

Determinants of local recruitment in a growing colony of Audouin's gull

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Summary

1. Local recruitment of Audouin's gull (*Larus audouinii* Payraudeau) was studied between 1988 and 1997 at the Ebro Delta colony (north-western Mediterranean). Since its establishment in 1981, the colony has dramatically grown to include, in 1997, 65% of the total world population. Several hypotheses were tested, involving the effects of a badger predatory event in 1994, and sex, age and cohort (year of birth) on recruitment.

2. Results supported the prediction that colony size influenced recruitment: the probability for any individual to have previously bred increased throughout the study, together with colony size. At the end of the study, 90% of breeders aged 4 years had already been recruited at age 3, the age of first reproduction by Audouin's gulls. As expected by the dramatic increase of breeding numbers, most local recruitment occurred at very young ages, especially when compared with other Laridae.

3. Neither food availability nor reproductive success affected recruitment. Recruitment was not affected by high nest predation by the badger, although after the event, the proportion of Ebro Delta birds nesting on the nearby Columbretes Islands tripled.

4. Probability of first reproduction depended on age: it was the highest at ages 3 and 4, and then decreased sharply with age to stabilize beyond age 6 to a value depending on the year and cohort but always very low (< 5%). Cohort and sex did not influence local recruitment.

5. Annual resighting rates ranged between 35% and 82%, and were higher for females. This may represent a sex-dependent suspension of breeding, probably as a trade-off between early recruitment and future survival.

Key-words: colony size, dispersal, food availability, *Larus audouinii*, predation.

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Introduction

Recruitment can be defined as the entry of new individuals into the breeding fraction of a population. These new individuals may have been born in the same population (i.e. local recruitment) or at other populations (i.e. non-local recruitment or immigration). As such, recruitment and age at recruitment in

particular play a major role in the dynamics and the growth of both populations and metapopulations (Stearns 1992; Nichols *et al.* 1994; Hanski & Gilpin 1997). In many bird species, especially in long-lived ones, different individuals start to breed at different ages. In seabirds in particular, the variation among individuals in the age of recruitment is quite large (see reviews in Bradley & Wooller 1991; Danchin *et al.* 1991). Two non-exclusive reasons are proposed in the literature for the delayed reproduction of apparently mature individuals (Curio 1983). Constraint hypotheses consider that young individuals are prevented from reproducing by social factors or by inadequate breeding capabilities (e.g.

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Aebischer, Potts & Coulson 1995; Spear, Sydeman & Pyle 1995) or by endocrine mechanisms (Hector *et al.* 1990). On the other hand, restraint hypotheses consider that young individuals delay breeding in order to avoid costs in survival or in their future reproductions (e.g. Forslund & Pärt 1995; Pyle *et al.* 1997). In this context, Boulinier & Danchin (1997) have recently suggested that delayed reproduction may be caused by the need of individuals to gather information about the suitability of the breeding sites where they can recruit.

Apart from age, space is another important determinant of recruitment. A philopatric strategy seems at first advantageous when site quality is highly predictable over time. However, in such cases high-quality sites will tend to become saturated. Young individuals will then be faced with the alternatives of delaying breeding altogether or dispersing to recruit elsewhere (Greenwood & Harvey 1982; Ens, Weissing & Drent 1995; Prévot-Julliard 1996). This may be the reason for the widespread existence of prospectors in seabirds (Harrington 1974; Porter 1988; Cadiou, Monnat & Danchin 1994). The prospecting period in the life of an individual may also provide an opportunity for the colonization of new high-quality breeding sites (Boulinier & Danchin 1997) but relevant empirical data are very limited. Such a phenomenon may have occurred with Audouin's gull (*Larus audouinii* Payraudeau) at the Ebro Delta colony, in the north-western Mediterranean. The total world population of the species has dramatically increased since the establishment in 1981 of this colony, where the numbers breeding have increased from 36 pairs up to more than 11700 pairs in 1997, then representing 65% of the total world population (Oro 1998). Such a dramatic growth rate (average annual increase of 47%) has never previously been reported for gulls or seabirds in general. A very high immigration rate must have occurred to explain this growth rate, but also local recruitment is expected to be particularly high in this newly founded fast-growing colony. Little is known about the mechanisms that attract young birds to established colonies and this has considerable importance in both conservation and evolutionary ecology. Three main hypotheses about the determinants of local recruitment in Audouin's gull were tested in the present study.

HYPOTHESIS 1: REPRODUCTIVE SUCCESS

If prospecting occurs, conspecific reproductive success may be used as a cue by potential recruits (e.g. Reed & Dobson 1993; Danchin & Wagner 1997). Reproductive success, as one of the most important fitness components, may be correlated with local recruitment to the breeding site (Lebreton 1987); Cadiou *et al.* 1994 have shown that the number of

prospectors that recruit in the following year is positively associated with reproductive success the year before. Similarly, we can predict that local recruitment of Audouin's gull at the Ebro Delta will be associated with reproductive success at the colony. Thus, we first tested the null hypothesis of constant local recruitment through time (i.e. not varying with the reproductive success at the colony the year before). During one year of the study (1994), reproductive success was particularly low due to a dramatic event. A badger (*Meles meles*) entered the colony, disturbing the gulls and preying on nests (both on eggs and chicks) (Oro, Pradel & Lebreton 1999). This event may be considered as a natural experiment in which reproductive success was manipulated. However, the trauma caused by this predation may go beyond the simple decrease in reproductive success. A previous study (Oro *et al.* 1999) has shown that a relatively large number of breeders ($\approx 10\%$) dispersed from the colony following this event. It would then be expected that the breeding dispersal in 1994 caused by the predation would increase the probability of recruitment for potential breeders, as has been recorded in other species (e.g. Pradel *et al.* 1997a). Therefore, predation by the badger in 1994 was also considered as a factor by itself. To confirm that predation caused emigration of local breeders, its influence on breeding dispersal of individuals born in the Ebro Delta colony to the closest neighbouring colony of the Columbretes Islands (80 km apart) was also assessed. In this archipelago, ecological conditions are not as suitable as in the Ebro Delta, in terms of food availability and competition with the predatory yellow-legged gull *Larus cachinnans* (Oro *et al.* 1996a). Reproductive success has always been high in the Ebro Delta since the establishment of the colony, whereas many cases of breeding failures have been recorded in the Columbretes Islands (Oro *et al.* 1996a). In many long-lived bird species, including gulls, individuals that breed successfully in year i are more likely to return to the same area in year $i + 1$ (Greenwood & Harvey 1982; Cuthbert 1988; Cadiou *et al.* 1994; Nager *et al.* 1996; but see Korpimäki 1993). Thus, we tested the hypothesis that the relative attractiveness of the Columbretes Islands to the individuals born in the Ebro Delta was low through the years of study, whereas it increased after the badger event.

HYPOTHESIS 2: COLONY SIZE

If colony size reflects the relative quality of the habitat in which each colony is located, a large colony may be more attractive to potential recruits than a smaller colony (Kharitonov & Siegel-Causey 1988; Stamps 1988; Brown, Stutchbury & Walsh 1990). Apart from reproductive success, gulls may also use

the presence of conspecifics as a cue to colony selection (Reed & Dobson 1993; Danchin & Wagner 1997). The conspecific attraction hypothesis (Stamps 1988) predicts that animals may use the presence of conspecifics to ascertain the suitability of the breeding habitat (see also Smith & Peacock 1990; Muller *et al.* 1997). In seabirds, the attractiveness of the natal colony may increase with its size (e.g. Porter & Coulson 1987; Weimerskirch & Jouventin 1987; but see Aebischer 1995). However, beyond a threshold of breeding numbers, density-dependent factors may act inversely, reducing site attractiveness for potential new recruits (Porter & Coulson 1987; Cairns 1992; Switzer 1993; Spindel *et al.* 1995), or deterring them for breeding because of the low availability of suitable nest sites (e.g. Nager *et al.* 1996). In practice, several studies have shown how density dependence influences recruitment: in herring gulls *Larus argentatus*, recruits are more attracted to dense areas (Duncan 1978), but if density is high they have greater difficulty in establishing a territory (Chabrzyk & Coulson 1976); when density decreases, new breeders may recruit at younger ages (Duncan 1978; Coulson, Duncan & Thomas 1982); in kittiwakes *Rissa tridactyla*, small colonies attract more young individuals than larger colonies (Coulson & Nève de Mévergnies 1992). In Audouin's gull, density dependence seems to operate in stable colonies where ecological conditions are not suitable for breeding successfully (Ruiz *et al.* 1998), whereas at the growing colony of the Ebro Delta some parameters, such as reproductive success, do not seem to be affected by density-dependent factors (Oro *et al.* 1996a, 1999). Thus, the null hypothesis of no variation of recruitment at the Ebro Delta depending on the colony size the year before was also tested.

HYPOTHESIS 3: FOOD AVAILABILITY

For a given density, recruitment may depend on the amount of food available during the breeding season (Porter & Coulson 1987; Ricklefs 1990; Aebischer & Wanless 1992; Spear *et al.* 1995), especially in temporally varying environments (e.g. Switzer 1993). In seabirds in particular, it has been suggested that food supplies may limit breeding populations and restrict the recruitment of young birds (Ricklefs 1990). Food availability for Audouin's gulls around the Ebro Delta is especially high because of the diversity and richness of foraging habitats, although it varies from year to year (Oro *et al.* 1997, 1999). Thus, we finally tested the null hypothesis that different levels of food availability did not cause variation in recruitment over the years. For all the hypotheses tested, the effects of age and sex of the individuals were also considered.

Methods

STUDY AREA AND COLLECTION OF DATA

Audouin's gull is an endemic seabird of the Mediterranean region, adapted to foraging during the night, mostly on clupeoid fish. It shows a large foraging range and is known to exploit fish discarded from commercial fisheries, especially from trawlers, a foraging resource which is very predictable in space and time (e.g. Oro *et al.* 1996a; Oro, Jover & Ruiz 1996b; Oro *et al.* 1997). The study was carried out between 1988 and 1997 on gulls breeding at the Punta de la Banya (Ebro Delta Natural Park, 40°37'N, 00°35'E; Fig. 1). The site is a sandy and flat peninsula of 2500 ha with several dunes covered by halophilous vegetation, where Audouin's gulls breed (called sub-colonies thereafter) (see details in Oro *et al.* 1996a). Since 1988, chicks have been ringed at the colony with an alphanumeric coded darvic ring, which can be read through a telescope from a distance of up to 150 m. The number of hours spent reading darvic rings was recorded each breeding season to estimate resighting effort (see below). Numbers ringed each year varied from 360 to 1035 depending on colony size (Oro & Martínez-Vilalta 1994) and, in total, 4595 chicks were ringed during the period 1988–94. Between 1992 and 1997, 11135 resightings of 2554 different individuals of known age were obtained at the colony during the breeding season. From the 2554 individuals we excluded: (a) immature birds (less than 3 years old, Oro & Martínez-Vilalta 1994; Oro 1998); (b) birds ringed in other colonies; and (c) birds resighted at least once in the clubs (even though they were observed also in the sub-colonies), since clubs are formed by non-breeders (Oro 1998). In the case of multiple resightings in the same breeding season, only one was retained to run the model, although additional information was retained when available (e.g. breeding status, sex). After that, 2080 individuals remained for the analyses. Whenever possible, the sex was determined from observation of copulations: in this way, 142 males and 170 females were identified. The resighting pressure throughout the different areas of the colony was evenly distributed in all the years to limit heterogeneity in recapture probabilities (Prévot-Julliard 1996; Pradel *et al.* 1997a).

The presence and movements of the badger throughout the colony during the breeding season of 1994 were easily detected by its tracks in the sand, which were checked daily during the whole season. The daily surveys of the tracks and food remains allowed us to determine that the badger preyed only on eggs and chicks, and not on adults (see also Oro *et al.* 1999). The badger stayed constantly in the colony from the pre-laying period until the chicks fledged, and predation rates were

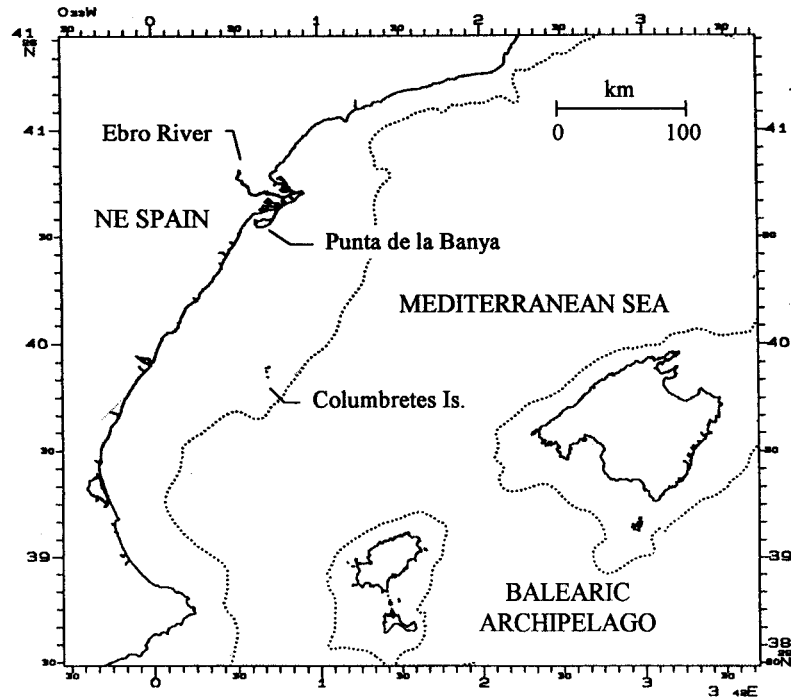


Fig. 1. Map of the study area showing the colonies of Audouin's gulls at the Punta de la Banya (Ebro Delta) and the Columbretes Islands, 80 km away. The dotted line shows the limit of the continental shelf, where most Audouin's gull forage.

very similar in all the sub-colonies (D. Oro, unpublished data).

Reproductive success (as chicks fledged per pair) was estimated from 1991 to 1996 as the ratio of the number of chicks raised to the total number of breeding pairs. First, the number of chicks produced was estimated using the Petersen method (Seber 1982; p. 59 et seq): chicks were marked each year as fledglings at two separate sessions 5 days apart during the fourth week of June when mortality is negligible. Each breeding season, this protocol was followed in 3–4 subcolonies selected randomly to account for intercolony differences in reproductive success (Oro 1998). An estimate of the number of fledglings (\hat{f}_k) at each subcolony (k) was obtained. Secondly, to estimate colony size, counts of gull nests were carried out from 1991 to 1996 during 2–3 days in the second week of May, when most pairs had laid but few broods had hatched (D. Oro, unpublished data). The number of nests was counted by a team of 4–12 people (depending on the size of the sub-colony) moving in a line back and forth through the dunes where Audouin's gulls breed. The estimation of the size (\hat{n}_k) of each subcolony (k) was close to the real number of nests (error less than 3%, D. Oro & G. Ruxton, unpublished data). Finally, a weighted mean of reproductive success (rs_i) was calculated for each breeding season (i) as:

$$rs_i = \frac{\sum_k (\hat{n}_k \cdot \hat{f}_k)}{\sum_k \hat{n}_k}$$

where \hat{f}_k is the estimated number of fledglings per pair in the k subcolonies sampled, and \hat{n}_k is the estimated number of breeding pairs in the k subcolonies sampled.

The amount of fish discarded and natural fish availability are associated with fishery catches in the Ebro Delta area (e.g. Oro & Ruiz 1997; Oro 1999). The total fishery catches (excluding shellfish catches, see Oro & Ruiz 1997) of April, May and June from 1991 to 1996 were then used to estimate food availability for gulls during breeding, from which an index was calculated correcting for the breeding numbers each year (Oro *et al.* 1999). Data were obtained from the fishermen guild bulletins of the harbour closest to the colony (Oro & Ruiz 1997).

DATA ANALYSIS

At the beginning of this analysis, it was known that Audouin's gull do not start to breed before age 3 (Oro & Martínez-Vilalta 1994; Oro 1998). Some attempts to model recruitment based on age-specific breeding probabilities have assumed that recapture probabilities were equal to 1 and adult survival was constant (Chabrzyk & Coulson 1976; Spear & Nur

1994). We used instead a recently developed capture–recapture approach which estimates resighting probabilities together with *seniority* probabilities with no assumptions concerning survival. This allowed us to test the effects of covariates on the probability of first reproduction (for details, see Pradel 1996; Pradel *et al.* 1997a). The parameters estimated are of two types: *seniority* probabilities (γ) and *resighting* probabilities (p). The seniority probability is defined as the probability that an animal breeding on a given year has already bred previously, i.e. that it is experienced (Pradel 1996). The proportion of first-time breeders (β) is simply $1 - \gamma$ and can be calculated cohort per cohort. The types of assumptions that are made in this approach are analogous to those made when studying survival from capture–recapture data, except that they apply to recruitment; namely, animals have independent fates and are identical (same recruitment and recapture parameters) within each identifiable group (such as males and females); no mark is lost or misread; and temporary emigration, if present, is random. Note, however, a possible difference with the CJS (Cormack–Jolly Seber) model: animals of the same group may have heterogeneous survival probabilities as long as they *recruit* in the same way. In fact, recapture histories are reversed in the recruitment analysis and then examined as a classical survival analysis and its general assumptions, and models were fitted using programs RELEASE and SURGE (see, for instance, Lebreton *et al.* 1992). Full details of the method and of its implementation are given in Pradel *et al.* (1997a) and only the main features are summarized here. A general starting model is identified involving the factors thought to influence recruitment. The adequacy of this model is checked using goodness-of-fit tests (Pradel *et al.* 1997a). Then, the significance of the factors considered and of their interactions is assessed by comparing models with or without the effects tested. There are different methods for selecting among models. These have been compared in a series of recent papers (e.g. Anderson, Burnham & White 1994; Burnham, Anderson & White 1994, 1995). Here, following the recommendations of these authors, selection of models is made on the basis of the Akaike's information criterion (AIC), the model with the smallest AIC value being selected. Furthermore, the value of 2 is the threshold below which two models are considered to be statistically equivalent (see for instance Anderson *et al.* 1994).

The set of models considered in the present analysis contains models correcting for the presence of transients in the data, i.e. of animals which, being in transit over the sampling area when captured, have no chance of being recaptured. Such models, developed in the context of survival analysis (Pradel *et al.* 1997b), have not been used previously in the context

of recruitment analysis. However, they can be used without change, the same line of reasoning outlined hereafter being applicable: Pradel *et al.* (1997b) first noticed that the presence of transients in a capture–recapture experiment leads to a mixture of two populations, one of which, the ‘transient population’, is comprised of animals of known fate: they are never recaptured after release. Pradel *et al.* (1997b) were then able to show that survival over the first interval after release is biased in a predictable way that depends on the proportion of transients among the unmarked captured (see Pradel *et al.* 1997b for details). Allowing for survival parameters specific to the first interval after release is then equivalent to fitting explicitly a mixture model. The same statement applies to a recruitment analysis, which is for all practical purposes a survival analysis of reversed capture histories (for the duality of the two types of analyses see Pradel 1996). The only change is that, because capture histories are analysed in the opposite direction (Pradel 1996), the seniority probability is biased at the time of the last observation depending on the proportion of transients among the animals seen for the last time. This proportion, which is of no particular interest, is denoted τ_b in the model notations below (subscript b denotes the ‘badger effect’). Although this proportion is not interesting in itself, its magnitude conditions the amount of bias expected when no correction is done for the presence of transients (see Fig. 1 in Pradel *et al.* 1997b). Seniority probabilities would then be underestimated for old ages giving the erroneous picture that recruitment is spread over a larger age span than is true.

Another difficulty in the present analysis is that sex is more likely to be identified for animals seen often than for animals seen rarely. From a statistical point of view, the determination of sex is not independent of the capture histories. It is then not possible to analyse the capture histories of individuals of known sex separately from those of individuals of unknown sex without running the risk of overestimating capture probabilities in the first case (and underestimating them in the second); this would lead in turn to bias in the estimation of recruitment. Although it is not possible to know exactly the sex-ratio on the colony, it is likely to be close to 1. Time spent at the colony is similar for males and females (Oro 1998), thus recapture rate was assumed to be equal for both sexes. The covariate sex was thus coded as 1 for males, 0 for females and 0.5 for unsexed individuals. This ensures that when using the covariate sex in the model, the capture probability of unsexed individuals will be approximately equal to the mean of the capture probabilities of males and females (exactly on a logit scale).

In summary, the models used in this analysis involve three types of parameters: seniority prob-

abilities (γ), resighting probabilities (p) and the proportion of transients among the animals seen for the last time (τ_b). The factors considered in the modelling process for seniority (γ) and resighting (p) probabilities are: time (as year of resighting from 1992 to 1997, t), age from 3 to 8 years (a), sex (s), cohort as year of birth from 1988 to 1994 (c) (e.g. Spear & Nur 1994), colony size varying from 3950 to 11 328 pairs (z , data transformed by the log function) (Oro 1998), breeding success (b), badger effect (m), food availability (f), and resighting effort (e). When two factors enter a model with their interaction, they are separated by a '*' in the model notation. When the interaction is not present, a '+' is used instead. For instance (γ_{a^*t} , p_{a^*t}) designates a model where seniority and recapture probabilities varies with age and time, each combination of the two factors being independent. It may be noted that not all combinations of factors can be distinguished. For instance, a^*t is not different from a^*c . However, when some simplification has been attained, the effects of time, age and cohort can be discriminated as in $t+a$ and $c+a$ which are no longer equivalent.

Theoretically, the seniority probability should increase with age from 0 (at age 3 when all breeders are first-time breeders) to 1 (at the unknown age when no more breeders are recruiting into the population). However, a seniority probability of 1 may never be attained if the age at which recruitment is completed is not represented in the sample or if there is always a residual flow of individuals coming back to their natal colony after first recruiting in another site. In this second case, it is still possible to look for an age beyond which seniority probability remains constant. For this purpose, once a satisfactory model in terms of factors involved has been selected with the procedure outlined above, other models with this same structure in which seniority probability is kept constant beyond an age each time younger are successively fitted. Our data allowed us to try all ages of stabilization from 4 to 8 years. The age of stabilization is assumed to be attained when the difference between the AIC of the new model and the lowest AIC among those of the preceding models in the series exceeds 2 (see above and Pradel *et al.* 1997a).

BREEDING DISPERSAL

Conditions at the nearest colony of the Columbretes Islands (Fig. 1) are likely to influence recruitment in the Ebro Delta colony. As a complement to the previous analysis, we attempted to measure the attractiveness of the Columbretes Islands to the individuals born in the Ebro Delta. At the Columbretes colony, chicks have also been ringed since 1988 (495 chicks through 1994), and resightings of marked birds were also carried out between

1992 and 1997. Thus, since a similar capture-recapture experiment was in progress at the Columbretes Islands during the period of the study, the numbers of individuals born in the Ebro Delta observed as breeders at the Columbretes Islands were available (387 individuals in total over the period). However, the numbers observed at the Columbretes depend not only on the attractiveness of the Columbretes Islands to the birds native from the Ebro Delta, the quantity of interest to us, but also on the numbers of chicks marked the previous years at the Ebro Delta colony, on the resighting pressure at the Columbretes Islands colony, and on the demographic processes of mortality and recruitment which control the numbers of breeders available at each age. Specifically, the expected numbers N'_i left available to breed at the Columbretes Islands in year t (from 1992 to 1997) from those ringed in year i (from 1988 to 1994) by the demographic processes is given by the formula:

$$N'_i = N_i \cdot \phi_j \cdot \phi^{t-i-3} \cdot b_{t-i}$$

where N_i is the number of individuals initially ringed in year i , ϕ_j is the juvenile survival from birth to age 3, ϕ is the adult survival probability of Audouin's gulls, b_{t-i} is the breeding propensity, i.e. the proportion of breeders among the survivors, at age $t-i$.

Given n'_{it} , the actual number of individuals born in year i and resighted in year t , the ratio of n'_{it} to N'_i estimates the probability of presence at the Columbretes Islands colony times the probability of observation on this colony. To simplify, we may assume that the demographic parameters do not depend on the origin of the birds (from the Columbretes Islands or from the Ebro Delta), nor on the year of ringing. Then, the ratio of ratios (n'_{it}/N'_i)_E/(n'_{it}/N'_i)_C where the numerator is calculated for birds ringed on the Ebro Delta (E) and the denominator for birds ringed on the Columbretes (C), is equal to (n'_{it}/N_i)_E/(n'_{it}/N_i)_C and estimates the relative presence (rp) of birds from the Ebro Delta colony at the Columbretes Islands colony. Assuming finally that this quantity does not depend on i , the year of ringing, but only on t , the year of observation, we get a more precise common-sense pooled estimate as

$$rp_t = \left(\sum_i (n'_{it}/N_i)_E \right) / \left(\sum_i (n'_{it}/N_i)_C \right)$$

An estimate of the variance of rp_t obtained by the delta method, is

$$\frac{\left\{ \sum_i \frac{n'_i(N_i - n'_i)}{(N_i)^3} \right\}_E}{\left\{ \left(\sum_i \frac{n'_i}{N_i} \right)^2 \right\}_C} + (rp_t)^2 \frac{\left\{ \sum_i \frac{n'_i(N_i - n'_i)}{(N_i)^3} \right\}_C}{\left\{ \left(\sum_i \frac{n'_i}{N_i} \right)^2 \right\}_C}$$

Table 1. Goodness-of-fit tests of the recruitment model (γ_{a^*t} , p_{a^*t}) by cohort applied to the reversed CMR histories. Only the cohorts of 1988, 1989 and 1990 included the results of the recruitment model after the predatory event in 1994. The values of the test 3.SR of RELEASE corresponding to the predatory event in 1994 are given for each cohort (see text)

Cohort	χ^2 value	d.f.	P-value	Test 3.SR		
				χ^2 value	d.f.	P-value
1988	30.88	17	0.02	3.97	1	0.033
1989	25.01	13	0.02	5.38	1	0.017
1990	28.25	9	<0.001	15.30	1	<0.001
1991	4.81	4	0.31	–	–	–
1992	2.42	1	0.12	–	–	–
1993	0.57	1	0.45	–	–	–
Total	91.95	45	<0.0001	–	–	–

Finally, 95% confidence intervals (CI) were calculated from this variance to assess whether there were significant differences between the different values of rp_t .

Results

PRELIMINARY TESTS

The fully time- and age-dependent model (γ_{a^*t} , p_{a^*t}) was not accepted (overall test, $\chi^2_{45} = 91.95$, $P < 0.0001$, see Table 1), because test 3.SR of RELEASE – which tests the assumption that all marked animals at $(i + 1)$ have the same probability of having been observed at (i) – was highly significant in the occasion corresponding to year 1994. In fact, when just the cohorts not affected by the badger were considered (i.e. those of 1991, 1992 and 1993) the goodness-of-fit test was not significant (overall test, $\chi^2_6 = 7.80$, $P = 0.25$). Thus, the badger effect was introduced in all the analyses of model selection using SURGE [models (τ_b , γ , p)].

MODELLING RECRUITMENT AND RESIGHTING PROBABILITIES

Seniority probabilities (γ) were first modelled, considering that resighting probabilities depended just on time [models (τ_b , γ , p_t), Table 2]. When the best model without effect of colony size on seniority probability was considered [i.e. the model (τ_b , γ_{t+A+s} , p_t), Table 2], a relationship between the maximum likelihood estimates of recruitment and the colony size (log transformed) the year before was observed (Fig. 2). In fact, AIC decreased considerably (-7.2) when the covariate of colony size was introduced in the model (Table 2). This result was independent of the increased number of chicks raised through time at the colony, since we dealt only with probabilities of having been resighted the year before. We then provisionally selected the model (τ_b , γ_{A+s+z} , p_t), where seniority probability depended on a linear trend of age (A), on sex and

on colony size the year before. An age effect on seniority probabilities was expected, since in some long-lived species breeding propensity may increase with age (Pradel *et al.* 1997a). However, quadratic effect of age (A^2) on seniority probability was rejected (Table 2). The effect of sex was provisionally kept in the model (see below), and females showed higher seniority probabilities than males, although differences were not significant. Tests of the effects of other covariates, such as the reproductive success

Table 2. Model selection for seniority probabilities (γ), when resighting probability depends hypothetically just on time, and the effects of badger on recruitment are considered [model (τ_b , γ , p_t), see text]. The deviance, the number of parameters (np) and the AIC of each model are also shown. Bold denotes the temporarily selected model for seniority probabilities. Model notation is adapted from Lebreton *et al.* (1992) with γ denoting seniority probability; t , time effect; a , age effect; A, linear effect of age on a logit scale; A^2 , quadratic effect of age on a logit scale; s , sex effect; c , cohort effect; z , colony size effect; b , breeding success effect; and f , food availability effect

Model for γ	Deviance	np	AIC
γ_{t+c+s}	6597.38	17	6631.38
γ_{a+c+s}	6596.45	17	6630.45
γ_{t+A+A^2+s}	6601.72	14	6629.72
γ_{t+A+A^2}	6604.60	13	6630.60
γ_{A+A^2+s}	6613.22	9	6631.22
γ_{t+A+s}	6601.79	13	6627.79
γ_{A^*s+t}	6640.64	12	6664.64
γ_{t+A}	6604.80	12	6628.80
γ_{t+s}	6673.49	12	6697.49
$\gamma_{A+s+z+b+f}$	6600.38	11	6622.38
$\gamma_{A+s+z+b}$	6600.24	10	6620.24
γ_{A+s+b}	6612.28	9	6630.28
γ_{A+s+f}	6613.05	9	6631.05
γ_{A+s+z}	6600.09	9	6618.09
γ_{A+s}	6613.68	12	6637.68
γ_{A^*s+z}	6638.03	8	6654.03

*Interactions between effects.
+ Additive models.

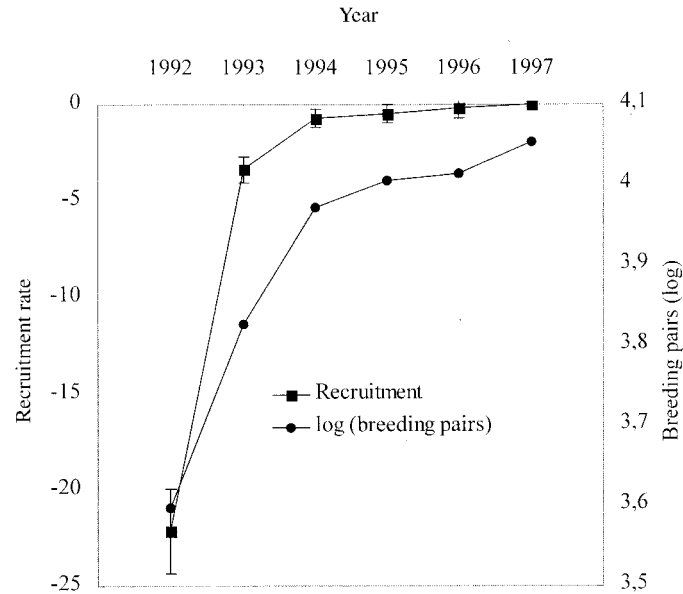


Fig. 2. Recruitment (\pm SD) over the study period (1992–97) estimated from the model ($\tau_b, \gamma_{t+A+s}, p_t$) and its relationship with the colony size year before expressed as number of breeding pairs (on a log scale). The proportions of new recruits are expressed as relative values to that in year 1997 on a logit scale under that model.

the year before (including a partial breeding failure when the badger entered the colony) and food availability, were not significant.

Starting from the model ($\tau_b, \gamma_{A+s+z}, p_t$), we then modelled resighting probabilities [models ($\tau_b, \gamma_{A+s+z}, p_t$), Table 3]. The model finally retained was ($\tau_b, \gamma_{A+z}, p_{t+s}$), where recruitment was modelled with an additive effect of age and colony size the year before, whereas resighting was modelled with an additive effect of time and sex. When the effect of sex was moved from seniority probabilities to resighting probabilities, the resulting model fitted the data better. In this model, resighting probabilities were affected by time and by sex. However, no differences in resighting probabilities depending on the sex of individuals were expected to occur at the colony. Then, the effect of sex on resighting probabilities may be interpreted as a sex-dependent intermittent or skipping reproduction, which may occur in long-lived birds especially early in the breeding life (e.g. Wooller & Coulson 1977; Viallefont, Cooke & Lebreton 1995; Pradel *et al.* 1997a). Under the selected model, resighting probability estimates varied from 34.7% (SD = 5.3) to 82.0% (SD = 1.6), and they were higher for females than for males (Fig. 3). The effects of resighting effort (e) on resighting probabilities were rejected in the final model (Table 3), probably because resighting probabilities were more sensitive to differences in ringing effort through the years (see also Oro *et al.* 1999). Linear effects of age (A) on resighting probabilities did not improve the fit of the model (Table 3).

Figure 4 shows the variations of the probability of first reproduction over age as predicted by the finally selected model ($\tau_b, \gamma_{A+z}, p_{t+s}$), expressed as the proportion of first-time breeders (β , estimable as $\beta = 1 - \gamma$). β rapidly decreased at age 4 and then remained near constant and at very low probabilities from age 6. An exploratory analysis showed that under the finally selected model, recruitment may be considered to stabilize at age 6 (Fig. 5).

With regard to breeding dispersal, we observed a marked increase in the numbers of individuals from the Ebro Delta that recruited to Columbretes Islands in 1995, after the badger event in 1994 which causes a high nest predation rate (Fig. 6). Looking at 95% CI in Fig. 6, rp was significantly higher in 1995 than in the other years.

Discussion

As usual in all areas of statistics, the test of the hypothesis using the seniority approach is based on selecting an appropriate model to describe the data. Thus, the hypotheses tested in our study are not mutually exclusive. It is likely that the decision in Audouin's gulls to recruit to the breeding population is dependent on the combined effects of environmental conditions at the colony, including food availability, presence of predators, reproductive success, number of conspecifics or nest site quality. However, one factor may be more important than others in determining local recruitment to the Ebro Delta colony.

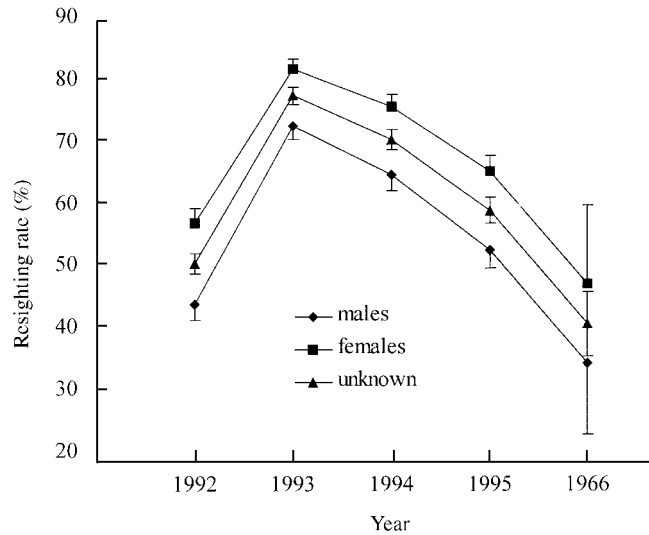


Fig. 3. Effects of sex and time on resighting probabilities. Sex- and age-specific resighting probabilities are expressed as relative values to that in year 1997 (on a logit scale), estimated from the finally selected model ($\tau_b, \gamma_{A+z}, p_{t+s}$); standard deviations (SD) are also shown (+ SD for females, -SD for males, \pm SD for unknown sex).

COLONY SIZE DETERMINES LOCAL RECRUITMENT

Local recruitment increased together with colony size (Fig. 2, see also Brown *et al.* 1990; Negro,

Hiraldó & Donázar 1997). Although Aebischer, Coulson & Colebrook (1990) found a parallel long-term trend between breeding parameters of kittiwakes and weather in the North Sea, we believe that the positive association between recruitment and colony size at the Ebro Delta is not a numerical artefact resulting from this type of phenomenon, since other demographic parameters, such as immigration rate or breeding success, estimated at the colony do not show the same trend (Oro *et al.* 1999; D. Oro & G. Ruxton, unpublished results) and environmental conditions in the last 30 years have varied greatly from year to year with no clear trend (e.g. Oro 1999). Individuals dispersing between patches are at significant risk; thus, there is a premium on rapid recognition and establishment at suitable sites (Smith & Peacock 1990). The high quality of this colony in terms of habitat suitability and food availability (Oro *et al.* 1996a; Oro & Ruiz 1997) may have counterbalanced density-dependent factors (Ruiz *et al.* 1998), reducing in turn the benefits of delaying breeding (see also Wooller & Coulson 1977; Mills 1989). As expected by the dramatic increase of breeding numbers at the Ebro Delta colony, most Audouin's gulls recruited at the youngest breeding ages (3–4-year-old birds). Previous studies in other Laridae showed that recruitment occurred at older ages (large and medium gulls, e.g. Coulson *et al.* 1982; Rattiste & Lilleleht 1986; Reid 1988; Pyle *et al.* 1997) or decreased slowly with age (terns and small gulls, e.g. Harrington 1974; Spindelov 1991; Prévot-Julliard 1996).

Table 3. Modelling resighting probabilities (p), when seniority probability (γ) depends hypothetically on age, sex and colony size [model ($\tau_b, \gamma_{A+s+z}, p$), see text]. The deviance, the number of parameters and the AIC of each model are also shown. Bold denotes the temporarily selected model for seniority probabilities. Model notation is adapted from Lebreton *et al.* (1992) with p denoting resighting probability; t , time effect; e , effort effect; a , age effect; and s , sex effect

Model for p	Deviance	np	AIC
p_{t+A}	6602.34	10	6622.34
p_t	6602.59	9	6620.59
p	6787.53	5	6797.53
p_{e+e^2}	6675.57	6	6687.57
p_e	6701.35	5	6711.35
$p_{\ln(e)}$	6701.05	5	6711.05
p_{e2}	6692.01	5	6702.01
p_{t+s}^\dagger	6590.23	9	6608.23
p_{t+s+A}^\dagger	6592.89	10	6612.89
$p_{t+s}^*A^\dagger$	6593.53	9	6611.53

*Interactions between effects.
+ Additive models.
†In these models, we moved the sex effect from seniority probability to resighting, resulting in the models (τ_b, γ_{A+z}, p).

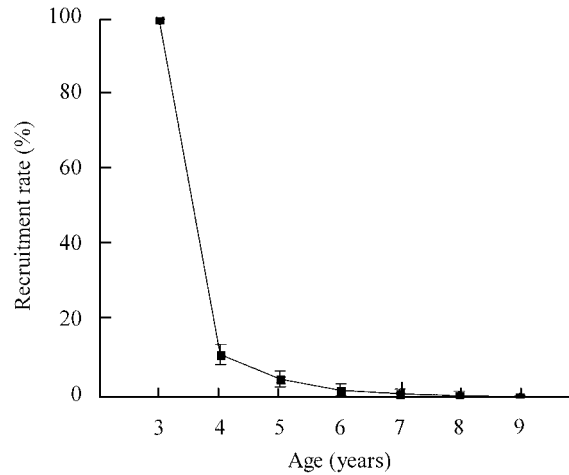


Fig. 4. Recruitment in year 1997 for the different age-classes under the finally selected model ($\tau_b, \gamma_{A+z}, p_{t+s}$). Recruitment is expressed as the proportion of first-time breeders ($\beta \pm \text{SD}$) estimable from the recruitment (i.e. seniority) probability (γ) as $\beta = 1 - \gamma$.

NO EVIDENCE OF REPRODUCTIVE SUCCESS AND FOOD AVAILABILITY HYPOTHESIS

Reproductive success did not affect recruitment the following year, even when a badger who entered the colony caused a breeding failure of many pairs. However, a dispersal (both natal and breeding) of some individuals to the Columbretes Islands was recorded that year, probably explaining the strong increase in breeding numbers (20% of growth) at this colony (Oro *et al.* 1996a). Only after unpredictable and detrimental events, such as the badger predation, some individuals – especially newer breeders,

Oro *et al.* 1999 – may disperse and breed elsewhere rather than return to their natal site for breeding (see also Cuthbert 1988; Switzer 1993; Nager *et al.* 1996; Boulinier & Danchin 1997). Results confirm the strong relationship between local recruitment and breeding dispersal in the dynamics of local populations and metapopulations (see also Birkhead & Furness 1985; Cairns 1992; Hanski & Gilpin 1997; Oro & Pradel 1999).

Spear *et al.* (1995) found that annual variation in food supply affected age at first reproduction in males of western gulls *Larus occidentalis*. However, food availability beyond a minimal threshold has

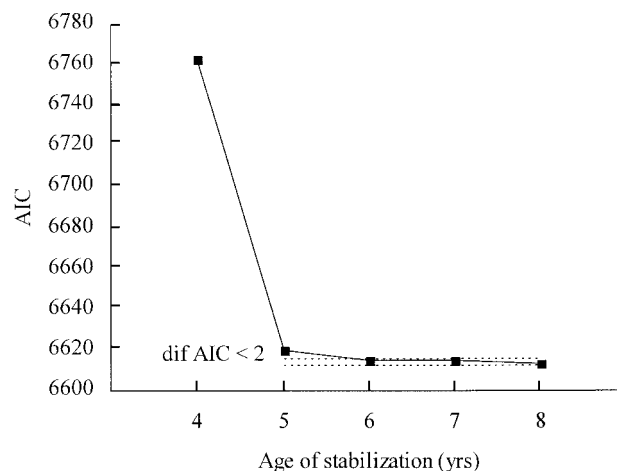


Fig. 5. The AIC values for models with different ages of stabilization (see Methods). Models used derived from the finally selected model ($\tau_b, \gamma_{A+z}, p_{t+s}$). In these models, seniority probability at age i was forced to be constant beyond age i , whereas the rest of the model at age i remained equal. All these models had the same number of parameters. The AIC values of models with age of stabilization 6 or more (points between dotted lines) differ by less than 2.

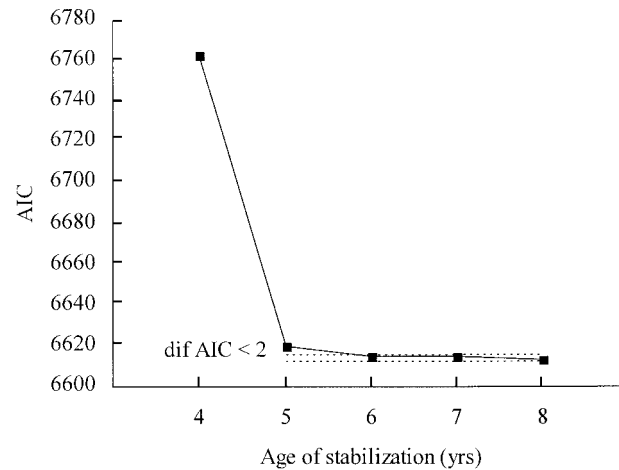


Fig. 6. Breeding dispersal of Audouin's gulls born in the Ebro Delta to the Columbretes Islands colony throughout the study expressed as a relative presence (rp , see Methods) probability ($\pm 95\%$ CI).

probably limited effects on some demographic parameters such as survival or recruitment, whereas it continues to cause changes in breeding performance (e.g. Pons & Migot 1995). The establishment since 1991 of a trawling moratorium overlapping with the breeding season of the gulls has negatively affected food availability and consequently their breeding performance, although breeding failure affecting the whole colony has never been recorded (Oro *et al.* 1996a). In spite of the trawling moratorium, availability of both natural prey and secondary foraging resources around the colony is high (Oro & Ruiz 1997; Oro *et al.* 1997), and gulls also showed behavioural mechanisms to buffer against this decrease in food supply (see Oro 1998 and references therein). Thus, recruitment in Audouin's gulls breeding at the Ebro Delta has not been affected by changes in food availability, as recorded also with adult survival (Oro *et al.* 1999).

EFFECTS OF AGE AND SEX ON RECRUITMENT AND LIFE-HISTORY CONSEQUENCES

As expected in a long-lived species, there were significant differences in the age at first reproduction in Audouin's gulls. Local recruitment to the Ebro Delta colony occurred at the youngest ages at which gulls were capable of breeding, and sharply decreased thereafter (Fig. 4). At the end of the study in 1997, $\approx 90\%$ of birds aged 4 years had already been recruited at age 3, the youngest age at first reproduction in Audouin's gulls (Oro & Martínez-Vilalta 1994). Beyond age 6, probability of first reproduction stabilized to a value depending on the year and cohort but always very low (< 0.05). This stabilization might indicate that individuals older

than 6 years observed breeding for the first time in the Ebro Delta had initially recruited in another colony before returning to their natal site (see also Ens *et al.* 1995; Prévot-Julliard 1996; Pradel *et al.* 1997a). In long-lived species and in gulls in particular, sex differences in recruitment are slight (Chabrzyk & Coulson 1976; Wooller & Coulson 1977; Rattiste & Lilleleht 1986; Mills 1989; Bradley & Wooller 1991; Spear *et al.* 1995; our study), although males are almost always most abundant in the earliest age class to breed.

Different life-history strategies selected to increase fitness may coexist in the same population at evolutionary equilibrium (Ens *et al.* 1995). Pugsek & Wood (1992) found that California gulls *Larus californicus* followed different strategies related to skipping breeding; in a population of western gulls, where skipping breeding was unusual, males recruited at younger ages than females to optimize their fitness (Pyle *et al.* 1997). Most Audouin's gulls start to breed at very young ages (3 and 4 years old), but results also suggest that, as in other gull species (e.g. Pugsek & Wood 1992; Pugsek *et al.* 1995), there is occasional skipping of breeding, especially at the youngest ages and higher for males than for females (see also Pugsek *et al.* 1995). If early reproductive effort reduces the physical condition of individuals, their condition the following year may be too low to breed, and gulls would skip breeding to avoid lifetime reproductive costs (Wooller & Coulson 1977; Nichols *et al.* 1994; McNamara & Houston 1996; Pradel *et al.* 1997a).

Conclusion

During the study, there was no nest site limitation at the colony, since only 20–26% of suitable vege-

tated dunes were occupied (D. Oro, unpublished data). Thus, the hypotheses tested in our study are based on the assumption that potential recruits (individuals physiologically mature enough to breed) have the option to delay breeding or to join the breeding population of the Ebro Delta. The decision to breed for the first time or to delay breeding may rely on cues that indicate the quality of the environment (e.g. Reed & Dobson 1993; Danchin & Wagner 1997). Our data were only consistent with the predictions of the colony size hypothesis: Audouin's gulls would recruit using the presence of conspecifics as an indicator of environmental conditions (see also Stamps 1988; Brown & Bomberger Brown 1996). This parameter would integrate multiple environmental factors occurring at the colony (such as predation events or those included in the other two hypotheses: reproductive success and food availability) which are crucial for proximate decisions when birds recruit.

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