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COLONIAL SEABIRD NESTING IN DENSE AND SMALL SUB-COLONIES: AN ADVANTAGE AGAINST AERIAL PREDATION[1]

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Key words: colony size; Audouin's Gull; Larus audouinii*; Peregrine Falcon;* Falco peregrinus*; Ebro Delta; Spain.*

Nesting in colonies is a form of social behavior in birds that is modified by adaptive pressures, with costs and benefits for the colony members (see review in Wittenberger and Hunt 1985). Seabirds have been widely studied to assess the importance of colony density on predation (Gotmark and Anderson 1984, Velarde 1992, Anderson and Hodum 1993). Lack (1968) asserted that breeding near conspecifics is a mode of nest defense in birds, and that the use of habitat may be influenced by potential predation risks (Wiens 1989). However, Anderson and Hodum (1993) stated that the importance of nesting near other birds for protection against predators is still not clear because results do not always agree. Moreover, the size of a colony is another factor that could influence the distance between nests (e.g., Brown et al. 1990).

The predation behavior of Peregrines (*Falco peregrinus*) on breeding Audouin's Gulls (*Larus audouinii*) is examined here with respect to density and size of the different sub-colonies within a colony. Quantitative variation of the two factors are considered among the sub-colonies to test how they influence aerial predation by Peregrines.

STUDY AREA AND METHODS

The Audouin's Gull colony is located on the Punta de la Banya, Ebro Delta, NW Mediterranean (40°37′N, 00°35′E). This colony was established in 1981 and since then has grown dramatically, now holding about 70% of the total world population (Pedrocchi and Ruiz 1995). The habitat is a sandy, flat peninsula of 2,500 ha with small dunes covered by halophilous vegetation. Audouin's Gulls only breed on these dunes, although not all the dunes are occupied by breeding gulls. Each dune occupied by breeding Audouin's Gull was considered

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TABLE 1. Probability of attack by Peregrines on Audouin's Gull sub-colony in the Ebro Delta colony, depending on its density and size. The total number of attacks recorded during the study (1992, 1993 and 1994) was 21. Probabilities were calculated with Baye's Rule (see text).

	No. attacks (%)	p[1]	p[2]	Fisher's exact
Density of the sub-colony				
Above the median	3 (14.3)	0.03	0.57	$P = 0.01$
Above the top quartile	1 (4.7)	0.15	0.70	$P = 0.04$
Size of the sub-colony				
Above the median	19 (90.4)	0.86	0.08	$P = 0.004$
Above the top quartile	12 (57.1)	0.76	0.12	$P = 0.03$

[1] Probability of attack given that a gull was in the most dense-large half of the sub-colony distribution (above the median), or in the most dense-large quartile of the sub-colony range (above the top quartile).
[2] Binomial probability if Peregrines attacked Audouin's Gull randomly with respect to density and size of the sub-colony.

a sub-colony (number of dunes occupied during the study = 18, median area = 0.57 ha, range = 0.1–4.54 ha).

The study was carried out during 1992, 1993 and 1994, from the establishment of the gulls in late March until mid-July, when most of the gulls disperse from the colony. All the edges of the dunes where Audouin's Gulls bred were systematically observed at least once a week and prey remains and pluckings were recorded. When a dead Audouin's Gull was found, the cause of the death was determined, and gulls not clearly depredated by Peregrines were not considered. To distinguish gulls depredated by Peregrines from those depredated or scavenged by Yellow-legged Gulls *Larus cachinnan* (Oro and Martínez-Vilalta 1994), I considered the tracks on the sand, the type of injury on the skull or back of the gull, the way it was plucked and eaten, and the parts of the gull left. There were no other potential aerial predators (large raptors or seabirds) in the colony. Although Peregrines do not carry or transport large prey (Dekker 1987), I only considered the corpses found at the edge of the sub-colonies. I assumed that a gull found dead at the edge of sub-colony "A" was predated in that sub-colony. Gulls found in the sand far from the dunes were not considered because I did not know whether Peregrines had caught the gull on the closest sub-colony or in flight. This assumption did not bias the results, because 21 of the 23 corpses found (91.3%) were at the edge of a sub-colony. Moreover, the three attacks observed were swoopings over sub-colonies, provoking the simultaneous flight of all the gulls there. No persecution behind the gulls was observed, as recorded with other potential prey of Peregrines, such as shorebirds.

For each gull found depredated, procedures similar to those of Anderson and Hodum (1993) were followed: for that sub-colony, the number of nests present were counted within circles with radius = 3 m around five nests chosen at random to estimate nest density (expressed as number of nests/20m^2). Nest density of the whole colony was measured taking a sample size of 30 circles randomly each year, and I considered whether the mean nest density of the sub-colony was below the median of the colony distribution that year. To assess greater densities, I used the top last quartile of each distribution. I then obtained the number of observed and expected depredations depending on the sub-colony density and size, and the null hypothesis of independence was tested by means of the Fisher exact test. The same procedure was used for the sub-colony size (expressed as number of nests/sub-colony). All the sub-colonies were censused each year by counting all the nests (varying from 290 pairs to 2,976 pairs), and a colony size distribution was obtained by counting all the sub-colonies each year.

RESULTS AND DISCUSSION

I found 21 Audouin's Gulls depredated by Peregrines during the study (five in 1992, ten in 1993 and six in 1994). Table 1 shows the probabilities of attack on sub-colony depending on both its density and size. The probability of being attacked by a Peregrine in a dense sub-colony (with a high density of breeding pairs) was 0.15, whereas the probability of being attacked in a small sub-colony (with a low number of breeding pairs) was 0.14.

Gulls breeding in dense and small sub-colonies within the colony enjoy greater protection against aerial predation by Peregrines than those in large, loose aggregations. Results indicated the importance of nesting density, independent of colony size. In Audouin's Gull, density is clearly the important aspect of social spacing. As in most colonial species (Clode 1993), density and colony size covary in Audouin's Gull. However, variation in size of the colonies in contrast to colony density has generally been ignored with respect to social costs and benefits for individuals (Brown et al. 1990). Several studies have stated that flocking (or grouping in breeding colonies) may help prey to detect, to confuse or to defend against predators (Kenward 1978, Velarde 1992, Anderson and Hodum 1993). However, prey or habitat characteristics are different in each case, and predator selection may vary. In the Ebro Delta, Peregrines captured adult gulls by dropping sharply on the different sub-colonies, just as they would act on groups of ducks or shorebirds resting or feeding on the ground. Most of the successful attacks were over large groups with low densities, so there could be a selection in gulls for breeding in dense and small groups as an anti-predator strategy against aerial predators. As Hamilton (1971) stated, aggregations of animals may reduce the risk of predation for each individual, but predators evolve to exploit such rich food patches. There appears to be a similar tendency against terrestrial intrusions per-

formed by the Yellow-legged Gull which commonly prey on nests of Audouin's Gull, especially in subcolonies with low densities (Oro and Martinez 1994, González-Solís et al. 1995). However, Clode (1993) suggested that seabird aggregations have evolved to utilize a dispersed and unpredictable food supply; as such, she stated that colonial nesting leads to increased vulnerability to predation, rather than being a strategy selected to combat it.

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THE CORTICOSTERONE STRESS RESPONSE IN GENTOO AND KING PENGUINS DURING THE NON-FASTING PERIOD[1]

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Penguins rely primarily on stored fat reserves as an energy source during fasting periods, such as molt or incubation, often for weeks or months (Watson et al. 1971, Cherel et al. 1988a, 1988b, Williams et al. 1992). During the final phase of fasting, when fat stores are depleted and food is not available, they begin mobilizing protein reserves as an energy source (Cherel et al. 1988a, 1988b). These energy reserves are derived primarily from skeletal muscle through the process of gluconeogenesis promoted by the adrenal glucocorticoid, corticosterone. Corticosterone secretion is under the control of adrenocorticotropin hormone (ACTH) released by the anterior pituitary which, in turn, is under the control of corticotropin releasing factor (CRF) from the hypothalamus (Holmes and Phillips 1976, Siegel 1980, Harvey et al. 1984). Corticosterone may be released rapidly into the bloodstream in response

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