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POPULATION TRENDS IN SOME FLORIDA BAY WADING BIRDS

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Abstract.—Roseate spoonbills (*Ajaia ajaja*), Reddish Egrets (*Egretta rufescens*), and Great White Herons (*Ardea herodias occidentalis*) have unique subpopulations that are largely restricted to Florida Bay. All three species are believed to have had relatively large populations in Florida Bay, but the birds were virtually extirpated from the area between the late 1800s and the mid-1930s by human harvesting for food and feathers. After the birds were protected, they reestablished small populations that initially grew quickly. The Great White Heron population in Florida Bay increased from a low of about 20 individuals after the 1935 hurricane to a population of 800–900 resident adults in the early 1960s. As many as 400 additional birds (juveniles and possibly seasonal migrants) were present in winter censuses. The population remained at about that level through the 1960s, after recovering from a 20–40% decrease caused by a 1960 hurricane. After 1968, the population was surveyed only once, in 1984, when about the same number of birds were censused. The Reddish Egret recovered more slowly from total extirpation around 1935 to an estimated 200–250 adults in the late 1970s. Casual observations in the 1980s suggest the population has remained at about that level. Roseate Spoonbills showed an exponential recovery from just a few individuals up to a maximum of 2400 breeding birds by 1978–79. Subsequent censuses (1984–1986) revealed only about 800–900 nesting adults.

The virtual absence of pre-1880s data precludes comparing present populations with those of the pristine environment. However, the most recently surveyed population of each of these species seems to be at a lower density than was historically present. The recent decline in the spoonbill population and low reproductive success of the Great White Heron population are causes for concern about the future of the populations. These findings point out the importance of continued monitoring and analysis of population trends. *Received 11 March 1988, accepted 26 Nov. 1988.*

Florida Bay supports one of the most species-rich piscivorous avifaunas in North America. The most diverse group, the Ciconiiformes (long-legged wading birds), is represented by 14 species (Table 1). In this paper, we review population data for three wading bird species, Roseate Spoonbill (*Ajaia ajaja*) Reddish Egret (*Egretta rufescens*), and the white phase of the Great Blue Heron, the Great White Heron (*Ardea herodias occidentalis*), that are closely associated with the Florida Bay ecosystem. All three species are dependent on the bay and associated euryhaline habitats (here-

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TABLE 1

CICONIIFORMES REPRESENTED IN FLORIDA BAY, MONROE COUNTY, FLORIDA

Common name	Scientific name
Least Bittern	*Ixobrychus exilis*
Great Blue/White Heron	*Ardea herodias occidentalis*
Great Egret	*Casmerodius alba*
Snowy Egret	*Egretta thula*
Little Blue Heron	*E. caerulea*
Tricolored Heron	*E. tricolor*
Reddish Egret	*E. rufescens*
Cattle Egret	*Bubulcus ibis*
Green-backed Heron	*Butorides striatus*
Black-crowned Night-Heron	*Nycticorax nycticorax*
Yellow-crowned Night-Heron	*N. violaceus*
White Ibis	*Eudocimus albus*
Roseate Spoonbill	*Ajaia ajaja*
Wood Stork	*Mycteria americana*

after we lump the euryhaline, mangrove-dominated habitats as part of the Florida Bay ecosystem) for nest sites and foraging substrate. In the eastern United States, about 50% of the Great White Herons and Reddish Egrets and 90% of the Roseate Spoonbills nest within Florida Bay. Because of their small, geographically restricted populations, and their high trophic positions in relatively complex food webs, these species are likely to be particularly vulnerable to habitat changes in south Florida.

The environmental sensitivity of wading birds, coupled with the relative ease with which they can be counted, has resulted in their being proposed as biological indicators of habitat quality (Custer and Osborn 1977, Powell and Powell 1986). The three species we have selected to analyze should function well as indicators because all have small populations that are concentrated in relatively few breeding colonies. These characteristics make them likely to respond quickly to environmental changes in a measurable fashion.

Our objectives were to determine population changes for adults of each species and to provide ecological interpretation of identified trends.

METHODS

The Great White Heron exists in Florida Bay in what is currently recognized as two distinct color morphs, the typical "blue" form, Great Blue Heron, and an all white form, Great White Heron. While the color morphs coexist throughout the bay, the Great White Heron has been the focus of attention because the south Florida coastal ecosystem appears to be the epicenter of its distribution; Florida Bay supports roughly half of the entire Florida population. The other 50% are distributed predominantly south in the lower keys (Robertson unpubl. data), with a few breeding records north along the east coast to Biscayne Bay and along the Gulf coast to Tampa (Robertson 1978a). We have limited our comments to the white morph because there are insufficient data to analyze population trends of the blue morph.

Great White Herons were surveyed from fixed-wing aircraft flown in an irregular grid designed to cover all islands and shallow mud banks in the bay. The large size and white color of this heron make individuals highly visible from low level (150–400 m) reconnaissance. Aerial counts were assumed to record the entire population, however, the accuracy of the surveys has never been tested. Potential sources of error include: diffculty in distinguishing between Great White Herons and Great Egrets (*Casmerodius albus*) in large breeding colonies, overlap or voids in coverage of extensive mud banks in the western bay, and difficulty in locating diurnally resting birds on mangrove islands in the eastern bay. The presence of large fledglings that were generally indistinguishable from adults made it impossible to determine population size during the protracted breeding season. Aerial counts (up to three in one year) were made intermittently between 1935 and 1968 and again in 1984 (Appendix I). Aerial surveys of the Great White Herons were estimates of the total population.

Reddish Egrets are difficult to detect from the air, so population estimates of this species have been based primarily on ground counts. Population estimates prior to 1977 were rough estimates based on partial nest counts and the number of birds observed foraging on banks. For two nesting seasons beginning in 1977–78, one of us (RTP) attempted to make complete counts of breeding Reddish Egrets in Florida Bay. Because the nesting season is protracted and Reddish Egrets may nest solitarily, a variety of methods were used to locate nesting pairs: previously known sites were checked repeatedly throughout the year, foraging adults with brightly colored soft parts (indicating breeding condition) were followed back to breeding sites, and vocalizations from begging young were used to identify islands with active nests. Furthermore, because adults were not individually recognizable, it was necessary to adjust the number of nests found to account for the possibility of multiple nesting attempts. Toward this end, two population values were generated: one based on the total number of nests observed, and a second controlling for duplication, based on the number of nests that successfully produced young. As mentioned, the first value is likely an overestimate because it includes renestings; the second is likely to underestimate by assuming that all pairs are successful.

Beginning in the 1930s, the number of spoonbill breeding pairs generally was determined by one of two methods. Both methods derive population estimates of breeding birds only and do not include the nonbreeding portion of the population. During most years, ground counts of active nests were made (Appendix II). In contrast to the Reddish Egrets, spoonbills nest in compact colonies and have a highly synchronous nesting season. Therefore, the ground counts produce highly accurate measures of the breeding population based on single annual censuses. Post-breeding censuses were made immediately after the last young had fledged to avoid inclusion of second nest attempts and minimize the loss of nests through stick thievery by later nesting wading birds. Nesting attempts that occurred two to three months after the initial breeding effort were assumed to be second attempts. For several years, primarily in the 1960s and early 1970s, the spoonbill population in the bay was estimated by aerial reconnaissance (Appendix II). Spoonbills nesting in dense mangroves are difficult to accurately detect from the air, however, so these counts must be considered as rough approximations of population size.

The survey techniques used for each species produced somewhat different results because for the Great White Heron all individuals were counted, while Roseate Spoonbill estimates were derived exclusively from nest counts, and Reddish Egret estimates were derived from a combination of both. For the latter two species, it is not known what percent of each population is reproductively active during a given year.

RESULTS

Overview.—Insufficient data are available to estimate wading bird populations that existed in Florida Bay prior to human influence on the system. Audubon reported that during his travels in relatively pristine Florida Bay in 1832 that at Sandy Key there were "flocks of birds that covered the shelly beaches" and "the air was darkened by whistling wings" (Proby 1974). Beyond these superlatives, the only insight Audubon provided regarding population sizes was through his reports of numbers of birds he saw in groups or the numbers he was able to shoot at one site. The next available reports date from the late 1800s when more quantitatively oriented ornithologists began to visit south Florida (Maynard 1881, Scott 1889, 1891). By that time, however, the millinery trade had focused on bird feathers as a source of adornment, and wading bird populations were devastated by plume hunters. Even after the plume hunting was largely terminated in 1912, Florida Bay colonies continued to be disrupted by local inhabitants and commercial sponge fishermen who collected eggs and nestlings for food (Sprunt 1935). Due to the early and persistent history of exploitation, there are no known sources from which to quantify pristine wading bird populations in Florida Bay. Consequently, for each of the three target species, we can only point to indicators of population size prior to man's influence.

Great White Heron.—Quantitative records of the Great White Heron population prior to human disturbance are nonexistent, with Audubon again providing the only information that allows us to speculate on population size. Though Audubon gave no estimate of the *Ardea* population, his reference to Great White Heron flocks indicates that the species was abundant in the bay. Audubon (Proby 1974) reported flocks "sometimes a hundred or more being seen together" to be a regular occurrence on the flats. For the next 100 years after Audubon's visit to the keys, data on *Ardea* populations in Florida Bay are limited primarily to nest records on isolated bay keys (Scott 1890, Bent 1926, Holt 1928). These data, plus the aggregation of records from a large series of clutches collected by Court in 1925, indicate the existence of a relatively large population at that time. Court collected at least 29 Great White Heron clutches from Palm Key and estimated there were 15 additional nests present on Oyster and Clive keys in western Florida Bay. Holt and Sutton (1926) reported Great White Herons were "common on the keys and mud banks off Flamingo" in

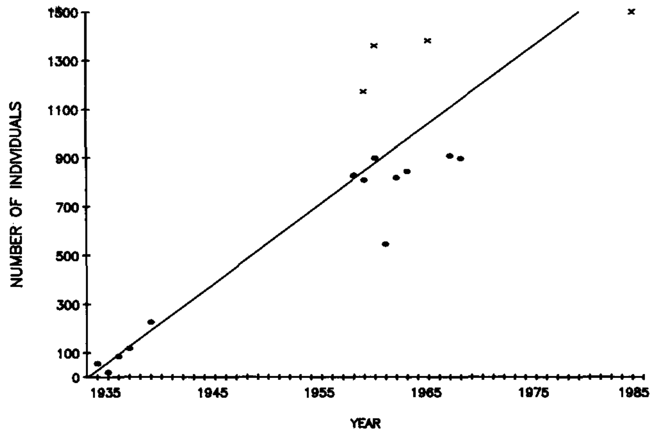

FIG. 1. Population growth of Great White Heron (*Ardea herodias occidentalis*) in Florida Bay. Data were collected from fixed-wing aircraft by three different observers (see Appendix I). Round points are summer censuses, X's mark winter censuses. Line is fitted to censuses through summer 1960 (Y = 28.6 + 32.7X).

1924. It is known, however, that as the human population grew in the mainline keys and areas adjacent to Florida Bay, the use of *Ardea* as a food source by humans had a major impact on the population (Holt 1928, Sprunt 1935). Sprunt (1935) made the first systematic survey of the entire bay and recorded only 56 individuals (Fig. 1, Appendix I; the area between the Florida mainland and Key West had 211 individuals). Sprunt concluded that this was the entire population for the area. However, it is unlikely that his 3.25-h survey could have canvassed all relevant habitat, as aerial surveys made at similar flight speeds by one of us (WBR) in the 1960s required about 50 h to cover the same area thoroughly. In any case, on the basis of his surveys, Sprunt predicted the Great White Heron would be extirpated within five years due to harvesting of nestlings for food. In the fall of 1935, the bay population was further reduced by a major hurricane that passed across the upper keys and Florida Bay. A month after the hurricane, Sprunt (1935) again surveyed the population and found only 20 Great White Herons in Florida Bay and 146 birds throughout the species' range as far west as Key West. In April 1936, Sprunt again flew the transects and recorded 39 Great White Herons in the bay (Sprunt 1936a). The next aerial survey in October 1936 recorded 86 birds (Sprunt 1936b). Sprunt (1937, 1939b) made aerial surveys of the population in September 1937 and January 1939, each of which revealed a continuing recovery of the population (Fig. 1).

Extensive surveys of the *Ardea* population were again made by one of us from 1959 through 1968 (Fig. 1; WBR, in 1958 through 1967; JCO in 1967, 1968). In 1959 and summer of 1960, WBR counted between 809 and 898 Great White Herons in Florida Bay. In August, 1960, a second major hurricane (Donna) passed across the upper keys and Florida Bay (Gentry 1974). This storm had a large impact on the *Ardea* population, as had the hurricane in 1935. A survey two months after the hurricane yielded 30–40% fewer Great White Herons in the bay than had been present the previous two years (Fig. 1). It is not known what portion of that decline resulted from mortality as opposed to relocation. However, more than 100 Great White Heron carcasses were found in limited searches of storm racks on keys in the bay and along the south shore of the mainland after the hurricane (WBR unpubl. data). This large number of carcasses indicates that much of the population reduction was the result of storm-induced mortality. The path of the hurricane had its greatest impact within the bay, and presumably bird mortality was primarily in that area. Therefore, the portion of the Great White Heron population that was located in the lower keys (estimated to be about half of the total) would have been largely unaffected, and storm-induced mortality might have been as much as 20% of the total population. Two years after the 1960 hurricane, the Florida Bay Great White Heron population had recovered to at least 90% of the pre-hurricane level. Continued surveys through the 1960s indicated a stabilization of the population at between 800–900 birds in summer and 1200–1400 birds in winter (Fig. 1). After 1968, the Great White Heron population was not surveyed again until the winter of 1984 by WBR, when 1509 birds were counted in the Bay. That count was similar to winter counts made in the 1960s (Fig. 1).

Reddish Egret.—Historically, Reddish Egrets nested in coastal colonies north to Clearwater Harbor, Pinellas Co., and probably North Anclote Key, Pasco Co., on the Gulf Coast, and were particularly abundant in Tampa Bay and Charlotte Harbor. On the Atlantic Coast, they were found at Pelican Island in the Indian River and possibly at Cape Canaveral, Brevard Co., but were not reported from other localities and may have been relatively uncommon. They were also widely distributed in Florida Bay and probably the lower keys (Audubon 1843, Maynard 1881).

Indications of Reddish Egret abundance in pristine Florida Bay are limited to anecdotal reports. When Audubon visited Florida Bay in 1832, he was told that "though still plentiful, this species was much more so when the keys were first settled" (Audubon 1843). He reported seeing as many as "twenty or thirty, sometimes as many as a hundred" foraging on shallow flats (Audubon 1843). Audubon found Reddish Egrets easy to collect, killing 12 in less than half an hour at one colony (possibly one of the Peterson or Buchanan Keys; see Audubon 1843). He also reported watching another hunter take 28 in an hour. In 1872, Maynard (1881) found white-morph Reddish Egrets abundant among the "interior keys" of Card Sound, an area he termed the "stronghold" of the "species" (*"Ardea pealii"* or Peale's Egret, then considered distinct from *"A. rufescens,"* the Reddish Egret). On the inhabited "outer keys," Maynard found "Peale's Egrets" "not uncommon" and the dark phase nearly absent. While Audubon's and Maynard's data are not sufficient to estimate the Reddish Egret population in the bay, they do indicate the presence of a substantially larger population than at present.

In the two decades following 1890, Reddish Egrets declined sharply in Florida, but are known to have persisted in Florida Bay at least until 1908. Scott (1889) still considered the species locally common in Florida, an opinion supported by Jamison (1891) who found about 60 nests in a small heronry in Pine Island Sound (Lee County) in 1891. However, one year later Scott (1892) reportes it rare in the Caloosahatchee region. In March 1902, Howe and King (1902) found only two Reddish Egrets (near "Tavanier Bank, Bay of Florida," probably the area now referred to as Upper Cross Bank) in a two-day trip in Florida Bay, and noted that this species still suffered from plume hunting. Bent and Job spent two weeks in April–May 1903 searching Florida Bay and Cape Sable for nesting herons with Audubon wardens Guy Bradley and William Burton. In separate accounts, Bent (1926) reported only scattered individuals, and Job (1905) noted that "several" birds flushed from one key—possibly Porjoe Key. Broadhead (1910) described Reddish Egrets as "not uncommon" at Upper Matecumbe Key in the spring of 1906, where she saw two birds "brought in." Chapman (1908) found six Reddish Egrets foraging at the head of Snake Bight (possibly Garfield Bight incorrectly identified) near Flamingo on 29 March 1908. In contrast to these estimates of a very low Reddish Egret population, Guy Bradley, chief Audubon warden for the area, estimated in 1904 that 300 Reddish Egrets survived, from Key West to Florida Bay and north along the Gulf Coast to Chokoloskee (Allen 1954, 1955). However, no details of Bradley's report have survived, so the basis for this estimate is unknown.

Soon after 1908, Reddish Egrets apparently disappeared entirely from Florida Bay and the rest of Florida (Howell 1932; Allen 1954, 1955). The species was not reported again from Florida Bay until 23 April 1937, when two birds in non-breeding plumage were found at Upper Matecumbe Key (Davis 1937). The following year a nest was discovered at Bottlepoint (now called Bottle) Key (Desmond 1939). For the next few years, the known population in Florida Bay was 4–5 birds (Fig. 2, Sprunt 1938, Poor 1941, Stimson 1942). During this time the species was limited to

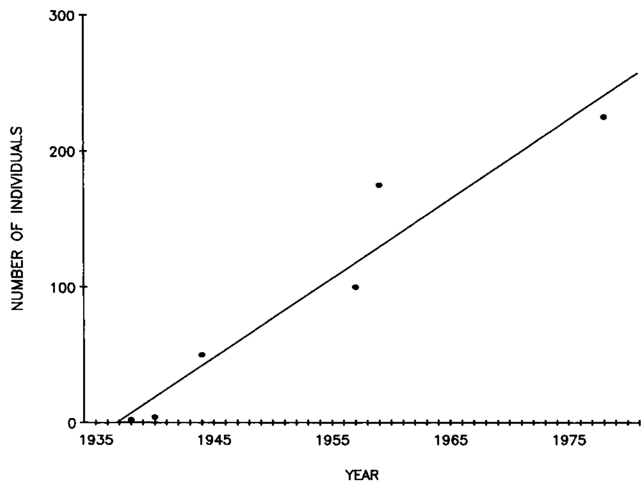

FIG. 2. Population growth of Reddish Egret (*Egretta rufescens*) in Florida Bay following recovery from probable extirpation in 1930s. Equation for line $Y = -12.1 + 6.0X$.

eastern Florida Bay, notably Bottle, Low, Stake and Manatee keys. Reddish Egrets also returned to the lower keys, with 2–5 birds reported near Key West in 1939–40 (Greene 1946). By 1944, Reddish Egrets had increased to perhaps 50 birds in eastern Florida Bay, with 38 recorded at one (unnamed) key (Baker 1944). The population continued to increase through the 1950s; Allen (1954, 1955) estimated 150 birds in Florida Bay and the keys in 1954 (Fig. 2). In 1959, Allen estimated that the Reddish Egret population was not over 200 individuals (Palmer 1962). Based on current distribution, we estimate the bay population would have been between 150 and 175 birds.

Reddish Egrets were not censused again until the mid-1970s, when the entire Florida population was roughly estimated to be about 300 individuals, with most nesting occurring in Florida Bay (Robertson and Kushlan 1974, Robertson 1978b). In 1977–78, 168 nest were located on 17 different keys (Table 2). Seventy-four of those nests were successful. The large number of failed nesting attempts and a nine-month breeding season makes it likely that renesting was wide-spread and that the Reddish Egret population was substantially lower than 168 pairs. At the same time, some pairs were probably unable to produce young throughout the season in spite of multiple nesting attempts. Therefore, a population estimate based on the 74 successful pairs would be a low estimate. On the basis of these considerations, we suggest a range of 100–125 pairs or 200–250 adults as a breeding population estimate for that year (Fig. 2). Repro-

TABLE 2
NUMBER OF NESTING ATTEMPTS BY REDDISH EGRETS IN FLORIDA BAY IN 1977–78 AND 1978–79

Key	1977–78	1978–79
Frank	54	32
Tern	38	39
Porjoe	28	25
Foxtrot/Bob Allen	15	10
Buchanan	9	10
Manatee	5	4
Bottle	3	6
Cowpens	3	2
Sandy	3	ND
Oyster	2	ND[a]
Peterson	2	1
Butternut	3	ND
Stake	1	3
Crane	1	1
Duck	ND	1
West	1	ND
Pigeon	1	ND
C. Jimmie	ND	1
Total	169	135

[a] ND = no data, status of colony unknown.

ductive data from the following season support that conclusion. In 1978–79, only 135 nesting attempts were recorded (Table 2), but nest success was generally high (RTP unpubl. data). Therefore, fewer second nesting attempts would have been expected, and most of the 135 nesting attempts probably represented different pairs.

There have been no attempts to survey the Reddish Egret population since 1980. Casual observation of active nests in the 1980s indicate that the major breeding sites in the eastern bay (Tern, Porjoe, and Buchanan keys) are still active.

Roseate Spoonbill.—Reports from travelers and naturalists in the mid-1880s indicated that a large spoonbill population existed in south Florida (summarized in Allen 1942). Major spoonbill colonies prior to 1850 included coastal colonies at Indian Key in Tampa Bay, Marquesas Keys, Boca Grande Key, and Pelican Island in the Indian River, and inland colonies at Alligator Lake, Cuthbert Lake, Corkscrew rookery, Okaloacoochee Slough, 17 Mile Swamp, Lake Poinsett (Allen 1942), and the Big Cypress (Sprunt 1939a). Scott (1889) reported that spoonbills had once

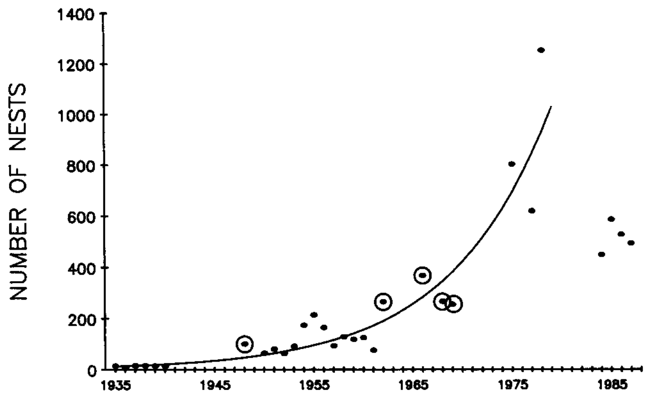

FIG. 3. Population growth of Roseate Spoonbill (*Ajaia ajaja*) in Florida Bay. Simple points are total number of nests counted on ground visits to colonies; encircled points are estimates derived from aerial counts which are relatively inaccurate. Equation for line during growth period (up to 1978–79) Y = 13.22 × exp(0.099X).

"bred in enormous rookeries" around Cape Romano and that large numbers of birds were present in that region as late as 1880. Further indication of colony size is evidenced by Bryant's (1859) report of a plume hunter killing sixty spoonbills in a day at Pelican Island. Historical records documenting spoonbill abundance in Florida Bay are even more limited than for the rest of the state. Audubon refers to spoonbills breeding among the Florida Keys (in Allen 1942) and foraging along the mangrove edges of Sandy Key during his trip through the keys in 1832 (Audubon 1960).

During the last half of the 1800s, and continuing through the early 1900s, the spoonbill population was greatly reduced. Although prohibition of plume hunting and protection of nesting colonies began in the early 1900s, the decline continued until, by the early 1930s, fewer than 200 pairs were thought to nest in Florida. These birds nested sporadically in small numbers (6–10 pairs) in mixed species colonies at Cuthbert Lake, Lane River, Shark River, and Charlotte Harbor (Allen 1942) and in one larger colony located at Bottle Key in eastern Florida Bay (Grimes and Sprunt 1936). By 1935, continued human predation on adults and eggs had probably eliminated all colonies except the Bottle Key colony which had been reduced to 15 pairs (Allen 1963) (Fig. 3). By 1941, it was thought to be the only remaining active colony in Florida (Fig. 3; Allen 1942).

After 1940, the next account of spoonbills breeding in Florida was by J. C. Watson of the U.S. Fish and Wildlife Service. Watson estimated 100 breeding pairs and up to 10 colonies in the Bay during the 1948–49 season (Allen 1963). Allen resumed his spoonbill surveys in Florida Bay in 1950 and found larger numbers of nesting birds and a greater number of active colonies, compared to his surveys in the 1930s, but fewer than estimated by Watson (Appendices II–IV).

Approximately every 10 years from 1955 through 1978, the nesting population doubled (Fig. 3). In the 1978–79 season there was a dramatic increase in the number of breeding spoonbills (based on nest counts) over the previous two years, with the population reaching 1254 breeding pairs (Fig. 3). During 1978–79, nesting also occurred at two sites in the mangrove fringe adjacent to the bay, Madeira Rookery and Lane River. Spoonbill nesting had been noted only once for each of these colonies since the 1940s: 6 nests at Madeira Rookery in 1967 (unpubl. data, ENP), 3 nests at Lane River in 1975 (Ogden 1975). In 1978–79, these 2 colonies had an additional 115 pairs of spoonbills. These nests were initiated in spring, 3–4 months later than the highly synchronous bay colonies and may have been renesting. For this reason, we have not included them in the total nesting population estimate. No information is available for five years subsequent to 1978–79, but by 1984 when population surveys were reinitiated, the nesting population was 64% smaller than the peak 1978–79 level (Fig. 3). Subsequent surveys in 1985, 1986, and 1987 revealed a breeding population similar to levels in 1984 (Fig. 3).

DISCUSSION

During the first third of this century, Florida Bay wading bird populations went through an extreme bottleneck period (Weins 1977). One species, the Greater Flamingo (*Phoenicopterus ruber*) that was represented by a nonbreeding population of up to several thousand individuals disappeared from the area and has never become reestablished. The three species we analyzed were similarly pushed to the brink of extirpation or possibly were temporarily extirpated during this same period. In each case, however, when the exploitation was terminated, the population recovered.

The history of exploitation and recovery for these bay species differs from that of adjacent, more interior wading bird populations (i.e., White Ibis [*Eudocimus albus*], Snowy Egrets [*Egretta thula*], and Great Egrets). Protection was achieved for the latter species by 1915. Their population responded with rapid growth so that by the 1930s their combined population was estimated to be greater than a million birds (Robertson and Kushlan 1974). In contrast, the Great White Heron, Reddish Egret, and Roseate Spoonbill were still being heavily exploited as a food resource throughout the 1930s (Sprunt 1935). This delay in the implementation of protection for these species is significant in that it precluded their becoming reestablished while south Florida was still relatively unaltered by human development. By the end of the 1940s, when Florida Bay species began to recover, south Florida hydrology had been seriously disrupted (Anonymous 1950). The delay in recovery of the Florida Bay populations is also significant in that it means there are no population data for these species from a period that can be considered as representative of relatively pristine conditions. Thus, while a relatively firm basis for comparison exists to assess current status of interior wading bird populations no equivalent data exist for the three Florida Bay populations. Consequently, we can only speculate about the population sizes of these species before human interference.

The populations of these three species did not begin to recover at least until the late 1930s, and in the case of the Reddish Egret, recovery probably was predicated on recolonization from outside the state. With cessation of major human disruption of colonies, the populations of all three species increased relatively rapidly. If Sprunt's initial surveys adequately reflect the population, the Great White Heron population had the greatest rate of recovery, with a calculated increase of 30–40 birds per year between 1936 and 1960 (Fig. 1). More likely, Sprunt's estimates were actually low and initial recovery was slower, but still robust. The Reddish Egret and Roseate Spoonbill, which were both recovering from even smaller populations, initially increased at a slower rate (Figs. 2 and 3). The spoonbill population curve was ultimately exponential, with increases of over 150 birds per year by the late 1970s. As with the Great White Heron, the results was a near doubling of the population every decade between 1940 and the late 1970s. The Reddish Egret appears to have continued a linear growth rate up until the late 1970s, though the paucity of data makes that conclusion tentative.

For at least two of these species, the population recoveries have not continued into the present. In the mid-1980s, when spoonbills were surveyed after a hiatus of five years, the population was only one-third as large as the actual nest count compiled in 1978–79. The largest colony, Tern Key, had declined to one-fourth its previously recorded maximum (Appendix II). Interpretation of the spoonbill population data is made difficult by the gap in surveys between 1979 and 1984. The population peak of about 2500 adult birds (1254 pairs) was recorded for only a single year (1978–79). Five years later, when the spoonbills were next surveyed, only 900 (450 pairs) birds nested in the Bay. We do not know whether the 1978–79 peak represents a single year and whether the subsequent decline occurred in a single year or was spread out over five years.

Based on the 1978–79 population size, subsequent surveys indicate that a major population decline occurred during the early 1980s. This decline presumably resulted from some combination of low reproductive success, a high mortality rate, or emigration of juveniles and adults between 1979–84. The estimated mortality rate of 20% per year calculated for some adult wading bird species by Henny (1972) would be sufficient to explain the population decline if reproduction failed for a period of several years. We have no information available to suggest that adult mortality would have been greater during those years. In both 1977–78 and 1978–79, reproductive success was very low with 0.06 fledglings per nest produced in 1977–78 (Robertson 1978b), and 0.45 in 1978–79 (Robertson 1979). As suggested by Roberston (1979), almost complete nesting failure in 1977–78 and 1978–79 would result in major year-class gaps. Because spoonbill maturity is reached in three years (Allen 1942), reduced recruitment of new adults into the breeding population would be expected in the early 1980s. Therefore, the observed population decline in the early 1980s conforms with these predictions.

It is too early to determine whether the spoonbill population has again stabilized, but surveys in 1984–1987 show a consistent number of breeding birds. Low reproductive success has also been noted during the 1980s: 1982–83 = 0.06 young/nest, 1983–84 = 0.5 young/nest, 1986–87 = 0.06 young/nest (Powell, unpubl. data). Again, with some year-classes nearly missing, we expect a further decline in the spoonbill breeding population.

As with the Roseate Spoonbill, gaps in the Great White Heron data make conclusions about the population trends tenuous. The heron data present an additional difficulty due to a 40–50% yearly variation in population estimates. This within-year variation appears to be a seasonal phenomenon, with populations being up to 50 percent larger in winter (Appendix I). Large nestlings and fledglings are indistinguishable from adults in aerial surveys, and probably account for much of the variability. These young leave the bay within two months of fledging from winter nests (Powell and Bjork, unpubl. data) so they would be absent from summer, fall, and, to varying degrees, spring surveys. In view of our inability to distinguish reliably between adults and juveniles, we have chosen to use the summer adult population as the base population for the species. Great White Herons reached this base level of about 900 birds by 1960. The population suffered a major decline during Hurricane Donna in 1960, but recovered to the pre-hurricane level within two years. For the rest of the decade, the population remained at about 900 adult birds. The winter surveys increased slightly throughout the decade (Fig. 1), but the 20% difference between the survey extremes probably reflects a combination of sampling error and differences in reproductive success rather than changes in the adult population.

The existence of only a single survey after 1968 makes conclusions about the current status of the population largely speculative. The 1984 survey was made in January and February when there were large numbers of nestlings and recent fledglings particularly at colonies along the eastern fringe of the bay. While the number of birds recorded in winter 1984 was up to 10 percent higher than comparable surveys in the 1960s, we do not consider that difference indicative of a significant change in the population. Our conclusion is that the Great White Heron population was the same size in 1984 as it was two decades before.

As with the Roseate Spoonbill, we attribute the absence of continued population growth to low reproductive success and a low rate of recruitment. A three-year analysis of reproduction by Great White Herons in the early 1980s (Powell and Powell 1986) indicated that only 24% of nests produced young and productivity of only 0.5 young fledged per nest attempt in natural colonies (N = 97 nests). This productivity is well below the 1.91 young per nest that Henny (1972) calculated to be necessary to sustain Great Blue Heron populations. Though the method Henny used to derive that value is flawed (Anderson et al. 1981), it is likely an approximation of required productivity. The magnitude of spread between Florida Bay productivity and Henny's value is probably indicative of real differences. However, Henny's data were obtained from birds banded in the northeastern U.S. where life expectancies may be substantially shorter than those of a non-migratory, sub-tropical population. At this point, we have no measures of adult survival rate and therefore cannot estimate the level of recruitment that would be necessary to maintain a stable population in the bay. It should be noted, however, that a majority of the Great White Heron productivity during the early 1980s came from more productive nests of food-supplemented birds (mean young/nest, Powell and Powell 1986). This raises the possibility that stability of the Great White Heron population is dependent on supplemental feeding by humans.

Through a food addition experiment, Powell and Powell (1986) identified insufficient food as the major cause for low Great White Heron productivity. They also compared their current data with measures of reproductive parameters collected in 1923 (Holt 1928) and found (comparing distributions by chi square) that both clutch size and productivity were significantly greater in 1923. These findings are corroborated by a comparison of clutch size data for Great White Herons nesting between 1889 and 1925 and those nesting between 1981 and 1984. Prior to 1925, clutches averaged 3.41 ± 0.58, N = 112 (Powell unpubl. data) which was significantly larger than the average clutch size produced by naturally foraging herons in the 1980s ($\bar{x} = 3.0 \pm 0.53$; N = 57; $\chi^2 = 33$, $P < 0.01$). There was no significant difference between the number of eggs laid by

Great White Herons prior to 1925 and supplemented birds in the 1980s ($\bar{x} = 3.59 \pm .79$, N = 32, $P > 0.01$). The clutch data from nests prior to 1926 are primarily from several large series collected by E. Court, H. J. Hoyt, and E. Holt, so they are probably an unbiased representation of clutch size.

The Reddish Egret is by far the least abundant of the three species and also has the weakest data set for deriving a population growth curve. After their return to the bay in 1937, the Reddish Egret population appears to have grown at least through the 1950s and possibly the 1960s. In the mid- to late 1970s, the population appears to have remained stable. Because the population was not monitored between the mid-1950s and mid-1970s, we cannot determine if the population stabilized, increased gradually, or peaked and declined during the 1960s and early 1970s. The absence of data beyond the 1979–80 breeding season makes it impossible to project a current population trend. Casual observations in the 1980s indicate that the major colonies are still active, but no recent attempts have been made to evaluate reproductive success or population size.

The apparent instability of the Roseate Spoonbill and Great White Heron populations is probably ultimately related to human manipulation of south Florida hydrology. Recent evidence obtained from the analysis of coral in Florida Bay indicates that, prior to 1915, twice as much freshwater reached the bay as post-1930 (Smith et al. 1988). Reduced freshwater input would be expected to have major impacts on the ecosystem as a habitat for piscivorous wading birds. A reduced freshwater runoff would alter sheet flow and the resultant hydropattern of associated euryhaline marshes, which has major impacts on the availability of food resources for the three species. Great White Heron juveniles, Roseate Spoonbills and, to a lesser extent, Reddish Egrets, must have access to fish and invertebrates concentrated in shallow pools and ponds by cyclic flooding and drying of euryhaline wetlands. A reduction of freshwater runoff would also affect fish and invertebrate communities through resulting increases in salinity. A strong positive correlation exists between high runoff years and high recruitment by sport fishes (Tilmant, in press) and pink shrimp (*Penaeus duorarum*) (Browder 1985). These species, and others, are dependent on low salinities during larval and post-larval stages (Robblee pers. comm.; Rutherford et al., in press). Schmidt (1979) reported the occurrence of salinities along the northern mangrove-seagrass ectone in the bay that were high enough to be fatal to most euryhaline species of fish. These high salinities would have been moderated by historic hydropatterns that maintained a higher water table in upland areas (Tabb 1967, Sculley 1986).

Another human impact on the ecosystem that negatively affected wading bird populations was modification of foraging habitat for commercial and residential land development along the mainline keys. Historically, these high marsh areas were the principal forgaing habitat for spoonbills (Sprunt pers. comm.). Transitional wetlands on the mainline keys are also important as alternative foraging habitats for Reddish Egrets when storm-induced high water levels prevent them from using most bank habitats in the bay (Powell 1987).

The aggregate of low reproductive success manifested as a consistent high rate of nestling starvation and nest failure in Great White Herons and the high frequency of complete colony failure in Roseate Spoonbills indicate that these populations are at best marginal under current habitat conditions. The recent decline in the spoonbill population may indicate submarginal habitat quality for that species. The heavy dependence of Great White Herons on supplemented food for successful reproduction points to an unstable population for that species, as well.

In view of the inadequacy of presently available data, we recommend monitoring all three species to determine their population trends under current water management conditions. Furthermore, any future manipulation of water release schedules should include an analysis of impacts on these species. The three species forage in different habitats with little overlap in either prey type or capture technique. An analysis of carbon isotope ratios of tissues from nestling Great White Herons indicates that the population is dependent on a seagrass-derived food chain, while Roseate Spoonbills show a mangrove-based dependency (Sternberg and Powell, unpubl. data). These differences underscore the need for a diverse research program that analyzes the interrelationships of freshwater input, productivity of the estuary, and wading bird foraging ecology.

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APPENDIX I
GREAT WHITE HERON SURVEYS

	Date	Survey time (h)	Coverage	Estimated population: Florida Bay	Estimated population: Lower keys
Sprunt	Feb. 1935	3.25	FL Bay & lower keys	56	155
Sprunt	Oct. 1935	4	FL Bay & lower keys	20	126
Sprunt	Apr. 1936	4	FL Bay & lower keys	39	211
Sprunt	Oct. 1936	11	FL Bay & lower keys	86	226
Sprunt	Sept. 1937	3	FL Bay	118	
Sprunt	Jan. 1939	4.5	FL Bay & lower keys	226	419
Robertson	Sept.–Oct. 1958	NA[a]	FL Bay	827	
Robertson	June 1959	NA	FL Bay	809	
Robertson	Oct.–Nov. 1959	NA	FL Bay	1172	
Robertson	Jan.–Feb. 1960	NA	FL Bay	1361	
Robertson	May 1960	NA	FL Bay	898	
Robertson	Sept.–Oct. 1960	NA	FL Bay	546	
Robertson	Aug. 1962	22	FL Bay	818	
Robertson	Sept. 1963	NA	FL Bay	844	
Robertson	Feb.–Mar. 1965	NA	FL Bay	1382	
Robertson	Nov. 1965	15	FL Bay	1430	
Robertson	Apr. 1967	NA	FL Bay	903	
Ogden	July 1967	NA	FL Bay	914	
Ogden	Apr. 1968	NA	FL Bay	897	
Robertson	Jan.–Feb. 1984	NA	FL Bay	1508	

[a] NA = not available.

Appendix II

Total Number of Roseate Spoonbill Colonies and Nests per Year

Year	Total colonies	Total nests	Total nests*
1935–36[1a**]	1	15	
1936–37[1a**]	1	5	
1937–38[1a**]	1	6	
1938–39[1a**]	1	16	
1939–40[1a**]	2	15	
1948–49[1b***]	10	100	
1950–51[2]	7	64	
1951–52[2]	8	80	81
1952–53	5	66	60[1]
1953–54[2]	3	81	101[1]
1954–55[4]	7	174	
1955–56[5]	8	214	
1956–57[2]	6	183	148[1]
1957–58[1***]	4	92	
1958–59[2]	6	145[2,11]	110[12]
1959–60[2]	6	119	117[1]
1960–61[1a]	5	125	
1961–62[2]	4	76	
1962–63	9	266	
1966–67	8	368	
1968–69	6	272	
1969–70	7	255	
1975–76[8]	11	802	
1977–78[13]	16	619	
1978–79[14]	18	1254	
1984–85[15]	13	448	
1985–86[15]	14	590	
1986–87[15]	16	527	
1987–88[16]	16	493	

* Number of total nests from a different reference.
** Reference number in this position applies to all counts for this year.
*** Individual counts not available for all colonies for this year.
A = Colony active with a small number of nests. No count made.
? = Status unknown.

[1] R. P. Allen. The present status of the Roseate Spoonbill, a summary of events 1943–1963. Unpublished report, National Audubon Society (NAS) Research Department, Tavernier, Florida.
[a] Ground counts.
[b] Estimate, J. C. Watson, U.S. Fish and Wildlife Service.
[c] Flight line counts of adults at nesting islands.
[d] Aerial counts, W. B. Robertson, Jr., ENP, Homestead, Florida.
[2] Ground counts, R. P. Allen field notes, NAS Research Department.
[3] Ground counts, Rangers Log, ENP.
[4] Ground counts, District Ranger Bean, ENP Memorandum, 25 Feb. 1955.
[5] Ground counts, R. P. Allen and ENP Rangers, ENP Memorandum, 22 Feb. 1955.
[6] Aerial survey, J. C. Ogden, ENP Memorandum, 9 Feb. 1967.
[7] Ground counts, W. B. Robertson, Jr. Bird Obervation Cards, ENP.
[8] Ground counts, J. C. Ogden field notes, ENP.
[9] Aerial survey, J. C. Ogden flight notes, ENP.
[10] Number of nests estimated by ground counts of young/2, J. C. Ogden field notes, ENP.
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[12] Aerial survey, W. B. Robertson flight notes, ENP.
[13] Ground counts, ENP June 1978 Progress Report.
[14] Ground counts, ENP 1979 Annual Report.
[15] Ground counts, George Powell field notes, NAS Research Dept.
[16] Ground counts, Robin Bjork field notes, NAS Research Dept.

APPENDIX III

NUMBER OF ROSEATE SPOOONBILL NESTS IN EAST CENTRAL FLORIDA BAY BY COLONY AND YEAR

Year	Bottle	Stake	Cowpens	Cotton	West	Low	Manatee	Crab	East	Crane	East Butternut	Middle Butternut	East Bob Allen	Pigeon	Jimmie Channel
1935–36	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1936–37	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1937–38	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1938–39	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1939–40	3	0	0	0	0	0	12	0	0	0	0	0	0	0	0
1950–51	5	12	3	18	0	0	0	0	0	0	0	0	0	0	0
1951–52	5	26	10	10	0	0	0	0	0	0	0	2	0	0	0
1952–53	0	34	8	0	0	0	0	0	0	0	0	4	0	0	0
1953–54	0[1a]	30[3]	28[1a]	0[1a]	0	0	0	0	0	0	0	0	0	0	0
1954–55	13	47	39	?	32	25	0	0	0	0	0	0	0	0	0
1955–56	4	55	70	27	5	18	0	0	0	0	0	0	0	0	0
1956–57	0	45	70	25	0	22	0	0	0	0	0	0	0	0	0
1958–59	5	5	75	20	0	0	0	0	0	0	0	0	0	0	0
1959–60	0	8	65	3	0	0	0	0	0	0	0	0	0	0	0
1960–61	0	?	70	?	0	0	0	0	0	A	0	0	0	0	0
1961–62	0	?	50	3	0	0	0	0	0	0	0	0	0	0	0
1962–63	0[1d]	35[1a]	75[1c]	15[1d]	0	0[1d]	0	0	0	45[1a]	0	0	0	0	4[1d]
1966–67	0	10[6]	0[9]	0	?	20[8]	20[9]	3[9]	0	24[8]	0	0	0	0	0
1968–69	5[8]	15[10]	A[9]	0	0[9]	2[9]	?	?	0[9]	A[9]	0	0	0	0	0
1969–70	5[8]	A[9]	?	0	?	0	?	?	0	A[9]	0	0[9]	0	0	0
1975–76	25	?	30	0	?	0	?	?	0	A	0	A	0	A	0
1977–78	?	41	13	0	A	0	1	A	0	31	8	0	0	A	0
1978–79	23	77	69	0	0	4	5	A	0	A	4	0	0	30	0
1984–85	0	0	12	0	?	0	0	0	12	14	0	26	?	0	12
1985–86	0	0	?	0	7	0	0	8	6	17	0	66	?	0	19
1986–87	0	0	15	0	2	0	0	0	7	27	0	42	8	0	6
1987–88	0	0	14	0	9	0	0	0	0	12	14	0	9	12	28

For meaning of superscripts, see Appendix II.

APPENDIX IV

NUMBER OF ROSEATE SPOONBILL NESTS IN NORTHEAST, SOUTHEAST, AND WEST FLORIDA BAY BY COLONY AND YEAR

	Northeast							Southeast			West		
Year	Tern	North nest	South nest	Projoe	North Park	South Park	Pass	East Buchanan	West Buchanan	Barnes	Frank	Oyster	Sandy
1935–36	0	0	0	0	0	0	0	0	0	0	0	0	0
1936–37	0	0	0	0	0	0	0	0	0	0	0	0	0
1937–38	0	0	0	0	0	0	0	0	0	0	0	0	0
1938–39	0	0	0	0	0	0	0	0	0	0	0	0	0
1939–40	0	0	0	0	0	0	0	0	0	0	0	0	0
1950–51	0	5	0	11	0	0	0	0	0	0	0	0	0
1951–52	0	5	0	14	0	0	0	0	0	0	0	0	0
1952–53	0	8	0	12	0	0	0	0	0	0	0	0	0
1953–54	0	23[3]	0	0[1,3]	0	0	0	0	0	0	0	0	0
1954–55	0	9	0	9	0	0	0	0	0	0	0	0	0
1955–56	0	26	0	9	0	0	0	0	0	0	0	0	0
1956–57	0	1	0	20	0	0	0	0	0	0	0	0	0
1958–59	0	20	0	20	0	0	0	0	0	0	0	0	0
1959–60	0	24	0	16	0	0	0	3	0	0	0	0	0
1960–61	0	10	0	20	0	0	0	25	0	0	0	0	0
1961–62	0	0	0	20	0	0	0	?	0	3	0	0	0
1962–63	50[1c]	0[1d]	0	15[6]	0	0	0	25[1d]	?	2[1d]	0	0	0
1966–67	181[7]	?	0	?	0	0	0	10[9]	100[9]	0	0	0	0
1968–69	175[10]	0[9]	0	0[9]	0	0	0	?	75[10]	0	0	0	0
1969–70	150[1]	A[9]	A[9]	?	0	0	0	?	100[10]	0	0[9]	0	0
1975–76	495	0	30	20	0	0	0	25	25	0	47	105	0
1977–78	272	0	10	64	0	0	0	20	42	A	36	56	25
1978–79	591	0	33	64	0	A	0	68	85	?	62	64	80
1984–85	170	0	?	77	20	3	0	27	8	0	0	3	62
1985–86	184	0	?	118	4	5	4	0	7	0	0	6	139
1986–87	158	0	21	99	0	6	2	8	9	0	0	0	107
1987–88	110	0	21	75	9	10	2	19	0	0	4	0	151

For meaning of superscripts, see Appendix II.