growth in the population over the last 17 years cannot be explained without large-scale immigration of individuals. Further, this immigration has continued into recent times. Even though population growth seems to have slowed considerably since 1994 (see Table 2 in the Appendix), net immigration into the population continued after this time, although the level of external recruitment generally showed a downward trend. This is not too surprising when we realize that the local recruitment must balance mortality of established breeders, in order for the population to be stable in the absence of external recruits. Lastly, in some years, the model suggests that there was net dispersal from the Ebro Delta. It is unknown whether there was immigration or not in these years, since our model can only estimate the net immigration or emigration rate. Audouin's gulls may skip breeding after adverse environmental conditions, especially young breeders (Oro 1998; Oro & Pradel 2000). However, the cumulative number of immigrants to the Ebro Delta colony at any point in time cannot be explained solely in terms of the return of birds that previously migrated from the delta. Although we predict net emigration in some years, Fig. 2 demonstrates that these numbers are considerably smaller than the net numbers of migrants



**Fig. 3.** Estimated median number of breeding females migrating from the Chafarinas Islands under two alternative hypotheses: that chick-rearing performance is always as poor as was measured in the Ebro Delta in the poor year of 1994, or always as good as measured in the good year of 1992.



**Fig. 4.** The median of model estimates of the cumulative number of breeding females that left the Chafarinas colony and the cumulative number of breeding females that joined the Ebro Delta colony.

in other years. Hence, a substantial fraction of the immigrants into the Ebro delta colony must have been born at other colonies.

Comparison between Figs 2 and 3 clearly shows that immigration of breeding females to the Ebro Delta cannot be explained by the simple shifting of breeding females from the Chafarinas Islands colony, even considering a scenario of high productivity there. For instance, our model predicts that around 1250 breeding females immigrated to the Ebro Delta colony in 1993 and 1994; yet the predicted number of such birds which could have left the Chafarinas colony in these years is very low, certainly less than 1000. We explore this possibility further in Fig. 4, where we plot, for each year, the cumulative estimated net number of immigrants that have entered the Ebro Delta colony since 1981, and also the cumulative number that have left the Chafarinas Islands since that year. It is clear that the rate of dispersal from the Chafarinas Islands is insufficient to explain the number of immigrants joining the colony at the Ebro Delta, especially during the first years. Further,

our simulations over-estimate the numbers leaving the Chafarinas colony in the first 2 years, because they assume that there are no juveniles maturing in these years (i.e. that no birds breed there prior to 1981). However, this effect should be quite small (affecting our estimates for these years by 20% at most). There was no significant correlation between the number of females emigrating from the Chafarinas in a given year and the number of females joining the Ebro Delta colony ( $r = 0.21$ ,  $n = 16$ ,  $P = 0.44$ ). Thus, it would appear that in order to explain the growth of the Ebro Delta colony in some years, we would require a number of immigrants from the Chafarinas Islands and also from another colony (or colonies) of approximately a stable size of 1000–2000 breeding females. Since the Chafarinas can only account for at most 50% of the migrants to the Ebro Delta, the rest must come from a colony or colonies of at least equal size to the Chafarinas. The other known large colonies in the western Mediterranean (the Balearic Archipelago, Columbretes Islands, Alborán Island and Grossa Island, see Fig. 1) have been

counted during the last 20 years and have grown from *c.* 600 breeding pairs in 1981 to *c.* 2800 pairs in 1997 overall (Oro 1998). Thus, our model predicts that it is likely that immigration from these colonies also occurred. However in some years (e.g. in 1994, see Fig. 4), the number of immigrants can only be explained by further immigration from the central and eastern Mediterranean Audouin's gull metapopulations.

The assumption that reproductive success was different among colonies taking account of the year effect was met (Friedman test,  $\chi^2_3 = 9.58$ ,  $P < 0.025$ ). The Ebro Delta and Grossa Island colonies showed higher reproductive success than the Columbretes (both Tukey tests for multiple comparison for non-parametric analysis of variance,  $P < 0.05$ ), whereas other comparisons tested were not significant (all Tukey tests,  $P > 0.05$ ). However, the average reproductive success of a given colony was not autocorrelated from one year to the next (partial correlation coefficient controlling for factors year and colony  $r = 0.21$ ,  $n = 24$ ,  $P = 0.31$ ).

## Discussion

### GROWTH OF COLONIES AND THE HYPOTHESES OF HABITAT SELECTION

Our results suggest that immigration is the main demographic parameter associated with an increase in seabird local populations (see also Ollason & Dunnet 1983; Ainley *et al.* 1990; Cairns 1992). This seems to be especially true when adult survival is not affected by environmental factors. Other demographic parameters, such as productivity, have smaller effects on the growth of these local populations (e.g. Cairns 1992). Although, when productivity is especially high, it may attract immigrants from other local populations (see below). Immigrants may come from other colonies within the metapopulation, but when dispersal capacity is high, immigrants from more distant metapopulations can also be involved (Hanski 1998). In fact, this capacity, which seems very high in Audouin's gulls (Oro & Martínez-Vilalta 1994; Oro & Pradel 1999), is essential for the extent of the colonization and immigration processes observed (Hengeveld 1989; Paradis *et al.* 1998). The predictive model clearly shows that immigration to the Ebro Delta cannot be explained by simple shifting of breeding females from the Chafarinas Island colony (655 km southwards), which was the most likely source of these birds (de Juana & Varela 1993), and that long-range immigration also occurred, presumably from central and, even the more distant, eastern Mediterranean colonies.

How immigrants decide where to breed away from their natal site seems to depend on the species and spatial and temporal variation of the environment. Site fidelity should increase with environmental predictability in time and environmental homogeneity in space at the different patches within the metapopulation (McPeck & Holt 1992; Switzer 1993; Holt 1997). Con-

trary to the prediction of the conspecific reproductive success hypothesis (e.g. Danchin *et al.* 1998), breeding success at the Ebro Delta colony was not autocorrelated from one year to the next. Thus, predictability of the environment was low (see also Erwin *et al.* 1998), not only at the Ebro Delta, but also in other local populations within the metapopulation, independently of their size or relative quality. While some species use the reproductive success of conspecifics to assess the quality of different patches in a given year (e.g. Boulinier & Danchin 1997; Danchin *et al.* 1998; Brown *et al.* 2000), some others may rely on the presence of conspecifics (e.g. Ray, Gilpin & Smith 1991; Spendelov *et al.* 1995; Oro & Pradel 2000) or on the individuals' past reproductive success (Switzer 1997). When dispersal capacities are low, or when local populations are far from each other, as is the case for Audouin's gull colonies, prospectors can be time-constrained in their inspection for suitable places to breed in the future during the short period of time when nestlings are close to fledging. However, individuals could prospect a larger geographical range and gather information on colony size at different local populations during the entire breeding season.

Our results suggest that immigration to the Ebro Delta was probably higher when breeding failures at other colonies occurred (Oro *et al.* 1996; Oro 1998; Oro & Pradel 2000), and that high patchiness in the quality of the environment favours dispersal of individuals (Holt 1997). Such environmental variability suggests that individuals plastically adapt through a process of habitat selection directed to increasing their fitness. Thus, dispersal directions within the metapopulation were probably not random (e.g. Greenwood & Harvey 1982; Ray *et al.* 1991; Spendelov *et al.* 1995; Boulinier & Danchin 1997; Danchin *et al.* 1998). Our results also suggest that environmental quality at local population level may vary with time. It is known that, at the Ebro Delta, partial breeding failure causes breeding dispersal to other colonies and skipping of reproduction, especially for younger breeders (Oro 1998; Oro *et al.* 1999; Oro & Pradel 2000; D. Oro & R. Pradel, unpublished results). In fact, the predictions of our model suggest that net emigration to other colonies occurred in these years, and that local populations may act as a source or as a sink depending on the temporal and spatial variability of environmental conditions for breeding. Thus, local population and metapopulation dynamics also depend on these variations, which determine in turn the changes in the rate of their components (dispersal or emigration, local recruitment and immigration). However, it is remarkable that annual immigration rate to the Ebro Delta, when positive, has normally represented a wave involving a relatively high number of individuals, whereas the number of prospectors recorded at the colony has been much lower (D. Oro, unpublished data). Away from the colonies, concentrations of large numbers of Audouin's gulls from different breeding populations occur at the wintering grounds (Oro & Martínez-Vilalta 1994;

Ruiz *et al.* 1996). At these grounds, individuals may take cues from conspecifics, firstly for food finding, but alternatively for deciding the migratory way to search for a breeding site.

#### FORMATION OF COLONIES

Colonization of an empty patch implies emigration from occupied patches. Two factors can increase the chances of individuals dispersing and colonizing new sites: low breeding success and, especially, breeding failure the previous year, caused by bad environmental conditions like short food supply or the presence of predators (Greenwood & Harvey 1982; Danchin & Monnat 1992; Switzer 1997; Oro & Pradel 1999; Oro *et al.* 1999; Oro & Pradel 1999, 2000; although see Erwin *et al.* 1998). Another important factor is density dependence, which may increase the dispersal rate through the rise of economic thresholds and competition over resources (e.g. den Boer 1968; Hansson 1991; Brown & Rannala 1995; but see Stiling 1987), at levels both intra- and interspecific (Oro *et al.* 1996; Ruiz *et al.* 1998). In colonies where such competition is very high, the chances of recruiting to the local population may decrease and colonizing a new patch may become an increasingly attractive strategy (den Boer 1968; Forbes & Kaiser 1994).

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There are differences in breeding site fidelity, and consequently in dispersal rates, depending on the species and their life-history strategies (Paradis *et al.* 1998). While some colonial species show a low colonization rate (e.g. Kharitonov & Siegel-Causey 1988), some others, such as Audouin's gulls and other Laridae, show a relatively high turnover (colonization–extinction) rate of local populations (Lambertini 1993; Erwin *et al.* 1998). This difference is probably linked, at least partially, with predictability of habitat quality. For instance, when predictability of breeding success is low, like that recorded in the present study (i.e. there is no autocorrelation between years), rates of colonization increase and low breeding site fidelity can be advantageous (e.g. McPeck & Holt 1992; Switzer 1993). Behaviour can also play an important role in the ability of social breeding species to colonize empty patches, and opportunistic species may show higher capacities than specialists (for both food and habitat). Herring gulls *Larus argentatus* and fulmars *Fulmarus glacialis* provide good examples of high colonization rates of such opportunistic species, exploiting increased amounts of food from human activities (e.g. Hengeveld 1989). However, results suggest that colonization may be determined mainly by several human-induced habitat changes: first, and most crucially, effective protection against human disturbances; and secondly, shortage of suitable breeding sites as a result of the spread of human settlements, tourism and industrial development, which may increase the chances of colonization (Hanski 1998; Paradis *et al.* 1998). These may be considered environmental and density-independent stochastic events, and the role of

chance is probably a more important influence on population dynamics than has been appreciated (e.g. Grant & Grant 1995; Benton & Grant 1996; Johst & Brandl 1997; Erwin *et al.* 1998).

Although it has been suggested that colonization success may depend on the number of colonizers (see Ims & Yoccoz 1997 and references therein), little is known about this relationship in birds, often because of the difficulty of estimating the number of the first settlers in studies of natural colonization in meta-populations (Valone & Brown 1995). While in the Manx shearwater *Puffinus puffinus* or in the kittiwake *Rissa tridactyla* colonies may be formed by an appreciable number of individuals selecting a new site (Storey & Lien 1985; Coulson & Nève de Mévergnies 1992, respectively), other species such as fulmars (Anderson 1982), Audouin's gulls (present study) or shags *Phalacrocorax aristotelis* (Martínez-Abraín, Oro & Jiménez 2000) show that colonization may be performed by very few pairs.

A prospecting period that may last several years normally precedes a colonization event (e.g. Kharitonov & Siegel-Causey 1988). The evolutionary function of prospecting probably relies on the importance of breeding habitat selection, which can affect most components of fitness (Boulinier & Danchin 1997; Danchin *et al.* 1998). To assess the quality of a breeding patch, individuals may use environmental cues, such as the presence of conspecifics or their breeding success (Smith & Peacock 1990; Reed & Dobson 1993; Boulinier & Danchin 1997; Danchin *et al.* 1998). Yet when the patch is empty, other cues must be used, and information could still be available through the presence of heterospecifics or their numbers (Kharitonov & Siegel-Causey 1988; Mönkkönen *et al.* 1999). This information could allow immigrants to reduce the uncertainty and risks associated with pioneering a new breeding site. Interspecific facilitation may occur (Ims & Yoccoz 1997; Mönkkönen *et al.* 1999), especially when interspecific competition is low (e.g. Danielson & Gaines 1987; Brooke *et al.* 1995; Oro *et al.* 1996; Erwin *et al.* 1998).

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**Appendix: model parameter values****Table 1.** Probability of a breeding female raising 0, 1, 2 or 3 fledglings during the study

Year	P (0)	P (1)	P (2)	P (3)
1981–90	0.05	0.41	0.33	0.21
1991	0.76	0.18	0.06	0.00
1992	0.38	0.34	0.26	0.02
1993	0.65	0.29	0.05	0.01
1994	0.87	0.08	0.03	0.02
1995	0.44	0.37	0.18	0.01
1996	0.50	0.35	0.12	0.03
1997	0.87	0.07	0.03	0.03

**Table 2.** Total number of breeding females at the Ebro Delta and the Chafarinas Islands colonies. As an example, in 1982 at the Ebro Delta, the estimate of the population size is drawn from a uniform distribution between 0.97% and 103% of 200. Similarly, in 1991, the uniform distribution lies between 0.91% and 100% of 3950

Year	Ebro Delta		Chafarinas Is.	
	Estimate	Error	Estimate	Error
1979	0	0	1350	±2%
1980	0	0	1870	±2%
1981	36	0	2220	±2%
1982	200	±3%	1710	±2%
1983	546	±3%	2020	±2%
1984	1 200	−9%	2194	±2%
1985	1 200	−9%	2198	±2%
1986	2 200	−9%	1930	±2%
1987	1 850	−9%	2845	±2%
1988	2 861	±3%	2800	±2%
1989	4 266	±3%	3200	±2%
1990	4 300	−9%	3600	±2%
1991	3 950	−9%	4000	±2%
1992	6 714	±2%	4300	±2%
1993	9 373	±2%	3540	±2%
1994	10 143	±2%	4136	±2%
1995	10 402	±2%	2124	±2%
1996	11 328	±2%	2412	±2%
1997	11 725	±2%	2700	±2%

