Comparative Nest Site Selection and Breeding Success in 2 Sympatric Ardeids, Black-crowned Night-Heron (*Nycticorax nycticorax*) and Little Egret (*Egretta garzetta*) in the Axios Delta, Macedonia, Greece

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Abstract.—We studied nest site selection and breeding success of Black-crowned Night-Herons (*Nycticorax nycticorax*) and Little Egrets (*Egretta garzetta*) in the Axios Delta (Greece) from 1988 to 1990. Both species nested above the middle of tamarisks and alders. Nest density varied each year from 333.3 nests/ha to 646.2 nests/ha for Black-crowned Night-Herons and 291.7 nests/ha to 421.5 nests/ha for Little Egrets. Black-crowned Night-Herons started to breed earlier than Little Egrets, also placing their nests higher (mean nest height: 4.21 ± SD of 0.80 m and 3.54 ± SD of 0.71 m for Black-crowned Night-Herons and Little Egrets, respectively). The nearest neighbors were conspecifics for Black-crowned Night-Herons and heterospecifics (Black-crowned Night-Herons) for Little Egrets. The mean distance of the nearest neighbor was similar in both species (1.02 ± SD of 0.46 m and 1.11 ± SD of 0.37 m for Black-crowned Night-Herons and Little Egrets, respectively). In contrast to late-nesting Little Egrets that located their nests lower, Black-crowned Night-Herons maintained a constant nest distance from the ground. The mean clutch size (3.40 ± SD of 0.60 and 4.32 ± SD of 0.81 for Black-crowned Night-Herons and Little Egrets, respectively) and the mean chick survival per nest (2.48 ± SD of 0.95 and 2.53 ± SD of 1.28 for Black-crowned Night-Herons and Little Egrets, respectively) of both species varied among the study years. No variation was observed in the means of clutch size and chick survival per nest of Black-crowned Night-Herons among the 3 sub-periods of the breeding season. Little Egret clutch size and mean number of eggs hatched was smaller in late nesters, but no difference was observed in chick survival per nest between early and late nesters. Nest placement did not affect chick survival in Black-crowned Night-Herons and only marginally in Little Egrets. *Received 5 March 1997, accepted 27 September 1997.*

Key words.—Axios Delta, Black-crowned Night-Heron, breeding success, *Egretta garzetta*, Greece, Little Egret, nest site selection, *Nycticorax nycticorax*.

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In mixed-species heronries, hundreds or thousands of breeding birds coexist, leading to dense nesting and partitioning of the available space (Jenni 1969, Maxwell and Kale 1977, Parsons 1995). Interactions result in a horizontal and vertical stratification, in which vegetation type and structure have been found to be very important in nest site choice (McCrimmon 1978, Beaver *et al.* 1980). In certain habitats, nest site selection critically affects breeding success (Frederick and Collopy 1989). Timing of clutch initiation has also been reported to affect breeding success (McNiel and Leger 1987).

Nesting and foraging resources are critical for herons during breeding (Hafner and Fasola 1992, Fasola 1994). Feeding habitats in the Axios Delta, northern Greece, do not seem to be a limiting factor to nesting ardeids (Kazantzidis and Goutner 1996). On the other hand, the lack of available breeding sites is a common problem throughout the Mediterranean, resulting mainly from land reclamation (Fasola and Allieri 1992a).

Black-crowned Night-Herons (*Nycticorax nycticorax*) and Little Egrets (*Egretta garzetta*) breed in a number of Mediterranean colonies (Cramp and Simmons 1977, Voisin 1991). Despite an overall regional increase (Perennou *et al.* 1996), populations are declining in Greece (Crivelli *et al.* 1988), and elsewhere (Tucker and Heath 1994).

In contrast to the Little Egret, considerable information exists concerning nest site requirements and breeding success of the Black-crowned Night-Heron, a cosmopolitan species (Wolford and Boag 1971, Burger 1979, Beaver *et al.* 1980, Tremblay and Ellison 1980, Custer *et al.* 1983, Findholt and Trost 1985, Burger and Gochfeld 1990, Kelly *et al.* 1993). In the Mediterranean, our knowledge of nest site selection of Black-

crowned Night-Herons and Little Egrets comes from studies in the Camargue (Hafner 1977, 1980) and Italy (Fasola and Allieri 1992b). Although the breeding performance of Little Egrets in the Mediterranean has been extensively studied (Hafner 1977, Tsahalidis 1990, Ashkenazi and Yom-Tov 1996, Prosper and Hafner 1996, Kazantzidis *et al.* 1996), such studies on Black-crowned Night-Herons are rather limited (Hafner 1977, Prigioni *et al.* 1985, Ashkenazi and Yom-Tov 1996).

Our objectives were to study nest site selection and breeding success of both species, to compare their seasonal and annual variations, and seek relations between nest site characteristics and survival per nest.

STUDY AREA AND METHODS

Study Area

The Axios Delta (40°30'N, 22°53'E) is part of a wetland complex at the Thermaikos Gulf, northern Aegean Sea, covering an area of 68.7 km^2 (Athanassiou 1990), and comprised by estuarine and deltaic areas of the rivers Axios, Aliakmon, Loudias and Gallikos. The complex is a Wetland of International Importance according to the Ramsar Convention, a Special Protected Area (according to the EU Directive 79/409) and an Important Bird Area in the European Union (Grimmet and Jones 1989).

The Axios Delta includes a variety of habitats such as salt and freshwater marshes, ricefields, lagoons, open sea, vegetated coastal islets, sandy shores, forested river banks and tamarisk shrubland. Ricefields are important cultivated habitats in the area, offering valuable food resources to nesting ardeids (Kazantzidis and Goutner 1996).

The Breeding Colony

During the last 15 years, the colony site has changed 4 times along the Axios River as a result of human activities (mainly sand extraction works) (A. J. Crivelli, pers. comm.). The most recent pertubation was in 1987 when the colony site, located on an island approximately 10 km north of the river mouth, was completely destroyed by logging and sand extraction works. The birds abandoned the site, joining a smaller colony at the river's mouth the object of the present study.

The current colony at the Axios Delta is one of the largest in Greece, both in number of breeding pairs and number of species. Most of the breeding population consists of Black-crowned Night-Herons (420-800 pairs) and Little Egrets (274-700 pairs). Other species breeding in the colony are Great Cormorants (*Phalacrocorax carbo,* 100-150 pairs), Pygmy Cormorants (*Phalacrocorax pygmeus,* 5-10 pairs; except 1990), Squacco Herons (*Ardeola ralloides,* 150-300 pairs), Spoonbills (*Platalea leucorodia,* 16-50 pairs) and Glossy Ibises (*Plegadis falcinellus,* 30-50 pairs). During the study period the colony was situated in an elongated and narrow riverine forest of tamarisks (*Tamarix* spp.), alders (*Alnus glutinosa)* and willows (*Salix* spp.), on an island near the mouth of Axios River. At the start of the breeding seasons, parts of the colony ground below the trees were inundated by rain water; this dried out completely by mid-May.

Methods

The study was carried out from 1988 to 1990. From early April to late June, in selected parts of the colony (2 in 1988 and 1989 and 3 in 1990), all newly constructed nests of both species were individually marked by small numbered wooden labels placed below the nest. We studied 4.1%, 16.7% and 7.6% of the Black-crowned Night-Heron nests in the colony and 7.0%, 28.8% and 22.1% of Little Egret nests during the 3 years, respectively. The colony area was determined as that demarcated by the peripheral nests. Nests were checked at least every 5 days from the beginning of the egg laying period with the aid of a mirror, fixed at the top of a pole. We recorded the number of eggs, hatchlings and number of chicks surviving per nest until approximately the age of 25 days (when, upon our approach, they were capable of climbing from the nest). Brood mates were banded with colored elastic bands placed on the tarsometatarsus, until the age of 15-25 days when individuals were given unique combinations of colored plastic bands above the tibio-tarsal joint (66 Little Egrets and 44 Black-crowned Night-Herons) or beige colored wingtags (polyester cloth impregnated in vinyl) with black letters and numbers (129 Little Egrets and 57 Black-crowned Night-Herons). Hatching success (number of eggs hatched per study nest) and chick survival (number of chicks at age approximately 25 days per study nest) were determined by directly checking the content of the nests. To reduce disturbance during breeding, other data were collected in early September, when all nestlings had fledged and had left the colony: area of the colony site; number of total nests; vegetation type at each nest; distance of each nest from the ground and the top of the tree (made with the aid of a scaled pole); the species and distance of the nearest nest neighbor (estimated by Euclidean theorem: $a^2 + b^2 = c^2$ where "a" and "b" are the vertical and the horizontal distance between the nests and "c" is the hypotenuse of the right-angled triangle formed by "a" and "b").

In each breeding season, the nesting period was divided into 3 equal sub-periods (a, b and c) in order to examine potential variability in nest placement during the course of nesting. Duration of the sub-periods depended on the duration of the total breeding period, being 15 days in 1988, 18 days in 1989 and 19 days in 1990.

Comparisons related to breeding success among years and sub-periods were made with 1-way ANOVAs (using Scheffe's test to assess differences). A 2-factor ANOVA was used to test whether the interaction of the factors "year" and "species" affected: (1) the nest distance from the ground and, (2) nest distance from the top of the tree. Sub-period, as a factor, could not be included in the multifactorial ANOVA, due to small sample sizes. Thus, for both species, differences among sub-periods in regard to the above variables as well as tree height were analyzed by 1-way ANOVAs. Student's t-tests compared means of habitat and breeding parameters between the species studied. Data were log-transformed

where appropriate. In cases of small samples, non-parametric procedures (Mann-Whitney U-test, Spearman Rank Correlation Coefficient) were used, while categorical data were analyzed by the Chi-square test (with Yate's correction on 2 × 2 tables). To evaluate the relative importance of nest site parameters to chick survival per nest, a stepwise multiple regression was applied for each species, separately. Nest distance above ground and nest distance from the top of the tree were the independent variables (tree height was excluded, because it was highly intercorrelated with these 2 variables); and chick survival per nest was the dependent variable (all years' data were compiled). Means are presented with standard deviations (SD).

RESULTS

Colony Site

Colony area varied among years, being larger in 1988 (Table 1). In 1988 and 1989, the number of nests per ha of Black-crowned Night-Herons was higher than that of Little Egrets but their median nest densities were similar ($U_2 = 5.0$, n.s.). Nest density of all species combined was negatively correlated with the colony area ($r_s = -1.00$, df = 2, $P < 0.001$), and varied among the years, with highest values in 1989 and lowest in 1988 (Table 1).

Nest Site Selection

The majority of nests of both species were located in tamarisks. Several nests were found in alder and only occasionally in willow. The number of nests of both species in alder increased significantly in 1990 (BNHE, $\chi^2_2 = 27.0$; LE, $\chi^2_2 = 117.0$; both $P < 0.001$; Fig. 1). Alders were taller than tamarisks in the colony (alder, $\overline{X} = 7.59 \pm$ SD of 0.57 m, N = 31; tamarisk, $\overline{X} = 6.54 \pm$ SD of 1.06 m, N = 241) ($t_{270} = 5.37$, $P < 0.001$).

Both species occupied trees of similar height (BNHE, $\overline{X} = 6.7 \pm$ SD of 1.0 m, N = 147; LE, $\overline{X} = 6.6 \pm$ SD of 1.1 m, N = 125) during the study period ($t_{270} = 0.966$, n.s.). Black-crowned Night-Herons nested in lower trees in 1988 than in the other 2 years (Scheffe test) ($F_{2,146} = 14.55$, $P < 0.001$; Fig. 2) and Little Egrets nested in trees of similar height among all years ($F_{2,124} = 1.17$, n.s.).

With the exception of Little Egret in 1988, both species nested above the middle of the nesting trees, having significantly greater mean distances from the ground than from the top of the tree (t-tests, $P < 0.05$; Fig. 2). The factors "species" and "year", significantly affected the mean nest distance from the ground ($F_{2,1} = 36.13$, $P < 0.001$; 2-factor ANOVA) increasing significantly through the years for both species, being greater in Black-crowned Night-Herons (Fig. 2). Similarly, both factors had a significant relation to the nest distance from the top of the tree ($F_{2,1} = 13.59$, $P < 0.001$; 2-factor ANOVA). In Black-crowned Night-Herons this distance increased through the years, whereas in Little Egrets it decreased (Fig. 2).

Most Black-crowned Night-Heron nests (56.3%, of a total 119) had a conspecific nearest neighbor, followed by the Little Egret (35.1%) and Squacco Heron (12.6%). Percentages of each neighboring species did not differ among years ($\chi^2_4 = 5.07$, n.s.). Most Little Egret nests (46.7%, of a total of 105) had also Black-crowned Night-Heron as a nearest neighbor, followed by Little Egret (37.1%), Squacco Heron (15.2%) and Spoonbill (0.9%). Percentages of each neighboring species differed significantly among years ($\chi^2_4 = 12.43$, $P = 0.01$) because the incidence of Little Egrets as a conspecific neighbor varied among the years ($\chi^2_2 = 6.35$, $P = 0.04$), being lowest in 1988 (23.8%, N = 5) and highest in 1989 (50.0%, N = 24).

The mean distance to the nearest neighbor did not differ significantly between species (BNHE, $\overline{X} = 1.02 \pm$ SD of 0.47 m, N =

Table 1. Colony area (ha) and nest density (nests/ha). Number of nests in brackets.

Year	Area (ha)	No. of species	Nest Density			
			Black-crowned Night-Heron	Little Egret	Other species	Total
1988	2.4	7	333.3 [800]	291.7 [700]	221.6 [532]	846.6 [2,032]
1989	0.65	7	646.2 [420]	421.5 [274]	509.2 [331]	1,576.9 [1,025]
1990	1.5	6	377.3 [566]	386.7 [580]	277.3 [416]	1,041.3 [1,562]

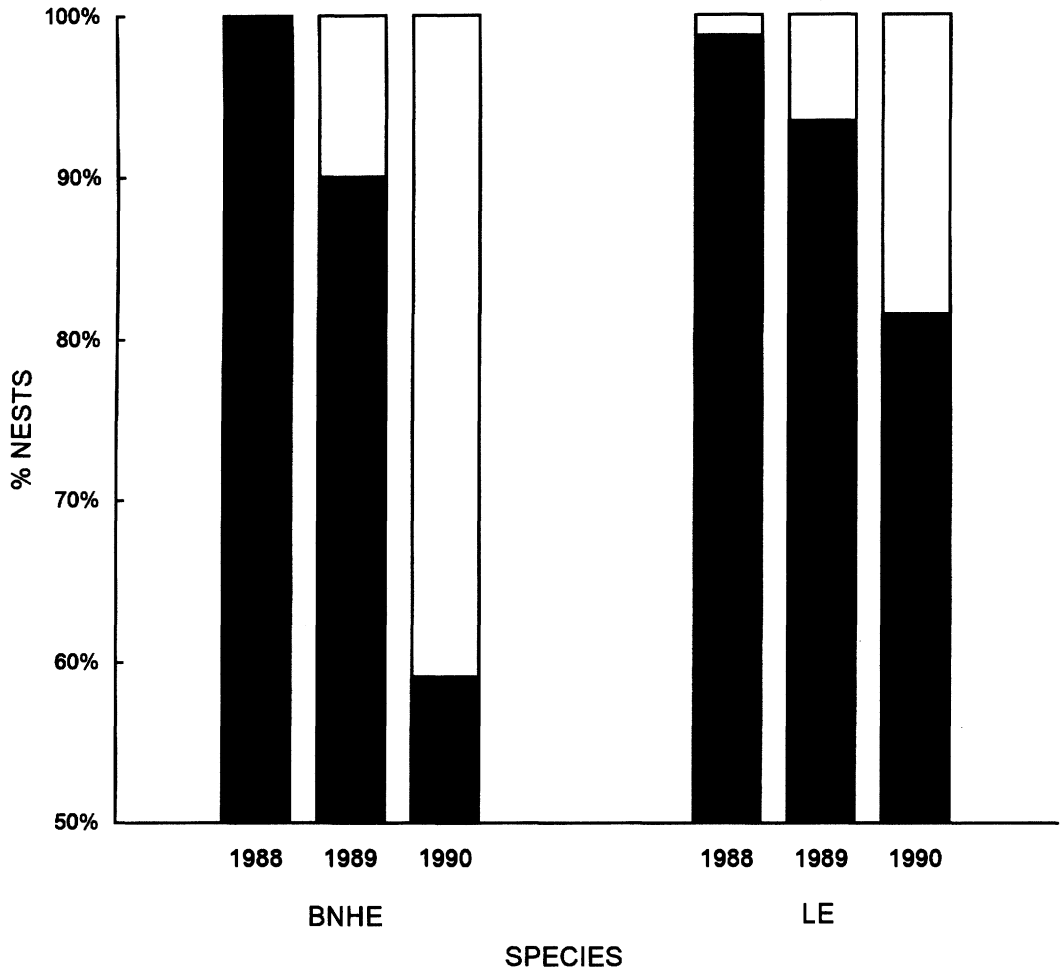

Figure 1. Distribution of Black-crowned Night-Heron (BNHE) and Little Egret (LE) nests on different tree species (Tamarisk-black fill, Alder-white fill) (1988-1990).

147; LE, $\overline{X}$ = 1.1 ± SD of 0.41 m, N = 125; t_{270} = 1.75, n.s.), although differences were found within each species through the years (BNHE, $F_{2,146}$ = 19.23; LE, $F_{2,124}$ = 15.14; both $P < 0.001$). This difference is mainly attributed to the mean distance from the nearest neighbor being greatest in 1988 (Scheffe test; Fig. 3). The species of nesting tree (tamarisk and alder), did not affect the nearest neighbor distance in either species (BNHE, t_{144} = 1.96; LE, t_{123} = 1.88; both n.s.).

Nest Placement in Relation to the Time of Breeding

Breeding by Black-crowned Night-Herons was initiated on 7 April in 1988 and 1989 and 10 April 1990, and reached a peak by the end of the month (Fig. 4). Little Egrets initiated breeding on 12 April 1988 and 1989 and on 18 April 1990, reaching a peak in the first 10 days of May (Fig. 4).

During the first and second sub-periods of the breeding season ("a" and "b"), Black-crowned Night-Herons nested in taller trees than in the last sub-period ("c") ($F_{2,146}$ = 5.86, P = 0.003; Table 2). The mean nest distance from the top of the tree decreased significantly through sub-periods ($F_{2,146}$ = 5.66, P = 0.004). As lower trees were gradually occupied, mean distances from the ground remained similar in all sub-periods ($F_{2,146}$ = 0.72, n.s.; Table 2). The distance to the nearest neighbor varied significantly among the 3

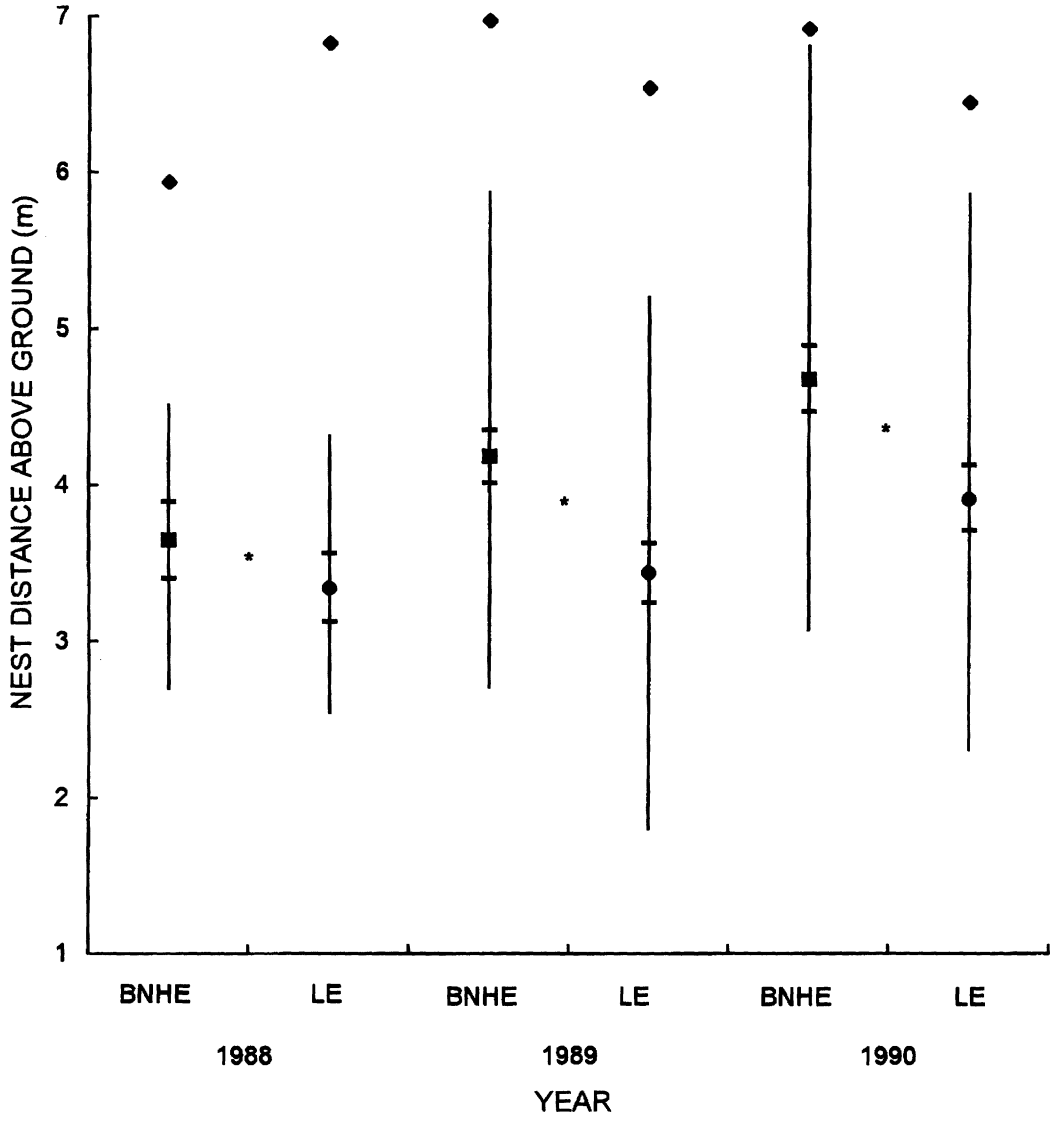

Figure 2. Mean nest distance (m) from the ground (95% confidence intervals and ranges included) and the mean nesting tree height (♦) used by Black-crowned Night-Herons (BNHE) and Little Egrets (LE) (1988-1990). Stars between BNHE and LE columns indicate a significant difference (t-test, P < 0.001).

sub-periods ($F_{2,146}$ = 5.25, P = 0.01), being closer during the first and similar in the other 2 sub-periods (Scheffe test; Table 2).

Little Egrets nested in trees of similar height ($F_{2,124}$ = 1.58, P = 0.21) and at similar distances from the top of the tree ($F_{2,124}$ = 0.58, P = 0.56) in all 3 sub-periods of the breeding season. By contrast, mean nest distance from the ground varied significantly among the sub-periods, being further in the first ($F_{2,124}$ = 4.07, P = 0.02; Scheffe test; Table 3). The mean distance of the nearest neighbor varied significantly in the 3 sub-periods ($F_{2,124}$ = 12.09, P < 0.001) being shortest in the first, and longest in the last (Scheffe test; Table 3).

Breeding Success

Black-crowned Night-Heron clutch size and chick survival per nest varied significantly among years (clutch size, $F_{2,145}$ = 12.67; chick survival, $F_{2,145}$ = 7.71; both P < 0.001),

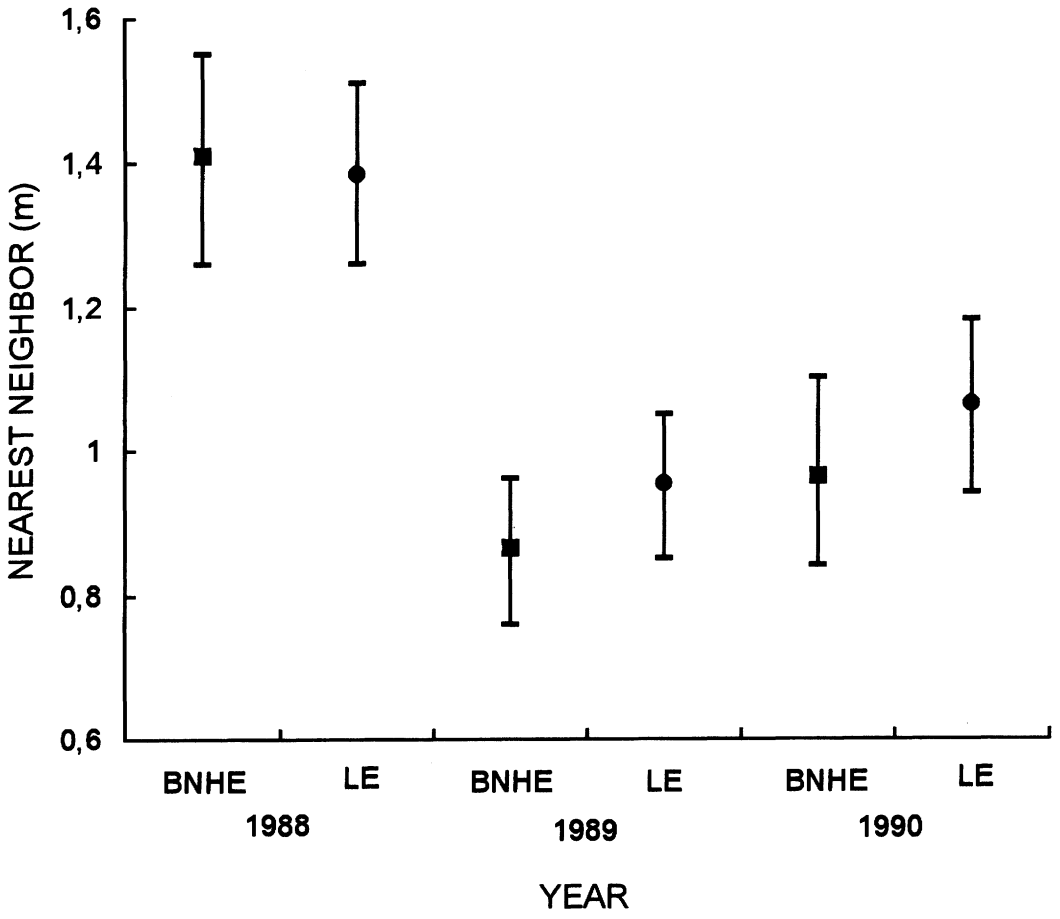

Figure 3. Mean distance (m) (and 95% confidence intervals) of nearest neighbor nests for Black-crowned Night-Herons (BNHE) and Little Egrets (LE) 1988-1990.

with smaller values in 1990, and similar in the other years (Scheffe tests). Mean number of eggs hatched did not differ during the same interval ($F_{2,145} = 0.55$, n.s.; Table 4).

Significant differences among years were observed in all breeding success parameters of Little Egret (clutch size, $F_{2,255} = 3.72$, $P = 0.02$; mean number of eggs hatched, $F_{2,255} = 3.26$, $P = 0.03$; chick survival, $F_{2,255} = 7.71$, $P < 0.01$). All variables had higher mean values in 1988 than in the other 2 years (Scheffe test; Table 4).

Egg losses in both species were mainly due to predation by Magpies (*Pica pica*), whose number of breeding pairs around the colony increased from 3 in 1988 to 7 in 1989. During the study period, Black-crowned Night-Herons and Little Egrets lost 11.1% and 21.2% of their eggs, respectively, (representing 0.4 ± SD of 0.5 and 0.9 ± SD of 1.2 eggs per nest, respectively; $t_{400} = 5.45$, $P < 0.001$). Percentages of unhatched eggs were similar in both species, being 2.3% of the total number of eggs laid by Black-crowned Night-Herons and 1.9% by Little Egrets.

During the study, 17.3% and 23.9% of the total number of chicks of Black-crowned Night-Herons and Little Egrets, respectively, were lost. Chick losses seem to have resulted from heavy rainfall, human disturbance, and probably brood reduction mechanisms; the last-hatched chicks usually starved, being unable to compete for food with older siblings, or were ejected from the nest to the ground and then were preyed upon by red foxes (*Vulpes vulpes*). Losses varied among years, being lowest in 1988 and highest in 1990 (BNHE, $\chi^2_2 = 12.92$; LE, $\chi^2_2 = 15.31$; both $P <$

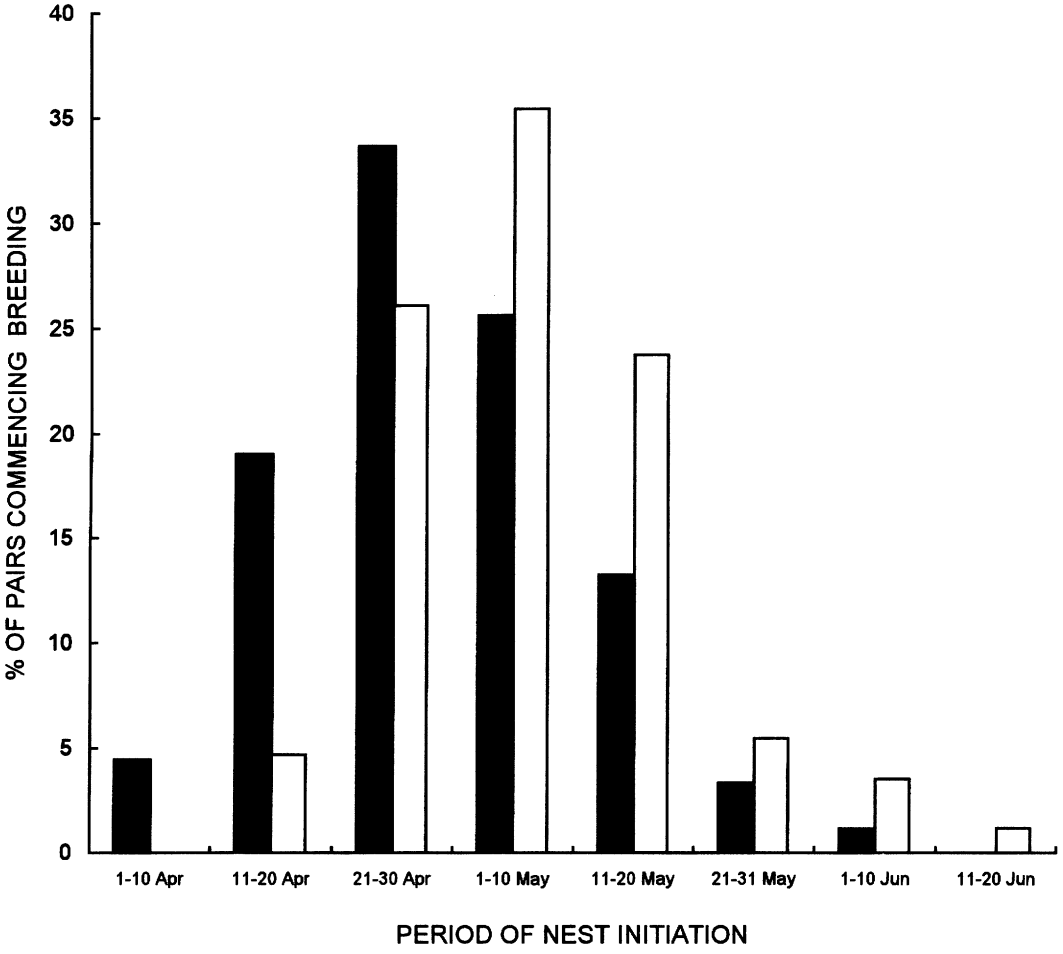

Figure 4. Timing of egg laying initiation for Black-crowned Night-Herons (black column) (N = 146 clutches) and Little Egrets (white column) (N = 256 clutches) (1988-1990).

0.001). As a result of these losses, chick survival was highest in 1988 and lowest in 1990. Mean number of chicks lost per nest was significantly higher for Little Egrets ($t_{400} = 3.48$, $P < 0.001$).

Variation of Breeding Success in Sub-Periods

Black-crowned Night-Herons demonstrated no variation in clutch size and chick survival per nest studied among sub-periods (clutch size, $F_{2,145} = 2.68$; chick survival, $F_{2,145} = 0.28$; both n.s.). Nevertheless, the mean number of eggs hatched per nest studied varied significantly among the 3 sub-periods ($F_{2,145} = 4.28$, $P = 0.02$), being higher in the first and lower in the last (Scheffe test; Table 5).

Little Egrets experienced a significant decrease in the mean clutch size during the breeding period ($F_{2,255} = 4.54$, $P = 0.01$). Mean number of eggs hatched also differed significantly ($F_{2,255} = 4.31$, $P = 0.01$), the differences being between the "a"-"c" and "b"-"c" sub-periods (Scheffe test); no variation appeared in the chick survival per nest ($F_{2,255} = 0.81$, n.s.; Table 5).

Chick Survival in Relation to Nest Placement

Nest distance from the ground had a marginally significant effect on Little Egret chick survival ($F_{1,124} = 3.998$, $P = 0.048$, $R^2 = 0.03$). In Black-crowned Night-Herons, neither distance from the ground nor distance from the top of the tree had a significant ef-

Table 2. Black-crowned Night-Herons mean nest height (m), mean nest distance below nesting tree-top (m), mean distance (m) from the nearest neighbor and mean height (m) of nesting trees during the 3 sub-periods of the breeding season, all years combined. N = sample size.

Sub-period	N	Nest distance from the ground ± SD	Nest distance from the top of the tree ± SD	Nest distance from the nearest neighbor ± SD	Tree height ± SD
a	61	4.30 ± 0.90a*	2.55 ± 0.91a	0.87 ± 0.39a	7.00 ± 1.00a
b	72	4.14 ± 0.73a	2.32 ± 0.74ab	1.13 ± 0.50b	6.61 ± 1.02ab
c	13	4.15 ± 0.64a	1.71 ± 0.45b	1.10 ± 0.55b	6.01 ± 0.84b
All periods	146	4.21 ± 0.80	2.36 ± 0.80	1.02 ± 0.46	6.72 ± 1.00
Ranges		2.69 - 6.80	0.86 - 4.56	0.37 - 3.46	4.06 - 8.72

*Means of each column sharing a common letter were not significantly different.

fect on chick survival ($F_{1,145} = 0.08$, $P = 0.99$, $R^2 = 0.001$). No differences in mean chick survival per nest were detected in relation to the tree species (tamarisk or alder) where nests were placed (BNHE, $t_{144} = 0.92$; LE, $t_{254} = 1.56$; both n.s.).

DISCUSSION

Black-crowned Night-Herons and Little Egrets, like other herons breeding in the Mediterranean region, are quite adept at exploiting available local nesting resources such as vegetation type and height (Voisin 1991, Perennou *et al.* 1996). The area occupied by the colony in the Axios Delta varied during the study period, due to the variable size of the breeding populations and the differences in nest densities. Nest density and area occupied by heron colonies vary considerably: in the Camargue, in southern France, a colony of more than 2,000 pairs covered an area of 4.5 ha, and nest density ranged from 1,285 to 6,071 nests per ha, depending on the location of the nests within the colony (Hafner 1977, 1980). In Oregon, USA, nest density in Great Blue Heron (*Ardea herodias*) colonies varied from 39 to 720 nests per ha (Bayer and McMahon 1981), while in Monroe County, Michigan, USA, nest density in a Black-crowned Night-Heron colony within a 1.4 ha woodlot was 88 nests per ha (Hoffman and Prince 1975). In Maine, USA, the mean nest density at 11 colonies was 149 nests per ha (Gibbs *et al.* 1987). Elsewhere in the USA, densities were much higher: in Florida, in a colony of 2.8 ha at Riomar Island, 2,657 nests of 13 species were counted (949 nests per ha; Maxwell and Kale 1977) while at Pea Patch Island, Upper Delaware Bay, density was 5,000-25,000 per ha (Parsons 1995). Inter-colony differences in nest density are not always easy to explain, but, as shown in the above literature, differences in vegetation structure and number of breeding pairs are the most probable reasons. In the previous studies, high nest density has been observed in highly populated mixed colonies while in small colonies (mixed or not) the density was lower. In comparison to these cases, the Axios Delta colony seems densely populated. This may be attributed to an extensive reduction in suitable nesting habitat, resulting

Table 3. Little Egret mean nest height (m), mean nest distance (m) below nesting tree-top, mean distance (m) from the nearest neighbor and mean height (m) of nesting trees during the 3 sub-periods of the breeding season, all years combined. N = sample size.

Sub-period	N	Nest distance from the ground ± SD	Nest distance from the top of the tree ± SD	Nest distance from the nearest neighbor ± SD	Tree height ± SD
a	55	3.75 ± 0.76a*	2.86 ± 1.03a	0.95 ± 0.33a	6.76 ± 0.99a
b	54	3.37 ± 0.68b	3.00 ± 1.10a	1.17 ± 0.41b	6.52 ± 1.17a
c	16	3.41 ± 0.61b	2.67 ± 1.45a	1.45 ± 0.38c	6.22 ± 1.44a
All periods	125	3.54 ± 0.71	2.90 ± 1.12	1.11 ± 0.37	6.59 ± 1.13
Ranges		1.80 - 5.85	0.00 - 5.40	0.49 - 2.36	2.54 - 8.61

*Means of each column sharing a common letter were not significantly different.

Table 4. Breeding success (means ± SD) of Black-crowned Night-Herons (BNHE) and Little Egrets (LE) during the study period at the Axios Delta. N = sample size.

	N		Clutch size		Eggs hatched per nest		Survival per nest	
Year	BNH	LE	BNHE	LE	BNHE	LE	BNHE	LE
1988	33	49	3.39 ± 0.56a* (103)1	4.55 ± 0.76a (223)1	2.91 ± 0.58a (93, 90.3)2	3.76 ± 0.84a (184, 82.5)2	2.70 ± 0.92a (65, 69.9)3	3.27 ± 1.19a (160, 87.0)3
1989	70	79	3.53 ± 0.63a (245)	4.39 ± 0.85b (347)	2.97 ± 0.76a (211, 86.1)	3.25 ± 1.42b (257, 74.1)	2.59 ± 0.92a (184, 87.2)	2.38 ± 1.51b (188, 73.2)
1990	43	128	3.19 ± 0.55b (148)	4.20 ± 0.78b (538)	2.84 ± 0.53a (122, 82.4)	3.21 ± 1.24b (411, 76.4)	2.14 ± 0.94b (113, 92.6)	2.34 ± 1.24b (300, 73.0)
All years	146	256	3.40 ± 0.60 (496)	4.32 ± 0.81 (1,108)	2.92 ± 0.64 (426, 85.9)	3.32 ± 1.28 (852, 76.9)	2.48 ± 0.95 (362, 85.0)	2.53 ± 1.28 (648, 76.1)

*Means of each column sharing a common letter were not significantly different.

[1]Number of eggs after clutch completion.

[2]Number of eggs hatched (first number) and % hatching success (second number).

[3]Number of chicks at approximate age 25 days (first number) and proportion of chicks surviving from those hatched (second number).

from continuous destruction or degradation of trees and bushes in the Axios Delta.

In 1988 and 1989, both species mainly nested in tamarisks. In 1990, they used alders more. This was probably due to the abandonment of nesting sites on alders by Great Cormorants, which nested contiguously in 1988 and 1989 and, in 1990, moved elsewhere in the colony area. The resulting available nest sites were partly occupied by Black-crowned Night-Herons and Little Egrets. The highest mean nest distance from the ground of both species in 1990, was due to a greater proportion of nests being placed on alders which were taller than tamarisks.

Nest distance from the ground and top of the tree in the Axios Delta colony seems to be determined by interspecific interactions. During the study period, Black-crowned Night-Herons nested higher than Little Egrets (Fig. 2). Since Black-crowned Night-Herons started breeding earlier, they had all the potential nesting sites available from which to choose, and the opportunity to occupy those most suitable. Later-nesting Black-crowned Night-Herons selected sites on the highest branches of the lower trees, keeping a rather consistent distance from the ground. This may be a function of antipredatory behavior, as higher nesting sites are possibly safer (Burger 1979). In contrast, Little Egret mean nest distance from the ground declined as the breeding season progressed, which is not consistent with antipredatory behavior. Thus, early occupation of the colony site by Black-crowned Night-Herons, coupled with their generally larger breeding population, may have forced Little Egrets to nest lower, in response to the absence of suitable higher sites.

Tree structure and timing of breeding affect selection of nesting sites of these species in other parts of the world, as well. Black-crowned Night-Herons nested higher than Little Egrets in the Camargue (Hafner 1977, 1980; Voisin 1979, 1991) and in Italy (Allieri *et al.* 1988, Fasola and Allieri 1992b), started egg laying earlier than the latter species. In contrast, in the USA and on Madagascar, in mixed colonies, Black-crowned Night-Herons nested close to the ground or even on it, starting incubation later than the other species which occupied the higher parts of the vegetation (Burger 1985, Burger and Gochfeld 1990).

The nearest neighbors of Black-crowned Night-Herons were most frequently conspecifics. In contrast, Black-crowned Night-Herons, were most frequently nearest neighbors to Little Egrets probably because the late-breeding Little Egrets tended to locate their nests in relation to Black-crowned Night-

Table 5. Breeding success (means ± SD) of Black-crowned Night-Herons (BNHE) and Little Egrets (LE) in the 3 sub-periods of the breeding season, all years combined. N = sample size.

	N		Clutch size		Eggs hatched per nest		Survival per nest	
Sub-period	BNHE	LE	BNHE	LE	BNHE	LE	BNHE	LE
a	61	12	3.49 ± 0.62a* (213)1	4.49 ± 0.81a (503)1	3.10 ± 0.65a (189, 88.7)2	3.48 ± 1.31a (390, 77.5)2	2.52 ± 0.99a (154, 81.5)3	2.48 ± 1.39a (278, 71.3)3
b	72	12	3.37 ± 0.57a (243)	4.23 ± 0.83b (474)	2.81 ± 0.66b (202, 83.1)	3.35 ± 1.24a (375, 79.1)	2.47 ± 0.89a (178, 88.1)	2.64 ± 1.35a (296, 78.9)
c	13	32	3.08 ± 0.64a (40)	4.09 ± 0.64c (131)	2.69 ± 0.48b (35, 87.5)	2.72 ± 1.46b (87, 66.4)	2.31 ± 1.11a (30, 85.7)	2.31 ± 1.63a (74, 85.1)
All periods	146	56	3.40 ± 0.60 (496)	4.32 ± 0.81 (1,108)	2.92 ± 0.64 (426, 85.9)	3.32 ± 1.28 (852, 76.9)	2.48 ± 0.95 (362, 85.0)	2.53 ± 1.28 (648, 76.1)

*Means of each column sharing a common letter were not significantly different.

[1]Number of eggs after clutch completion.

[2]Number of eggs hatched (first number) and % hatching success (second number).

[3]Number of chicks at approximate age 25 days (first number) and proportion of chicks surviving from those hatched (second number).

Herons. Squacco Herons were the nearest neighbor of both species in only a few cases, because they started breeding in mid-May when the only remaining suitable sites were widely scattered throughout the colony site.

For both Black-crowned Night-Herons and Little Egrets, the distance to the nearest neighbor increased as the breeding season progressed. This occurred because colony formation originated from a core area, expanding gradually to adjacent areas, where (especially for Little Egrets) the suitable nesting sites likely were more distant to each other. Information regarding changes in the distance of the nearest neighbor during the breeding season is generally lacking. Distance to the nearest neighbor differs among colonies and species. In mixed-species colonies of Black-crowned Night-Herons in America, this distance varied from 0.95 m to 7.8 m (Burger 1979, Beaver *et al.* 1980), depending mainly on vegetation structure.

The mean clutch size of Black-crowned Night-Herons in the Axios Delta (3.4 eggs) was slightly lower than was observed in the Camargue (3.6 eggs; Hafner 1977, Voisin 1991) and in Italy (3.6 eggs; Prigioni *et al.* 1985) but higher than in Israel (2.8 eggs; Ashkenazi and Yom-Tov 1996). Chick survival per nest was similar to that in the Camargue (2.2-2.5 chicks; Hafner 1977, Voisin 1991) and Italy (2.4 chicks; Prigioni *et al.* 1985). In North America, clutch size of Black-crowned Night-Herons varies from 2.5 to 4.1 eggs and survival from 0.5 to 2.4 chicks per nest (Wolford and Boag 1971, Tremblay and Ellison 1980, Custer *et al.* 1983, Findholt and Trost 1985, Kelly *et al.* 1993) although all latter figures are probably not readily comparable with ours, due to differences in methods used.

The mean clutch size of Little Egrets in the Axios Delta (4.3 eggs) was higher than that found in the Camargue (4.1 eggs; Kazantzidis *et al.* 1996) and in Israel (3.4 eggs; Kashkenazi and Yom-Tov 1996), and similar to that in Spain (4.3-4.6 eggs; Prosper and Hafner 1996) but lower than that at Lake Kerkini, Greece (4.7 eggs; Tsahalidis 1990) or in Japan (4.9 eggs; Inoue 1985). Mean chick survival per nest in the Axios Delta (2.5 chicks) was lower compared to that at Lake Kerkini, Camargue (both 3 chicks) and Spain (3.0-3.8 chicks; Hafner 1977, Tsahalidis 1990, Prosper and Hafner 1996). Clutch size of Little Egrets breeding in Mediterranean wetlands is dependent on the availability of food and body condition of the female at the onset of breeding (Hafner *et al.* 1994, Kazantzidis *et al.* 1996). Chick survival is presumably dependent on the quality of diet, mainly during the peak of their development period (Kazantzidis *et al.* 1996).

All breeding success parameters of each species differed significantly among years, with the exception of Black-crowned Night-Herons number of eggs hatched (Table 4). Such differences are often determined by a variety of factors, such as, weather conditions, shifts in prey and predation (Owen 1960, Quinney 1982, Frederick and Collopy 1989), which should be further investigated in the Axios Delta.

Despite the fact that Little Egrets lay, on average, more eggs than Black-crowned Night-Herons, the mean number of eggs hatched per nest were relatively similar, especially in the third sub-period, denoting a higher egg predation in Little Egrets, particularly at this stage. No interpretation is possible, since in the present study, no data were collected on nest attendance or antipredator behavior. In the Camargue, losses during the egg stage differed significantly between the species (where Little Egrets suffered higher egg predation). In contrast to the Axios Delta, no difference between species was observed in chick losses (Hafner 1977).

A gradual decline in clutch size during the breeding season was observed in Little Egrets only. In ardeids and other wading birds, clutches laid later in the season are usually smaller than clutches laid earlier (Jenni 1969, Hafner 1977, Pratt and Winkler 1985, Rodgers 1987, Ranglack *et al.* 1991). No specific pattern in the variation of chick survival per nest of both species among the sub-periods was found. However, in other studies, chick survival varied considerably, being lower in late nesters of some colonies, or differed in the same colonies among years and different species (McNiel and Leger 1987, Rodgers 1987, Ranglack *et al.* 1991).

We expected to find stronger relationships between chick survival and nest placement. Several authors found that nest site selection affects breeding success: Ranglack *et al.* (1991) found that nests of Cattle Egrets which were placed higher had higher hatching success and chick survival than those placed lower. In the Camargue, peripheral nests constructed later in the breeding season (corresponding to the third sub-period of the present study), had lower success than those in the center (Hafner 1980). In other studies, nest site selection varied depending on the height of nesting trees, availability of suitable nesting sites (vegetation structure), and the timing of nest building (McCrimmon 1978, Beaver *et al.* 1980, Hafner 1980, Burger 1985, Arendt and Arendt 1988, Baxter 1994). Nest height and timing of breeding also affect breeding success in Blackbirds (*Turdus merula;* Ludvig *et al.* 1995). On the other hand, Ranglack *et al.* (1991) found that clutch size in Cattle Egrets was not correlated with nest height, while Baxter (1994) did not find relationships between fledging success and tree height or tree species in 4 heron species.

In summary, nest placement did not affect chick survival in Black-crowned Night-Herons and only marginally in Little Egrets.

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