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COMPETITION BETWEEN CATTLE EGRETS AND NATIVE NORTH AMERICAN HERONS, EGRETS, AND IBISES

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Cattle Egrets (*Bubulcus ibis*) recently invaded and spread across North America, nesting in existing heronries. The spread of this species into the Western Hemisphere is well documented (Crosby 1972, Weber 1972), yet many aspects of its breeding biology are incompletely understood. Cattle Egrets do not appear to compete with native herons and egrets for food since their foraging methods and food items differ (Jenni 1969, 1973). Cattle Egrets tend to breed later than native North American ardeids, thus eliminating competition for nest sites (Dusi 1966, Dusi and Dusi 1968, Jenni 1969, Dusi et al. 1971, Weber 1972). In 1968, Dusi suggested that Cattle Egrets may compete with Little Blue Herons (*Florida caerulea*) when some late-arriving Cattle Egrets take over deserted nests, often adding their own eggs to those already present. Dusi, however, stated that the existing competition was not "greatly harmful" to the Little Blue Herons. Further study, however, indicated that Cattle Egrets arrive when Little Blue Herons have chicks, and that the egrets take over nests by forcing some of the heron chicks out of their nests (McKitrick 1975). While Cattle Egrets steal nest material from each other in Africa (Siegfried 1971a, 1972) and Colombia (Lancaster 1970), they have not been reported to steal material from other nesting herons in North America. Presumably, nesting much later than the native species eliminates some competition for nest sites and materials, as well-established incubating herons can successfully defend their nests.

Observations in northern heronries, unlike those in the south, suggest that Cattle Egrets do not breed later than native species. Thus, direct competition for nest sites and nesting materials may occur. I observed the behavior and ecology of Cattle Egrets in a mixed species colony of herons, egrets, and ibises during the 1975 breeding season to determine the niche overlap among these species and the effect of Cattle Egrets on native species. I was particularly interested in comparing the times of arrival at the heronry, the dates of egg-laying, competition for nest sites and nests remaining intact from the previous year, competition for nest materials, aggressiveness during the breeding period, and nest success.

One of the aims of studies of resource partitioning is to analyze how interspecific competition limits the number of coexisting species (Schoener 1974). Competition, here defined as the simultaneous demand by two or more organisms of different species for limited resources such as food or space (Koplin and Hoffmann 1968), has been studied by experimentation and observation. Experimentalists (e.g., Connell 1961) who perturb the system and observe the results, demonstrate the existence of competition, but do not elucidate the mechanisms. Observationalists (e.g., MacArthur 1959, Johnson 1971, Pearson 1971) tend to infer competition by hypothesizing a mechanism. The natural invasion of a species, such as the Cattle Egret, into an existing system provides an ideal evolutionary situation for both approaches to the study of competition; field behaviorists normally have the opportunity to examine competition only among long-established species.

MATERIALS AND METHODS

During 1975 I worked on Islajo Island just south of the Brigantine National Wildlife Refuge near Atlantic City, New Jersey. This spoil island contained a small sand dune surrounded by an extensive area of *Phragmites* and poison ivy (*Rhus toxicodendron*). The *Phragmites* were surrounded by *Spartina alterniflora* salt marsh, *Iva* bushes and open mudflat. The vegetation in the colony area could be classified into four heterogeneous types: dense *Phragmites*, sparse *Phragmites*, dense *Phragmites* with sparse *Rhus*, and sparse *Phragmites* with dense *Rhus*. High tides regularly inundated the mudflat and *Spartina* marsh. Tide levels infrequently reached the edge of the *Phragmites*, occasionally seeping into the lower areas. Nesting on the island were: 30 pairs of Great Egrets (*Casmerodius albus*), 300 pairs of Little Blue Herons, 125 pairs of Louisiana Herons (*Hydranassa tricolor*), 350 pairs of Snowy Egrets (*Egretta thula*), 25 pairs of Black-crowned Night Herons (*Nycticorax nycticorax*), 325 pairs of Glossy Ibises (*Plegadis falcinellus*), and 45 pairs of Cattle Egrets. Cattle Egrets began breeding in this colony in 1968 (Adams and Miller 1975). The birds nested in all of the available *Phragmites* and *Rhus* areas.

I made observations on Islajo Island from early March until early July 1975. I checked the island for signs of herons two or three times per week from March until late April, when I took up residence on the island until early July. During the pre-egg and incubation phase, I made daily observations from the blind from 0600 until 2000. The two areas used for these studies each had the same species composition

TABLE 1. Arrival and egg-laying times in a mixed species heronry in New Jersey.

	First arrival	Half had arrived	First egg-laying	Peak
Common Egret	12 April	20 April	6 May	10 May
Little Blue Heron	26 April	2 May	8 May	16 May
Louisiana Heron	26 April	5 May	10 May	13 May
Snowy Egret	12 April	18 April	8 May	14 May
Black-crowned Night Heron	28 March	15 April	9 May	16 May
Cattle Egret	2 May	6 May	8 May	16 May
Glossy Ibis	20 April	25 April	6 May	15 May

except that one area contained Cattle Egrets and the other did not. These areas had similar nest densities; the mean distance between nests in the area with Cattle Egrets ($\bar{x} = 92.1$ cm, SD = 35 cm) did not differ significantly ($t = 1.12$) from that in the area without Cattle Egrets ($\bar{x} = 102.4$ cm, SD = 50.8). The two areas were similar in structural appearance and had similar vegetation, i.e. sparse *Phragmites* and dense *Rhus*.

During the observation periods, I recorded all aggressive encounters, the species involved, who "won," the distance at which the interaction began, and "intensity" of the response. "Intensity" was based on posturing, vocalizations, and pecking behavior of the opponents. I also noted trips for collecting nest material, source of material gathered (the ground, another nest, or broken from bushes), responses of the nest owner when an intruder stole nest material, responses of incubating birds to flying predators, and behavior of nestlings (feeding activities, movements away from nests).

Before entering the blind each morning, I checked nest contents and marked all nests, eggs, and chicks. All chicks were banded and weighed daily with a Pesola field balance. I determined chick survival for all species by checking nests on alternate days and observing live chicks on the nests from my blind. Nest checking was possible only until chicks were 13 or 14 days old. Chicks then began to leave frequently, making it necessary to watch from a blind. I remained in the blind at least until all chicks had returned to their nests to be fed by their parents.

RESULTS

PHENOLOGY

Black-crowned Night Herons arrived on the colony site in late March, two weeks before the arrival of any other species (Table 1). Twenty-five to 250 night herons roosted in the colony until nesting began, when their numbers decreased. Great Egrets, Snowy Egrets, and Glossy Ibises arrived in mid-April, and Little Blue Herons and Louisiana Herons in late April. The first Cattle Egrets arrived in the colony in early May.

All species began egg-laying from 6 to 10 May, with Great Egrets and Glossy Ibises first, and Louisiana Herons last (Table 1). For Cattle Egrets, only 6 days elapsed between their arrival and first egg-laying, whereas, for all native species more than two weeks elapsed.

NEST SITE SELECTION

Upon arrival, the birds established perch sites which they defended from intruders. The species present did not nest in all areas of the colony, but selected particular habitats. All the Great Egrets nested on the ground in one sparse *Phragmites* area, Black-crowned Night Herons nested on the ground in dense *Phragmites* areas, and Glossy Ibises nested on the ground in all areas. Snowy Egrets nested on the ground as well as above ground in *Rhus*. Louisiana and Little Blue herons nested only in the *Rhus* bushes. Cattle Egrets nested only in *Rhus* areas, and tended to nest in bushes although a few nested on the ground (Table 2).

The island is swept by tides during the winter, yet many nests remain intact on the ground and in the bushes. When birds arrived, they either claimed old nests, took material from old nests to build new nests, or constructed new nests from twigs or scattered *Phragmites* stems. Before any herons arrived, I marked and measured 70 ground nests made of *Phragmites*, and 70 bush nests of twigs. The birds reused 73% of the tree nests and dismantled the remaining tree nests to construct new nests by the first week of egg-laying. Only 29% of the ground nests were reused, and only 6% were dismantled, leaving 65%.

Cattle Egrets, Little Blue Herons, Louisiana Herons and Snowy Egrets all used the twigs from the tree nests, whereas, Glossy Ibises and Black-crowned Night Herons used the *Phragmites* from the ground nests. The fewer number of ibises and night herons and the abundance of old *Phragmites* at least partly accounts for the low usage of old nests on the ground. However, there was intense competition for the tree nests among Cattle Egrets, Little Blue Herons, Louisiana Herons, and Snowy Egrets.

TABLE 2. Habitat selection at Islajo Island, 1975.[a]

	Dense *Phragmites*	Sparse *Phragmites*	Dense *Phragmites*, sparse *Rhus*	Sparse *Phragmites*, dense *Rhus*
Great Egret	----	G	----	----
Little Blue Heron	----	----	B	B
Louisiana Heron	----	----	B	B
Snowy Egret	----	B	B	B, G
Glossy Ibis	G	G	G	G
Black-crowned Night Heron	G	G	----	----
Cattle Egret	----	----	B, G	B, G

[a] G = ground nesting. B = bush nesting.

Cattle Egrets were significantly more successful ($\chi^2 = 11.77$, df = 3, $P < 0.01$) at competing for old nests than their percentage occurrence suggests. They occupied half of the reused tree nests in my study area even though they arrived last. Intense fighting, described below, occurred during the establishment of nest sites.

Competition for nest material continued through the pre-egg and incubation periods. Usually nest material was stolen while nests were unattended (80%). Only Cattle Egrets removed material from nests being defended by other species. Six times I collected twigs from outside of the heronry and constructed nests near my blind. Cattle Egrets quickly dismantled these undefended nests and tended to defend this source of nest material from each other as well as from other species. Cattle Egrets needed less material because they had smaller nests than other species (Table 3). For this species, mean nest width (35.8 cm) was similar to that found in Africa (36.3 cm, Siegfried 1971a).

I recorded heights of nests from the ground in two areas with Little Blue Herons, Louisiana Herons, Snowy Egrets, and Glossy Ibises, and in two other areas with these species plus Cattle Egrets. Areas were chosen for their similarity in bird composition, flora, and structure of vegetation. Areas with the same species of birds had similar nest heights so I pooled the data for analysis. The native species situated the height of their nests in direct relation to body length (Table 4). Little Blue Herons, the largest species, had the highest mean nest height, while Glossy Ibises, the smallest native species, had the lowest. Cattle Egrets had a higher mean nest height than predicted by the body length relationship found for native species. Mean nest heights differed significantly among species in both study areas (analysis of variance). In the study area without Cattle Egrets, mean nest heights differed significantly for all species ($F = 28.3$; df = 3,30; $P < 0.001$). In the area with Cattle Egrets, there were also significant differences ($F = 12.37$; df = 5,36; $P < 0.01$). Comparing nest heights between the two areas, the Little Blue Heron ($t = 0.58$), Louisiana Heron ($t = 1.22$) and Glossy Ibis ($t = 0.8$) means did not differ significantly, but the Snowy Egret's did ($t = 2.23$, df = 26, $P < 0.05$). The presence of Cattle Egrets lowered the Snowy Egret nests significantly. The mean nest height of the Cattle Egret did not differ significantly from that of the Snowy Egret in the non-Cattle Egret area ($t = 0.82$).

TABLE 3. Nest sizes in centimeters (± SD) for species in a mixed species colony.

Species	N	Width	Depth
Little Blue Heron	15	40.7 ± 6.9	21.2 ± 5.9
Louisiana Heron	15	43.6 ± 1.9	23.0 ± 1.2
Snowy Egret	20	41.0 ± 5.0	27.0 ± 6.5
Cattle Egret	20	35.8 ± 7.9	20.1 ± 7.7
Glossy Ibis	20	41.8 ± 7.0	36.5 ± 22.4

Cattle Egrets nested from 3 to 112 cm (difference = 109 cm, Table 4) above the ground, whereas all other species had a nest height variation of 40 to 60 cm within the area with Cattle Egrets. Cattle Egrets overlapped with all species present and had a broader range of nest site heights.

TABLE 4. Heights (in cm) of nests from the ground on Islajo Island, New Jersey.

	Area with Cattle Egrets				Area without Cattle Egrets			
Species	N	$\bar{x}$ ± SD	Range	Difference[a]	N	$\bar{x}$ ± SD	Range	Difference[a]
Little Blue Heron	15	79.1 ± 15.3	54–106	52	16	79.1 ± 12.0	62–112	50
Louisiana Heron	9	62.5 ± 14.9	46–98	52	5	71.1 ± 11.0	50–112	61
Snowy Egret	18	40.0 ± 16.0	20–74	54	17	60.1 ± 23.0	30–101	71
Glossy Ibis	10	26.0 ± 10.7	15–55	40	15	28.0 ± 8.8	15–43	28
Cattle Egret	16	70.0 ± 31.5	3–112	109				

[a] Difference between highest and lowest value.

TABLE 5. Aggressive behavior in a mixed heronry. Percent occurrence of the behavioral sequences sampled.

Species	N[a]	Stand	Erect crown feathers	Erect back feathers	Vocalize	Chase	Peck at
Little Blue Heron	154	100	97	98	55	55	22
Louisiana Heron	84	100	100	100	61	58	18
Snowy Egret	134	100	100	97	70	78	32
Cattle Egret	135	100	100	100	97	86	80
Glossy Ibis	24	100	0	0	98	40	47

[a] Number of sequences observed for each species.

AGONISTIC INTERACTIONS

I recorded agonistic interactions among all species in one study area containing seven pairs of Little Blue Herons, three pairs of Louisiana Herons, eight pairs of Snowy Egrets, four pairs of Glossy Ibises, and eight pairs of Cattle Egrets. Observations were for 8 to 14 h a day from 8 May until 13 June. This area, chosen for its species composition, had synchronous breeding activities: 8 to 15 May pre-egg laying period for all species, 16 May to 4 June incubation period, and 5 to 12 June hatching period. Agonistic encounters usually involved chasing and displacing any intruder (non-neighbor) that landed close to a perch or nest site. Nest owners usually ignored neighbors landing at their own nests.

I computed the mean number of agonistic interactions (inter- and intraspecific) per bird-hour (Aggression Index) for the five weeks described above. Cattle Egrets ($\bar{x}$ = 0.47) acted more aggressively than Snowy Egrets ($\bar{x}$ = 0.27), Louisiana Herons ($\bar{x}$ = 0.21) or Little Blue Herons ($\bar{x}$ = 0.18). Glossy Ibises, the only exclusively ground-nesting species, were less aggressive than the other species ($\bar{x}$ = 0.12). I found that 80% of all agonistic interactions of Cattle Egrets ended in pecking at the intruder compared to under 50% for all other species (Table 5).

Since intraspecific aggression can be used as an indication of seasonal agonistic levels, I computed the intraspecific aggression index as a function of date (Fig. 1). Agonistic interactions, highest in the pre-egg phase, generally decreased throughout incubation. At hatching, aggressive interactions decreased in Snowy Egrets, increased in Louisiana Herons

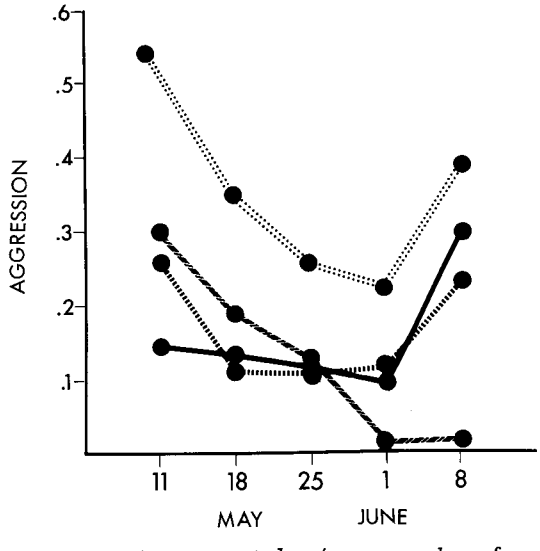

FIGURE 1. Aggression index (mean number of encounters·bird^{-1}·hr^{-1}) as a function of season. The first week was pre-egg, and the last week was hatching. Dotted line, Cattle Egret; diagonal line, Snowy Egret; dashed line, Louisiana Heron; and solid line, Little Blue Heron.

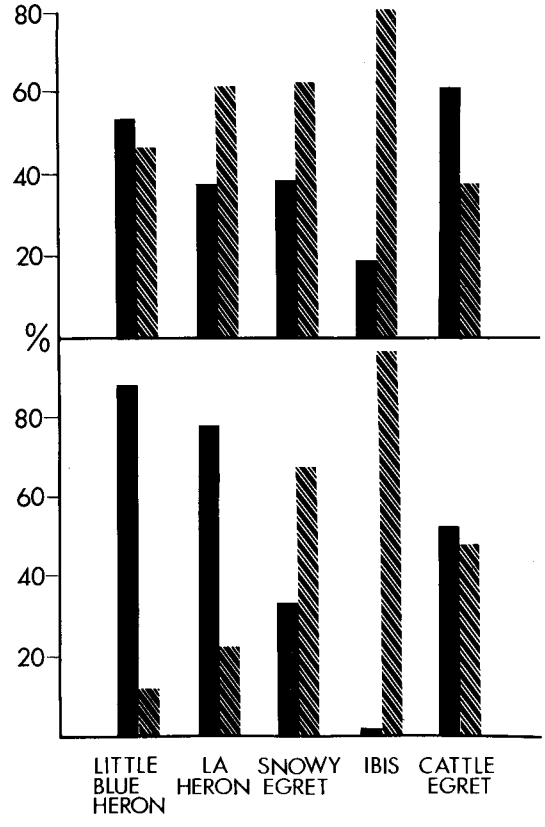

FIGURE 2. Upper graph: percent interspecific (hatched bar) versus intraspecific aggression (solid bar). Lower graph: percent interspecific wins (solid bar) versus losses (hatched bar).

TABLE 6. Percent chases as a function of distance from the nest.

Species	N[a]	Distance (m) 0–1	1–2	2–3	3–4	Over 4
Little Blue Heron (55)[b]	110	61	29	9	1	–
Louisiana Heron (55)	75	71	21	8	–	–
Snowy Egret (50)	150	62	30	7	1	–
Cattle Egret (42)	150	49	36	10	4	1
Glossy Ibis (47)	50	60	40	–	–	–

[a] Number of chases for each species.
[b] Body length in cm (after Robbins et al. 1966).

and Cattle Egrets, and increased dramatically in Little Blue Herons. In the pre-egg phase, agonistic levels were inversely related to body length of the species. In the post-hatch phase, aggressive interactions were positively related to the size of the bird for the native species. Cattle Egrets were more aggressive throughout the breeding season.

I compared the percentage of intraspecific interactions to the percentage of interspecific interactions (Fig. 2). Except in the Cattle Egret, the percentage of intraspecific aggression related directly to body length, and the percentage of interspecific aggression related inversely to body length. For interspecific aggression, the percentage of wins (except for the Cattle Egret) also related directly to body length (Fig. 2). These data indicate that the larger the bird, the higher the percentage of intraspecific aggression and the higher the percentage wins of interspecific interactions. Again, the Cattle Egret is an exception to the pattern.

I then compared the mean aggression indices for the entire reproductive cycle in the study areas with and without Cattle Egrets. The aggression indices were similar for Little Blue Herons (0.18, 0.20) and Louisiana Herons (0.21, 0.19). However, Snowy Egrets' aggression index was higher (0.27) in the area with Cattle Egrets compared to an area without them (0.22). Similarly, Snowy Egrets won fewer of their encounters in areas with Cattle Egrets (33%) compared to areas without them (58%, $\chi^2 = 4.9$, df = 1, $P < 0.05$).

I also recorded the distance from the nest an individual chased another species during the incubation period. Most chases and supplantings occurred within 1 m of the nest site (Table 6). Only Cattle Egrets started most of their chases at distances greater than 1 m from their nests. The mean distance at which chases began for each species was plotted against the species being supplanted (Fig. 3). For example, Little Blue Herons supplanted each other at a mean distance of 1.09 m, Louisiana Herons at 1.4 m, and Cattle Egrets at 0.61 m. For the native North American species, the smaller the intruder species (as measured by body length), the farther from the nest a supplant began. Also, the larger the bird defending its nest, the farther from the nest it started chasing and supplanting. Cattle Egrets did not fit the pattern, but supplanted or chased all intruders at the same distance from their nests; a distance which was greater than that for most other species. They were also able to land

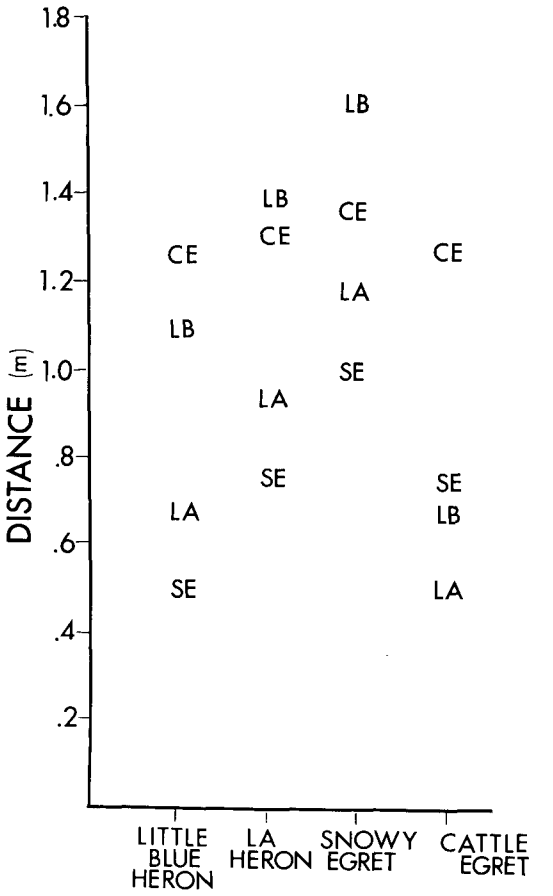

FIGURE 3. Mean distance defended by each species as a function of the species being chased (abscissa). Species chased are ordered by decreasing body length.

TABLE 7. Mean clutch size and nesting success at hatching and at two weeks post-hatching.

Species	N	Clutch ($\bar{x} \pm SD$)	Hatching ($\bar{x} \pm SD$)	14 days post-hatching ($\bar{x} \pm SD$)
Little Blue Heron	10	3.83 ± 0.6	3.6 ± 0.8	2.48 ± 0.9
Louisiana Heron	10	3.60 ± 0.8	3.0 ± 0.9	1.77 ± 1.2
Snowy Egret	20	3.25 ± 0.6	2.2 ± 1.2	0.95 ± 1.3
Cattle Egret	20	3.40 ± 0.8	3.3 ± 0.8	2.54 ± 0.9
Glossy Ibis	20	2.38 ± 1.1	2.3 ± 1.0	1.03 ± 0.9

closer to the nests of other species before being chased than would be predicted from their body length.

NEST SUCCESS

I followed nest success in all nests for 14 days after hatching for Little Blue Herons, Louisiana Herons, Snowy Egrets, Cattle Egrets, and Glossy Ibises. The mean number of young at hatching and the mean number of chicks surviving to 14 days of age indicated that Cattle Egrets had the highest success, and Snowy Egrets the lowest (Table 7).

I compared the mean number of young hatching per nest for Snowy Egrets and Little Blue Herons in the areas with and without Cattle Egrets. Hatching success did not differ between the two areas for the Little Blue Heron ($\bar{x}$ = 3.6, 3.7), but for the Snowy Egret it was significantly higher (t = 2.3, df = 22, $P < 0.05$) in the area without Cattle Egrets ($\bar{x}$ = 3.0 ± 0.3, N = 18) compared to that in the area with Cattle Egrets ($\bar{x}$ = 2.2 ± 1.2, N = 18).

In order to determine the ability of Cattle Egret parents to feed and fledge young successfully, I recorded the mean weights of chicks (N = 15) until 15 days of age. To measure fledging success, it is essential to show not only that a certain percentage of chicks reach 14 days of age, but also that these young are healthy enough to survive. Therefore, in Figure 4 I compared the mean weights of these chicks with those of chicks raised in South Africa (Siegfried 1973). Comparable data do not exist for Cattle Egrets in their native central Africa. However, chicks of this species in New Jersey had similar weights to those in South Africa, where they have bred since the turn of the century (Siegfried 1971b, 1971c).

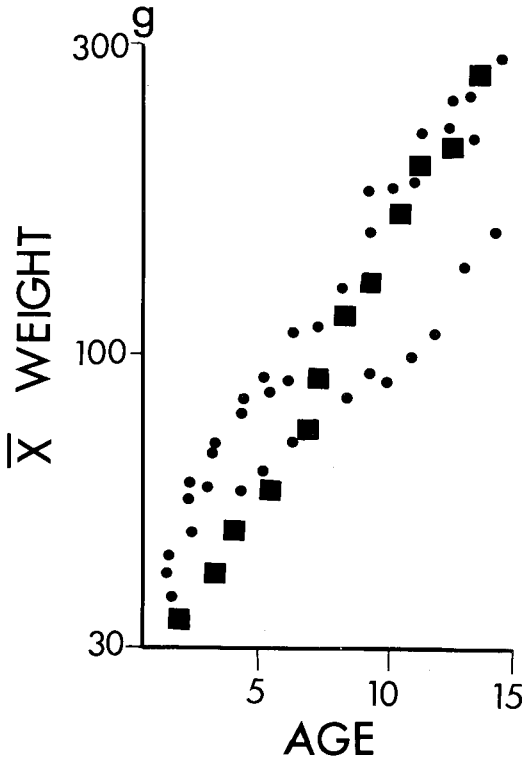

FIGURE 4. Mean weights of Cattle Egret chicks at Islajo Island (squares) compared to means reported by Siegfried (1973) from Africa (circles). See text for an explanation.

DISCUSSION

COMPETITION FOR NEST SITES AND MATERIALS

In the United States, Cattle Egrets first bred in the heronries of Florida in the early 1950's and gradually spread northward (Crosby 1972). Previous studies of this species in the U.S. (all from southern areas), showed that they arrived in the colonies and started breeding well after the native species (Dusi 1966, Dusi and Dusi 1968, Dusi et al. 1971, Jenni 1969, Weber 1975). The simultaneous arrival and nesting of Cattle Egrets with the native North American ardeids in the New Jersey colony increases the possibility of competition for nest sites and materials. The heronry at Islajo Island covers all the available *Phragmites* and *Rhus* bush area, increasing the likelihood of nest site competition. Indeed, the increased levels of aggression I found for the bush-nesting species may reflect the scarcity of bushes for nesting.

Evidence of competition for poison ivy

bushes includes: (1) increased levels of aggression in these areas compared to pure stands of *Phragmites*; (2) lowering of mean nest height in Snowy Egrets; and (3) the placement of nests on the ground by Snowy Egrets only in the areas used by Cattle Egrets.

Burger (1978) examined 14 colonies of mixed ardeid species in Argentina, Mexico, and the U.S. and divided them into two types according to vegetation structure. "Homogeneous colonies" contained either a pure stand of one plant species *or* several species of plants so intermixed that every area of the colony looked alike. "Heterogeneous colonies" contained dissimilar sub-areas with respect to plant species, density, height, or amount and location of open spaces. In heterogeneous colonies, bird species selected nest sites on the basis of the above parameters. In homogeneous colonies, the native species usually situated their nests vertically in a direct relation to body length. The largest species always nested highest and the smallest species nested lowest. Cattle Egrets, present in only two of these colonies, nested higher than would be predicted by the model for indigenous species. I also suggested that homogeneous sections of heterogeneous colonies may exhibit the pattern of homogeneous colonies.

The study areas selected at Islajo Island were homogeneous, and the mean nest heights corroborated the above hypothesis. The Cattle Egret's mean nest height was below that of the Little Blue Heron and above that of the Louisiana Heron and Snowy Egret. Jenni (1969) reported mean nest heights in a colony at Lake Alice, Florida: Cattle Egret, 2.38 m; Little Blue Heron, 2.19 m; Louisiana Heron, 1.74 m; and Snowy Egret, 1.74 m. Cattle Egrets nested relatively higher in this colony than on Islajo Island.

In the present study, Cattle Egrets had the highest aggression rates indicating competition for these high nest sites, but they had a lower percentage of victories than either Little Blue Herons or Louisiana Herons, suggesting that these latter two species would nest higher or at the same height as Cattle Egrets. The data, however, indicate that Snowy Egrets were considerably less aggressive than Cattle Egrets, that they were involved in a higher percentage of interspecific encounters, and that they lost a higher percentage of these encounters than did Cattle Egrets. In areas without Cattle Egrets, Snowy Egrets won significantly more of their interspecific encounters (58% wins compared to 33%). Although Cattle Egrets compete with Little Blue Herons and Louisiana Herons, they seem to be particularly successful when competing with Snowy Egrets. Competition between Snowy Egrets and Cattle Egrets has not been studied previously because of the rarity of Snowy Egrets in the colonies examined (Dusi and Dusi 1967, 1968). Previous studies (Dusi and Dusi 1968, Jenni 1969, Weber 1975) noted relatively low interspecific aggression rates; I attribute this to the late arrival of Cattle Egrets, and the abundance of nest sites and nest material. Although Dusi (1968) and Jenni (1969) reported that Cattle Egrets take over abandoned nests, they did not note the stealing of nest material from active and defended nests that I observed. Only McKitrick's (1975) study indicated that Cattle Egrets decrease nest success of Little Blue Herons by taking over their nests.

The winter tides on Islajo dislodge and remove some old nests as well as debris from the island. Few twigs lie scattered around the edge of the heronry. Evidence for the scarcity of twigs used for constructing nests includes: (1) the complete usage of all old twig nests by the end of the first week of egg-laying when some birds still had not constructed nests; (2) the rapid use and defense of artificially provided nests and twigs; and (3) the frequent stealing of twigs from unattended nests by all species, and from attended nests by Cattle Egrets. In some other colonies, nesting seems to be limited by the supply of nest material as the birds steal nest material from each other (Siegfried 1971a, Lancaster 1970) or from other species (Milstein et al. 1970, Dickerman and Juarez L. 1971). In other colonies, however, the herons neither steal nest material nor take over abandoned nests (Meanley 1955).

BREEDING SUCCESS

Competition for nests and nest sites, although interesting in itself, is far more important because of its effect on the breeding success of the species involved. Success can be measured in terms of the acquisition of territories and nest sites described above, clutch size, hatching success, and fledging success, all of which contribute to the overall success of the species.

Mean clutch sizes for Cattle Egrets in the New World have been reported as 2.42 (Alabama, Dusi and Dusi 1970), 2.86 (Florida, Weber 1975), 3.40 (this study), and 3.50 (Florida, Jenni 1969). Clutches in New Jersey are as large as those elsewhere in the U.S., which indicates that food resources are suf-

ficient in early May. Mean clutch sizes of other herons in the New Jersey colony were within ranges reported for these species (Palmer 1962).

Jenni (1969) reported that Cattle Egrets had the highest hatching success of the species present (Little Blue Herons, Louisiana Herons, and Snowy Egrets) in a Florida colony. My findings were similar. In both studies Snowy Egrets had the lowest hatching success. On Islajo Island, Snowy Egrets had a significantly lower hatching success in the area with Cattle Egrets (68%) compared to that without Cattle Egrets (88%). In Florida, 94% of the Snowy Egret eggs survived (Jenni 1969) compared to 67% in Georgia (Teal 1965). Percentage egg survival of Little Blue Herons and Louisiana Herons at Islajo Island did not differ from values in the literature (Meanley 1955, Jenni 1969).

Chick success is often not reported. When it is, the term "fledging" may mean the age of first flight, the age of leaving the nest, or some date in between. Furthermore, percentage of success and mean number of young per nest are not comparable because authors rarely state whether they included nests that failed to raise any young. In computing success, I included all nests in which any eggs hatched. In this study, the number of hatchlings per nest for Cattle Egrets at 14 days post-hatching averaged 2.54. Jenni (1969) reported a mean of 2.9 at 14 days post-hatching, and Weber (1975) reported a mean of 1.8 at "fledging." If fledging in Weber's case means leaving the nest at 5 to 6 weeks, then these data may be comparable. Dusi and Dusi (1970) reported lower "fledging" success (14.8%). I estimated "fledging" success (5 weeks post-hatch) to be 65% in the Islajo Island colony.

The success of other species in the Islajo colony varied (Table 7). I compared my data with Jenni's (1969) from Florida, where similar species composition and similar clutch sizes occurred. At 14 days of age, Little Blue Herons had similar percent success in New Jersey (69%) and Florida (72%). Louisiana Herons had lower percent success in New Jersey (59%) than in Florida (75%), and Snowy Egrets had even lower percent success in New Jersey (45%) than in Florida (72%). Jenni (1969) attributed the higher success of Cattle Egrets to their exploitation of a food source not used by the other herons. In addition, Cattle Egrets in Florida nested considerably later than the indigenous species. The lower success of native species in New Jersey may have been partly a product of the higher levels of aggression and disturbance during the nestling period. Cattle Egrets consistently chased and supplanted other species throughout the breeding period and even chased young Snowy Egrets.

Overall, Cattle Egrets in New Jersey appear more successful than the native North American herons and ibises. Cattle Egrets arrived slightly later than the indigenous species but laid eggs at the same time. Cattle Egrets, more aggressive than the other species, successfully defended higher perches than those of much larger species. They were also able to win more than half of their interspecific encounters despite their smaller size. I suggest that differences in nest site selection, egg-laying, and egg hatching success are due to direct competition. The Cattle Egrets are more able to acquire and defend nests and nest materials, and are more aggressive throughout the incubation period. Subsequent differences in success from hatching through fledging may be the result of increased disturbance due to the aggressiveness of Cattle Egrets and to differences in their ability to feed the young.

SUMMARY

I observed the behavior of Cattle Egrets in a mixed colony of herons and ibises in New Jersey, where all species laid eggs during the same period. All the herons competed for stick nests in the bushes from the previous year. Cattle Egrets acquired significantly more nests than predicted by their percent occurrence.

In two similar study areas, the native species situated the height of their nests according to body length. Little Blue Herons nested highest in the bushes, and Glossy Ibises nested on the ground. Cattle Egrets had a higher mean nest height than predicted by the body length relationship found for the native species.

Cattle Egrets were twice as aggressive as any other species, and their conflicts were more vigorous than those of other species. They fought more with each other and won more of their interactions with other species. Eighty percent of their interactions ended in pecking at the intruder, compared to less than 50% for all other species. Cattle Egrets supplanted most intruders at distances greater than 1 m from their nests, whereas, for other species most such actions were at distances less than 1 m. For the native species, larger species defending nests chased intruders that

landed farther from the nest than did smaller species. Larger intruding species could more closely approach the nests of others before being chased than could smaller species.

The mean number of young at hatching and the mean number of chicks surviving to 14 days indicated that Cattle Egrets had the highest breeding success while Snowy Egrets had the lowest breeding success.

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LITERATURE CITED

ADAMS, B., AND J. MILLER. 1975. The Absecon Bay heron colony. EBBA News 38:103–108.

BURGER, J. 1978. The pattern and mechanism of nesting in mixed-species heronries. *In* Wading birds. Research Report No. 7. Natl. Audubon Soc., New York.

CONNELL, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle, *Chthamalus stellatus*. Ecology 42:710–723.

CROSBY, G. T. 1972. Spread of the Cattle Egret in the Western Hemisphere. Bird-Banding 43: 205–212.

DICKERMAN, R. W., AND C. JUAREZ L. 1971. Nesting studies of the Boat-billed Heron *Cochlearius cochlearius* at San Blas, Nayarit, Mexico. Ardea 59:1–16.

DUSI, J. L. 1966. The identification characters of nests, eggs, and nestlings of some herons, ibises and anhingas. Alabama Birdlife 14:2–6.

DUSI, J. L. 1968. The competition between Cattle Egrets and Little Blue Herons. Alabama Birdlife 16:4–6.

DUSI, J. L., AND R. T. DUSI. 1967. The status of the Cattle Egret in Alabama, 1966. Alabama Birdlife 15:2–6.

DUSI, J. L., AND R. T. DUSI. 1968. Ecological factors contributing to nesting failure in a heron colony. Wilson Bull. 80:458–466.

DUSI, J. L., AND R. T. DUSI. 1970. Nesting success and mortality of nestlings in a Cattle Egret colony. Wilson Bull. 82:458–466.

DUSI, J. L., R. T. DUSI, D. L. BATEMAN, C. A. MCDONALD, J. J. STUART, AND J. F. DISMUKES. 1971. Ecological impacts of wading birds on the aquatic environment. Res. Bull. 5. Auburn Univ., Auburn, Alabama.

JENNI, D. A. 1969. A study of the ecology of four species of herons during the breeding season at Lake Alice, Alachua County, Florida. Ecol. Monogr. 39:245–270.

JENNI, D. A. 1973. Regional variation in the food of nestling Cattle Egrets. Auk 90:821–826.

JOHNSON, D. W. 1971. Niche relationships among some deciduous forest flycatchers. Auk 88:796–804.

KOPLIN, J. R., AND R. S. HOFFMANN. 1968. Habitat overlap and competitive exclusion in voles (*Microtus*). Am. Midl. Nat. 80:494–507.

LANCASTER, D. A. 1970. Breeding behavior of the Cattle Egret in Columbia. Living Bird 9:167–194.

MACARTHUR, R. 1959. On the relative abundance of bird species. Proc. Natl. Acad. Sci. U.S.A. 45:293–295.

MCKITRICK, S. R. L. 1975. Growth and development of nestling Cattle Egrets, *Bubulcus ibis*, and Little Blue Herons, *Florida caerulea*, in an upland heronry in Macon County, Alabama. M.S. thesis, Auburn Univ., Auburn, Alabama.

MEANLEY, B. 1955. A nesting study of the Little Blue Heron in eastern Arkansas. Wilson Bull. 67:84–99.

MILSTEIN, P. L., I. PRESTT, AND A. A. BELL. 1970. The breeding cycle of the Grey Heron. Ardea 58:171–256.

PALMER, R. S. 1962. Handbook of North American birds. Vol. 1. Yale Univ. Press, New Haven, Connecticut.

PEARSON, D. L. 1971. Vertical stratification of birds in a tropical dry forest. Condor 73:46–55.

ROBBINS, C. S., B. BRUUN, AND H. S. ZIM. 1966. Birds of North America. Golden Press, New York.

SCHOENER, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

SIEGFRIED, W. R. 1971a. The nest of the Cattle Egret. Ostrich 42:193–197.

SIEGFRIED, W. R. 1971b. Population dynamics of the Cattle Egret. Zool. Africana 6:289–292.

SIEGFRIED, W. R. 1971c. Plumage and moult of the Cattle Egret. Ostrich Suppl. 9:153–164.

SIEGFRIED, W. R. 1972. Breeding success and reproductive output of the Cattle Egret. Ostrich 43:43–55.

SIEGFRIED, W. R. 1973. Food requirements and growth of Cattle Egrets in South Africa. Living Bird 11:193–206.

TEAL, J. M. 1965. Nesting success of egrets and herons in Georgia. Wilson Bull. 77:257–263.

WEBER, W. J. 1972. A new world for the Cattle Egret. Nat. Hist. 82:56–63.

WEBER, W. J. 1975. Notes on Cattle Egret breeding. Auk 92:111–117.

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