THE INFLUENCE OF ANNUAL VARIATION IN RAINFALL AND WATER LEVELS ON NESTING BY FLORIDA POPULATIONS OF WADING BIRDS

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INTRODUCTION

Colonial wading birds are highly mobile species known to move throughout large geographical regions in response to environmental factors. Both the locations of nesting colonies and the number of birds in them are influenced by year-to-year changes in the locations of wader concentrations. Kushlan (1976) reported that White Ibis (*Eudocimus albus*) changed nesting sites in and adjacent to the Florida Everglades almost annually, and that the sequence in which colony sites were utilized corresponded with changes in feeding areas by the birds prior to each nesting season. In a later paper Kushlan (1977) also showed that the number of White Ibis that nested in southern Florida changed considerably from year to year. More birds nested during the two wet years, 1972 and 1973, than during the dry year 1971. Similar shifts in numbers of nesting birds and locations of colonies have been reported for the White-faced Ibis (*Plegadis chihi*) in Nevada and Utah (Ryder, 1967), for the Scarlet Ibis (*Eudocimus ruber*) in Trinidad and Surinam (ffrench and Haverschmidt, 1970), and for the Sacred Ibis (*Threskiornis aethiopicus*) in Ethiopia (Urban, 1974).

Although colonial species of ibis are frequent participants in colony relocations, other colonial waders apparently make similar movements. Byrd (1978) reported a tendency for wading birds banded as nestlings to return to colonies in the same geographical region in following years, although some banded birds returned in summer to colonies of regions that were great distances from where they had fledged. He listed Cattle Egrets (*Bubulcus ibis*) banded as nestlings in Alabama that appeared in Texas in a subsequent breeding season, a Black-crowned Night Heron (*Nycticorax nycticorax*) banded in a Saskatchewan colony and later recorded on the Atlantic coast, and a Glossy Ibis (*Plegadis falcinellus*) banded in a Virginia colony that was later found breeding in Maine. Circumstantial evidence of shifts from one area to another by herons and egrets has also been provided by repeated annual censuses of some colonies over a period of several years, where numbers of pairs may change considerably between consecutive years, while long-term trends by each species may be much more stable. The implication is that birds utilize a particular colony site only when local conditions are favorable. Such a pattern of use

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was shown, most strongly for Cattle Egrets and Louisiana Herons (*Hydranassa tricolor*) at Alligator Bay, North Carolina (Grant, 1971), and for Little Blue Herons (*Florida caerulea*) and Great Egrets (*Casmerodius albus*) at McKinney's Pond, Georgia (Shanholtzer *et al.*, 1970). Ogden (1978) provided additional examples of relocation of colonies by large numbers of waders, and pointed out the difficulty of determining population trends because of the high mobility of these species.

It appears that a major factor that influences waders to use different colonies in different years is food availability in wetland habitats. Kushlan (1978, 1979) reviewed wading bird feeding ecology and feeding behavior, and discussed the factors that determine colony and feeding locations. He suggested that, barring changes in colony site habitat, location of food resources is the major factor that determines colony sites. Urban (1974) speculated that there was a correlation between timing of nesting, food supply, rainfall, and the numbers of pairs of birds in Sacred Ibis colonies. Our observations in Florida suggest a strong correlation between the timing of nesting and the location of colonies and surface water levels. Although the extent and duration of surface flooding is an obvious factor that relates to colony locations, we assume that the influence of water on food resources is probably of ultimate importance.

As a basis for understanding regional population dynamics and long-term population trends by waders in the southeastern coastal plain, this study was designed to ascertain the frequency and magnitude of shifts in nesting sites by regional wading bird populations, the relationship between those shifts and climatological factors, and the effect of these relationships on nesting success. Specifically, we need to answer the following questions:

1. What are the number of birds and the location of nesting sites for each species of colonial wading bird?
2. Can we determine population trends, either on a regional or species basis, by comparing our census data with historical census data?
3. What are the characteristics of nesting sites presently being used by each species?
4. Are the annual variations in numbers and locations of nesting waders related to climatological factors?
5. Are the seasonal, annual, and regional variations in species productivity related to colony characteristics, colony locations, and climatological factors?

In this paper we report on our initial analysis of one phase of the project, the relationship between colony locations and size and annual climatological factors. These data were obtained during aerial surveys of all active nesting colonies in peninsular Florida, exclusive of the western Panhandle. We considered that a geographically large study area is essential in order to assess wading bird dynamics on a regional basis. For example, if the number of waders declines in one colony, or in one type of colony, does the number concurrently increase at other sites?

Methods

We organized this study into two phases. The first consisted of a series of aerial surveys conducted by fixed-wing, single-engine aircraft during April–May, repeated in June–July, for three consecutive years, 1976 through 1978. Objectives of these surveys were to locate active nesting colonies, determine species composition and make gross estimates of numbers of each species, and determine various characteristics (vegetation substrate, presence or absence of standing water, proximity to human activities, etc.) of each site. North Florida surveys were flown by Nesbitt, east-central and southeastern Florida (south to Broward Co.) by Kale, and west-central and south Florida by Ogden. Colony data from Everglades National Park were provided by James Kushlan and Oron Bass.

The second phase of this study, to begin in 1979, will consist of ground studies to more accurately determine numbers of birds in selected representative colonies, and to correlate nesting success with colony type and annual climatological conditions. Limited aerial surveys will also be conducted during this second phase.

Results and Discussion

For the following analyses we selected five

herodius), Great Egret, Wood Stork (*Mycteria americana*), Cattle Egret, and White Ibis. The first three species listed were chosen because they nest conspicuously in the tops of woody vegetation, and the latter two species because they are white-plumaged and nest in easily recognizable dense aggregations. These characteristics of visibility are prerequisites for accurate aerial surveying of colonial birds.

Figure 1 shows the location of 295 wading bird nesting colonies that were active in at least one year in each region (southern, central, northern) of the peninsula. In some cases a symbol on the map represents more than one colony. The 295 colonies represent 211 inland and 84 coastal sites. We define coastal colonies as those in saltwater or brackish zones, including several colonies a few miles inland in the broad mangrove forest in extreme southwestern Florida. Data from a few south Florida colonies were not available in time for inclusion in these analyses.

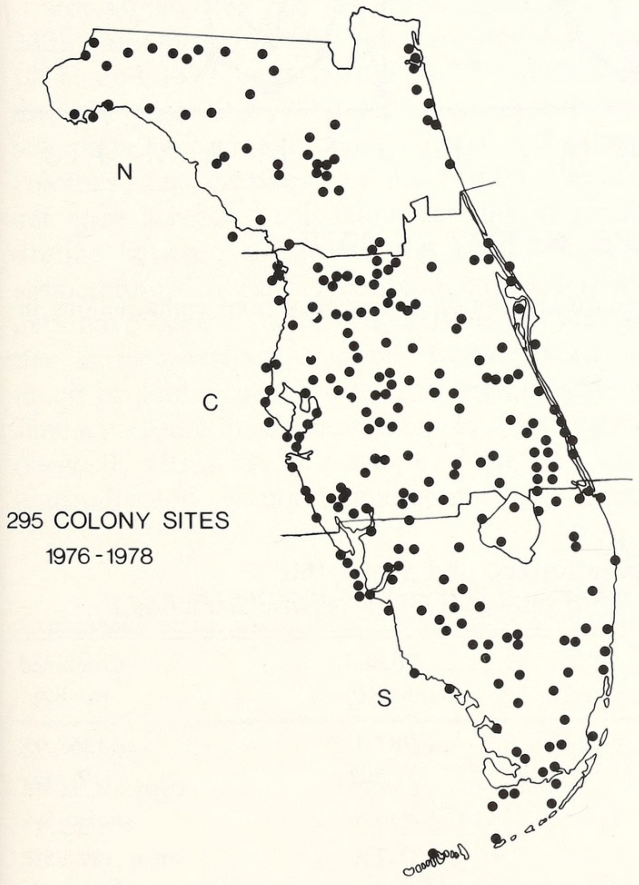

Figure 1. Location of 295 active nesting colonies of colonial wading birds, 1976–1978.

Rainfall data in each region are presented in Figure 2, which compares the historical mean rainfall with mean rainfall for each of the years, 1976 through 1978, as calculated from rainfall at eight scattered stations throughout Florida. These stations were Tallahassee, Jacksonville, Daytona Beach, Orlando, Tampa, Fort Myers, Belle Glade, and Homestead. Data are presented for the months January through July, the major wader nesting period, including the one or two months immediately preceeding actual nesting by most species. The combined means for each region were derived by adding the monthly mean rainfall from each station within that region.

In this preliminary analysis, we have not used surface water data because surface water conditions in most interior swamps and marshes in Florida are directly correlated with rainfall, and thus the extent and depth of water in fresh water wetland habitats increase proportionately with increasing rainfall. In coastal colonies surface water is related to sea level and varies imperceptibly between breeding seasons.

These data show that 1976 rainfall rates were slightly on the dry side of the historical means, that rainfall during 1977 was well below the means, and that 1978 was slightly wetter than the means. It is important to note the relative pattern of rainfall during the three years, as most changes in number and location of waders nesting each year appear to be related to this rainfall pattern.

Table 1 presents the combined total number of pairs of Great Egrets, Cattle Egrets, and White Ibis, and the mean number of pairs per colony for inland and coastal colonies in each year, 1976–78. Great Blue Herons and Wood Storks were omitted from this analysis because these two species, especially the latter, often nest separately in single-species colonies. These data were compiled from 82 colonies that were active all three years, and that contained one or more of these three conspicuous species. Colonies that were not detected until the second or third year of the survey were excluded from this comparison because in most cases we could not determine whether these colonies were inactive during the first survey year or were active and not detected.

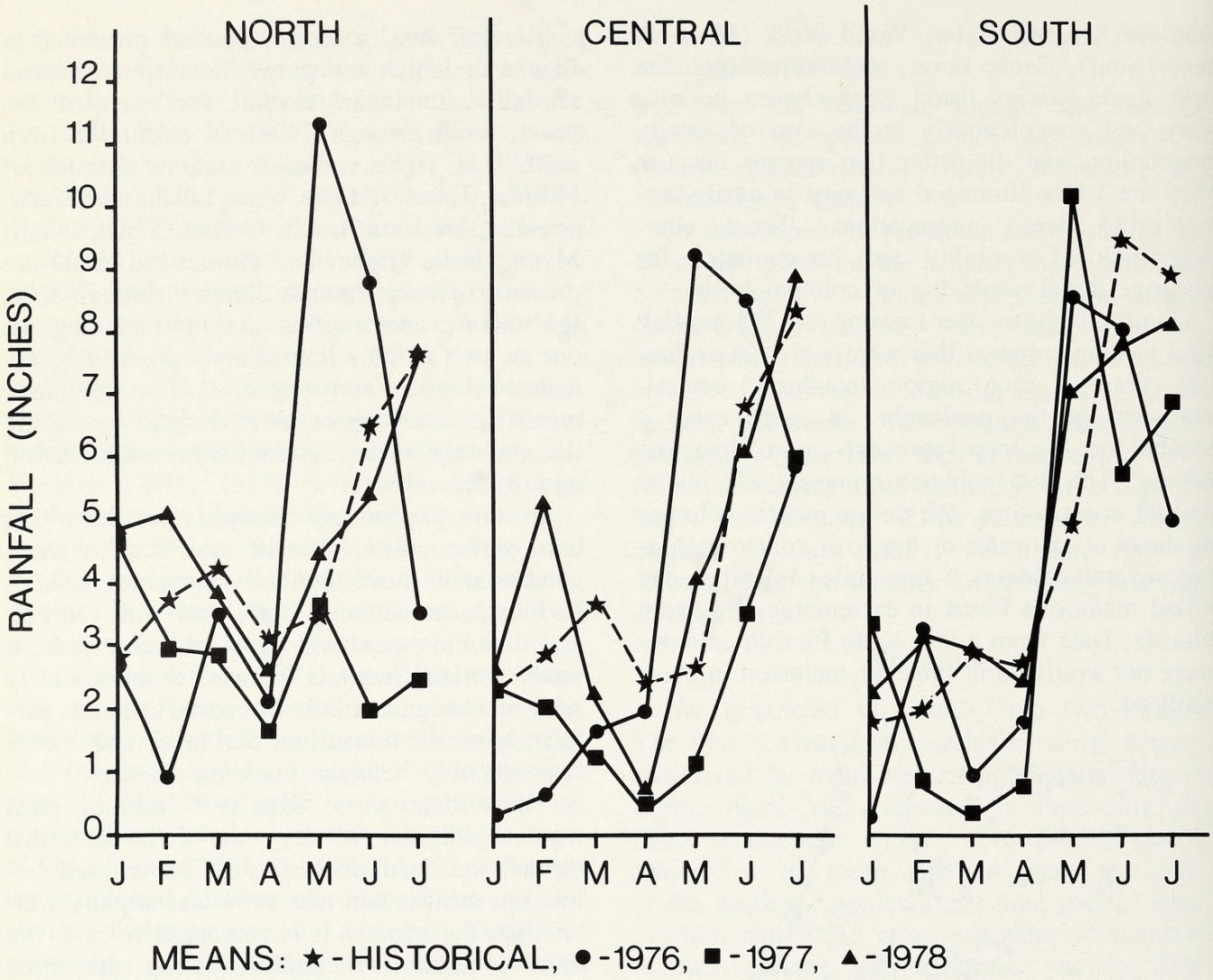

Figure 2. Comparison of historical mean rainfall in peninsular Florida with means from eight stations in 1976, 1977, and 1978.

TABLE 1
Nesting Pairs of Great Egrets, Cattle Egrets, and White Ibis
(in inland and coastal colonies which were active 1976 through 1978 in peninsular Florida.)

		Inland (n=42 colonies)	Coastal (n=40)	Combined (n=82)
1976	Mean No. of pairs	1922.1	787.5	1368.6
	Total No. of pairs	80,730	31,502	112,232
1977	Mean No. of pairs	1468.1	779.9	1132.4
	Total No. of pairs	61,663	31,196	92,859
1978	Mean No. of pairs	1634.4	1164.8	1405.3
	Total No. of pairs	68,646	46,595	115,241

Similar numbers of nesting pairs were present in the two near-average years, 1976 and 1978, with slightly more pairs present in the wetter year 1978. Approximately 20,000 fewer pairs nested during the dry year 1977, with the reduction occurring entirely in the inland colonies. The relative stability of coastal colonies when compared to that of the inland colonies is shown by the total number of colonies active in 1976 that remained active in 1978 (Table 2). Fewer than one-half (46%) of inland colonies were still active in the third year, while 78% of the coastal colonies remained active.

TABLE 2
Numbers of 1976 Colonies Still Active in 1978

	Inland	Coastal
1976	94	61
1978	44	48
Active in 1978	46%	78%

The relationship between rainfall and nesting for each species of wader is revealed by comparing the total number of inland and coastal colonies that contained these species, the mean number of pairs per colony, and the total numbers of pairs in all colonies in the dry and wet years, 1977 and 1978. These data are presented separately for each of the five species analyzed (Tables 3, 5–8).

For Great Blue Herons (Table 3), a total of 2328 pairs nested in 66 colonies in the dry year 1977, and 1397 pairs nested in 75 colonies in the wet year 1978. The reduction in number, 931 pairs, occurred in both coastal and inland colonies, but primarily in the former. We do not have a ready explanation for this dramatic decline between a dry and wet year, although temperature differences between the two years may have been a factor. Great Blue Herons are the earliest-nesting colonial wading bird in much of peninsular Florida, and lay as early as January (sometimes December) in some years (Howell, 1932). It is possible, therefore, that unusually low winter temperatures may affect either the timing of nesting or the number of pairs that attempt nesting. Table 4 shows deviations from historical mean temperatures at six Florida stations scattered throughout the peninsula for the main Great Blue Heron nesting months, January through April in each year 1976–78. Temperatures in 1976 were near normal, 1977 showed a cumulative 8.9 degrees below normal, and 1978 showed a cumulative deviation of 14.4 degrees below normal. Temperature and rainfall are compared with the pattern of Great Blue Heron nesting in Figure 3. Only colonies active in all three years are included in this comparison, so that the total number of pairs and colonies is less than that indicated in Table 3. Figure 3 shows a positive correlation between the number of pairs of Great Blues in inland colonies and cumulative temperature deviations from January through April, and a reverse correlation between numbers of pairs in coastal colonies and mean annual rainfall from January through July. More birds nested in inland colonies in the warmest spring of 1976, and fewer in the coldest spring of 1978, while more birds nested in coastal colonies in the dry year 1977, and fewer in the wet year 1978.

These relationships may not be fully understood until ground studies are concluded; how-

TABLE 3
Comparison of 1977 and 1978 Great Blue Heron Nestings in Peninsular Florida

	1977			1978		
	Inland	Coastal	Total	Inland	Coastal	Total
No. colonies	33	33	66	34	41	75
Mean no. pairs per colony	29.79	40.76		20.59	17.00	
Total no. pairs all colonies	983	1345	2328	700	697	1397
% total	42%	58%		50%	50%	

TABLE 4
Deviations from Historical Mean Temperatures for January through April at Six Florida Stations

	1976					1977					1978				
	J	F	M	A	Cum. Sta.[a] Deviation	J	F	M	A	Cum. Sta.[a] Deviation	J	F	M	A	Cum. Sta.[a] Deviation
Tallahassee	−5.2	2.0	2.6	−1.1	−1.7	−8.7	−5.6	3.6	−0.5	−11.2	−7.8	−9.6	−4.0	−1.6	−23.0
Gainesville	−3.4	2.3	4.5	−1.2	2.2	−8.7	−4.1	5.2	−0.5	−8.1	−5.2	−7.7	−1.7	−0.1	−14.7
Orlando	−3.8	2.2	4.5	0	2.9	−9.7	−4.1	3.8	−0.7	−10.7	−3.5	−5.7	0.4	2.1	−7.5
Tampa	−3.8	1.3	4.5	−1.4	0.6	−9.2	−4.3	4.9	−0.5	−9.1	−5.4	−8.6	−1.8	0.3	−15.5
Ft. Myers	−2.6	0.3	3.0	−2.1	−1.4	−7.6	−3.7	2.4	−1.9	−10.8	−4.3	−7.5	−2.8	−0.5	−15.1
Belle Glade	−1.9	0.5	3.9	−0.2	2.3	−5.7	−1.6	4.5	0.7	−3.5	−3.6	−6.0	−0.8	−0.2	−10.6
Monthly Mean Deviation [b]	−3.4	1.4	3.8	−1	0.7[c]	−8.2	−3.9	4.0	−0.5	−8.9[c]	−4.9	−7.5	−1.7	0.0	−14.4[c]

[a]Cumulative station deviation derived by totaling January-April deviations for each station.
[b]Monthly mean deviation derived by averaging station deviations for each month.
[c]Four-month total of monthly mean deviations.

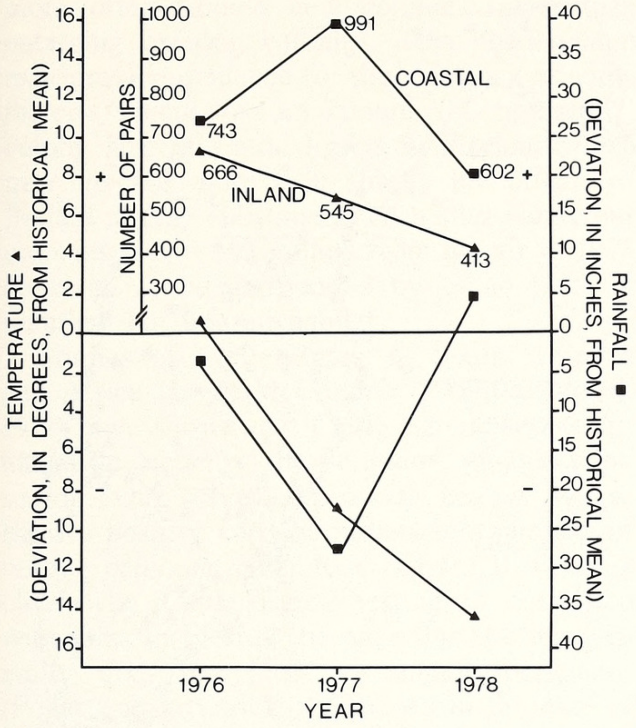

Figure 3. Correlations between rainfall, temperature, and number of nesting pairs of Great Blue Herons in peninsular Florida, 1976 through 1978.

ever, it appears that Great Blue Herons in peninsular Florida are a relatively mobile population that shifts nesting locations in response to several complex environmental factors. Two patterns appear to be evident from these three years of observations. First, the increase in numbers in coastal colonies in 1977 may be a result of birds forced to move from inland sites where many swamps were dry. Secondly, extremely cold temperatures late in winter, such as occurred in 1978, may have depressed the total number of Great Blues in both coastal and inland colonies. We do not know if fewer pairs initially attempted to nest in 1978, or if greater nesting failures resulted from the cold weather early in the nesting season before our surveys were conducted. The fact that the decline in numbers in 1978 was less in inland colonies than it was in coastal colonies may have been a result of better nesting conditions inland due to higher water levels.

With the four remaining species—Great Egret, Cattle Egret, Wood Stork, and White Ibis—patterns of nesting were compared only with rainfall, because these species initiate nesting in most of peninsular Florida later than Great Blue Herons, generally between late February and April when temperature is usually not a limiting factor. Thus far in our analyses, we have detected no relationships between low winter temperature and numbers or location of nesting sites by these four species, as seemed to occur with the Great Blue Heron.

The dry year-wet year nesting pattern of Great Egrets is shown in Table 5. Total numbers of nesting pairs in the two years were similar, 11,546 *vs.* 10,755. The greater rainfall of 1978, however, created numerous inland nesting sites that were not available to, or at least not used by, Great Egrets in 1977. Seasonal marshes and swamps, ponds, and low ground in pastures, all dry in 1977, were flooded in 1978. The result was a shift from coastal to inland sites by approximately 1500 or more pairs, and a 30% increase in inland colonies. The widely scattered nature and small size of many of the new inland colonies in 1978 suggests that it is very unlikely that all colonies were located during our surveys.

TABLE 5
Comparison of 1977 and 1978 Great Egret Nestings in Peninsular Florida

	1977			1978		
	Inland	Coastal	Totals	Inland	Coastal	Total
No. colonies	53	47	101	76	50	126
Mean no. pairs per colony	110.7	120.7		93.6	72.7	
Total no. pairs all colonies	5869	5677	11,546	7119	3636	10,755
% total	51%	49%		66%	34%	

The distribution of Great Egret colonies in 1977 and 1978 is presented in Figure 4, which shows that most new colonies formed in central and south Florida, mainly located in a region of prairie, pasture, and phosphate-mining country and extending south into the Big Cypress Swamp. Colonies that contained Great Egrets both years were primarily those at the relatively stable coastal sites. As with most other wading birds in Florida, Great Egrets nest in woody vegetation over dry ground only when they nest on islands. We do not know if the shift to inland sites in 1978 was because the higher surface water levels created more nesting sites over water or because feeding conditions in the area were improved, but we suspect a combination of both factors. Cypert (1958) reported that the number of Great Egrets in the Okefenokee Swamp region is primarily regulated by local surface water conditions, with more birds scattered throughout the marshes when they are well flooded. A comparison of 1978 nesting success by Great Egrets at two inland colonies during spring nesting (relatively low water) and at one inland colony during summer (higher water) revealed that 50% of 76 nests in the spring colonies produced full-sized, feathered nestlings, while only two of 16 (13%) nests in the summer colony produced large young (B. Warren, unpub. data). If this pattern is representative, which we doubt, it would suggest that high water years may provide good nesting habitat, but not necessarily provide good feeding conditions. In the case of the summer colony, water was generally 8 to 15 inches or more in depth over most of the country within several miles of the colony.

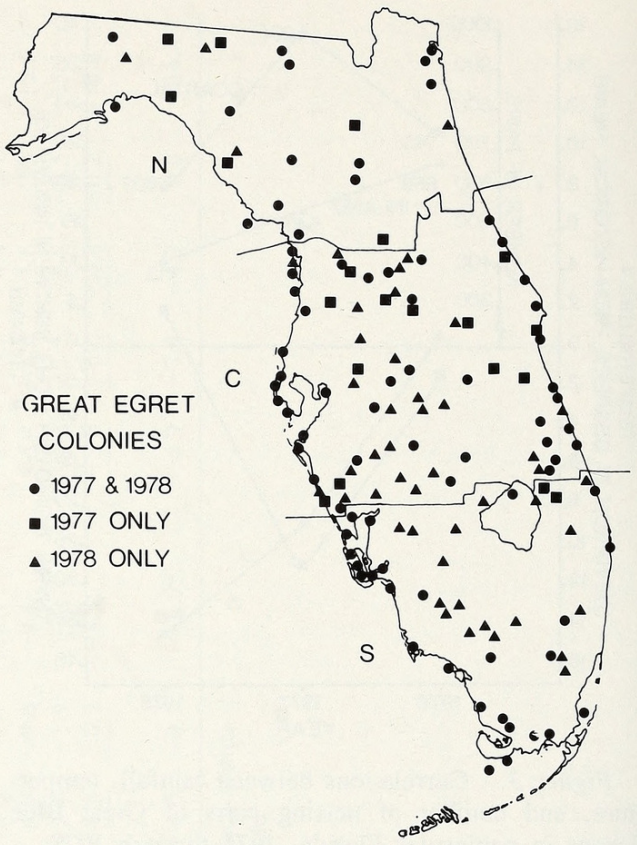

Figure 4. Distribution of Great Egret nesting colonies in peninsular Florida in 1977 and 1978.

The number of pairs and number of colonies of Cattle Egrets in both inland and coastal sites showed considerable increase, 38% and 35%, respectively, in the wetter year 1978 (Table 6). The higher inland numbers resulted primarily from establishment of new colonies, while the increase in the coastal zone was caused by greater numbers of pairs in the existing colonies. The mean colony size in inland colonies did not increase, suggesting that Cattle Egrets

TABLE 6
Comparison of 1977 and 1978 Cattle Egret Nestings in Peninsular Florida

	1977			1978		
	Inland	Coastal	Totals	Inland	Coastal	Totals
No. colonies	67	17	84	108	28	136
Mean no. pairs per colony	1353.1	700.0		1227.8	1138.3	
Total no. pairs all colonies	90,658	11,900	102,558	132,608	31,875	164,483
% total	88%	12%		81%	19%	

more often formed new colonies rather than enlarging existing colonies. This phenomenon may provide evidence for the existence of some factor(s) regulating maximum (= optimum?) colony size of Cattle Egrets in Florida, which may involve more than simply the effects of limited nesting substrate at each site. Numerous colonies that we examined from the air in 1978 appeared to be surrounded by broad belts of identical but unused habitat.

Studies of Cattle Egrets in South America and Africa (Lowe-McConnell, 1967; Siegfried, 1971) have shown that Cattle Egrets were stimulated to nest by the initiation of the rainy season. Our survey appears to be the first to show a positive correlation between numbers of nesting pairs and magnitude of rainfall. It is not clear why Cattle Egret nesting is correlated with rains in Florida, because this species generally does not feed on aquatic organisms (Fogarty and Hetrick, 1973). As in the case of Great Egret nesting, higher rainfall results in a greater number of potential nesting sites, and numerous 1978 colonies were located in sites that were dry in 1977. The correlation between rainfall and initiation of nesting in Cattle Egrets may be related to their origin in the dry regions of Africa (Siegfried, 1978), although wading birds (especially Cattle Egrets?) appear to be sufficiently flexible in many other respects to suggest that this consideration is probably unimportant.

The numbers of nesting pairs and active colonies of Wood Storks were both higher in the dry year 1977 (Table 7). This species has been intensively studied in Florida (Kahl, 1964; Ogden *et al.*, 1976; Browder, 1978). The stork's grope feeding technique for obtaining food requires the presence of relatively high concentrations of small fish, especially when food requirements are greatest during the nesting season. Favorable feeding conditions occur when fish are concentrated by dropping water levels, such as happens during annual dry seasons and in dry years. Studies in the Florida Everglades show good correlation between drying rates and timing of colony formation by storks (Kushlan *et al.*, 1975). Colony formation is delayed, or storks are most likely to desert established colonies, when water levels are high or are rising. Thus, a pattern of increased nesting in the drier year 1977 was not surprising. The change in percentage of storks nesting in inland versus coastal colonies between the two years, as shown in Table 7, is primarily a result of the failure of three major coastal colonies in the Everglades region to form in 1978. Our aerial surveys covered essentially the entire breeding range of the Wood Stork in the United States (excluding 1–3 very small intermittent colonies in southeastern Georgia). Hence our counts confirm that in years when habitat conditions are poor for stork feeding, not all adult storks attempt to nest.

Both the total number of pairs of White Ibis and the number of colonies that contained ibis were similar during 1977 and 1978 (Table 8). Between the two years, mean colony size declined in inland sites and increased in coastal sites, and the percentage of ibis in coastal colonies increased during the second year.

Although our figures do not indicate a great amount of shifting of nesting sites by White Ibis, it does appear that they may have re-

TABLE 7
Comparison of 1977 and 1978 Wood Stork Nestings in Peninsular Florida

	1977			1978		
	Inland	Coastal	Totals	Inland	Coastal	Totals
No. colonies	15	5	20	13	2	15
Mean no. pairs per colony	194.3	281.6		145.2	200.0	
Total no. pairs all colonies	2915	1408	4323	1888	400	2288
% total	67%	33%		82%	18%	

sponded to the heavier rainfall in 1978 by either forming smaller inland colonies or moving to the coastal colonies. Just why this may have occurred is uncertain, although ibis, like storks, are more efficient feeders when water levels are low or dropping. Kushlan (1976, 1978, 1979) reported that peak nesting by White Ibis in subtropical zones occurs during dry seasons when food is concentrated, and that heavy rains during dry seasons can cause colony abandonment. Ibis colonies in Florida typically form during March, late in the annual dry season. The spring of 1978 in peninsular Florida was characterized by above normal rainfall during February, which presumably either dispersed ibis food or increased the depths of water over nearby feeding grounds to the point where ibis could not feed immediately prior to the normal time of colony formation. Although heavy rainfall affects all wetlands, coastal estuaries subject to tidal influence are less affected than inland basins and may provide better feeding habitats when water is high inland. An indication that this is so is seen annually in the Everglades region, where feeding flocks of ibis move to the coast during the summer rainy season. Thus in 1978 some ibis may have shifted to coastal colonies in response to the heavy February rains. Further indication that inland marshes in 1978 did not provide adequate food for ibis, at least locally, was the absence of ibis at the Andytown East colony in the interior Everglades, where they nested in large numbers in prior years. In addition, they also abandoned another inland site in the Okaloacoochee Slough when many of their nests already contained eggs.

Conclusion and Summary

The three years of aerial surveys over peninsular Florida demonstrated that both total numbers of nesting pairs and the location of nest colonies varied between years in response to rainfall, and for at least one species, in response to low temperature as well. Although it appears that wading birds may move over large geographical regions when selecting nesting sites, precise information about the distance that individual birds move will require marking large numbers of birds in such a way as to recognize colony of origin.

Each of five species of wading birds analyzed here showed different responses to the 1977–78 rainfall pattern. Total numbers of Great Egrets and White Ibis remained approximately the same between dry and wet years, with the majority of egrets in inland colonies and an increase in numbers of ibis in coastal colonies in the wetter year. Great Blue Herons showed a shift to coastal colonies in the dry year, while the number of nesting pairs was reduced during the breeding season of 1978 following the coldest winter on record. Higher rainfall in 1978 was correlated with a sharp increase in the number of nesting pairs of Cattle Egrets, and a reduction in the number of nesting Wood Storks.

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TABLE 8
Comparison of 1977 and 1978 White Ibis Nestings in Peninsular Florida

	1977			1978		
	Inland	Coastal	Totals	Inland	Coastal	Totals
No. colonies	12	15	27	15	14	29
Mean no. pairs per colony	1048.7	1301.2		689.2	1680.9	
Total no. pairs all colonies	12,585	19,518	32,103	10,339	23,533	33,872
% totals	39%	61%		31%	69%	

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Literature Cited

Browder, J. A. 1978. A modeling study of water, wetlands, and Wood Storks. *In* A. Sprunt, IV, J. C. Ogden, and S. Winckler (eds.). Wading Birds. National Audubon Society Res. Rep. No. 7: 325–346.

Byrd, M. A. 1978. Dispersal and movements of six North American Ciconiiforms. *In* A. Sprunt, IV, J. C. Ogden, and S. Winckler (eds.). Wading Birds. Nat. Audubon Soc. Res. Rep. No. 7: 161–185.

Cypert, E. 1958. The relation of water level to populations of Common Egrets in the Okefenokee Swamp. Oriole 23(1):9.

ffrench, R. P. and F. Haverschmidt. 1970. The Scarlet Ibis in Surinam and Trinidad. Living Bird 9: 147–165.

Fogarty, M. J. and W. M. Hetrick. 1973. Summer foods of Cattle Egrets in north central Florida. Auk 90: 268–280.

Grant, G. S. 1971. Three-year study of the heronry at Alligator Bay, North Carolina, Chat 35(1): 5–9.

Howell, A. H. 1932. Florida bird life. Coward-McCann, Inc. New York. 579 pp.

Kahl, M. P. 1964. Food ecology of the Wood Stork (*Mycteria americana*) in Florida. Ecol. Monogr. 34: 97–117.

Kushlan, J. A. 1976. Site selection for nesting colonies by the American White Ibis *Eudocimus albus* in Florida. Ibis 118: 590–593.

Kushlan, J. A. 1977. Population energetics of the American White Ibis. Auk 94: 114–122.

Kushlan, J. A. 1978. Feeding ecology of wading birds. *In* A. Sprunt, IV, J. C. Ogden, and S. Winckler (eds.). Wading Birds. Nat. Audubon Soc. Res. Rep. No. 7: 249–297.

Kushlan, J. A. 1979. Feeding ecology and prey selection in the White Ibis. Condor 81:376-389.

Kushlan, J. A., J. C. Ogden, and A. L. Higer. 1975. Relation of water level and fish availability to Wood Stork reproduction in the southern Everglades, Florida. U.S. Geol. Surv. Open File Rep. No. 75-434. Tallahassee, Florida.

Lowe-McConnell, R. H. 1967. Biology of the Immigrant Cattle Egret *Ardeola ibis* in Guyana, South America. Ibis 109: 168–179.

Ogden, J. C. 1978. Recent population trends of colonial wading birds on the Atlantic and Gulf coastal plains. *In* A. Sprunt, IV, J. C. Ogden, and S. Winckler (eds.). Wading Birds. Nat. Audubon Soc. Res. Rep. No. 7: 137–153.

Ogden, J. C., J. A. Kushlan, and J. T. Tilmant. 1976. Prey selectivity by the Wood Stork. Condor 78: 324–330.

Ryder, R. A. 1967. Distribution, migration and mortality of the White-faced Ibis (*Plegadis chihi*) in North America. Bird-Banding 38: 257–277.

Shanholtzer, G. F., W. J. Kuenzel, and J. J. Mahoney. 1970. Twenty-one years of the McKinney's Pond Rookery. Oriole 35: 23–38.

Siegfried, W. R. 1971. Feeding activity of the Cattle Egret. Ardea 59: 38–46.

Siegfried, W. R. 1978. Habitat and the modern range expansion of the Cattle Egret. *In* A. Sprunt, IV, J. C. Ogden, and S. Winckler (eds.). Wading Birds. Nat. Audubon Soc. Res. Rep. No. 7: 315–324.

Urban, E. K. 1974. Breeding of Sacred Ibis *Threskiornis aethiopica* at Lake Shala, Ethiopia. Ibis 116: 263–277.

Comments:

Unidentified: There are several parameters interacting with several species. You probably have considered this; but in the case of Cattle Egrets, they apparently like to nest in associations over water. On the one hand, water may stimulate large numbers to breed; on the other hand, it will also either directly or indirectly produce more prey items for Cattle Egrets. If you take this strategy and apply it to Great Egrets, it doesn't necessarily work.

Ogden: I am not sure that I understand yet why a lot more water will produce more food for Cattle Egrets. At least in these subtropical areas both Cattle Egrets and Great Egrets are capable of breeding for a good part of the year, and what actually triggers nesting may be the creation of nesting sites, the summer rains for instance. Of these 280 sites, except for colonies that were on islands, I think 57% of them were in vegetation over standing water. So, at least in Florida, it looks like they require either iso-

lation by being on an island, or they require vegetation over standing water. Both Cattle Egrets and Great Egrets might have been stimulated to breed by the creation of nesting sites. I agree that once they start nesting the rising water might have different effects on food for the two species of egrets.

Blacklock: Colonial waterbirds have been counted in Texas since 1967. One observation of particular interest is that during dry periods many colonial waterbirds apparently do not attempt to breed. Breeding populations during wet periods are almost double that for populations during dry periods.

Thompson: In 1957, R. P. Allen wrote a paper on populations of wading birds entitled, "An Urgent Appeal for Information on the Wading Birds," *Audubon Field Notes,* 11: 458–460. He documented population declines in numerous species nesting in Florida up to that time. He also described a sudden influx of Great Egrets into the upper Midwest in 1947 and 1948. Apparently egrets were displaced from Florida and established new colonies far to the north. This is another example of the need for a large study area when monitoring population trends.

Ogden: Yes, it may turn out that the peninsular of Florida is not a big enough study area for us to see the full extent of seasonal or year-to-year shifts in wader populations.