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WADING BIRD COLONY FORMATION AND TURNOVER RELATIVE TO RAINFALL IN THE CORKSCREW SWAMP AREA OF FLORIDA DURING 1982 THROUGH 1985

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ABSTRACT.—Thirty-seven colony sites were used by nine species of nesting wading birds (Ciconiiformes) in the Corkscrew Swamp area (2320 km²) of southwestern Florida during a four-year census. Yearly turnover in colony site use averaged 30–40% with a maximum of 25 active colonies in any one year. The number of species nesting in a colony was correlated with the year to year stability of the colony. Fewer colonies formed during drought years. Colony formation occurred later in a season that followed 18 months of below normal rainfall. *Received 12 Feb. 1987, accepted 20 July 1987.*

The location and timing of nesting by colonial wading birds (Ciconiiformes) are correlated with surface water conditions and feeding opportunities (Kahl 1964, Kushlan et al. 1975, Kushlan 1976, Ogden et al. 1980). This study was designed to document the species abundance in an area around Corkscrew Swamp Sanctuary of the National Audubon Society in southwestern Florida, and to examine the relationship between rainfall, nesting, and colony locations. The goal of this study was to show responses by nesting wading birds to annual rainfall patterns on a regional rather than individual colony basis.

METHODS

The study site was within a 32-km radius (3217 km²) of the observation tower at Corkscrew Swamp Sanctuary in northern Collier County, Florida. Of this area, 27% was in the Gulf of Mexico and not suitable for wading birds. The four major natural habitats in the area were coastal lagoons with mangrove swamps, freshwater marshes, cypress swamps, and pine-live oak uplands. Much of the upland vegetation had been cleared for farming, ranching, and housing.

We conducted aerial censuses from fixed-wing, single engine aircraft flying at either 200 or 600 m above ground level along 10 transect lines spaced 6.4 km apart in the study area. We flew censuses monthly from March through August, 1982–1985, and during September 1982. To maximize our chances of locating all active colonies, the compass direction of the transects and the altitude flown was alternated between censuses. A constant altitude was maintained throughout a census until a colony was found. Colonies were circled at 200 m to determine activity. We estimated the total number of pairs present regardless of species. Numbers of Wood Storks (*Mycteria americana*) and Great Egrets (*Casmerodius albus*) could

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be separated from the total count. We did not attempt to count small dark herons. Snowy Egrets (*Egretta thula*) were not abundant in the area (pers. obs.), and we considered all small white herons to be Cattle Egrets (*Bubulcus ibis*). We classified colony sites into saltwater and freshwater habitats. The freshwater sites were further classified based on vegetation that supported the nests: tall-woody vegetation (>10 m), low-woody vegetation (<10 m), and mixture of tall- and low-woody vegetation.

We summed the maximum count of the number of pairs at each colony to determine the total number of breeding pairs in the study area. This procedure provides a minimum estimate of pairs because it does not account for failures before the peak count, or for birds that settle to nest after the count.

We calculated colony site turnover rates using the following formula (Erwin et al. 1981, McCrimmon and Parnell 1983):

$$T_n = \left(\frac{S_1}{N_1} + \frac{S_2}{N_2}\right)$$

where T_n is the turnover between two years; S_1 = number of sites occupied only at first census; N_1 = total number of sites, first census; S_2 = number of sites occupied only at second census; N_2 = total number of sites, second census. T can be converted to a percentage (T_{max} = 1). When more than one year exists between surveys, annual turnover rates can be calculated as T_n/number of years.

RESULTS

During the four-year study, 37 different colony sites were used by nesting wading birds (Table 1) (Fig. 1). In 1982 and 1984, 20 sites were active; in 1983, 25 were active; and in 1985, 14 sites were active. Of the 37 total colony sites, 6 were used in all 4 years, 7 were used in 3 years, 10 were used twice, and 14 were used once. The 6 sites active in all 4 years were in large relatively permanent wetlands. Two of these were found on islands in coastal lagoons, three were found in large natural marshes and swamps, and one site was located in a manmade water impoundment. Of the 6 sites used in all years, one coastal colony and two inland colonies moved short distances (<0.5 km) between years.

Colony turnover (see McCrimmon and Parnell 1983) was 32% between 1982–1983, 35% between 1983–1984, and 39% between 1984–1985. Comparing colony use in 1982 to 1984 showed a turnover rate of 55%. Between 1982 and 1985 the turnover rate was 51%. Three colony sites used in 1982 were abandoned during 1983 or 1984, but reused in 1984 or 1985 (Table 1). Of the 37 sites used during this study, ten were known to have been used previously. Two additional sites (Ft. Myers Airport, 1976; Big Hammock, 1980) were active in one of the previous six years but were not active during this study, although several hundred birds settled in Big Hammock during one month of 1985, but did not nest.

Nine species were found nesting in the area during the study (Table 2). White Ibis (*Eudocimus albus*) and Glossy Ibis (*Plegadis falcinellus*) nested

TABLE 1

ACTIVE COLONY SITES FROM 1982 THROUGH 1984 IN A 32-KM RADIUS CIRCLE AROUND CORKSCREW SWAMP SANCTUARY IN SOUTHWEST FLORIDA

Colony site	Year			
	1982	1983	1984	1985
1. Baucom Cypress	+[a]	+	+	+
2. Biggar	+	+	+	+
3. Camp Keais	+	+	+	+
4. Coconut Road	+	+	−	−
5. Corkscrew Cypress	+	+	+	+
6. Corkscrew Sawgrass	+	+	+	−
7. Cow Lake	−	+	−	−
8. East of Corkscrew Island	−	+	+	−
9. East of Cow Lake	−	+	−	−
10. East of Ft. Myers Jetport	+	+	−	−
11. East of Koreshan	+	+	−	−
12. Estero Bay	+	+	+	+
13. Halfmoon Pond	−	+	+	+
14. Immokalee	−	−	−	+
15. Lehigh Acres	+	+	−	+
16. New Pass	−	+	+	+
17. North of Catherine Island	+	−	−	−
18. North of Coconut Road	−	−	+	−
19. North of Lake Trafford	+	−	−	−
20. North of Sadie Cypress	+	−	−	+
21. Northeast of Felda	+	−	+	−
22. Northeast of Immokalee Airport	+	+	−	−
23. Northwest corner of Lake Trafford	−	−	+	−
24. Northwest of Lake Trafford	−	+	+	−
25. Sadie Cypress	−	+	−	−
26. South Estero Bay	+	+	+	+
27. South of Ft. Myers Jetport	+	+	−	−
28. South of Keri Tower	−	+	−	−
29. Southeast of Felda	−	−	+	−
30. Southwest of Berry Groves	+	+	−	−
31. Southwest of Corkscrew Tower	−	+	+	+
32. Southwest of Fire Tower	−	+	+	+
33. Southwest of Lake Trafford	−	−	+	−
34. Sunniland North	−	−	+	−
35. Sunniland South	+	+	+	−
36. 12-mile Slough	−	−	−	+
37. West of 12-mile Slough	+	−	−	−

[a] A + indicates the site was active that year, a − indicates no activity.

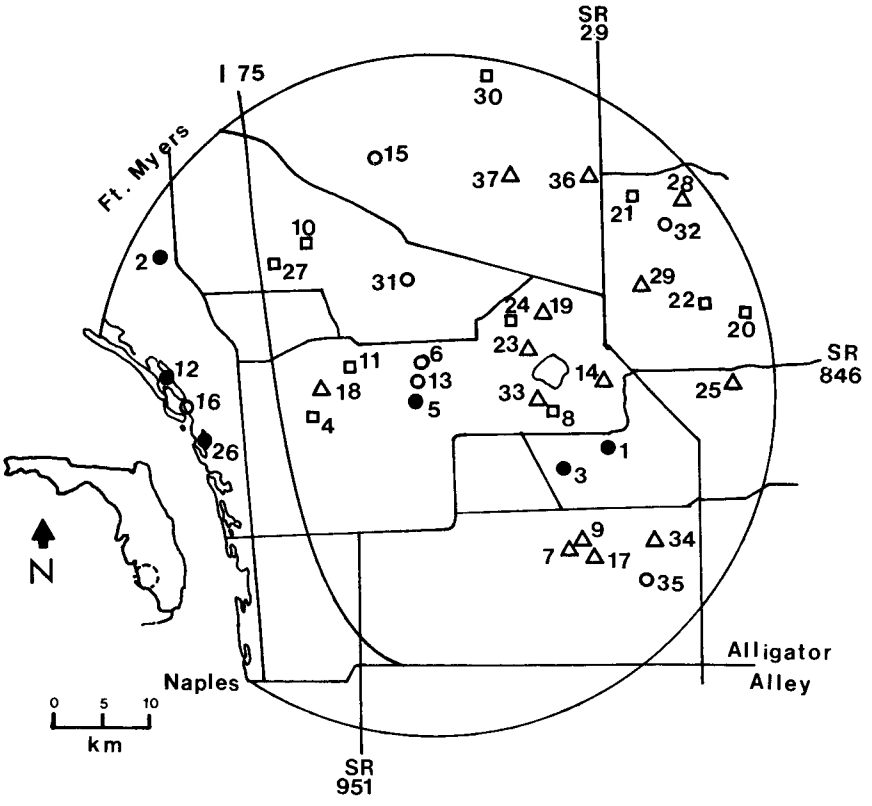

FIG. 1. Wading bird colony sites active during 1982–1985 in the Corkscrew Swamp area of southwest Florida. Sites are numbered as in Table 1 (closed circle = active 4 times, open circle = active 3 times, square = active twice, triangle = active once).

only in 1983. Wood Storks nested each year in Corkscrew Swamp Sanctuary, and in 1983 at Sadie Cypress Swamp. Cattle Egrets were found at the greatest number of colony sites each year (Table 2).

The number of species nesting at a site appeared to be related to the yearly use of the site ($\chi^2 = 20.6$, $P < 0.06$). Fewer than 3 species nested at all 14 sites used only once, compared with 3 or more species nesting at 83% of the 23 sites used more than once. More species tended to nest at sites that were active more often. Of the 14 sites used only once, 9 contained only one species, 4 contained 2 species, and the species present in one were not recorded (probably only Cattle Egrets). Cattle Egrets nested in at least eight of the 14 sites used only once. The one site used in all

TABLE 2

NUMBER OF ACTIVE WADING BIRD COLONIES AND NUMBER OF PAIRS NESTING IN A 32-KM RADIUS AROUND CORKSCREW SWAMP SANCTUARY

	Year							
	1982		1983		1984		1985	
Species	Colonies	Pairs	Colonies	Pairs	Colonies	Pairs	Colonies	Pairs
Wood Stork	1[a]	18[b]	2	2200	1	990	1	1010
Great Egret	12	650	14	400	12	350	8	210
Cattle Egret	13	8500	20	6500	15	10,000	9	2100
Little Blue Heron	11	+	13	+	7	+	2	+
Tricolored Heron	2	+	7	+	7	+	1	+
Snowy Egret	3	+	3	+	6	+	3	+
Great Blue Heron	6	15	12	15	4	6	6	35
White Ibis	0		1	+	0		0	
Glossy Ibis	0		1	+	0		0	
Total number of colonies and pairs	20	>9183	25	>9115	20	>11,346	14	>3355

[a] Number of active colonies with that species nesting.
[b] Estimated number of pairs nesting in study area, + indicates species present, but no total count made.

four years that contained only two species was Corkscrew Cypress, which had Wood Storks and Great Egrets.

The three coastal sites (<0.5 km from the coast), which had mangroves as the dominant vegetation, were active in 11 of the 12 colony years. Of the inland sites, five sites had only tall-woody vegetation (>10 m), six had a mixture of tall- and low-woody vegetation, and 23 sites had only low-woody plants (<10 m). For inland sites, the proportion of times a site was active varied significantly with the vegetation type ($\chi^2 = 15.8$, $df = 2$, $P < 0.001$). Pair-wise comparisons at the 0.01 level for significance showed that sites with a mixture of tall- and low-woody vegetation were active a significantly greater proportion of the time (83% of 24 colony-year records) than those with only low-woody vegetation (39%). Sites with only tall vegetation (60%) did not differ significantly from either low or mixed vegetation types in the proportion of times they were active. Cypress (*Taxodium* spp.) were the dominant plants at all but one of the colony sites that had tall-woody vegetation. Willows (*Salix* spp.) were the dominant plants at all except one of the sites with low-woody vegetation.

Nesting populations of wading birds fluctuated greatly among the four years (Table 2). About 9000 pairs nested in 1982 and 1983, 11,000 pairs nested in 1984, and 3300 pairs nested in 1985. Much of the total and annual variation was due to changes in the numbers of nesting pairs of Cattle Egrets (Table 2).

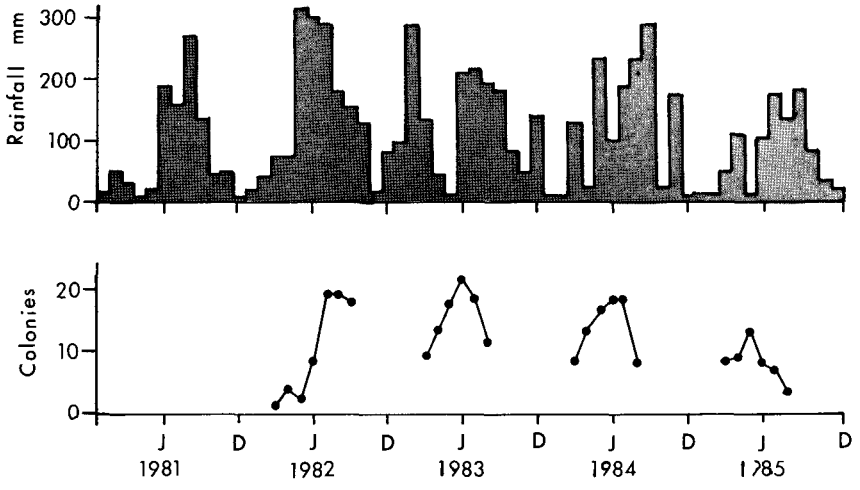

FIG. 2. Monthly rainfall (mm) at Immokalee Airport from January 1981 through August 1985, and the number of active wading bird colonies during 1982 through 1985 in the Corkscrew Swamp area of southwest Florida (D = December, J = July).

In 1982 the number of colonies active each month peaked between July and September (Fig. 2). In 1983 the peak was in June, in 1984 it was in June–July, and in 1985 a much lower peak occurred in May. In 1982, numerous colonies were still active in September, whereas the number of active colonies had decreased substantially by August in the other 3 years. Fewer than 500 pairs were recorded nesting during March through June of 1982, whereas over 4000 pairs had begun nesting by May of 1983. Although colonies began to form in 1985, as they had in 1983 and 1984, the number of pairs nesting in 1985 was substantially lower than the number of birds that first appeared in colony sites. In addition, in 1985, birds briefly occupied four additional sites, but abandoned each before they began to nest (counts not included in totals for 1985).

Variation in the timing and intensity of nesting seems to be related to the annual pattern and variation in rainfall (Fig. 2). Southwest Florida is characterized by a dry winter–spring and a wet summer (Thomas 1974). In southwest Florida, monthly rainfall averages 40–60 mm from November through April and increases to 180–210 mm from June through September (Thomas 1974, N.O.A.A. 1981–1985). The calendar years of 1981 and 1985 were dry with less than 1000 mm of rainfall at Immokalee Airport (N.O.A.A. 1981, 1985) (Fig. 2). Total annual rainfall ranged from 1450 to 1700 mm in 1982–1984 (N.O.A.A. 1982, 1983, 1984) (Fig. 2).

The delay in the onset of nesting exhibited in 1982 compared with

1983–1984 appears related to the dry year in 1981 and dry winter–spring of 1982 (Fig. 2). Only 225 mm of rain fell from January 1982 to 21 May 1982 (compared to 560 mm in 1983 and 354 mm in 1984 during the same period). When more typical rains began in early summer 1982, wading birds that had not nested earlier began to do so. Presumably the rains triggered nesting activity by reflooding nesting habitats (waders in south Florida rarely nest over dry habitats) and by increasing feeding habitats. That nesting wading birds failed to increase to the levels of the previous three summers in 1985 was almost certainly caused by the relatively small amounts and the lateness of the summer rains (Fig. 2). During 1985 at Immokalee Airport, only 9 mm fell in May and 107 mm in June, which was substantially less than the rainfall in May and June of 1982 (617 mm), 1983 (221 mm), or 1984 (338 mm). In 1985, colonies formed initially but most were abandoned by the end of June when many of the sites were dry. The dryness probably resulted in a lack of suitable nest sites. Through mid-July, most of the study area was quite dry with no water under many of the willow "heads" used for nesting and the marshes were dry. Few feeding herons and egrets were observed throughout the circle. Although marshes finally became wet in late July and August 1985, nesting did not resume.

DISCUSSION

Only 16% of the colonies in our census area were active in all four years. For colonies throughout peninsular Florida that were censused at least five times between 1976 and 1982, we found that of 46 coastal sites (estuarine and marine), 80% were active in at least five years, whereas only 39% of the 79 inland sites (freshwater) were active that often (Nesbitt et al. 1982; National Audubon Society, unpubl. data). Black et al. (1984) using data from Nesbitt et al. (1982) found that 83% of the 52 colony sites in southwestern Florida used in 1976 were also used in 1977 and 1978. For coastal colonies along the Atlantic Coast from Florida to Maine, Custer et al. (1980) found that 91% of the 186 active colonies in 1975 were also active in 1976. Similarly, other studies have found lower turnover rates for wading bird colonies in coastal North Carolina and coastal Massachusetts (Erwin 1978, McCrimmon and Parnell 1983).

Two factors contribute to making our turnover estimates higher than others. First, because we ran transects across our study area, we were confident that we found all active colonies in each year. For other studies done over larger areas the researchers were less certain that all active colonies were located annually, and therefore, they looked at turnover by considering only those colonies that had been censused in all years. This would make their turnover estimates lower than they actually may have

been (e.g., Black et al. 1984). The second explanation for our higher turnover estimates is that coastal colonies have a much higher probability of being active each year than do inland colonies (National Audubon Society, unpubl. data). Coastal colonies are in habitats in which the total area of inundated wetlands surrounding each colony is more consistent among years than is the case for many inland freshwater sites. Some of the inland colony sites we observed were used in years when they were flooded and not when they were dry.

The timing of the maximum number of active colonies varied among years. Ogden (1978), using data collected by R. P. Allen, reported that the historical pattern for southern Florida was for colonies to form in the spring, with peak number of colonies active during May and June. During the mid-1970s, more colonies were active later in the summer with peak numbers of active colonies occurring in June and July (Kushlan and White 1977, Ogden 1978). Our data show both patterns. Following the extremely dry 1981 summer and dry winter–spring of 1981–1982, we found a higher frequency of summer nesting after the initiation of rains during May–June 1982. During the relatively normal rainy seasons (see Thomas 1974) of fall 1982 through fall 1984, we found nesting starting earlier than in 1982 (Fig. 2). During the extremely dry year of 1985, little nesting occurred, and much of that was not successful. Because many birds abandoned colonies before they would have completed nesting in 1985, peak nesting occurred in May.

The quantity and timing of rainfall affects the chances of successful nesting by wading birds by determining the availability of suitable colony sites and by influencing the availability of food. Nests were placed in trees over water in all freshwater sites except one island site in a borrow pit. When these sites were not flooded, the birds did not nest in them (pers. obs.). Secondly, rainfall influences the amount of food in the environment and the food's availability to the birds. Average or above average rainfall during the preceding summer probably allows fish populations to increase to high levels (Kahl 1964, Kushlan et al. 1975). A dry period results in the concentration of fish into pools where herons, egrets, and storks feed on them. This seasonal dry period appears to be critical for successful nesting by wading birds in southwest Florida (Kahl 1964, Kushlan et al. 1975, Kushlan 1976, Browder 1984). Although Cattle Egrets are terrestrial feeders, rainfall may trigger nesting not only by increasing the availability of suitable nesting sites, but also by increasing the abundance of their primary prey, orthopterans (Lowe-McConnell 1967, Fogarty and Hetrick 1973, Siegfried 1978). Thus, the high summer peaks in nesting were largely caused by heavy Cattle Egret nesting during "normal" summer rainfall years.

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