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Nest Survival in a Large Ibis-Heron Colony During a Three-year Decline to Extinction

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Abstract.—I studied nest survival of seven species of Ciconiiformes on a dredge-spoil island in South Carolina, USA. In 1984, about 24,450 pairs nested in the colony. By 1986, only 3,682 pairs remained, and the site was abandoned in 1987. White Ibis (*Eudocimus albus*) numbers declined rapidly, while heron populations were stable, or decreased slightly. In 1985 the total nest success (percentage of nests producing climb-out young) of herons (47%) did not differ from that reported from other mixed-species colonies in the Southeast. In 1986, the nest success of most species was lower than that reported for any other viable colony. Nest survival of White Ibises was significantly lower than that of most of the heron species throughout the three years, and in 1986, ibises produced no fledglings, while total nest success for all heron species was 18%. Most nest mortality was caused by Fish Crows (*Corvus ossifragus*) and large mammals. Interspecific differences in nest survival were correlated with differences in nest heights and nest stability, characteristics that probably reflect ease of access to predators. In most White Ibis-heron colonies, ibises have lower success than herons. Other than the higher mortality of White Ibis nests from drought and flooding, their low survival, compared to heron nests in the same colony, may be explained in part by different susceptibility to predation. Although most species were subjected to intense predation for two years, they did not abandon the colony immediately, and the lack of response of these populations appears to be related to (1) site tenacity of more successful, nuclear species and (2) the limited opportunities for information exchange in a large colony dispersed through a dense canopy. *Received 14 December 1988, accepted 16 September 1989.*

Key words.—Black-crowned Night-Heron, Cattle Egret, diet, dredge-spoil, drought, Fish Crow, Great Egret, habitat selection, Little Blue Heron, nest-site selection, nest survival, predation, Snowy Egret, Tricolored Heron, White Ibis.

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The population dynamics of large ibis-heron colonies are not fully understood, and only a few detailed studies have been made of all species that occupy a single colony (e.g. Weise 1977, 1978). At the same time, suitable sites for large colonies, particularly in urbanized areas of the coast, are becoming rare (Erwin 1980). As wading birds may be regarded as indicators of the health of estuaries (Custer and Osborn 1977), it is important to understand the habitat requirements of their breeding populations (Burger 1978, McCrimmon 1978, Beaver *et al.* 1980, Custer *et al.* 1980).

Drum Island, in Charleston Harbor, South Carolina, was once the largest mixed-species wading bird colony on the Atlantic coast (Osborn and Custer 1978). The site was created when dredge-spoil was put on a marsh island in 1946. Herons began nesting there by 1948. Although a large body of data exists on the habitat use of dredge-spoil islands in early succession (Mendoza and Ortiz 1974, Buckley 1978, Lewis and Lewis 1978, Schreiber and Schreiber 1978, Parnell *et al.* 1978, Soots and Landin 1978, Parnell and Soots 1979, Parnell and McCrimmon 1984, Parnell *et al.* 1986), little information is available on wading birds occupying these sites in late succession.

Up to 1984, only one study (Custer and Osborn 1977) provided information on the reproductive biology of wading birds nesting on Drum Island. Because of urbanization taking place in the vicinity, I began to study the population size, reproductive success, mortality factors, diets and habitat-use patterns of all species breeding on the island.

STUDY AREA AND METHODS

Drum Island is 76 ha, roughly elliptical, and 275 m from the mainland. The island is composed of three cells, each divided by a 2-3 m high dike. The northern part of the island (10.3 ha) is wooded, the central section (56.1 ha) is bare and the southern section (9.1 ha), separated from the central area by two highway bridges, is the site of the nesting colony. It is covered ≥ 95% by an even-age, closed-canopy stand of white mulberry (*Morus alba*), averaging 8.0 ± 2.1 (SD) m high. No significant understory is present.

On 26 May 1984 I estimated population size by counting all nests that contained young or eggs, and which were in a N-S strip, 395 m x 6 m (0.24 ha) along the length of the nesting colony. The nests of Great Egret (*Casmerodius albus*), Tricolored Heron (*Egretta tricolor*), Black-crowned Night-Heron (*Nycticorax nyctricorax*), Yellow-crowned Night-Heron (*Nyctanassa violacea*) and White Ibis (*Eudocimus albus*) were marked with numbered plastic flagging. To study reproductive success, I checked nests at least once per week during 11 April - 18 June. Contents of high nests were examined by a mirror attached to a pole.

During February and March 1985 I marked a 9 ha area with 1 m-high stakes in a 25 x 25 m grid, and gave each grid intersection an alpha-numeric designation. Beginning in late March of both 1985 and 1986, the site was visited at least twice per week, until all nesting was over. The 1985 and 1986 census plots (98 and 115 respectively) consisted of circles (100 m^2) surrounding randomly-chosen grid intersections. Total colony size was estimated by extrapolation from density per unit area to the total area occupied by the colony. The censuses were conducted during the estimated peaks of nesting activity, when all species had either young or eggs (27 May - 3 June 1985, 4 June - 11 June 1986).

To study nest success, 2-3 individuals worked together on randomly-chosen, alternating grid lines to minimize disturbance to local areas. A 100 m^2 plot was established around each intersection and all nests were marked. In 1985, 36 such plots were established, and in 1986, 25. We used the same procedures for nest marking and examination that we used in 1984, except that all species were identified whenever possible. Nest content data were entered on a nest survival worksheet (Mayfield 1961). From this I calculated the time period that nest contents were exposed to risk, and used the modified (Johnson 1979) Mayfield (1961, 1975) method to calculate reproductive success. Success estimates are based on the survival of the nest (nest success of Mayfield 1975). I estimated survival through the time that nestlings started to climb out of the nest, and did not use nests whose fates were unknown. Young that had left the nest could usually be associated with specific nests. The Z-statistic (Hensler and Nichols 1981) was used to test for differences between nest survival estimates of two groups; the Bonferroni method was used for multiple comparisons (Miller 1966). I used the following day intervals for the period that eggs or young were in the nest: Great Egret, 24 and 26; Snowy Egret, 23 and 24; Little Blue Heron, 23 and 21; Tricolored Heron, 24 and 24; Cattle Egret, 24 and 27; Black-crowned Night-Heron, 24 and 21; White Ibis, 21 and 21.

During the egg stage, nests of three species, the Little Blue Heron (*Egretta caerulea*), Tricolored Heron and Snowy Egret (*Egretta thula*), are difficult to separate from each other. In order to reduce the bias that might result from excluding many nests that were found during the egg stage, I created a pool of nests that belonged to one of these three species, but that could not be further identified. Nests were randomly assigned to each of the three species, in proportion to the numerical representation of each species. Therefore, estimates of nest survival for these species during the egg stage were based on a combined set of randomly-drawn nests, and nests whose identity was known.

To determine if frequency of visitation affected nest success, I established five reproductive success study plots that were visited only once per fortnight, and compared nest success (percentage of nests that produced climb-out young) of the infrequently-visited plots with that of five plots randomly chosen from the pool of 25 weekly-visited plots. In August 1985 five structural characteristics of all nests ($N = 273$) on 23 of the 36 reproductive success study plots were measured. Characteristics were: (1) nest height, (2) height of nest tree, (3) tree diameter at 1 m above ground, (4) distance from center of nest to center of support tree, (5) vertical deflection distance when a 1200 g weight was attached under the center of the nest (Beaver *et al.* 1980). Structural characteristics of 58 plots (100 m^2) were also measured, including number of trees, height of tallest tree, diameter at 1 m of largest tree, and distance of plot from edge of colony.

Food samples (regurgitations) were taken opportunistically. Food was fixed in 10% formalin, and stored in 50% isopropyl alcohol. Most intact food items were identified to either species or genus. Prey items were classified as inhabitants of either saltwater or freshwater sites, based on specimen data in the Charleston Museum, or on published information.

RESULTS

History of the Colony

Drum Island was first reported as a colony site for Snowy Egrets in 1948 (Sprunt and Chamberlain 1949). Allen (*pers. comm.* in Teal 1965) stated that Drum Island had 4 pairs of White Ibises in 1958, and that the population increased to about 3,000 pairs in 1959. Cutts (1959) estimated numbers of pairs in the north cell in 1958 as: White Ibis, 6,000 - 7,000; Great Egret, 450; Little Blue Heron, 200; Snowy Egret, 400; Tricolored Heron, 400; Black-crowned Night-Heron, 100; Yellow-crowned Night-Heron, 15; Glossy Ibis, 100. Beckett (1964) estimated that 100-150 pairs of Black-crowned Night-Herons and 3,000-4,000 pairs of White Ibises nested in 1964. Finally, Osborn and Custer (1978) estimated that 20,000 pairs of White Ibises and 4,400 pairs of herons nested on the island in 1975. Indirect evidence (Ogden 1978) suggests that the White Ibises began to abandon the colony site in 1975. In 1976, the north cell colony had 2,750 pairs of White Ibis (Osborn and Custer 1978). In 1976, the remaining populations apparently began to shift to the south cell of the island.

Population Sizes

In 1984, I estimated that 18,485 pairs

of ibises and herons nested in the south cell. The total number decreased to 4,847 in 1985, to 3,682 in 1986, and finally, all species abandoned the island in 1987 (Table 1). White Ibises showed a continuous decline throughout the 3-year period. Their mean nest density on 115, 100 m^2 plots in 1985 was 1.07 ± 1.96 (SD), while the comparable figure for 98 plots in 1986 was 0.50 ± 1.30, a significant reduction in density ($t = 2.45$; $p < 0.05$). Most heron populations remained the same between 1984 and 1986. Great Egrets declined from about 797 nests in 1984, to 411 in 1986 (Table 1). Other than the White Ibis, this was the only species that had a significant decline in nest densities during 1985 - 1986. The mean nest density of Great Egrets in 1985 was 0.88 ± 1.12, versus 0.53 ± 1.10 in 1986 ($t = 2.27$; $P < 0.05$).

Nest Survival

The success of 48 nests on five plots visited weekly was 16.7%, while the success of 87 nests visited bi-weekly was 21.8%, a non-significant difference ($\chi^2 = 0.52$, 1 df, $P > 0.5$). These results suggest that the frequency of nest checks did not differentially affect the nest success of birds on the study plots.

White Ibis nest success fell rapidly over the 3-year period, and the Cattle Egret appears to have had a similar pattern of decline (Table 2). The decline in success of the other herons seemed to be more gradual, especially for the two largest species, the Great Egret and Black-crowned Night-Heron. The smaller Tricolored Heron did not fit this pattern, in that its success rate did not fall as rapidly as other herons of its size range. An estimated 26% (37.7% X 68.8%; Table 2) of 238 White Ibis nests produced at least one young in 1984. This value fell to 1% of 166 nests in 1985 and to zero in 1986. In comparison, most species of herons had significantly higher success than the ibises throughout the 3-year period (Table 2).

Nest survival rates during the egg stage fell for all species from 1984 to 1985. Only Great Egrets and White Ibises had reduced success during the nestling stage of 1985. Except for Snowy Egret nests during the nestling stage, nest success for all species of herons was reduced from 1985 to 1986 during all stages (Table 2). In 1986, Black-crowned Night-Herons had nest survivorship of about 18%, the highest in the colony. Great Egrets had a nest survival rate of 11%, whereas the success rate of all other species was below 10%. Because of high nest mortality in 1986, few interspecific differences are evident, except that all species had higher success than White Ibises and Cattle egrets, neither of which produced climb-out young.

Table 1. Population estimates of Ciconiiformes on Drum Island, South Carolina, USA, 1975; 1984-1986.

	Total number of nests (nests / 100m² [x̄ ± S.D.])			
Species	1975[1]	1984[2]	1985[3]	1986[4]
Great Egret	300	797	781 (0.88 ± 1.12)	411 (0.53 ± 1.10)
Tricolored Heron	1,500	720	932 (1.06 ± 1.29)	759 (0.98 ± 1.29)
Black-crowned Night-heron	100	683	524 (0.59 ± 1.07)	589 (0.77 ± 1.39)
Yellow-crowned Night-heron	—	76	27	31
White Ibis	20,000	13,763	950 (1.07 ± 1.96)	387 (0.50 ± 1.30)
Glossy Ibis	50	—	0	23
Small herons[5]	2,500	2,209	1,633 (3.48 ± 6.43)	1,482 (1.92 ± 2.97)
TOTAL	24,450	18,485	4,847	3,682

[1]Censused 23 May 1975 (Osborn and Custer 1978).
[2]Censused 26 May. Total population size based on extrapolation of densities on one transect, 2,370 m^2. The colony occupied 9.49 ha.
[3]Censused 27 May - 3 June. Population size estimates are based on extrapolations from densities on 115, 100 m^2 plots.
[4]Censused 4-11 June. Population size estimates are based on extrapolations from densities on 98, 100 m^2 plots.
[5]Small herons are Snowy Egret, Little Blue Heron and Cattle Egret.

Table 2. Nest survival rates, expressed as percentages, Drum Island, South Carolina, USA 1984-1986.

Species (No. of nests in each year	1984		1985		1986	
	$\hat{S}e$[1]	$\hat{S}n$[2]	$\hat{S}e$	$\hat{S}n$	$\hat{S}e$	$\hat{S}n$
Great Egret (8, 42, 51)	100.0	100.0	74.2 ± 7.4[6]	95.4 ± 4.5	27.0 ± 6.3[6]	41.4 ± 4.7
Snowy Egret (67, 38)	—	—	83.1 ± 5.4	50.4 ± 7.7[4]	24.7 ± 7.4[6]	38.0 ± 13.9
Little Blue Heron (16)	—	—	78.5 ± 9.7	67.2 ± 12.6	—	—
Tricolored Heron (14, 70, 94)	90.4 ± 9.1	80.5 ± 12.4	69.8 ± 5.9	80.8 ± 6.1	31.7 ± 4.9[6]	45.9 ± 8.7
Cattle Egret (35, 20)	—	—	86.0 ± 6.5	25.3 ± 8.7[5]	29.3 ± 9.3[6]	0
Black-crowned Night-Heron (7, 34, 47)	100.0	86.5 ± 12.6	75.6 ± 8.6	85.5 ± 6.7	51.2 ± 7.7[7]	35.1 ± 8.9
White Ibis (238, 166, 37)	37.7 ± 3.4[3]	68.8 ± 4.8[4]	24.6 ± 3.4[3]	5.4 ± 2.1[4]	1.7 ± 1.6[3,6]	0

[1]Estimated nest survival probability during egg period. See methods for duration of periods.
[2]Estimated nest survival probability during nestling period.
[3]Significantly lower than other species in that year. For paired comparisons, Z-statistic used (Hensler and Nichols 1981). For multiple comparisons, Bonferroni method used (Miller 1966). $P < 0.05$ in this and subsequent tests.
[4]Significantly lower than all species except Great Egret and Black-crowned Night-Heron.
[5]Significantly lower than all species except White Ibis and Little Blue Heron.
[6]Significantly lower than in previous years.
[7]Significantly lower than in 1984.

Comparisons with Other Colonies

The average, across-species nesting success of herons on Drum Island in both 1984 and 1985 was comparable to figures reported from other mixed-species colonies in southeastern North America (Table 3). Nest success during the nestling stage for three heron species on Drum Island in 1984 averaged 54.8%, which exceeded that for Sapelo Island, but was about the same as Green Island. However, in 1985, the average success of six heron species on Drum Island (47.0%) was near that reported from Sapelo Island and Green Island.

Pea Patch Island had about the same total nest success in 1975 as Drum Island in 1985. In 1977, a drought year in Delaware, average success fell to 29.2%. Large mammals were not present, and the low success during all three years was attributed to avian predation, starvation, and endoparasites. The status of this colony, which was also one of the few urban colonies in North America, has not been reported since Wiese's (1978) study.

White Ibises generally have lower success than herons in mixed-species colonies, and this relationship held for Drum Island in 1984. However, in 1985 and 1986, success of White Ibis was the lowest reported for any viable colony. In contrast, ibises on Green Island (72 km inland) had a total success of 45.8% in 1985.

Food Brought to Young

Regurgiated prey was classified according to whether it occured in freshwater or salt water habitats (Table 4). Little Blue Herons concentrated on amphibians (mainly *Rana*) and on two genera of crustacea (*Palaemonetes* and *Alpheus*). About 31% of the Little Blue Heron's diet consisted of prey taken outside freshwater sites. In contrast to the Little Blue Heron, Tricolored Herons and Snowy Egrets fed mainly in saltwater sites. Over 50% of the items recovered from the Tricolored Herons were top minnows (*Fundulus* spp.) Snowy Egrets took mainly saltwater fish, but they took a greater proportion of grass shrimp (*Palaemonetes*) than Tricolored Herons. Cattle Egrets specialized on Orthoptera. I also recovered amphibians (mainly *Bufo*) and rodents (*Rattus* and *Mus*). Cattle Egrets nesting on Drum Island frequently foraged in a garbage dump that was 1 km from the colony. Several samples contained chicken bones and rubber bands, probably taken from the dump.

The White Ibis diet contained about 82% crustacea. Of these, 62% were mainly saltwater genera (*Uca, Sesarma, Palaemonetes*), and 20% freshwater (crayfish, Astacidae). *Uca* made up the bulk of the White Ibises's diet. They also took a number of insects, mainly beetle larvae.

All species except the Cattle Egret used saltwater foraging sites more frequently

Table 3. Reproductive success of herons and ibises in mixed-species colonies in southern North America.

	Nesting success[1] of:	
Study site	Herons	White Ibises
Pea Patch Island, Del., 1975 (Wiese 1978)	39.6	–
Pea Patch Island, 1976 (Wiese 1978)	35.2	–
Pea Patch Island, 1977 (Wiese 1978)	29.2	–
Drum Island, 1984	54.8	39.2
Drum Island, 1985	47.0	2.9
Drum Island, 1986	18.0	0
Green Island, S.C., 1985 (unpubl. data)	51.6	45.8
Sapelo Island, Georgia (Teal 1965)	43.0	27.7
Lake Alice, Florida (Jenni 1969)	67.3	–
Riomar Island, Florida (Maxwell and Kale 1977)	74.2	–
Sunken Island, Florida (Rodgers 1980, 1987a)	65.3	–
Barataria Bay, Louisiana (Hammatt 1976)	48.9	10.1

[1]Success estimates are for individual nest contents, and are not corrected for exposure. Success is for the period until young climb out of the nest, except for Lake Alice and Sunken island, for which success is calculated through 14 days, and Riomar Island, for which success is calculated through 10 days.

Table 4. Composition of food brought to nestling Ciconiiformes in 1985 on Drum Island, South Carolina, USA.

Species (N)[2]	Arthropoda & misc.[3]	Crustacea FW	Crustacea SW	Fish FW	Fish SW	Amphibia	Terrestrial vertebrates
	Per cent composition (by number) of prey group[1]						
Great Egret (55)	2.1	0	24.7	0	73.4	0	0
Snowy Egret (45)	0.3	0	35.1	4.1	60.1	0	0
Little Blue Heron (24)	13.6	0.3	51.5	1.5	17.2	15.8	0.1
Tricolored Heron (90)	0.5	0	19.3	9.7	76.7	0	0
Cattle Egret (37)	85.3	0	0	0	0	13.2	1.5
Black-crowned Night-heron (70)	0	0	14.3	0	83.3	0	2.7
Yellow-crowned Night-heron (17)	0	0	100.0	0	0	0	0
White Ibis (23)	11.8	20.4	62.0	0	4.3	0	0

[1]FW = freshwater; SW = saltwater.
[2]N = number of samples collected from all young in one nest (one sample per day).
[3]Molluscs and annelids.

than freshwater. Among the piscivorus herons, only the Little Blue Heron obtained a significant proportion of its food away from saltwater, and this was mainly amphibians and arthropods. Tricolored Herons and Snowy Egrets took about 10% and 5%, respectively, of their food in freshwater sites, and for both species, the freshwater component was composed of fish.

Nest Site Selection

Great Egrets and Black-crowned Night-Herons nested significantly higher than the smaller species (Table 5). Black-crowned Night-Herons nested significantly lower than the Great Egrets. White Ibises differed from the other species in using lower trees for nesting. Cattle Egrets also tended to nest lower, but overlapped slightly with Little Blue Herons and Tricolored Herons. This pattern of vertical stratification agrees with that reported from other colonies (Maxwell and Kale 1977, Jenni 1969, Burger 1978).

Horizontal differences in nest placement were less pronounced. The three largest herons put their nests closest to the tree centers, whereas the ibises and smaller herons nested farther out. These differences may be expected on the basis of variation in nest sizes alone. Tricolored Herons differed from both Cattle Egrets and White Ibises in placing their nests farther from the tree center. This difference is reflected in the greater deflection of Tricolored Heron nests, which was significantly greater than all species except Snowy Egret and Little Blue Heron (Table 5).

Deflection distances were plotted against nest height to assess accessability to predators. This procedure assumes that nests that are higher in the canopy are more accessible to aerial predators, while lower nests, built in more stable positions, are more easily reached by climbing predators. The seven species formed a continuum from the Tricolored Heron nests relatively low on unstable substrate, to Black-crowned Night-Heron and Great Egret nests relatively high, and in more stable positions (Fig. 1). Nest survival (Table 2) and nest placement data (Table 5) tend to confirm that accessibility to predators influenced success. Among the low-nesting species, Tricolored Herons had the highest survival and the greatest nest deflection distances. White Ibises had the lowest survival rates and the lowest deflection distances. The two high-nesting species had about the same egg survival and deflection distances.

Nearest neighbor distances varied directly with species size (Table 5) and thus perhaps dominance (Burger 1978). The largest species (Great Egret) has the largest

Table 5. Characteristics of nest sites of Ciconiiformes in 1985 on Drum Island, South Carolina, USA.

Species (N)	Nest height (m)	Tree height (m)	Distance to tree center (cm)	Deflection[1] (cm)	Nearest neighbor (m)
	Nest site characteristics ($\bar{x} \pm$ S.D.)				
Great Egret (11)	5.51 ± 1.09[2]	7.55 ± 1.63[4]	27.73 ± 42.28	0	2.16 ± 0.93[7]
Snowy Egret (32)	3.18 ± 0.77	6.63 ± 1.58[4]	42.03 ± 52.23	1.11 ± 1.80	1.35 ± 0.75[8]
Little Blue Heron (10)	2.60 ± 0.46	6.36 ± 0.94	39.90 ± 30.02	0.91 ± 2.05	1.20 ± 0.66
Tricolored Heron (34)	3.27 ± 0.74	6.45 ± 1.54[5]	68.22 ± 60.74[6]	2.56 ± 3.67[6]	1.65 ± 1.00[4]
Cattle Egret (54)	3.04 ± 0.51	5.71 ± 0.58	31.94 ± 32.92	1.58 ± 3.52[5]	0.73 ± 0.03
Black-crowned (20) Night-Heron	4.13 ± 1.14[3]	7.07 ± 1.46[4]	22.68 ± 28.04	0.04 ± 0.13	1.73 ± 0.67[4]
White Ibis (104)	2.95 ± 0.93	5.51 ± 1.09	33.03 ± 44.92	0.35 ± 1.10	1.04 ± 0.69

[1]Vertical distance through which the nest moved when a 1200 g weight was attached under the center of the nest (Beaver *et al.* 1980).
[2]Significantly larger than for all other species (Tukey's test, with $\alpha = 0.05$, used in this and all subsequent comparisons).
[3]Significantly larger than for all species except Great Egret.
[4]Significantly larger than White Ibis and Cattle Egret.
[5]Significantly larger than White Ibis.
[6]Significantly larger than all species except Snowy Egret and Little Blue Heron.
[7]Significantly larger than Cattle Egret, White Ibis and Little Blue Heron.
[8]Significantly larger than Cattle Egret.

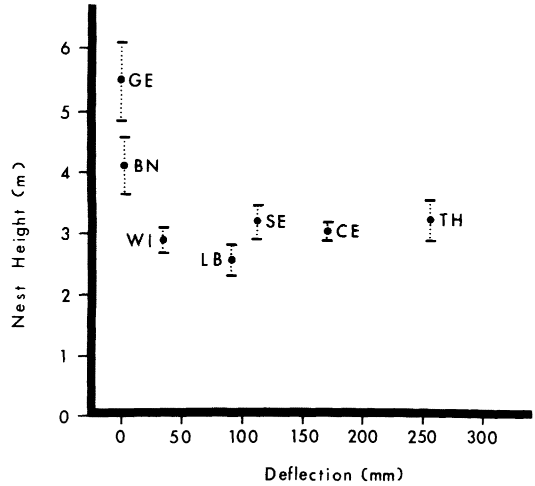

Figure 1. Mean nest heights (± 95% confidence interval) as functions of mean deflection distances of nests. The deflection distance is the vertical distance through which a nest moves when a 1200 g weight is attached under the center of the nest (Beaver *et al.* 1980). BN = Black-crowned Night-Heron; CE = Cattle Egret; GE = Great Egret; LB = Little Blue Heron; SE = Snowy Egret; TH = Tricolored Heron; WI = White Ibis.

internest distance, followed by the Black-crowned Night-Heron. The smallest species, Cattle Egret, had the smallest internest distance. Although White Ibises are intermediate in size, they had about the same average nearest neighbor distance as Cattle Egrets.

To examine the hypothesis that availability of suitable habitat influenced nest dispersion, I tested for a relationship between nest density and four structural characteristics on 58 plots, each 100 m^2. Mean nest density was 7.7 ± 9.4 (SD)/ 100 m^2. Tree height and tree diameter were correlated ($r = 0.82$, $df = 56$, $P < 0.01$). I found no correlation between nest density and any of the independent variables (tree diameter, tree density, or distance to edge of colony) and concluded that nest dispersion in this colony cannot be related directly to the structural characteristics measured.

DISCUSSION

The census totals obtained in 1984 are similar to those that Osborn and Custer (1978) reported in 1975. Although different sites on the island were being used, it is possible that the same populations were involved, and that after the rapid abandonment of the north cell by White Ibises in 1975, herons, and later ibises, began to colonize the south cell. This trend was already apparent in Osborn and Custer's (1978) survey, as they reported an increase in herons in the south cell between 1975 and 1976, and a colonization by ibises in 1976. The 1984 population size and composition suggest that the colony in the south cell was indeed composed of the north cell birds, and that it had been stable during the 9-year period before 1984.

I found that 1) most species aligned themselves vertically in order according to body size, 2) mean species nest height correlated with vegetation height, 3) most species had high horizontal overlap, 4) nearest neighbor distance was directly related to body size, and 5) nest density was not related to vegetation structure. These findings agree with those of Burger (1978), that social interactions are the main organizing force in intracolony nest dispersion. They contrast with those of Beaver *et al.* (1980), who argue that availability of suitable vegetation influences nest dispersion more than social factors. I conclude that in this homogeneous habitat, vegetation features are of secondary importance in determining dispersion.

Custer and Osborn (1977) gave 1975 egg success data for Snowy Egrets and White Ibises of 83% and 25%, respectively. These estimates are identical to the 1985 nest survival estimates for the egg stage of these two species. This correspondence suggests that the conditions of the colony in 1975 and 1985 were the same.

Although the abrupt population decline of White Ibis was evident between 1984 and 1985, the more gradual decline of ibises between 1985 and 1986, and the gradual decline of herons over the whole 3-year period, were not obvious. By analyzing the nest density on the basis of sampling plots, I was able to detect a significant change in Great Egret numbers between 1985 and 1986. However, other than that for the White Ibis, this was the only change which presaged the complete failure of the colony in 1987. Comparing the nest densities of the other five heron species between years did not provide reliable information on the colony's health. The reproductive success of herons on Drum Island in 1984-1985 was similar to other estimates available for southeastern North America. This similarity is despite an abundance of large mammals on the island. Nesting success of White Ibises was consistently lower than reported from other sites. By 1986, reproductive success for all species on the island was lower than that reported from any other viable colony.

In most cases, as I had no direct information on the causes of nest mortality, the cause of loss was inferred from the condition of the nest at the time of failure. In 1984, while Fish Crows (*Corvus ossifragus*) were seen in the colony, no direct predation was seen. In 1985, 3,000 - 4,000 crows used the island as a nocturnal roost, were in the colony in the early morning and late afternoon, and foraged at other times in a garbage dump 1 km from the colony. In 1986 many flocks, of up to 1,000 birds, were in the colony during the day, and punctured eggs were found throughout the study area.

In 1984, I found 1 - 3 partially eaten ibis young on each visit. In 1985, raccoons (*Procyon lotor*), house cats (*Felis cattus*), and opossums (*Didelphis virginiana*) were live-trapped in the area, and in 1986, $\geq$ 10 freshly-killed young and adult wading birds were found on every visit, usually within 100 m^2. In January-February 1987, the South Carolina wildlife department removed 67 raccoons (M. Dodd, *pers. comm.*)

Teal (1965) reported that crows and raccoons caused most mortality on Sapelo Island, which may explain the similarity of the nest survival estimates for Drum and Sapelo Islands. Three Florida colonies, one in the interior at Lake Alice, and the other two on the coast, had higher success than I found on Drum Island. The success estimates for these sites were only for the period through 10 to 14 days, and therefore may be slightly inflated. But if mortality from starvation or from mammals is not heavy, survival to 10 days or two weeks may give a good estimate of fledging success (Kushlan 1977, Shields and Parnell 1986). Therefore, the main difference between Drum Island and the Florida colonies would appear to be the latters' absence of significant predation by mammals.

The results of my study, and limited comparative data from elsewhere, suggest that outside peninsular Florida, nesting success of Ciconiiformes in the Southeast is low. Shields and Parnell (1986) analyzed the productivity of White Ibises in coastal North Carolina, and concluded that though mortality rates were high, productivity was sufficient for population maintenance. However, why is White Ibis reproductive success consistently lower than herons' in most mixed-species colonies?

The low success of White Ibises, in comparison to herons nesting in the same colony, is not unique to this study. The difference between the nest success of herons and ibises on Drum Island in 1985 was 37.8%. In Louisiana, Hammatt (1976) found a difference of 48.9%, and in Georgia, Teal (1965) reported a difference of 14.3%. The low success of ibises in Louisiana was related to flooding, which did not significantly affect herons in the same colony (Hammatt 1976).

The nesting success of White Ibises, Little Blue Herons and Cattle Egrets, who feed away from saltwater sites, should be affected more by drought than that of species who feed mainly in salt water habitats. Rainfall during the 6-month period preceding 1 June 1984 was 42% above normal (30-yr average, 1951-1980), but a prolonged drought began in June 1984, and rainfall in the 6 months preceding 1 June 1985 was 58% below normal. The corresponding figure for 1 June 1986 was 41% below normal. In 1985, but not 1984, I found marked White Ibis nests containing well-grown young, all of which were dead or moribund. This type of whole-nest mortality indicates abandonment (Ricklefs 1969), and it is possible that adult ibises abandoned nests when they were unable to find enough food for young (Bildstein *et al.* 1990).

However, even in the absence of flooding and droughts, White Ibises had lower nesting success than herons in the same colony. If mortality from sources other than predation affect all species in the colony equally, then the lower success of White Ibises may be related to greater susceptibility to predation. Predation rates could be affected by nest attendance pattern, sensitivity to disturbance (Shields and Parnell 1986), and accessibility of nests to predators (Ricklefs 1969, McCrimmon 1978).

The hypothesis that different susceptibility to predation accounts for different survival patterns of heron and Ibises nests is supported by comparing the results of this study with the Green Island study (Table 5). Neither Green Island nor Drum Island had significant mortality from parasites, such as reported from other sites (Wiese 1977, Snyder *et al.* 1984). In 1985, Green Island was in the same drought zone as Drum Island. However, while the discrepancy in breeding success between herons and ibises was 44.1% on Drum Island, it was only 5.8% on Green Island. The main difference between the two sites was in their predator populations: Green Island had no large mammals, and no more than four Fish Crows were seen per visit. On Drum Island the main difference between White Ibis nests and those of herons nesting at the same height was nest stability (deflection), which is a measure of access to climbing predators.

The failure of this colony was related to extensive predation by large mammals and Fish Crows. Vegetative changes that took place over the three years of the study were too gradual to explain the abrupt abandonment of a site that was relatively successful in 1984. Although the low success rate of White Ibises in 1985 may in part be attributable to the drought, heron nesting failure in that year cannot be assigned to that cause. Little Blue Herons obtained a significant proportion of food away from saltwater, but the 1985 nestling survival of Little Blue Herons did not differ from that of herons that fed mainly in saltwater sites. Further, only Great Egrets, but not Tricolored Herons and Black-crowned Night-Herons, had reduced nestling survival between 1984, a non-drought year, and 1985, a drought year.

Colony stability is not affected by predation, as long as levels are low (Teal 1965, Jenni 1969, Burger and Hahn 1977, Shields and Parnell 1986). Conversely, most studies that have documented heavy predation have reported rapid site abandonment (Baker 1940, Cutts 1955, Dusi and Dusi 1968, Taylor and Michael 1971, Bjorklund 1975, Rodgers 1987b). Usually these rapidly abandoned colonies covered a small area, were in relatively low, open vegetation, and had one or a few species of nesting birds. Colonial waterbirds may use interspecific cues to assess site suitability, but the reliability of these cues is probably correlated with potential for spatial and temporal contagion. White Ibises failed to abandon Drum Island despite massive nesting failure in 1984. Further, all heron species had lower reproductive success in 1986 than in 1985, but only Great Egret population density decreased between years. The apparent lack of response of ibises and most herons to high nest mortality suggests that interspecific cues about predation may be ineffective when a large colony is dispersed through a dense habitat. The colony was spread over 9 ha of closed-canopy, homogeneous woodland, and predation on one side of the site may not have been detectable on the other.

In discussing the behavior of Ring-billed Gulls (*Larus delawarensis*) subjected to continuous predation by foxes, Southern *et al.* (1985) suggested that their site persistence was related to the behavior of a nucleus of experienced breeders that continued to return to the site annually. Under these circumstances, site fidelity may have been disadvantageous. As the Drum Island colony had existed for at least 10 years, it is possible that such a nucleus was present there. In the case of Drum Island, it is also possible that the site tenacity of the more successful herons influenced the ibises to continue to return despite their low nesting success.

Coloniality does not necessarily provide protection via swamping of predators (Rodgers 1987b). The swamping effect may not operate with predators like foxes and raccoons, which, once attracted to a colony, may remain until most nests are destroyed (Southern *et al.* 1985). I found many partially-eaten young and adult birds, which implies that predators were engaged in surplus killing (Kruuk 1972). The fact that 67 raccoons were removed from the island in 1987 and that the island probably had a limited food base, other than the bird colony, implies that the raccoons were recruited annually from a wide area (Greenwood 1982).

Dredge-spoil islands are recognized as refugia for colonial waterbirds in disturbed coastal areas (Urner 1926). Their importance was demonstrated in a study comparing habitat use patterns in New

Jersey and Virginia, which showed that in more disturbed coastal areas, colonial waterbird rely more on dredge deposition sites (Erwin 1980). This reliance, however, may lead to an over-concentration of regional populations, which Erwin (1980) considers analagous to the "island dilemma" of Diamond (1975). If a large proportion of the region's wading bird population is located in a few colonies, higher priority should be placed on monitoring the health of these colonies.

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