FACTORS AFFECTING THE NEST HEIGTH OF THREE HERON SPECIES IN HERONRIES IN THE SOUTH-WEST OF SPAIN

FACTORES QUE AFECTAN A LA ALTURA DE LOS NIDOS DE TRES ESPECIES DE GARZAS EN EL SUROESTE DE ESPAÑA

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Differential resource selection is one of the principal factors which permit species coexistence (Schoener, 1974; Rosenzweig, 1981). In studies of niche partitioning, nest location has received much less attention than food or habitat, perhaps because suitable nest sites are presumed to be readily available for most species. However, when a species has specific nesting requirements, suitable nesting locations may be difficult to obtain (Wiens, 1989; Burger & Gochfeld, 1990). This may bring about the overlap of nest sites and, consequently, predation costs for breeders as a consequence of the attraction of predators due to the increase in cumulative nest density (Martin, 1996).

For colonial herons, the existence of a vertical nest stratification of species within mixed colonies in relation to body size has been suggested, with the larger species nesting at higher levels (Burger, 1982; Burger & Gochfeld, 1990; Fasola & Alieri, 1992). Species nesting higher are presumed to acquire these territories through dominance linked to body size (Burger, 1978b) and/or because they arrive earlier at colonies (Burger & Gochfeld, 1990). The two exceptions to this pattern are Purple Herons Ardea purpurea, that nest lower than expected according to its size and time of nest occupation as a consequence of the competitive exclusion by Grey Herons Ardea cinerea (Fasola & Alieri, 1992), and Cattle Egrets Bubulcus ibis, that nest higher than expected when they are not native in an area apparently because they are more aggressive in these new areas (Burger, 1978a).

In this paper we examine the vertical nest stratification of Cattle Egrets, Little Egrets *Egretta garzetta* and Night Herons *Nycticorax* *nycticorax* in two mixed heronries in the southwest of Spain, where Cattle Egrets are not native. We aimed at determining whether these three species align themselves vertically according to their body size or arrival times, and whether the non-native status of Cattle Egrets would modify the expected relationship between body size or arrival times and nest height (Burger, 1978a; Burger, 1982).

During the 1995 breeding season we studied two mixed heronries, one situated on the Guadiana river in the city of Badajoz (38°53' N $6^{\circ}58'$ E; Badajoz colony from now on), and the other (Morante colony from now on) situated on the border of an artificial pond about 30 km away from the former $(39^{\circ}03' \text{ N } 6^{\circ}41' \text{ E})$. The Badajoz colony was divided into subcolonies located on islands about 1 m above the water level. Islands are covered by *Tamarix* sp., *Phragmites* sp., *Populus* sp. and *Eucalyptus* sp. All the islands contained Cattle Egrets, Little Egrets and Night Herons. The Morante colony was on a small stand of Quercus ilex and Fraxinus angustifolia in the pond edge and the nesting species were Cattle and Little Egrets.

Data were collected in study plots located within each of the two studied colonies (two plots in Badajoz, each one in a different subcolony, and a plot in Morante). Before the settlement of birds in the colonies, we installed in the plots wooden stakes of known height to use them as references of distance. We made large scale photographs of the study areas where nests were placed when they were being constructed, so that nests could be individually identified. We visited the colonies weekly and observed them from the same place where we had taken the photographs. The amount of vegeta-

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tion suitable for nesting of each of the study plots was estimated by means of the photographs, which were parcelled from down to top in areas of 2×2 m, obtaining 455 parcels in the Badajoz colony and 92 in the Morante colony. When more than $\frac{3}{4}$ parts of a parcel were filled with vegetation, we gave them a value of 4 m², assigning fractions of this value in the rest of cases according to the surface of the photograph covered by vegetation. We assumed that this measure of the amount of vegetation in a parcel was directly related to the available area to place nests. This method allowed us to obtain the availability of places for nest building according to height (A: 0-2 m; B: 2-4 m; C: 4-6 m; D: 6-8 m; E: 8-10 m) in which nests were included. To avoid the effect of depth of the colony on the assignation of nests to the discrete height classes we only took into account those nests situated in the foreground as seen from our sampling point. Data collected for each nest included species, nest height above water level and hatching date.

As likely variables to explain the different success in getting the best places in colonies, we explored the following:

- 1. The body size, measured as the mean body mass of each species, which were obtained from Voisin (1991). This measure was taken as an estimate of the competitive ability of each species (Schoener, 1974; Burger, 1978a; Burger & Trout, 1979).
- 2. The laying date for each nest, that was estimated by subtracting the mean incubation period of each species (Voisin, 1991) from the hatching dates observed in the field. From these estimates we obtained the mean laying date for each species in each colony.

We compared nest heights and laying dates among heron species with the Kruskall-Wallis test (more than two groups) or Mann-Whitney test (two groups) and, in the first case, differences among groups were tested by the Scheffé test. Nest height selection by each species was tested by means of the Savage electivity index $W_i = U_i/D_i$ (Savage, 1931), where $U_i = u_i/u_*$, u_i is the observed number of nests of the species in the habitat i and u_* is the total number of nest of this species in the study area; $D_i = d_i/d_+$, d is the total surface of the habitat i available in the colony and d_{+} the total surface of the study area (measured by means of photographs because we knew the real surface that photos represented). The index ranges from 0 to infinite; values approach 0 for increasing avoidance, and to infinite for increasing preference. The index assumes the value 1 when use is proportional to availability. The departure of the use of each habitat type from a distribution proportional to its availability was tested using the statistic $(W_i - 1)^2/es (W_i)^2$, which follows a χ^2 distribution with 1 degree of freedom. [es (W_i)] is the standard error of the index approximately given by $\left[\frac{1-D_i}{u_+D_i}\right]$ (Manly et al., 1993). Data from the two study plots of the Badajoz colony were pooled for all analyses.

In Badajoz colony we found statistically significant differences between nest heights of species (H = 41.03, df = 2, n = 565, P < 0.01). Night Herons placed their nests higher than Little (P = 0.01) and Cattle (P < 0.01) Egrets (Table 1), whereas nest height differences between Cattle and Little Egrets were not significant (P = 0.24). The use of the Savage index confirms these results, showing a significant negative selection for the lowest parts of the colonies by all heron species. The values of the obtained available habitat of each class as well as the number of nests included in them are given in Table 2. Cattle Egrets showed a significant negative selection for the lower three meters of the colony ($W_i = 0.38, P < 0.05$), Little Egrets for the lower six meters ($W_i = 0.39$, P > 0.05 for the 0-3 m class; $W_i = 0.19$; P < 0.05 for the 3-6 m class) and Night Herons for the lower nine meters ($W_i = 0, P > 0.05$ for 0-3 m class; $W_i = 0.14$, P < 0.05 for 3-6 m class; $W_i = 0.31$, P < 0.05 for 6-9 m class).

In reference to phenology, in Badajoz all species began egg-laying from 29 April to 1 May. Cattle Egrets and Night Herons began earlier than Little Egrets. Laying dates were different for the three species (H = 10.03, df = 2, n = 187, P < 0.01). The Night Heron was the earliest species, followed by Little and Cattle Egrets. There were differences between Cattle Egrets and Night Heron laying dates (P < 0.01) and between Cattle Egret and Little Egrets (P = 0.04). However, Little Egret and Night Heron laying dates were not significantly different (P = 0.69).

TABLE 1

Parameters for each species and localities. Body mass values were obtained from Voisin (1991). Laying date is expressed as days from January 1st.

[*Parámetros considerados para cada especie y localidad. Los pesos corporales se obtuvieron de Voisin (1991). La fecha de puesta se expresa en días a partir del 1 de enero.*]

		Bada	ajoz	Morante		
Species	Body weight (g) [Peso corporal]	Nest height (m) [Altura de los nidos] $(\bar{x}\pm sd) (n)$	Laying date [Fecha de puesta] $(\bar{x}\pm sd) (n)$	$\begin{tabular}{c} \hline & Nest height \\ (m) \\ [Altura de los nidos] \\ (\bar{x} \pm sd) (n) \end{tabular}$	Laying date [Fecha de puesta] $(\bar{x}\pm sd) (n)$	
Bubulcus ibis Egretta garzetta Nycticorax nycticorax	350.0 417.5 583.5	9.0±3.2 (22)	156.5±20.7 (152) 144.8±15.9 (21) 138.9±14.1 (14)	2.5±1.4 (303) 3.7±1.3 (14)	115.8±8.8 (96) 121.5±11.2 (8)	

TABLE 2

Habitat availability and habitat use by each heron species in the two studied colonies. Habitat availability was measured as the amount of vegetation in 2x2 m parcels depicted on photographs of the study areas (see text for details). Habitat use was measured as the number of nests located in the foreground of such parcels. [Disponibilidad de hábitat y uso del mismo por cada especie de garza en las dos colonias estudiadas. La disponibilidad de hábitat fue medida como la cantidad de vegetación que aparecía en parcelas de 2x2 m definidas sobre fotografías de las áreas de estudio (véase el texto para más detalles). El uso del hábitat fue medido como el número de nidos ubicados en la parte frontal de tales parcelas.]

		Badajoz	s	Morante			
	Availability (m ²) [<i>Disponibilidad</i>]	Use (number of nests) [Uso (núm. de nidos)]		Availability (m ²) [<i>Disponibilidad</i>]	Use (number of nests) [Uso (núm. de nidos)]		
Height classes [Clases de altura]		Bubulcus ibis	Egretta garzetta	Nycticorax nycticorax		Bubulcus ibis	Egretta garzetta
A (0-2 m)	396	45	2	0	136	131	1
B (2-4 m)	396	116	1	1	121	124	7
C (4-6 m)	369	157	5	2	60	51	6
D (6-8 m)	324	138	12	10			
E (8-10 m)	216	57	2	17			
Total	1710	513	22	30	317	306	14

In Morante colony, Little Egrets nested higher than Cattle Egrets (U = 1184.5, $n_1 = 14$, $n_2 = 303$, P < 0.05). In this case the Savage index shows a negative selection by Little Egrets for the lower two meters above water level ($W_i = 0.17$, P < 0.05). However, no significant selection by Cattle Egrets was apparent. In relation to phenology, Cattle Egrets began the egg-laying on 15 April and Little Egrets on 17 April. The mean laying dates were not different between these species (U = 230, $n_1 = 8$, $n_2 = 96$, P > 0.05). Our results are in agreement with the hypothesized vertical nest stratification model developed for the north-eastern United States, Texas, Mexico, Argentina, Africa (see review in Burger & Gochfeld, 1990) and Italy (Fasola & Alieri, 1992). The vertical stratification pattern was not altered by the fact that the Cattle Egret is a recent breeder in the study area (Fernández-Cruz, 1975). The only factor that altered the vertical stratification was the species composition of the two colonies. In Badajoz, Night Herons placed their nests higher while Cattle and Little Egrets showed an important overlap in nest height, but when only Cattle and Little Egrets were breeding in a colony (Morante) nest heights were significantly different. This can be attributed to the similar values of the measured variables, body size and laying dates, for these two egrets, segregating only when other competitors are absent (Fasola & Alieri, 1992). As they have similar laying dates in the two-species colony, this fact could suggest a dominance by Little Egrets over Cattle Egrets, because Cattle Egrets prefer to nest higher in vegetation too, as has been shown by their higher nesting in areas where no other species are breeding at the same time, and early-nesting individuals nest highest in the vegetation (Burger, 1982).

Body size has been considered by other authors (Schoener, 1974; Burger, 1978a, 1979, 1982; Fasola & Alieri, 1992) as the main cause of the success in the acquisition of preferred nest sites and it seems to act even when there are an important similarity in the species body size, which has been proposed as a factor causing the overlap in nest heights (Fasola & Alieri, 1992). With respect to laying dates, we cannot affirm that this is an important factor in the acquisition of the preferred sites in the colonies because, though mean laying dates in Badajoz are pointing towards the existence of an order in occupation chronology that could give some advantages to the first species, the results are not consistent in both colonies.

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