

LIVING IN A GHETTO WITHIN A LOCAL POPULATION: AN EMPIRICAL EXAMPLE OF AN IDEAL DESPOTIC DISTRIBUTION

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Abstract. Merging patterns and processes about the way individuals should be distributed in a habitat is a key issue in the framework of spatial ecology. Here the despotic distribution of individuals in two distinct and neighboring patches within a local population of a long-lived colonial bird, the Yellow-legged Gull (*Larus michahellis*), was assessed. There was no density dependence for suitable habitat at the study population, but behavioral data suggested that birds from the good patch precluded birds from the bad patch from breeding in their patch. Younger breeders were almost exclusively found in the bad patch, where individuals were probably attracted by conspecific attraction from the good patch. Most breeding parameters were lower in the bad patch, resulting mainly from a higher vulnerability to environmental perturbations and a higher rate of intraspecific nest predation. Attempts at breeding dispersal between the two patches were only observed from the bad to the good patch. Strikingly, adult survival and large-scale dispersal, two life history parameters that are very conservative in long-lived organisms, were also more affected at the bad patch when catastrophic predation occurred. The study was consistent with an ideal despotic distribution at small spatial scale, and suggests that individual behavior can influence local population dynamics.

Key words: capture–recapture modeling; colonial seabird; despotic distribution; environmental perturbations; habitat heterogeneity; *Larus michahellis*; life history traits; patch quality; Yellow-legged Gull.

INTRODUCTION

The spatial distribution of animal populations has always attracted the attention of ecologists. It is assumed that habitat quality is heterogeneous and that organisms are looking for high-quality patches to optimize their fitness. This searching for high-quality habitat was the core of the first evolutionary models of breeding habitat selection, which postulated two alternatives: (1) that individuals were free to move among sites, average fitness at equilibrium being stabilized across habitats by density dependence (also called the ideal free distribution, IFD; see Fretwell 1972); and (2) that some individuals were able to occupy the best habitats and force others in a despotic way to poorer patches where their fitness should be lower (i.e., the ideal despotic distribution, IDD; see Brown 1969). The IDD applies under situations in which habitat selection by subordinate individuals is constrained by territoriality of dominant individuals. Under this scenario, animals guard resources, violating the “free” assumption of the IFD, and the average success of nondominants will be lower than the habitat average. Because these first models were vague and conceptual (i.e., they did not lead to testable predictions), several variations and corollaries have been pointed out, e.g., the ideal

preemptive distribution (IPD) model introduced later by Pulliam and Danielson (1991) broadened the IDD idea, postulating that some individuals may obtain resources in a manner that makes them unavailable to others, not only by despotism, but also by other causes. Furthermore, the presence of individuals in a given habitat may not be positively related to habitat quality (e.g., Pulliam 1988, Caughley 1994), and competition for nest sites does not necessarily imply despotism (Petit and Petit 1996, Kokko et al. 2004). Thus, in the absence of behavioral or life history information, there is no way to know if detected differences have any bearing on choices of individuals or on their aggressive tactics toward conspecifics. To disentangle real despotism from variation in ability to select the optimal sites, behavioral observations should show that animals breeding in the suboptimal patch are trying to settle in the optimal patch, and that individuals already reproducing in the good patch exert aggressive interactions to preclude conspecifics from occupying these patches (see Serrano and Tella 2007).

It is widely accepted that habitat can differ in quality and that some local populations occupy suitable patches (where fitness components are higher) while some other local populations are placed in poor, low-quality sites. Such spatial distribution of local populations has been commonly explained through competition for the best places (Tregenza 1995). More recently, other potential factors to explain habitat selection have also been cited, such as positive density dependence (or Allee effects)

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and the existence of ecological traps (Green and Stamps 2001, Morris 2003, Battin 2004). However, much less is known about heterogeneity in patch quality within a local population, i.e., at a smaller spatial scale. Many local populations of social organisms (such as seabirds) are sufficiently large that they extend over discrete areas where quality of the breeding sites is not uniform, although they necessarily share other resources such as food (e.g., Bosch and Sol 1998, Rodway and Regehr 1999, Cam and Monnat 2000a, Kokko et al. 2004). Here I analyzed the potential despotic distribution of breeding individuals by long-term monitoring of a local population (i.e., a colony) of the Yellow-legged Gull *Larus michahellis*, a social seabird that fight to holding territories that must be held long enough to breed. Within this local population, two distinct breeding patches with different habitat features and quality could be clearly defined (see Appendix A). Several studies have suggested that the poor habitat was probably colonized following an immigration wave of individuals from a culled neighboring colony (Bosch et al. 2000, Oro 2003). Birds breeding at both patches shared the same foraging grounds and food availability per capita was expected to be equal for all breeders. Further, I assessed whether there was limitation in within-patch habitat availability, another resource that could trigger competition between individuals (e.g., Calsbeek and Sinervo 2002, Kokko et al. 2004). Under density dependence for such resource, an increasing number of individuals should settle in nonoptimal sites resulting in a reduction in mean population fitness. Moreover I analyzed several life history traits to assess the influence of environmental stochasticity (including environmental perturbations such as predation and flooding) on the heterogeneity of individual quality at each breeding patch. Under the IDD models, the hypothesis tested here was that fitness parameters measured in the present study should be lower at the poorer patch than at the good patch. Adult survival was also incorporated as a measure of fitness, addressing one of the less explicit assumptions of the IDD models: while life history theory would predict that the most sensitive parameter of long-lived organisms (i.e., adult survival) should be constant, I tested the hypothesis that such parameter was again lower at the bad than at the good patch. Finally, behavioral observations were performed to validate whether the unequal distribution of individuals was despotic as predicted by the IDD models, and not the result of individual heterogeneity at selecting the most suitable sites.

METHODS

Study site

The study was carried out from 1992 to 2003 at the peninsula of Punta de la Banya (Ebro Delta, northwestern Mediterranean, 40°33' N, 0°39' E). The site is a salt marsh, sandy, bare, and flat with spatially discrete dunes covered by halophilous vegetation (Oro et al. 1995),

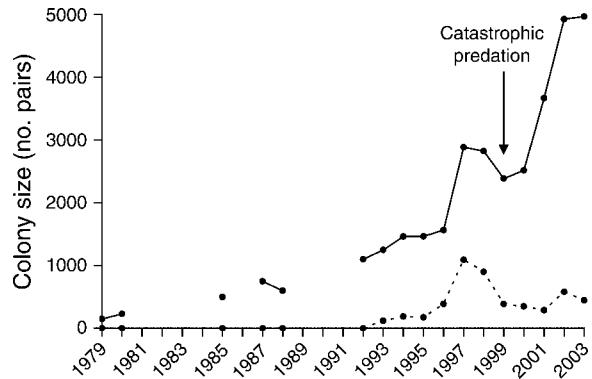


FIG. 1. Number of nests (pairs of Yellow-legged Gulls, *Larus michahellis*) estimated at the study site on the Ebro Delta, Spain, during 1979–2003. Colonies are grouped by habitat: the solid line shows the size of the colony at the several occupied dunes, and the dashed line shows the size of the colony at the bare patches, where nests were never recorded before 1993. The year (1999) when a fox entered the colony and caused catastrophic predation is also shown.

where most Charadriiformes (i.e., terns, gulls, shorebirds, and flamingos) breed (see Appendix A). Exceptionally, some terns *Sterna* spp. use parts of the bare areas, where vegetation is absent and there is always a risk of seawater flooding or chick overheating. Total surface area of the site is ~2500 ha, with only 12% occupied by dunes (called “vegetated patches” hereafter; see Appendix A). Subcolonies of gulls in 2003 occupied 59 patches, the maximum during the study, when population size was highest. I distinguished two study patches contiguous in space but different in features: (1) the largest dune (i.e., the vegetated, spatially discrete patch), holding the largest subcolony of gulls; and (2) the closest area of bare patch (not spatially discrete but identified by the occupancy of nests), partially colonized by gulls in 1993 (i.e., the bare patch) (see Appendix A).

Nest density and patch breeding numbers

Monitoring of the distribution and size of discrete groups of nests (i.e., subcolonies) occupying the patches (vegetated and bare) was begun in 1979 and has continued, uninterrupted, since 1992. Even though several other bare patches were colonized after 1993, close to the study area, I only monitored the first one because it remained the most important numerically. I estimated the number of nests for each subcolony (i.e., each dune) through standard methods already tested in the study site (e.g., Oro et al. 2006) (see Fig. 1). I assumed that colonizers were not limited by behavioral constraints linked to the maximum distance of dispersal, owing the small spatial scale of the study area (see Appendix A) compared to the much higher dispersal and foraging ranges of the species. To test the prediction that new settlers did not encounter a shortage of breeding habitat, I compared nest density (as mean number of nests counted per surface unit) at the vegetated patch

with nest density at seven long-term monitored colonies, all in the western Mediterranean, for which I estimated the number of nests using linear transects methods (Bosch et al. 2000, Oro et al. 2006). I took the value from the Medes Island, one of the largest colonies in the world and with most available habitats saturated (e.g., Bosch et al. 1994, 2000), as a reference value for a breeding site with a scarcity of nest site availability.

Age structure, breeding dispersal, and adult survival: field procedures and statistical modeling

During 1995–2001, 294 incubating adults were caught using cage traps in the two study patches (see details in Appendix B). Although exact age could not be estimated, younger breeders (3 and 4 years of age) could be identified by their plumage (Monaghan and Duncan 1979). To test for differences in the frequency of age groups (younger breeders vs. older breeders) between the two patches, I applied a contingency table analysis. Once caught, adults were marked with a unique combination of four Darvic color bands (Pro-Touch, Saskatoon, Canada). I searched for marked birds around the study patches and in other patches of the colony and identified birds from a distance using a spotting telescope. This procedure allowed me to record breeding dispersal of marked birds between the two patches. The effort of reading bands was distributed uniformly through the two study patches, thus limiting heterogeneity in resighting probabilities.

Adult survival was estimated through standard capture–recapture statistical methods (see Lebreton et al. 1992). First, a goodness-of-fit test (GOF) using U-CARE software (Choquet et al. 2003) was performed to assess the fit of the data to the more general Cormack-Jolly-Seber (CJS) model [ϕ_{t^*h} , p_{t^*h}], where ϕ is the local survival probability, p is resighting probability, t is time, and h is habitat (bare and vegetated patches). Models were fitted by the maximum likelihood method using MARK software (White and Burnham 1999), and model selection was carried out using the Akaike Information Criterion (QAIC; see Lebreton et al. 1992). Several models were built to test for potential effects of predation by an individual red fox *Vulpes vulpes* (distinguished by f in model notation) that entered the colony in 1999 and preyed upon gulls: following one of the predictions of IDD models, I tested the hypothesis that the predation was higher at the bad patch than at the good patch. Models included the fox effect for 1999 and 2000, because some birds were killed by the predator before being resighted in 1999, whereas others were preyed upon after being resighted within the 1999 season. Although several marked birds were found killed by the fox, the relatively low number of records did not allow for a multistate modeling for estimating mortality from this catastrophic event. At the same time, I could not estimate the dispersal probability (also by multistate models) between the two habitats due to the small number of observations made during the study.

Because the GOF tests showed some deviations from the more general model (see *Results*), I thus modified the model by adding an extra parameter, specifically a transient effect at each habitat, only for the occasions affected by the fox [τ^f , ϕ_{t^*h} , p_{t^*h}]: $\tau^f(\omega, e)$ was the probability that an unmarked animal ω captured at e was a transient, and their estimators were calculated as

$$\tau^f(\omega, e) = 1 - \frac{\phi^*(\omega, e)}{\phi(\omega, e)}$$

where $\phi^*(\omega, e)$ was the initial survival rate for transients, and $\phi(\omega, e)$ that for non-transients.

Agonistic interactions

During resighting efforts, I also recorded agonistic interactions (territorial aggressions and nest predation) between individuals from the two study patches. Because observations were performed after the settlement period, I concentrated on the behavior of birds that failed to breed during laying due to predation, and that tried to resettle. During the seven years of marking and resighting, 235 hours of observations were spent recording 61 cases of nest predation (mostly on eggs) and 143 aggressive interactions between gulls in which at least one marked bird was involved.

Breeding parameters

To record clutch size and average egg volume in modal clutches of three eggs, an arbitrary linear transect through both patches was established each year during 1993–2003. Transects were searched once every two days to establish clutch size. This could underestimate clutch size when egg predation was high (as it was recorded in the bare patch; see *Results*), because in the study area birds do not normally replace eggs when they are lost (see Oro et al. 1995). Thus, only clutches that were completed (i.e., with no additional eggs recorded during the visits longer than the average laying intervals of two days in the species) were considered. Nevertheless, the relatively high frequency of visits made this bias likely to be low. Nests that suffered predation during the two days following the laying of the last egg were not considered for clutch size estimation, nor were nests with four eggs because they were extremely rare (~1%, on average). I applied three-dimensional contingency tables to test for differences in clutch size between habitats and years using a chi-square statistic. In total, I used 1286 nests for clutch size analysis over the study years. Length and width of all of the eggs were measured with calipers to ± 0.1 mm. Egg volume (mL) was calculated using the equation of Oro et al. (1995) with a species-specific constant of $K_v = 0.477$, and the average egg volume was subsequently calculated for every completed clutch with three eggs, the modal clutch size (out of 530 nests). For gulls, average egg volume in a clutch and clutch size are reliable indicators of female condition just prior laying, which depends on the interaction between physiological state (depending in turn on age and genetic quality of

the individual) and food availability (e.g., Oro et al. 1999, Ruiz et al. 2000). Within a local population, all females should exhibit lower variance in egg parameters (clutch size and egg volume) than that between local populations exposed to variability in food availability. In our study, it was expected that such egg parameters did not vary between the vegetated and the bare patches, both being under the same conditions of food availability. Furthermore, comparisons of the average egg volume in three-egg clutches between the two patches had the advantage of avoiding potential biases due to predation, because I assumed that a three-egg clutch was complete and did not correspond to a second laying clutch (D. Oro, *unpublished data*). I used a two-factor ANOVA to test for potential differences in average egg volume in three-egg clutches between years and patches.

To estimate breeding success, each year a group of nests (327 in total over the study) was surrounded in a chicken wire enclosure 50 cm high just before hatching to allow an unbiased record of the number of fledglings per pair (see Oro et al. 1995). Nests were selected following the same proportions of clutch sizes recorded for each year and patch. In the bare patch, the enclosures were provided with a refuge to allow chick to reduce overheating and predation. Enclosures probably reduced chick predation artificially, but they allowed estimation of breeding success to be better adjusted to individual state (Oro et al. 1995). It was also expected that because both study patches were under the same conditions of food availability, breeding success should be similar in the two patches. Potential differences in any breeding parameter analyzed here would indicate a different structure of age and quality between vegetated and bare patches, once corrected for potential differences in nest predation rates. To test for the potential effects of the breeding patch, the year, and their interaction on breeding success, I used a general linear model.

RESULTS

Nest density

Nest density in the study area was considerably lower (median values of 13 and 19 nests/ha in the vegetated and bare areas, respectively) than that recorded in six other gull colonies in the same geographical region (Kruskal-Wallis $\chi^2 = 65.67$, $df = 7$, $P < 0.001$; range of median values 30–344 nests/ha). This result was confirmed by the fact that, on average, (considering all the years of monitoring), only 48% of the 101 dunes where gulls have bred at least once were occupied each season. Furthermore, territories here were extremely large for this species (probably as a result of being far from the carrying capacity for suitable space; see Bosch et al. 2000) and birds spent a large amount of time in their defense (D. Oro, *unpublished data*).

Age structure at each patch

There were significant differences in the percentage of younger breeders between the bare and vegetated

patches (40% and 6%, respectively, $\chi^2 = 248.61$, $df = 1$, $P < 0.001$). The five birds breeding at three years old (an exceptionally low age of first breeding for the species) were only caught in the bare patch.

Local survival and dispersal between patches

The GOF test of the more general capture–recapture model [ϕ_{t^*h} , p_{t^*h}] showed a slight lack of fit ($\chi^2 = 74.09$, $df = 36$, $P < 0.05$) generated by a transient effect (directional test for grouped transient, $z = 4.874$, $P < 0.001$) rather than by a trap-dependence phenomenon (directional test for grouped trap-dependence, $z = 0.313$, $P = 0.754$). Components of TEST3.SR (GOF test) showed that the transience was concentrated on the last two occasions, that is, those influenced by the predator event, almost equally between the two habitats. Without these two components, TEST3.SR was no longer significant ($\chi^2 = 5.980$, $df = 6$, $P > 0.05$). The more general model thus included a transient effect at each habitat only for the occasions affected by the fox [$\tau_{t^*h}^f$, ϕ_{t^*h} , p_{t^*h}]. Note that the transient effect was probably caused by an additive effect of permanent emigration after first capture (i.e., dispersal out of the study area; see Oro et al. 1999, Tavecchia et al. 2007) and an actual decrease of survival caused by the predator. I began model selection by modeling adult local survival (see Table 1); models with survival depending on habitat (such as model 9, namely, the more general model) were generally better than models with survival changing equally in the vegetated and bare patches (e.g., model 10 respective to model 11; Table 1). Furthermore, the best models (models 1 and 2) were obtained when survival was kept constant and varied only with a fox effect. Models with recapture probabilities varying with time yielded better QAIC values than models with recaptures changing with the interaction of time and habitat features, with constant values or varying only with habitat (e.g., model 7 compared with models 9, 16, and 17, respectively). The two best-ranked models (models 1 and 2) were nested, i.e., they had in common that the influence of predation was different at each habitat, whereas they differed in survival the years without predation: model 1 suggested that this survival was also lower in the bare than in the vegetated patch, and model 2 indicated no interaction of survival and habitat. This last model [τ^f , ϕ_{h^*f} , p_d] was retained as the finally selected model because it had one less parameter and the inclusion of such a parameter (i.e., the habitat effect; see model 1) did not improve the model significantly (likelihood ratio test, LRT, $\chi^2 = 2.043$, $df = 1$, $P = 0.153$). Furthermore, field observations did not suggest any particular survival threat in the bare patch in years without predation. From model 1 (Table 1), survival probability was estimated at 0.900 (95% confidence interval, CI, 0.879–0.916), whereas the fox caused a decrease in local survival to 0.777 (95% CI 0.736–0.813) at the vegetated patch and a higher decline to 0.681 (95% CI 0.641–0.719) at the bare patch (Fig. 2). Consistently, dispersal and mortality probabilities caused by the fox and expressed by the τ^f parameter showed a higher value from

TABLE 1. Modeling survival (ϕ) and recapture (p) probabilities of Yellow-legged Gulls (*Larus michahellis*) at the Ebro Delta, Spain, 1995–2002.

Model no.	Hypothesis on factors in survival	ϕ, τ	p	QDEV	np	QAIC	Δ QAIC	w_i
1	Constant but different for each habitat, and different fox effects at each habitat	$h, [h * f]$	t	324.78	10	2731.31	0	0.47
2	Constant and different fox effects at each habitat	$h * f$	t	326.82	9	2731.32	0.01	0.46
3	Additive effect of time and habitat	$t + h$	t	322.02	14	2736.70	5.39	0.03
4	Constant but different with fox predation	f	t	334.58	8	2737.05	5.74	0.03
5	Additive effect of time, habitat, and predator	$t + h + f$	t	334.58	9	2739.08	7.77	0.01
6	Time dependent	t	t	332.21	12	2742.81	11.50	0.00
7	Time dependent and different for each habitat	$t * h$	t	321.86	18	2744.73	13.42	0.00
8	Time dependent	t	$t * h$	328.74	18	2751.62	20.31	0.00
9	Time dependent and different for each habitat	$t * h$	$t * h$	321.75	24	2757.00	25.69	0.00
10	Habitat dependent	h	t	355.92	8	2758.39	27.08	0.00
11	Constant survival	\cdot	t	365.73	7	2766.18	34.87	0.00
12	Habitat dependent	h	$t * h$	355.36	14	2770.04	38.73	0.00
13	Constant survival	\cdot	$t * h$	360.61	13	2773.25	41.94	0.00
14	Time dependent	t	\cdot	381.10	7	2781.56	50.25	0.00
15	Time dependent	t	h	379.85	8	2782.33	51.02	0.00
16	Time dependent and different for each habitat	$t * h$	\cdot	372.38	13	2785.02	53.71	0.00
17	Time dependent and different for each habitat	$t * h$	h	372.25	14	2786.93	55.62	0.00
18	Habitat dependent	h	\cdot	430.03	3	2822.42	91.11	0.00
19	Habitat dependent	h	h	430.00	4	2824.40	93.09	0.00
20	Constant survival	\cdot	\cdot	439.42	2	2829.80	98.49	0.00
21	Constant survival	\cdot	h	437.85	3	2830.24	98.93	0.00

Notes: All models included a transient parameter for the year with fox predation (e.g., $[\tau^f, \phi_{t^*h}, p_{t^*h}]$ for the more general model). QDEV is the model deviance, np is the number of model identifiable parameters, QAIC is the corrected Akaike's Information criterion, Δ QAIC is the difference between the model tested and the model with lowest QAIC value, and w_i is the Akaike weight of each model, scaled to sum 1. The symbols “*”, “+” and “.” indicate interaction between effects, additive effects, and constant effects, respectively. Retained models are in boldface.

the bare patch (0.191) than from the vegetated patch (0.127). Recapture probabilities, which were time dependent and equal at both patches, ranged from 0.600 (95% CI, 0.529–0.666) to 0.874 (95% CI, 0.840–0.902). Observational data showed that during the study, 13 out of the 153 birds marked at the bare patch (i.e., 8%) were observed breeding at the vegetated patch in following years, whereas none of the 141 birds marked at the vegetated patch was observed dispersing to the bare patch. From the 13 dispersal events recorded, all but three were recorded in the year following the fox predation event.

Agonistic interactions

Behavioral observations showed that 97% of intra-specific nest predation ($N = 61$) occurred in the bare patch; from the 21 cases in which the individual was identified, 86% were performed by a bird breeding in the

patch. Excluding these predation encounters, aggressive interactions were related to territoriality, most of them (84%) occurring at the bare patch. All of the 16 failed marked birds from the bare habitat trying to reneest were observed doing so at the vegetated patch, and in all cases ($N = 41$ observations) they received aggressive interactions from resident marked birds. Observations showed that all of these birds failed to reneest within the same breeding season. These data clearly suggested that the distribution of individuals was despotic: birds from the good patch prevented birds from the bad patch from breeding in the good patch.

Breeding parameters

A three-dimensional contingency table indicated that there were significant differences in clutch size between habitats and years ($\chi^2 = 248.61$, $df = 21$, $P < 0.001$);

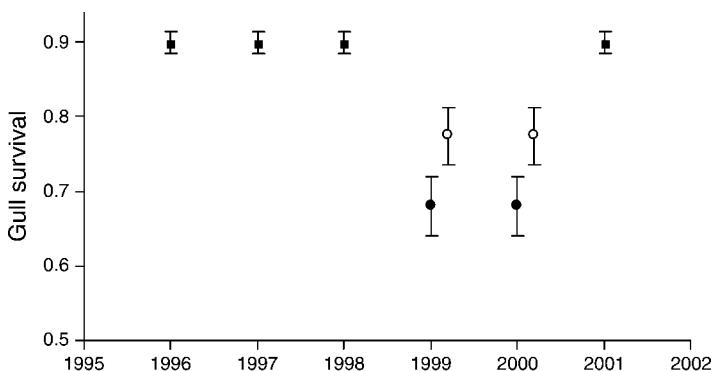


FIG. 2. Survival estimates (mean with 95% CI) for Yellow-legged Gulls breeding at the Ebro Delta during 1995–2001 from the finally selected model $[\tau^f, \phi_{h^*f}, p_i]$ (model 2 in Table 1), calculated by capture–recapture modeling. Squares show survival in years without predation, equal at the two patches; open and solid circles show survival affected by the catastrophic predator at the vegetated and bare patches, respectively (see Results).

here, one of the hypotheses under the IDD models was confirmed: clutch size was lower in the bare patch than in the vegetated patch ($\chi^2 = 195.37$, $df = 17$, $P < 0.001$) (see Fig. 3a). However, average egg volume in clutches of three eggs was not significantly different between years ($F_{9,486} = 1.684$, $P = 0.092$) or between patches ($F_{1,486} = 0.119$, $P = 0.730$) (Fig. 3b). These last two results suggest that birds able to lay three-egg clutches in the bare patch were probably birds of good quality, but the proportion of such birds was lower than in the vegetated patch (i.e., heterogeneity in individual quality was probably higher in the bare patch than in the vegetated patch). Results for breeding success also supported the IDD hypothesis that fitness parameters should be lower at the poorer patch than at the good patch: a GLM model showed that breeding success differed between the two study patches ($\chi^2 = 148.77$, $df = 3$, $P < 0.001$), being higher in the vegetated patch (1.53 ± 0.074 chicks/pair, mean \pm SE) than in the bare patch (0.44 ± 0.045 chicks/pair). There was no significant effect of year ($\chi^2 = 27.19$, $df = 27$, $P = 0.454$) nor of the interaction of year with habitat ($\chi^2 = 13.30$, $df = 27$, $P = 0.987$) on breeding success (Fig. 3c). As expected, flooding (caused by water pushed from the sea to the flat peninsula by strong winds) affected only the bare patch, specifically in 1994 and 1998 (minimum of 26% and 34% of nests flooded, respectively); the vegetated patch was never affected by this environmental perturbation.

DISCUSSION

Results found here supported some of the IDD predictions (see also Ens et al. 1995): younger breeders mostly recruited into the low-quality patch, and birds from this patch tried to renest (within the same or at the following season) in the high-quality patch after breeding failure caused by environmental perturbations. This was so even though density dependence for breeding sites was unlikely to operate within the local study population: a large number of vegetated, high-quality patches remained empty each year. Under this scenario of no density dependence (an essential mechanism invoked to explain the IDD model; see Morris [2003] and references therein), one question naturally arose: why did hundreds of birds select such a bad, poor-quality, and peculiar patch? Several nonexclusive hypotheses might account for this phenomenon: birds colonizing the bare patch were attracted by conspecifics to the largest, denser subcolony, as is commonly recorded, especially in social species (i.e., the conspecific attraction; see Stenhouse and Montevecchi 2000, Green and Stamps 2001, Martínez-Abraín et al. 2001, Serrano et al. 2004). Thus, birds probably used a social cue to erroneously select a poor patch for breeding. If this was true, the social mechanisms of conspecific attraction would represent a type of evolutionary trap that has not been described previously (Schlaepfer et al. 2002). Alternatively, birds occupying the bad patch had an

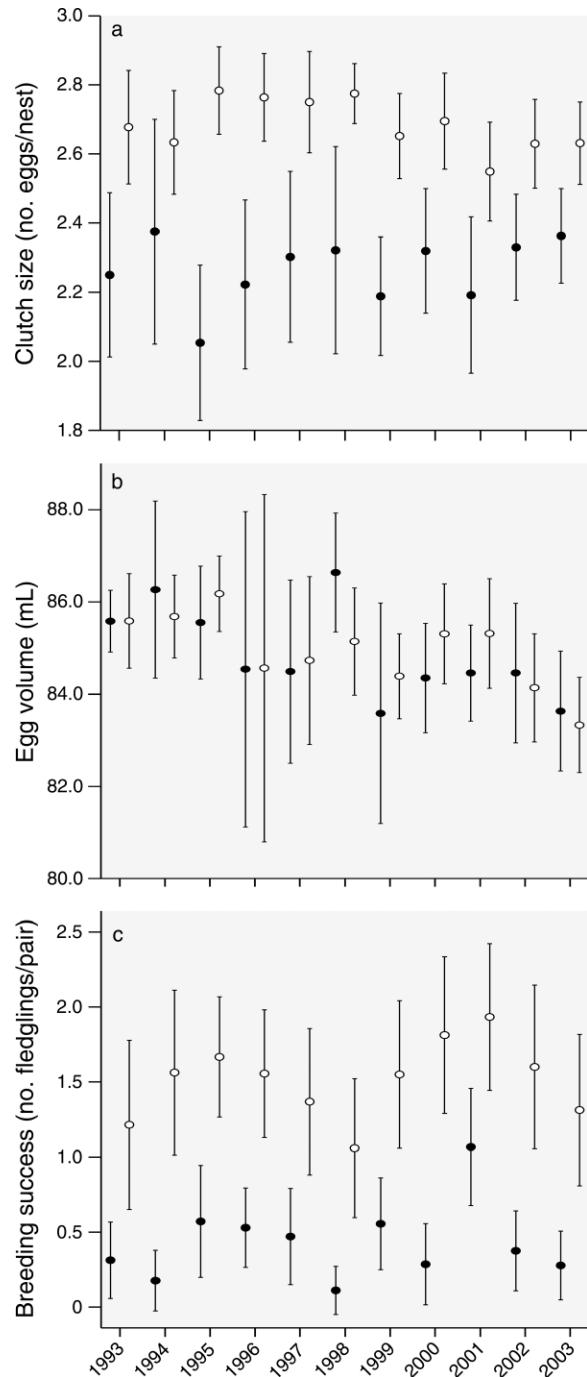


FIG. 3. Breeding parameters at the Ebro Delta during the study: (a) clutch size (mean number of eggs laid per nest with 95% CI); (b) egg volume (mean with 95% CI) in clutches of three eggs (the modal clutch size); and (c) breeding success (mean number of fledglings per nesting pair, with 95% CI). Open circles show the parameters at the vegetated patch, and solid circles show those at the bare patch.

imperfect knowledge of its profitability, described sometimes as “perceptual constraints” (e.g., Abrahams 1986, Rapport 1991), which would violate one of the few (and more difficult to demonstrate) assumptions of the

IDD (Tregenza 1995). Nevertheless, this explanation did not seem to apply in the study case: animals should be able to distinguish clearly between bare (bad patch) and vegetated (good patch) habitats, especially after the first years of colonization of the former patch. The bare patch was a sort of habitat never recorded before for any gull species, which always select vegetated habitats, or at least those with rough profile (e.g., stones, rocks), for breeding (e.g., Fasola and Canova 1992). Finally, differences in patch quality were consistent during the study, which should allow individuals to assess accurately the profitability of each patch in the long term (Maclean et al. 2005). Whatever the process involved in such unequal distribution of individuals in space, age probably played a major role, as suggested by the presence of very young recruits only in the bare patch. It has been commonly found that younger first-time breeders (i.e., less experienced and less capable individuals) have relatively low breeding success and breed in less suitable patches (e.g., Coulson 1968, Holmes et al. 1996, Serrano and Tella 2007). In the present study, differences in demographic parameters between patches were probably triggered by differences in both age structure and habitat features (see further examples in Holmes et al. 1996, Murphy 2001, Carrete et al. 2006, Serrano and Tella 2007), although they could not be disentangled here because of the small sample size for accurately testing such age effects. Results for Yellow-legged Gulls showed that even in situations where there was no density dependence for suitable space, a part of the population (probably with a younger age structure) bred in a very poor habitat. This was unexpected because, in heterogeneous habitats, poorer sites should be used at higher population densities through density-dependent mechanisms (Chamberlain and Fuller 1999, Velando and Freire 2001, Kokko et al. 2004).

Behavioral observations supported the despotic, agonistic prediction of the IDD: gulls from the bare patch trying to breed again after nest loss did so in the vegetated patch and were actively excluded by residents. These observations were essential to test this crucial prediction of the IDD model (Serrano and Tella 2007), i.e., that some individuals were excluded from habitat by conspecifics in a despotic way (Fretwell 1972). This assumption has often been missed by only observing the distribution of individuals in space with heterogeneity in patch quality, which may rather fit with the broader model of the ideal preemptive distribution, IPD (Pulliam and Danielson 1991; see also Tregenza 1995). Results also suggested that this behavioral dominance was likely to be age related and was one of the possible mechanisms to explain this despotic distribution (Marra 2000, Rendón et al. 2001, Rohwer 2004, Serrano and Tella 2007). A few birds from the bad patch were able to disperse to the vegetated patch, probably as a result of an increase in experience and performance with age, and being forced by breeding failures following catastrophic events, events that also decreased density (and in turn

competition) at the good patch (Oro et al. 1999, Cam and Monnat 2000a, b, Serrano et al. 2001, 2003, Serrano and Tella 2007). Even though it was not possible to fully demonstrate a choice of habitat for all colonizers in the bare patch (probably immigrants from a neighboring population, see Oro 2003), it was likely that they tried to occupy territories within the vegetated patch at the beginning of the season, from which they were probably precluded despotically by resident birds.

Another feature included in the IDD models was assessed here: the fitness consequences associated with the different habitats selected for breeding. Most of the parameters analyzed here (survival, dispersal, clutch size, and productivity) were higher in the high-quality patch, not only as a result of a lower vulnerability to perturbations, but also because of a lower rate of conspecific agonistic interactions (mainly intraspecific nest predation) than in the bare patch. The fact that different local populations and territories of social and territorial animals show different life history parameters has been found often at several spatial scales (e.g., Brooke 1979, Ens et al. 1995, Danchin et al. 1998, Murphy 2001, Frederiksen et al. 2005). Many of these studies have identified (often without full substantiation) such distributions as examples of IDD (e.g., Tome 2003, Zimmerman et al. 2003). In contrast, less is known about differences in vital rates between groups of individuals within a local population (often called subcolonies for social organisms), in which they have all the same resources per capita (e.g., food, mates). Most of these studies have found changes in breeding success, easily explained by differential predation rates depending on differences in microhabitat physical features or in densities between subcolonies or subpopulations (Birkhead 1977, Parrish 1995, Barbosa et al. 1997, Regehr et al. 1998, Genovart et al. 2003, Parejo et al. 2006).

Although scaling has been recognized as an important issue in ecology (see Wiens 1989), results shown here suggest a pattern of distribution of individuals traditionally studied and associated with larger spatial scales. Furthermore, the present study is, to my knowledge, the first to assess quantitatively the differences between neighboring breeding patches within a local population (under the same environmental conditions) in the most conservative and sensitive life history traits in long-lived organisms, i.e., survival and dispersal. The bare patch was clearly more affected by environmental stochasticity, such as flooding and mammalian predation, and variance in fitness components (breeding parameters and adult survival) was higher here than in the vegetated patch. It is now broadly accepted that environmental stochasticity plays an important role in population densities, dynamics, and distribution (e.g., Jonzén et al. 2004, Sæther et al. 2005). In comparison to large-scale patterns of population and metapopulation dynamics, this study also showed that particular individual

behavior and despotic distributions at small habitat scales can influence local population fluctuations.

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APPENDIX A

A map of the Punta de la Banya peninsula showing the main vegetated dunes where gulls can breed (*Ecological Archives* E089-047-A1).

APPENDIX B

Diagonal m -array of the number of birds $R_{(i)}$ released for the first time or in later occasions, at each year i and resighted at year j ($m_{(i,j)}$) at each study patch (*Ecological Archives* E089-047-A2).