BREEDING BIOLOGY OF FIVE SPECIES OF HERONS IN COASTAL FLORIDA

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ABSTRACT.—The breeding biology of the Louisiana Heron, Snowy Egret, Cattle Egret, Little Blue Heron, and the Great Egret was studied on Riomar Island, a 2.8-ha mangrove island in Indian River County, Florida from March through May 1973.

The Louisiana Heron and Cattle Egret nests were built increasingly more distant from the shoreline as the breeding season advanced. Nests of the Little Blue Heron were not horizontally stratified and the seasonal differences in siting of the Snowy Egret and Great Egret nests were not significant. The Louisiana Heron nests showed vertical stratification and were built significantly higher as the season advanced. Snowy Egret and Great Egret nests were built at lower elevations in midseason, but later nests were at the same height as the earlier nests. The heights of Cattle Egret and Little Blue Heron nests did not change during the season.

The Louisiana Heron, Snowy Egret, Cattle Egret, and Great Egret completed clutches the last week of March and the first week of April. Little Blue Herons completed their clutches the second and third weeks in April. The Louisiana Heron, Snowy Egret, and Cattle Egret laid eggs on the average at slightly greater than 2-day intervals and the Little Blue Heron and Great Egret at slightly less than 2-day intervals. All five laid replacement clutches when the original clutch was destroyed. Little Blue Heron clutches were significantly larger than Snowy Egret and Great Egret clutches. Louisiana Heron clutches were significantly larger than Great Egret clutches.

Incubation began after the first egg was laid in most Snowy Egret, Cattle Egret, and Great Egret nests and was delayed until after the second egg in Louisiana Heron and Little Blue Heron nests. The time interval between hatching of successive eggs in the clutch increased in all species except the Little Blue Heron, which showed a decrease in interval.

Nests failures were caused mainly by Brown Pelicans, whose clumsy landings at or near their own nests knocked eggs from nearby heron nests or crushed them. Still nesting success of the Riomar herons was better than any reported in the literature. The Little Blue Herons had the highest nest success because of their relative isolation from the other nesting species.—*Rice Creek Biological Field Station, State University College, Oswego, New York 13126*, and *Florida Medical Entomology Laboratory, Vero Beach, Florida. Present address of second author: Division of Ornithological Research, Florida Audubon Society, 35 1st Court, S.W., Vero Beach, Florida 32960.*
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INTEREST in the Ardeidae has increased in recent years due, in part, to their wetland habits that make them good indicator species of man's disturbances of these habitats. Some species appear to be declining in parts of their range; others are increasing in numbers (Lowe-McConnell 1967, Belknap 1968, Maxwell and Putnam 1968, Crosby 1972, Tate 1972). The reasons for varying success among the ardeids are often unexplained and will remain so until sufficient data on breeding requirements in different habitats are available.

This study provides data on the breeding biology of the Louisiana Heron (*Hydranassa tricolor*), Snowy Egret (*Egretta thula*), Cattle Egret (*Bubulcus ibis*), Little Blue Heron (*Florida caerulea*), and the Great Egret (*Casmerodius albus*) nesting on a mangrove spoil island in the Indian River at Vero Beach, Florida (27°38′N, 80°22′W). Spoil islands are created in the Intracoastal Waterway by dredging and pumping the spoil into piles outside the channel. Vegetation soon develops on them and provides nesting substrate for birds. Spoil islands have provided new nesting grounds for ardeids along coastal Florida. Reports in the literature on vertical and horizontal stratification of nest sites in these species are limited (Meanley 1955, Ralph and Ralph 1958, Bowen et al. 1962, Blaker 1969, Pratt 1970). Jenni (1969) summarized and presented quantitative data on vertical stratification of the Snowy Egret, Cattle Egret, Little Blue Heron, and Louisiana Heron in the inland Lake Alice, Florida heronry. This paper presents similar data for a coastal heronry.

DESCRIPTION OF THE STUDY AREA

Vero Beach, Indian River County, Florida, is on the Atlantic Coastal Plain about midway along the Florida peninsula. The Indian River, actually a tidal bay or lagoon, runs parallel to the coast and separates a barrier beach from the mainland. Observations were made on Riomar Island (sometimes called Crane Island), a 2.8-ha island 1.6 km south of the Merrill Barber Bridge, which crosses the Indian River at Vero Beach. This island contains one of the largest concentrations of herons and pelicans in the Indian River between the Sebastian and Fort Pierce Inlets.

Riomar Island has been undergoing uninterrupted vegetational development since the last dredging of the waterway in the late 1950's. The dominant canopy species, determined by quadrat analysis by Maxwell and Kale (1974) and listed in decreasing order of abundance with relative density (Curtis and Cottam 1969) are as follows: black mangrove (*Avicennia nitida*) 35%, white mangrove (*Laguncularia racemosa*) 28%, Australian pine (*Casuarina equisetifolia*) 18%, Florida privet (*Forestiera porulosa*) 10%, red mangrove (*Rhizophora mangle*) 7%, button mangrove (*Conocarpus erecta*) 1%, and Brazilian pepper (*Schinus terebinthifolius*) 1%.

The quantitative data on the breeding biology of the herons were collected on the south and west portions of the island. These tracts consist of thick growths of black and white mangrove and, along the waters edge, red mangrove. The northern portion of the island is similar, but Australian pine is scattered in clearings in the mangrove. The east portion is a pure stand of Australian pine fringed with small black mangroves along the shore. An open sandy space in the center of the island supports an herbaceous layer.

Nest sites for all species of birds were fairly evenly distributed in the mangroves, with few nests in the eastern portion and none in the center clearing. An approximate total of 2,657 breeding pairs of 13 species nested on Riomar Island in the spring of 1973. The ardeids and their relative abundance (%) included: Louisiana Heron 37.1, Snowy Egret 29.5, Cattle Egret 12.7, Great Egret 3.9, Little Blue Heron 2.7, Black-crowned Night Heron (*Nycticorax nycticorax*) 0.2, Yellow-crowned Night Heron (*Nyctanassa violacea*) 0.1, Great Blue Heron (*Ardea herodias*) 0.1, and Green Heron (*Butorides virescens*) 0.1. One other ciconiiform, the White Ibis (*Eudocimus albus*) 0.9, also nested on Riomar. Pelecaniforms nesting were Brown Pelican (*Pelecanus occidentalis*) 11.1, Double-crested Cormorant (*Phalocrocorax auritus*) 1.5, and Anhinga (*Anhinga anhinga*) 0.1 (Maxwell and Kale 1974).

METHODS

Studies were made inside the heronry from 13 March through 22 May 1973 for a total of 290 h. During 27 March–13 April, 279 nests were tagged and the fate of the eggs was followed to hatching and the young to day 10, when they left the nest and could no longer be identified with their particular nest. A mirror on a pole was used to check nest contents. Nests were checked daily and all changes were recorded. Nest heights were measured with a meter stick and distance of each nest from shore was estimated by pacing. Binoculars, spotting telescope, and telephotography were used during longer periods of observation from a blind in the clear center of the island. Positive identification of many nests was difficult until the nestlings were 4 to 5 days old, especially Snowy Egret and Cattle Egret nests. Therefore many nests that were destroyed before the nestlings were old enough for identification were not identified. Data were accumulated on 221 marked and identified nests, including 79 Louisiana Heron nests, 77 Snowy Egret nests, 31

TABLE 1

STRATIFICATION OF HERON NEST SITES ON RIOMAR ISLAND, INDIAN RIVER COUNTY, FLORIDA

Species	Date hatching week	N	Distance from shoreline Mean ± SE (range)	Height above ground Mean ± SE (range)
Louisiana Heron	13–20 April	34	4.0 ± 0.64 (0–16.8 m)	2.1 ± 0.06 (1.2–2.7 m)
	21–28 April	32	11.6 ± 1.50 (0–21.3 m)	2.2 ± 0.07 (1.2–3.1 m)
	29 April–16 May	11	11.8 ± 3.00 (0–21.3 m)	2.4 ± 0.14 (1.8–3.4 m)
	Total	77	8.3 ± 0.91 (0–21.3 m)	2.2 ± 0.04 (1.2–3.4 m)
Snowy Egret	16–23 April	45	7.8 ± 0.87 (0–21.3 m)	2.4 ± 0.04 (1.5–3.1 m)
	24 April–1 May	16	7.4 ± 1.75 (0–27.4 m)	2.2 ± 0.06 (1.8–2.7 m)
	2–21 May	10	9.6 ± 1.85 (3.1–21.3 m)	2.4 ± 0.12 (1.8–3.1 m)
	Total	71	8.0 ± 0.71 (0–27.4 m)	2.3 ± 0.03 (1.5–3.1 m)
Cattle Egret	16–23 April	15	3.7 ± 0.28 (1.8–6.1 m)	2.2 ± 0.06 (1.8–2.4 m)
	24 April–1 May	7	7.4 ± 2.45 (3.1–18.3 m)	2.2 ± 0.12 (1.8–2.7 m)
	2–14 May	5	4.6 ± 1.33 (1.8–9.1 m)	2.3 ± 0.12 (2.1–2.7 m)
	Total	27	4.8 ± 0.72 (1.8–18.3 m)	2.2 ± 0.05 (1.8–2.7 m)
Little Blue Heron	30 April–7 May	9	21.3 ± 0.00 (21.3 m only)	2.5 ± 0.18 (1.8–3.4 m)
	8–15 May	12	20.8 ± 0.34 (18.3–21.3 m)	2.7 ± 0.13 (1.8–3.4 m)
	Total	21	21.0 ± 0.20 (18.3–21.3 m)	2.6 ± 0.11 (1.8–3.4 m)
Great Egret	17–24 April	7	8.5 ± 1.75 (4.6–18.3 m)	2.8 ± 0.06 (2.7–3.1 m)
	25 April–2 May	3	8.5 ± 3.39 (4.3–15.2 m)	2.5 ± 0.10 (2.4–2.7 m)
	3–14 May	2	5.3 ± 2.29 (3.1–7.6 m)	3.1 ± 0.00 (3.1 m only)
	Total	12	8.0 ± 1.30 (3.1–18.3 m)	2.8 ± 0.06 (2.4–3.1 m)

Cattle Egret nests, 21 Little Blue Heron nests, and 13 Great Egret nests. Means are presented ± Standard Error of the mean and the t-test was used to compare two means and a paired t-test when more than two samples (Downie and Heath 1970). The level of significance was 0.05, unless otherwise noted.

RESULTS AND DISCUSSION

On Riomar Island a rectangular area 120 m by 60 m (0.72 ha) contained 1,352 active nests. These included 279 marked and 917 unmarked nests of five heron species under study plus 153 Brown Pelican and three Black-crowned Night Heron nests. This density is equivalent to 1,731 nests per hectare (700/acre).

Nest sites.—In order to determine the extent of intra- and interspecific differences in mean nest height (vertical stratification) and mean distance of the nest from the shore (horizontal stratification), data were collected during the 1st week of hatching, 2nd week of hatching, and 3rd and 4th (combined) weeks of hatching. The 1st-week interval includes those nests in which the last egg hatched during the first 7 days of hatching for each species, the second week includes nests in which the last egg hatched during 8 to 14 days after the first nests hatched of each species, etc. The hatching week dates vary for each species, reflecting variation in onset of breeding (Table 1).

The Louisiana Heron sited its nests increasingly more distant from the shore as the breeding season advanced. The mean distance from nest to shoreline for nests completing hatching between 13–20 April was significantly different (paired t-tests) from the mean distance of nests hatching between 21–28 April (t = 4.8) and 29 April–16 May (t = 3.9). Nests of the Cattle Egret that completed hatching during the second hatching week (24 April–1 May) also were significantly more distant from the shoreline (t = 2.2) than were nests that hatched a week earlier, but later nests (2–14 May) were closer to the shoreline, similar to the earlier nests. This shift by the Cattle Egret back to its site of first nesting and the failure of the Louisiana Heron also to make this shift may indicate that the Cattle Egret, whose breeding numbers in the colony increased daily until they reached a peak in June and July, was out-competing the Louisiana Heron for these more preferred sites.

Nests of the Snowy Egret, Great Egret, and Little Blue Heron exhibited no significant horizontal stratification. Nests of the Snowy Egret that completed hatching during 12–21 May appeared somewhat more distant from the shoreline than earlier nests, but the differences were not significant. Too few Great Egret nests were followed to permit comparisons. The Little Blue Heron was consistent in the siting of its nests from the shoreline. All nine nests hatching between 30 April and 7 May were exactly 21.3 m from it, and the mean distance of later hatching nests was 20.8 m (see Table 1).

Extent of change in vertical stratification differed among species as the season progressed. Louisiana Herons and Cattle Egrets generally nested lower than the other three species. The mean elevation of Louisiana Heron nests that completed hatching the first 2 weeks (13–28 April) was significantly lower ($t = 2.5$) than the mean elevation of nests hatching during 29 April–16 May. Jenni (1969) noted that the Louisiana Heron built the lowest nests in the Lake Alice colony.

Mean elevation significantly decreased ($t = 2.3$) in Snowy Egret nests that hatched 24 April–1 May compared to the means of nests that completed hatching the previous week and the following 2 weeks, but the differences between the means amounted to only 0.2 m, hence we attach no biological significance to it.

A similar pattern is shown by the Great Egret, although the reliability of the data may be questioned because of the few nests observed. Nests showed a significant ($t = 2.8$) decrease in mean elevation between the 1st and 2nd week and then an increase to a higher elevation the 3rd and 4th week ($t = 3.9$). The Great Egret is a considerably larger bird than the other four species, and it invariably nested near or on the top of the vegetation.

Cattle Egrets and Little Blue Herons did not change nest site elevations during the period of this study (March–May). Jenni (1969) found a significant increase in average nest height of Little Blues at Lake Alice, from 2.04 m for nests with clutches completed before April 28, to 2.59 m for nests with clutches completed between 10–30 June. The termination of our study at the end of May precluded observation of any such change on Riomar (see Table 1).

Louisiana Herons built 65% of their nests in black mangrove, 28% in white mangrove, and 7% in red mangrove. The Snowy Egret built 78% of their nests in black mangrove, the remainder in white mangrove and the Cattle Egrets built 81% in black mangrove, and 19% in white mangrove. Little Blue Herons nested exclusively in black mangrove at the fringes of the mixed heron colony and the Great Egrets placed 77% of their nests in black mangrove and 23% in white mangrove.

The Louisiana Heron, with the largest breeding population early in the season, appeared to be under the greatest pressure from competition as it showed significant changes in horizontal and vertical nest stratification during the nest site selection period. In contrast the Little Blue Heron, with a rather small nesting population, continued to nest in the same sites as at the start of their season. It generally nested apart from the other herons and may perhaps be less tolerant of competition. During interspecific encounters, both in their nesting sites and elsewhere on the island, they were invaribly subordinate to other species of herons. The Cattle Egret nested farther from shore as the season progressed, but it was able to find nest sites at a relatively constant height during the entire season. As its numbers increase it may also show vertical nest site stratification. The Cattle Egret has been able to nest in

TABLE 2
NUMBER AND PERCENT OF NESTS[1] WITH FULL CLUTCHES COMPLETED DURING 2-WEEK PERIODS ON RIOMAR ISLAND

	Louisiana Heron		Snowy Egret		Cattle Egret		Little Blue Heron		Great Egret	
	N	%	N	%	N	%	N	%	N	%
22 March–6 April	69	87	60	78	24	77	0	0	11	85
7–22 April	9	11	10	13	6	19	18	86	2	15
23 April–8 May	1	2	7	9	1	4	3	14	0	0
Total nests	79		77		31		21		13	

[1] Data from nests marked during period 27 March–13 April.

heronries with varying physical and biological characteristics in North and South America where it has been spreading in recent years. On the Guyana coast it has been taking over long-established heronries from indigenous herons (Lowe-McConnell 1967). It shares its feeding niche with few or no other competitors and is not dependent upon wetlands for survival; but we believe it exerts nest site competition with native herons. This undoubtedly has caused changes in relative numbers of herons nesting in established colonies with Cattle Egrets.

Egg laying.—Dates of clutch completion were determined in nests marked during the first 18 days (27 March–13 April) of the study period. The majority of Louisiana Heron, Snowy Egret, Cattle Egret, and Great Egret nests contained clutches by the last week of March or the first week of April, but nests of the Little Blue Heron did not contain their full complement until the second and third week in April (Table 2). At Lake Alice the peak of clutch completion for the Louisiana Heron and the Little Blue Heron occurred in the first 2 weeks of April; for the Snowy Egret it occurred in late April and for the Cattle Egret in early May (Jenni 1969).

Average time interval between eggs for the Louisiana Heron, Snowy Egret, and Cattle Egret was slightly greater than 2 days and for the Little Blue Heron and Great Egret the interval was slightly less than 2 days. In contrast, Jenni (1969) reported no time interval greater than 2 days. The Louisiana Heron and Snowy Egret laid eggs on the average every 2.1 ± 0.08 days (47 nests), and 2.1 ± 0.04 days (57 nests), respectively, with the time between laying of successive eggs increasing slightly. The mean interval between eggs for the Cattle Egret was 2.2 ± 0.13 days (21 nests). The Little Blue Heron and Great Egret laid their eggs on the average every 1.9 ± 0.16 days (18 nests) and 1.9 ± 0.37 days (8 nests) respectively, slightly more than the 1.7 days reported by Jenni (1969) for the Little Blue Heron. Both species showed a decrease in mean interval between successive eggs laid in the clutches (Table 3).

All five species apparently laid replacement clutches when the original clutch was destroyed. It was assumed the same pair maintained their territory around the nests in which replacement clutches were laid. Because the birds were not marked confirmation was not possible; but no increase in territorial disputes were noted as one might expect if a new pair were on territory. Furthermore, replacement clutches were always of the same species as the previous clutch in identified nests. Louisiana Herons laid eight replacement clutches in eight nests, beginning to do so a mean 5.3 ± 1.15 (range 2–10) days after loss of the clutch. Snowy Egrets laid 14 replacement clutches in 12 nests. Two successive replacement clutches were laid in two nests. An average of 8.1 ± 1.33 (range 2–22) days elapsed between the loss of one clutch and the laying of the first egg in the replacement clutch. Cattle Egrets laid seven

TABLE 3
DAYS BETWEEN EGGS LAID ON RIOMAR ISLAND

	Days	Laying interval between Eggs 1–2 (nests)	Eggs 2–3 (nests)	Eggs 3–4 (nests)
Louisiana Heron	1	1	4	1
	2	13	17	2
	3	0	7	2
Mean ± SE		1.9 ± 0.08 (N = 14)	2.1 ± 0.12 (N = 28)	2.2 ± 0.37 (N = 5)
Snowy Egret	1	1	1	0
	2	23	23	2
	3	1	5	1
Mean ± SE		2.0 ± 0.06 (N = 25)	2.3 ± 0.03 (N = 29)	2.3 ± 0.34 (N = 3)
Cattle Egret	1	1	0	0
	2	6	9	0
	3	3	1	1
Mean ± SE		2.2 ± 0.20 (N = 10)	2.1 ± 0.10 (N = 10)	3.0 ± 1.00 (N = 1)
Little Blue Heron	1	0	2	2
	2	5	6	2
	3	0	0	0
	4	0	1	0
Mean ± SE		2.0 ± 0.00 (N = 5)	2.0 ± 0.29 (N = 9)	1.5 ± 0.29 (N = 4)
Great Egret	1	0	1	0
	2	3	4	0
Mean ± SE		2.0 ± 0.00 (N = 3)	1.8 ± 0.60 (N = 5)	–

replacement clutches in seven nests. The average time between the loss of the clutch and the laying of the first egg in the replacement clutch was 8.7 ± 2.12 (range 1–17) days. The Little Blue Heron and the Great Egret both laid three replacement clutches in three nests 6.7 ± 3.69 (range 3–14) days for the Little Blue Heron and 8.0 ± 3.01 (range 5–14) days for the Great Egret after loss of the clutch.

Some evidence of indeterminate laying was found at three nests. A Snowy Egret laid 2 eggs, then lost 1 egg, and continued to complete a 3-egg clutch (28 March 1 egg, 29 March 2 eggs, 30 March 1 egg, 31 March 2 eggs, 2 April 3 eggs) and all eggs hatched. A Louisiana Heron had only 1 egg in the nest for 7 days, then completed a 3-egg clutch and all eggs hatched. Egg removal and replacement were the probable cause of the 7-day interval with only 1 egg (29 March 1 egg, 4 April 2 eggs, 6 April 3 eggs). After completing a 3-egg clutch, one Little Blue Heron lost 2 eggs and then laid another egg before the nest was destroyed (14 April 1 egg, 16 April 2 eggs, 17 April 3 eggs, 18 April 1 egg, 19 April 2 eggs). Jenni (1969) reported indeterminate laying by the Snowy Egret and Louisiana Heron at three nests where twice the normal number of eggs were laid to replace egg losses to predators. Most replacement clutches were laid about 1 week after the original clutch was destroyed in this study indicating that determinate laying is probably the primary method of egg-laying by the herons studied. Additional observations and experiments including artificial egg manipulation are needed to clarify these phenomena.

Clutch size.—Louisiana Heron clutches, completed 22 March–24 April, averaged 3.1 ± 0.05 eggs (range 2–4 eggs, N = 79) on Riomar. On Sapelo Island, Georgia, Teal (1965) found a mean clutch size of 3.1 eggs for 15 nests. At Lake Alice, Jenni (1969) reported a mean clutch size of 4.1 eggs for 36 nests, significantly larger (t = 9.1, P = 0.001) than Riomar clutches.

Snowy Egret clutches, completed 23 March–2 May, averaged 2.9 ± 0.06 eggs (range 2–4 eggs, N = 77) on Riomar. This is significantly smaller (t = 15.0,

$P = 0.001$) than the 4.1 ± 0.05 eggs (N = 89) Jenni (1969) reported for early clutches in April at Lake Alice, but is equal to the clutch size he reported for May clutches (2.9 ± 0.17 eggs, N = 13). Teal (1965) found a mean clutch size of 3.2 eggs for 29 nests in Georgia.

Cattle Egret clutches, completed 23 March–30 April, averaged 3.0 ± 0.13 eggs (range 2–5 eggs, N = 31) on Riomar. At Lake Alice mean clutch size was 3.5 ± 0.07 eggs, N = 85 (Jenni 1969) significantly larger ($t = 3.3$, $P = 0.01$) than Riomar clutches, but in South Africa (Siegfried 1972) the mean clutch size (3.1 eggs, N = 302) was similar. In Alabama, Dusi and Dusi (1970) reported a mean clutch size of 2.4 eggs (N = 50); this small size was attributed to a period of drought before the nesting season.

Little Blue Heron clutches, completed 8–24 April, averaged 3.3 ± 0.16 eggs (range 2–5 eggs, N = 21) on Riomar. Meanley (1955) gave an average of 4.04 eggs from 50 nests in Arkansas, significantly greater ($t = 4.4$) than the Riomar clutch size, and the clutch size of 3.7 ± 0.10 eggs (N = 58) at Lake Alice ($t = 2.96$) reported by Jenni (1969). The Riomar nests had significantly fewer eggs per clutch than those at Lake Alice ($t = 2.1$). In Texas, Taylor and Michael (1971) reported an average clutch size of 2.9 eggs from 127 nests.

Great Egret clutches, completed 23 March–19 April, averaged 2.8 ± 0.17 eggs (range 2–4 eggs, N = 13) on Riomar. Teal (1965), in Georgia, found an average clutch size of 3.0 eggs in 31 nests. In California, Pratt (1972) gave an average of 3.2 eggs per clutch for 87 nests, which is significantly greater than the Riomar clutch size ($t = 2.2$). In Louisiana, Simmons (1959) reported an average clutch size of 2.9 eggs for 63 nests and Taylor and Michael (1971) found an average of 2.7 eggs in three clutches in Texas.

Little Blue Heron clutches were significantly larger than Snowy Egret and Great Egret clutches on Riomar ($t = 2.8$ and 2.1 respectively), and Louisiana Heron clutches were significantly larger than Great Egret clutches ($t = 2.1$). None of the other possible comparisons on Riomar were significantly different. Jenni (1969) detected no significant clutch size differences among the same species mentioned immediately above, but he did find Louisiana Heron clutches significantly larger than those of the Cattle Egret and Little Blue Heron ($t = 4.32$ and 3.00 respectively), and Snowy Egret clutches significantly larger than Cattle Egret clutches ($t = 3.93$).

The Lake Alice herons all laid significantly more eggs per clutch on the average than the Riomar birds did. Clutch size is thought to be subject to geographic variation (Moreau 1944), but these two colonies are only 300 km apart. Differences in food availability, social stress from crowded nests and competition, optimal or suboptimal weather conditions before and during the egg-laying period, and the level of toxins (Peakall 1970) in the colony members are probably of greater significance in determining clutch size than is latitude. These data suggest that colonies situated in marine environments may tend to have smaller clutches than those in freshwater habitats.

Incubation and hatching.—Nice (1954) defined incubation period as used here as the number of days from the laying of the last egg to the hatching of that egg, when all eggs in the clutch hatch. Incubation periods determined in this study did not differ significantly from those Jenni (1969) found at Lake Alice (Table 4).

Both inter- and intraspecific variation occurs in the onset of incubation. The onset of incubation was estimated from the hatching time, realizing that other factors, such

TABLE 4

FREQUENCY DISTRIBUTION OF INCUBATION PERIODS ON RIOMAR ISLAND

	Incubation period in days							
	20	21	22	23	24	25	26	Means ± SE
Louisiana Heron	0	0	4	8	6	2	0	23.3 ± 0.21
Snowy Egret	2	4	13	9	1	0	0	22.1 ± 0.17
Cattle Egret	0	0	3	7	0	0	0	22.7 ± 0.15
Little Blue Heron	2	0	5	2	1	0	0	22.0 ± 0.40
Great Egret	0	0	0	0	0	0	3	26.0 ± 0.00

as differential egg development and incubation attentiveness, may cause variation in development time. In 55% of the Louisiana Heron nests incubation began with the laying of the 2nd egg and in 24% with the 3rd egg; the remaining 21% started incubation with the 1st egg. In the Snowy Egret nests incubation began with the 1st egg in 54% of the nests and with the 2nd egg in 44%. In 78% of the Cattle Egret nests incubation began with the 1st egg, 15% after the 2nd egg, and 7% after the 3rd egg. Little Blue Herons began incubating after the 2nd egg in 65% of the nests and after the 3rd egg in 14%. Incubation began with the 1st egg in 55% of the Great Egret nests, and after the 2nd egg in the remaining 45%.

Hatching was variable for all species, with most young hatching the 1st or 2nd day, while the eggs in some nests hatched over a period of 5 days or more. In comparing the Riomar and Lake Alice (Jenni 1969) studies (Table 5) some variation was noted in the number of young in the nests after each day of hatching in all species except the Cattle Egret, which had nearly identical numbers of young in the nest for each hatching day in both places. The mean number of Louisiana Herons hatching per nest was 2.8 ± 0.07 and the average clutch took 3.1 (range 1–5) days to complete hatching. Snowy Egrets had 2.7 ± 0.08 young per nest and hatching extended over 3.8 (range 1–5) days. An average of 2.6 ± 0.16 Cattle Egrets hatched per nest over a

TABLE 5

MEAN NUMBER OF YOUNG HERONS IN NESTS AFTER EACH DAY OF HATCHING ON RIOMAR ISLAND IN 1973 AND AT LAKE ALICE,[1] FLORIDA IN 1960

	Day after hatching						
	1st	2nd	3rd	4th	5th	6th	7th
Louisiana Heron							
Riomar (N)[2]	1.6 (76)	2.5 (65)	2.7 (29)	3.1 (8)	3.7 (3)	—	—
Lake Alice (N)	2.2 (25)	2.7	3.1	3.1	—	—	—
Snowy Egret							
Riomar (N)	1.5 (70)	2.1 (56)	2.1 (32)	3.0 (5)	3.0 (1)	—	—
Lake Alice (N)	1.5 (80)	2.4	2.9	—	—	—	—
Cattle Egret							
Riomar (N)	1.2 (27)	1.6 (24)	2.1 (21)	2.5 (12)	3.1 (9)	4.0 (3)	—
Lake Alice (N)	1.1 (49)	1.6	2.1	2.6	3.0	—	—
Little Blue Heron							
Riomar (N)	1.7 (20)	2.2 (16)	3.1 (10)	3.5 (2)	—	—	—
Lake Alice (N)	1.6 (37)	2.5	2.9	—	—	—	—
Great Egret							
Riomar (N)	1.5 (12)	1.9 (10)	2.3 (7)	2.5 (4)	2.5 (2)	3.0 (2)	3.0 (1)

[1] From Jenni 1969.
[2] N = number of nests and refers to all nests containing eggs that were still in the process of hatching.

TABLE 6
DAYS BETWEEN HATCHING ON RIOMAR ISLAND

	Days	Hatching interval between: Eggs 1–2 (nests)	Eggs 2–3 (nests)	Eggs 3–4 (nests)
Louisiana Heron	0	41	14	0
	1	30	32	1
	2	3	13	5
Mean ± SE		0.5 ± 0.07 (N = 74)	1.0 ± 0.09 (N = 59)	1.8 ± 0.16 (N = 6)
Snowy Egret	0	31	9	1
	1	30	22	2
	2	9	13	2
	3	1	0	0
	4	0	1	0
Mean = SE		0.7 ± 0.09 (N = 71)	1.2 ± 0.12 (N = 45)	1.2 ± 0.38 (N = 5)
Cattle Egret	0	4	1	0
	1	10	6	0
	2	10	5	3
	3	2	3	0
	4	0	0	1
Mean ± SE		1.4 ± 0.17 (N = 26)	1.7 ± 0.23 (N = 15)	2.5 ± 0.15 (N = 4)
Little Blue Heron	0	13	2	1
	1	5	8	2
	2	2	4	1
Mean ± SE		0.5 ± 0.15 (N = 20)	1.1 ± 0.18 (N = 14)	1.0 ± 0.41 (N = 4)
Great Egret	0	5	0	0
	1	4	1	0
	2	1	4	0
	3	0	1	1
	4	1	0	0
Mean ± SE		0.9 ± 0.37 (N = 11)	2.0 ± 0.41 (N = 6)	3.0 (N = 1)

period of 4.2 (range 1–6) days. The mean number of Little Blue Herons hatching per nest was 2.9 ± 0.20 and the average clutch took 2.6 (range 1–4) days to hatch. A mean of 2.6 ± 0.25 Great Egrets hatched per nest and hatching extended over 5.2 (range 1–7) days.

The time interval between hatching of successive eggs in the clutch increased in all species except for the Little Blue Heron and Snowy Egret where little change in hatching interval occurred in later hatchings (Table 6). Hatching of the first two eggs occurred on the same day in a majority of nests of all species except the Cattle Egret, which had a 1- or 2-day interval between hatchings. The hatching interval between the 2nd and 3rd was 1 day in a majority of nests of all species except the Great Egret, which had a 2-day interval.

Mortality of eggs and young and nest success.—Percent mortality of eggs and young was determined for various periods during the laying, hatching, and nestling stages (Table 7). Most nestlings had strayed away from their nests by the 10th day after hatching, so mortality data were not available past this date. For these and other species of herons, Jenni (1969) summarized mortality figures from the literature. His Lake Alice data are included in Table 7 for comparison.

A nest was considered successful if at least one nestling survived beyond 10 days of age. Nesting success for each species during the period March through May 1973 is summarized in Table 8. Meanley (1955) calculated a 93% nesting success for the Little Blue Heron in Arkansas. In Alabama, in 1965 (Dusi and Dusi 1968) the Little Blue Heron and the Cattle Egret had 14.5% and zero nesting success, respectively. The same colony was studied again in 1967 and at that time Cattle Egrets had a 30%

TABLE 7
EGG AND NESTLING MORTALITY ON RIOMAR ISLAND

	Louisiana Heron[1]		Snowy Egret[2]		Cattle Egret[3]		Little Blue Heron[4]		Great Egret[5]	
	N[6]	%	N	%	N	%	N	%	N	%
Laying to day before hatching	11	4.5	15	6.6	9	9.6	1	1.4	5	13.9
Day before hatching through hatching	21	8.6	25	11.1	12	12.8	8	11.6	3	8.3
2nd day after last egg hatched	5	2.4	9	4.8	1	1.4	1	1.7	1	3.6
10th day after last egg hatched	13	6.1	16	8.6	7	9.6	1	1.7	3	10.7
Total egg loss	32	13.1	40	17.7	21	22.3	9	13.0	8	22.2
Total nestling loss	18	8.5	25	13.4	8	11.0	2	3.3	4	14.3
Mortality from laying through 10 days	50	20.5	65	28.8	29	30.9	11	15.9	12	33.3
Overall mortality from laying through 2 weeks at Lake Alice[7]		35.8		42.5		17.9		37.7		—

[1] 79 clutches, 244 eggs, 212 nestlings.
[2] 77 clutches, 226 eggs, 186 nestlings.
[3] 31 clutches, 94 eggs, 73 nestlings.
[4] 21 clutches, 69 eggs, 60 nestlings.
[5] 13 clutches, 36 eggs, 28 nestlings.
[6] N = number of eggs and nestlings lost.
[7] Jenni 1969.

nest success (Dusi and Dusi 1970). Teal (1965) in Georgia, reported the following nest successes: Louisiana Heron 47%, Snowy Egret 37%, and Great Egret 39%. For Great Egrets in California, Pratt (1972) reported nesting success of 52% in 1967, 41% in 1968, 33% in 1969, and 28% in 1970.

Nesting success of the Riomar herons in 1973 was higher than any reported in the literature, probably a result of the heronry's isolated location, good weather condi-

TABLE 8
NESTING SUCCESS ON RIOMAR ISLAND

	Louisiana Heron	Snowy Egret	Cattle Egret	Little Blue Heron	Great Heron
Active nests	79	77	31	21	13
No. of nests containing at least 1 bird at 10 days[1]	75	65	28	21	11
% nesting success	95	84	90	100	85
No. of eggs	244	226	94	69	36
No. hatching	212	186	73	60	28
% hatching	87	82	78	87	78
No. of 10-day-old birds	194	161	65	58	24
% of nestlings reaching 10 days	92	87	89	97	86
% of eggs producing 10-day-old birds	80	71	69	84	67

[1] Young herons were considered successful if they survived a 10-day nestling period. The young 10-day plus herons scattered throughout the colony and could no longer be identified with their birth nests.

tions, and the fact that other nest success data probably included birds beyond 10 days of age. The Great Egret and Snowy Egret had the lowest nest success because of the juxtaposition of Brown Pelican nests. The pelicans made clumsy landings that dislodged heron eggs and nestlings near their nests. The Little Blue Herons that mated on the fringe of the main nesting colony away from the pelican nests had the most success. The Fish Crow (*Corvus ossifragus*) was the next greatest cause of egg and nestling loss. Congregating mainly in the Australian Pines, 50 crows used the island for resting, feeding, roosting, and nesting. Crows were seen pecking eggs and carrying away nestlings, but specific numbers were not recorded. The only other possible predators were black rats (*Rattus rattus*), which lived in and under the debris on the ground, but we never saw rats attacking eggs or nestling herons. We estimate that about 75% of the egg and nestling losses were due to the pelican and crow, and the remainder to infertile or addled eggs.

An unusual mixing of one Snowy Egret and two Louisiana Heron nestlings in a Louisiana Heron nest resulted in the death of the 6-day-old Snowy Egret nestling apparently from starvation. The Louisiana Heron nestlings were 5 and 3 days older than the Snowy Egret nestling and were, therefore, much more aggressive and successful in obtaining food from the parents.

It is interesting that the Cattle Egret had the highest overall mortality (30.9%) from laying through 10 days of age in this study, but in Jenni's (1969) study the Cattle Egret had the lowest mortality (17.9%) of all species observed. Reasons for these differences are unknown, but Brown Pelican interference could account for the difference. The nesting of the Cattle Egret seems to be timed to peak later than that of the native herons (Jenni 1969, Maxwell and Kale 1974), so that competition with native herons for optimal nesting sites is reduced. The availability of nest sites, abundance of food, and territorial aggressiveness are the probable reasons for the spectacular spread and population increase of the Cattle Egret in North America. We did not notice that the Cattle Egret was more pugnacious than the more aggressive native species, as incidents of egg destruction or twig stealing did not seem more intense than those by the native species. It is hoped that future studies of mixed heron colonies, especially those containing the Cattle Egret, will help determine the relationship of this species with others and the reasons for its success.

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