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BREEDING POPULATIONS OF THE WOOD STORK IN THE SOUTHEASTERN UNITED STATES[1]

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Abstract. Wood Storks (*Mycteria americana*) in the southeastern United States decreased from 10,000 breeding pairs in 1960 to 2,500–5,000 pairs in the late 1970s. The number of breeding pairs appeared to increase to 5,000–6,000 by the mid-1980s. Since the mid-1970s, the center of breeding in the southeastern United States has shifted north. Fewer birds have nested in the traditional southern Florida colonies, while the number of pairs nesting in northern Florida, Georgia, and South Carolina has been increasing annually. Storks nesting in the northern colonies appear to be reproductively more successful than those in the south, which may explain the increase in total numbers.

Key words: Aerial census; breeding range shift; colony census; population trends; southeastern United States; Wood Stork; Mycteria americana.

INTRODUCTION

Historically, Wood Storks (*Mycteria americana*) nested in all coastal states between Texas and South Carolina (Wayne 1910, Bent 1926, Howell 1932, Oberholser 1938, Dusi and Dusi 1968, Cone and Hall 1970, Oberholser and Kincaid 1974), although colonies outside Florida formed irregularly and contained relatively few birds. Traditionally, the largest Wood Stork nesting colonies were located in southern Florida (Ogden and Nesbitt 1979).

The number of breeding pairs in the southeastern United States decreased from an estimated 20,000 pairs in the 1930s, to about 10,000 pairs in the early 1960s, and to 5,000–6,000 pairs in 1975–1976 (Ogden 1978a, Ogden and Nesbitt 1979, Kushlan and Frohring 1986). Between the late 1950s and mid-1970s, nesting outside of Florida had become extremely infrequent. Increased agricultural and urban land development and the associated drainage of freshwater wetlands have eliminated many former nesting and feeding sites (Robertson and Kushlan 1974, Ogden and Nesbitt 1979). These land-use changes are likely the causative factors for the severe decline in stork populations, particularly in southern Florida.

Because the disjunct population of Wood Storks in the southeastern United States recently has been classified as endangered (Federal Register 28 February 1984), it is critical to the recovery efforts that the storks' recent status be evaluated in order to understand and predict future trends. Thus, we present census data for all known Wood Stork nesting colonies in the southeastern population, collected between 1958 and 1960 and from 1976 to 1985. Additionally, for the historically large nesting colonies in southern Florida (defined as Broward, Collier, Dade, Hendry, and Monroe counties) we have estimates of the number of nesting pairs for an uninterrupted 28-year period from 1958 to 1985. These data demonstrate two population trends that were not previously apparent (Ogden and Nesbitt 1979, Ogden and Patty 1982): a recent stabilization or possible increase in the total breeding population, and a considerable northward shift in the center of breeding for Wood Storks.

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METHODS

One or more aerial censuses were made during each stork breeding season over all of peninsular Florida from 1958 through 1960 (A. Sprunt, IV, pers. comm.; data on file Natl. Audubon Soc. Research Dept.). From 1976 through 1985 two aerial censuses wre flown annually over peninsular Florida and portions of coastal Georgia and South Carolina, usually during April and late June. These censuses were timed to locate active colonies and to count or estimate the number of pairs nest building and incubating (April) and the number of pairs that were successful in raising young (late June). The estimate of successful pairs (June census) was a crude measure at best, because of the spread in timing of nesting within and between colonies. The year to year variation in nesting success was great enough, however, that our counts or estimates of successful nests did provide a relative measure of nesting success that we feel revealed actual events at the regional level. Additional earlier censuses were flown in southern Florida, usually on a monthly basis, where nesting started as early as December. All censuses were flown with single-engine, fixed-wing aircraft. The censuses were designed to check all known or suspected stork colonies and systematically search for unknown colonies in regions where habitat appeared suitable or where numbers of feeding storks were seen. Although not all newly formed colonies were located in the year of their formation, the combination of aerial searches and a network of ground observers who regularly report colony locations has convinced us that no substantial portion of the total stork population was uncensused for long periods. At each colony, we either counted active nests, or closely estimated the total number of nests, as the airplane made three to six slow overhead passes at altitudes of 50 to 100 m. Two experienced observers independently made the nest estimates. A nest was considered active if it had either one or two adults in attendance, or contained eggs or young. In addition, during the April censuses when some pairs of adult storks could still have been in various stages of nest construction, we also included in the totals any discrete pairs of birds standing close together where no nest could be seen. Censuses taken later in the nesting season indicated that these "new pairs" should be counted, as in most cases active nests appeared where groups of these paired birds had been standing. We used the largest aerial count or estimate made each year for the number of nesting pairs at each colony. In this paper, and for historical reasons (Kahl 1964), we consider that the five southern Florida counties listed above contain the southern colonies. All remaining colonies are considered as the northern colonies.

Even though aerial estimates are less precise than ground counts, aerial censuses have decided advantages compared to ground-based census methods for assessing long-term trends for colonially nesting species that nest in geographically widespread colony sites (e.g., Kushlan and White 1977, Nesbitt et al. 1977, Osborn and Custer 1978, Buckley and Buckley 1980, McCrimmon 1982). The accuracy of aerial censuses has been repeatedly examined (e.g., Kushlan 1979, Drury 1980, Portnoy 1980). The challenge, as was well stated by Drury (1980), has been to conduct censuses with a level of accuracy that is "well within the limit of the [population] change to be detected." Drury felt, and we agree, that for at least some species, long-term population trends can be properly measured so long as three census criteria are met: (1) estimates must be collected by similar techniques over a period of years, (2) changes in the number of birds must be much greater than what might be explained by census error, and (3) the census takers must have a good understanding of the biology of the species being censused to interpret changes, both seasonal and long-term, that are seen.

Aerial censusing is a particularly appropriate means for estimating a nesting population of Wood Storks. Storks are large white birds that nest in discrete colonies, and which usually build their nests conspicuously on the upper or outer branches of trees and shrubs. A check on the accuracy of the stork census technique has been possible by comparing the aerial estimates with ground counts of nests in some of the same colonies in northern and central Florida (data of James A. Rodgers, Florida Game and Fresh Water Fish Commission). For 32 paired counts collected from nine colonies over a 4-year period (1981, 1982, 1983, 1985), the aerial estimates differed from the ground counts as follows: 1981 = 17% higher, 1982 = 3% higher, 1983 = 18% lower, and 1985 = 3% higher. We believe that the aerial estimates were more accurate than is indicated by these figures. Differences between the air and ground counts were caused only in

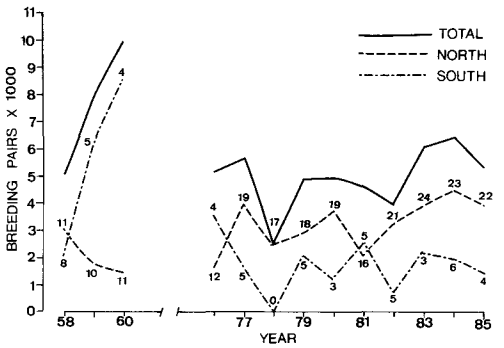

FIGURE 1. Number of nesting pairs of Wood Storks in the southeastern United States. The numbers adjacent to the lines for the north and south are the number of colonies during each calendar year.

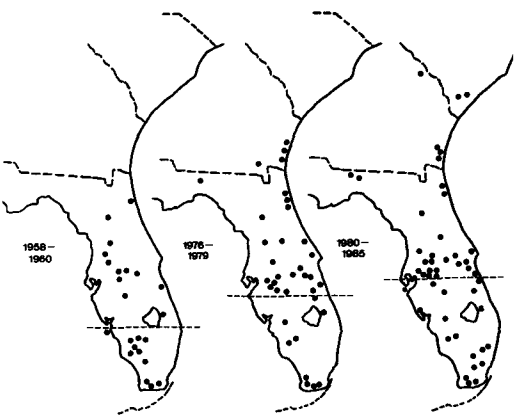

FIGURE 2. Location of Wood Stork colonies during 1958–1960 (n = 23), 1976–1979 (n = 35), and 1980–1986 (n = 47). The line across each map indicates the north-south weighted center of nesting during each time interval.

part by inherent differences in the accuracy of the two techniques. In most cases the estimates/counts were not made on the same day (usually within 1 week), while the number of nests in a colony was constantly changing, sometimes abruptly, due to nesting failures and new birds settling in colonies. In a few cases where nests were scattered or access to all nests was particularly difficult on the ground, aerial estimates were more accurate than ground counts.

Aerial census data used in our analyses were collected by biologists of the National Audubon Society, U.S. National Park Service, Florida Game and Fresh Water Fish Commission, Florida Audubon Society, Georgia Department of Natural Resources, South Carolina Division of Game and Fresh Water Fisheries, and the Savannah River Ecology Laboratory (see Acknowledgments).

RESULTS

Wood Storks breeding in the southeastern United States decreased from more than 10,000 pairs in 1960 to recent counts of about 6,000 pairs (total northern and southern colonies) in the best year (1984) and fewer than 2,500 pairs in the worst (1978, Fig. 1). The total number of pairs reached a low between 1976 and 1982, when numbers fluctuated between 2,500 and 5,200 pairs. During the 1958 through 1960 and 1976 through 1985 periods, Wood Storks nested at a total of 71 different sites in Florida, Georgia, and South Carolina (Fig. 2). Storks used 23 sites during 1958 through 1960, 35 during 1976 through 1979, and 47 during 1980 through 1985. Only eight sites were used in all three time periods. These included four colonies in southern Florida: Cuthbert Lake and East River in Everglades National Park, and Corkscrew Swamp and Sadie Cypress Swamp in Collier County. The remaining four colonies were scattered in central and northern Florida: Barley Barber Swamp in Martin County, Pelican Island in Indian River County, Reedy Creek in Polk County, and River Styx in Alachua County. Overall, 59% of the colony sites used in 1958 through 1960 were still used in the period 1975 through 1979, while 41% of those sites used in 1958 through 1960, and 58% of those used in 1975 through 1979, were also used in 1980 through 1985.

Two new trends have been apparent since the late 1970s. The total number of nesting pairs has increased and the geographical center of nesting has shifted well to the north.

Over 6,000 pairs nested in 2 out of 3 years since 1982 (1983, 1984), which was more than nested in any other year since 1975 (Fig. 1). The increase in number of pairs has occurred entirely in the northern colonies, while colonies in southern Florida may still be declining.

The second trend revealed by recent censuses was the northward shift in the breeding range (Fig. 2). During the 1958 through 1960 period, the north-south weighted center of the breeding population was along latitude 26°38′N, south of Lake Okeechobee in southern Florida. The weighted center of nesting shifted significantly north in each of the 1976 through 1979 and 1980 through 1985 periods (one-way ANOVA F = 4,325.6, $P < 0.001$). During 1976 through 1979, the center had shifted 87 km north to latitude

TABLE 1. Annual estimates of nesting pairs of Wood Storks, and percentage of pairs that produced large nestlings in northern and southern colonies.

Year	Northern colonies			Southern colonies		
	Maximum total pairs nesting[a]	Total pairs that produced large young[b]	Percent producing large young	Maximum total pairs nesting[a]	Total pairs that produced large young[b]	Percent producing large young
1977	3,939	2,650	67	1,708	0	0
1978	2,478	1,500	61	0	0	—
1979	2,845	2,300	81	2,059	500	24
1980	3,710	3,250	88	1,226	725	59
1981	2,087	1,000	48	2,526	550	22
1982	(3,236)[c]	—	—	(753)	—	—
1983	3,874	2,135	55	2,223	700	32
1984	4,476	3,080	69	1,971	755	38
1985	3,900	1,740	45	1,455	685	47
Total	27,309	17,655	65	13,168	3,915	30

[a] Total of highest count for each colony.
[b] Number of nests containing at least one young during second (usually late June) annual census.
[c] No estimate of number of successful pairs.

27°25'N. Between 1980 and 1985, it shifted another 45 km north to 27°49'N, across the southern part of Polk County in central Florida. Concurrent with this shift, the southern colonies declined 84% from 8,835 pairs in 1960 to 1,455 pairs in 1985. The number of pairs in the northernmost colonies located in Georgia and South Carolina increased from 0 pairs in 1960 to 605 pairs in 1985.

Since 1977, a significantly higher proportion of Wood Stork pairs that nested in the northern colonies than in the southern colonies were able to raise large young (Table 1; $\chi^2 = 4{,}350$, $P < 0.001$). For the 8 years 1977 to 1981 and 1983 to 1985, the aerial censuses indicated that 65% of the pairs that had been active in April in the northern colonies were still active during late June/July (nests contained large young in most cases), compared to only 30% in southern Florida colonies at comparable nesting stages. The summer census in 1982, taken after many young fledged, was excluded from analyses. In 7 of the 8 years, pairs in the north were more successful than those in the south. Only in the dry spring of 1985 was the percentage of pairs still active late in the nesting cycle similar in both regions (see Ogden et al. 1980 for discussion of wet-dry effects on nesting by storks).

Annual aerial or ground census data for Wood Stork colonies in southern Florida for a 28-year period from 1958 to 1985 are shown in Figure 3. Comparison of the mean annual number of pairs in two 10-year periods (1958 to 1967, 1976 to 1985) showed that significantly fewer pairs nested in the 1976 to 1985 period ($\bar{x} = 1{,}750$, SD = 985; $t' = 3.0$, $P < 0.05$) than in the 1958 to 1967 period ($\bar{x} = 4{,}969$, SD = 3,192). By plotting 3-year running averages we reduce the effects of abrupt annual variations in breeding numbers, usually caused by local climatological events, and graphically illustrate the decline (Fig. 3). The last major breeding in southern Florida occurred in 1966, 1967, and 1968 when 6,500 to 8,000 pairs nested. A small recovery occurred during 1974 through 1976 when 3,000 to 4,500 pairs nested. The 1976 breeding season was the last year when more pairs nested in southern Florida than in the northern range. The number of pairs nesting in southern Florida ranged between 750 and 2,500 pairs annually during 1979 to 1985.

The decline in total number of pairs in the southern colonies and the increase in pairs in the northern region are related in an important way to changes in the number of active colonies in the two regions (Fig. 1). In the south the annual number of colonies has virtually remained unchanged. During 1958 through 1967 between one and eight colonies were active in years that storks nested (no storks nested in southern Florida in 1962) and during 1976 through 1985 between three and six colonies were active in nesting years (none nested in 1978). A different pattern occurred in the northern region where the annual number of colonies increased from 10 to 11 per year in 1958 through 1960 to 21 to 24 per year in 1982 through 1985.

Although the number of colonies in the south did not change, the mean colony size decreased significantly from the 1958 through 1967 period

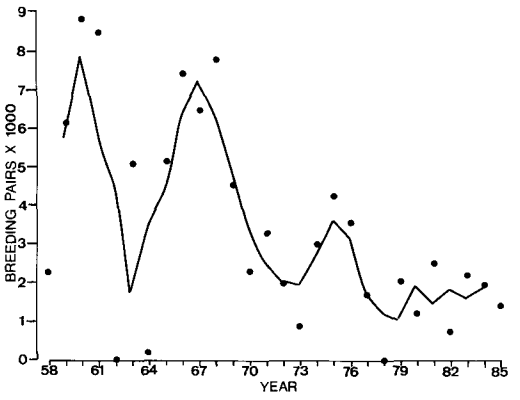

FIGURE 3. Wood Stork pairs (dark circles) and 3-year running average of the numbers of pairs in southern Florida (Broward, Collier, Dade, Hendry, and Monroe Counties) during a 28-year period.

($\bar{x}$ = 1,242 pairs per colony, SD = 1,584, n = 40 colonies; t' = 3.01, $P < 0.05$) to the 1976 through 1985 peroid ($\bar{x}$ = 437, SD = 590, n = 40 colonies). The decrease in colony size in the south is further illustrated at Corkscrew Swamp where more than 3,000 pairs nested in six different years between 1958 and 1967, whereas in the 1976 to 1985 period Corkscrew never had 3,000 pairs in any single year (maximum = 2,300). Also, within Everglades National Park at least 1,500 pairs nested in six different years during the 1958 to 1967 period, whereas that number of pairs never nested within the park between 1976 and 1985 (maximum = 1,233).

The recent population increase in the northern part of the range resulted from the formation of more colonies rather than a change in colony size. In the north, mean colony size has not changed significantly between 1958 and 1960 ($\bar{x}$ = 195, SD = 177, n = 32 colonies; t = 0.910, P = 0.364) and 1976 to 1985 ($\bar{x}$ = 168, SD = 152, n = 191 colonies). However, the 1958 to 1960 mean annual number of pairs nesting in the north increased from 2,082 in 1958 to 1960, to 2,704 pairs in 1976 to 1979, and 3,547 pairs in 1980 to 1985.

DISCUSSION

Kahl (1964) described three distinct geographical regions in Florida where Wood Storks nested, without commenting on whether he considered Florida storks in these regions to represent separate subpopulations. The apparent distinctness of these regional breeding areas has disappeared since the 1960s, with colonies now scattered more generally throughout peninsular Florida (Ogden and Nesbitt 1979). We consider the Wood Storks that nest in the southeastern United States to be a single population and find no evidence for the existence of discrete subpopulations. No interchange is known between the southeastern U.S. population and those that nest in southern Mexico (Palmer 1962, Ogden 1978b, Sprunt and Knoder 1980), and none of the 1,500 storks color-marked in Florida have been reported from west of the Mississippi (Ogden, unpubl.).

The recent northward shift in the geographical center of nesting by Wood Storks in the southeast may have been caused by several factors. The two factors that we find to be most consistent with the data gathered during the censuses are (1) that the much better nesting success in the northern colonies compared with the southern colonies has resulted in annual production exceeding annual mortality in the former region, while the reverse has been true in the latter; and (2) that adult storks that once nested in the south, and/or their offspring, have shifted to nest in northern colonies in some or most years, as a response to deteriorating feeding opportunities in the south.

Without large numbers of marked birds, the extent to which either of these factors has operated cannot be known. We believe, however, that both have contributed to the population shift. While the imbalance between the two regions in recent reproductive success almost certainly means that the first factor has contributed to the increase in the north, a case for the second factor requires a closer look at the recent census data. Storks were first detected nesting in Georgia in 1976, and in South Carolina in 1981. The initial breeders in South Carolina must have come north from either Georgia or Florida. The combined number of pairs in the two states increased from 16 in 1976 in one colony to over 600 in 1985 in five colonies. This increase means an average annual increase of 50% for the 9 years 1977 to 1985. We suggest that such a rapid increase has in part been due to a continuation of the same northward population shift that originally carried nesting storks to these two states.

The case that some of the increase in storks in the north is due to movement from the southern colonies is strengthened by comparing the relative changes in the number of pairs in the north and south regions between consecutive years

during the 1958 to 1960 and 1976 to 1985 censuses. For 7 of 11 years when the number of pairs in the south either increased or decreased between one year and the next, the reverse occurred in the northern colonies. We interpret this to mean that some storks that nested in the south in winter (colonies form November to March) in some years may move to northern colonies to nest in the spring (colonies form March to April) in different years when feeding conditions in the south are poor.

Although this pattern is not significant (binomial test, $P = 0.264$), an examination of the 4 years when it did not occur still suggests the interrelatedness of the population. The number of nesting pairs either increased or decreased in both regions in 1978, 1979, 1983, and 1985 (Fig. 1). These 4 years were associated with either unusually dry or wet conditions, which may have had enought influence on storks throughout their full range to mask any interregional shifts by nesting birds. Wet or dry extremes are generally very disruptive to stork foraging success, and correlate with reduced nesting efforts or success (Kahl 1964, Ogden et al. 1980). Reduced nesting in both regions during 1978, when unusually heavy rains throughout Florida apparently caused a general dilution of food resources, was followed by a recovery year in both regions in 1979 when rainfall was more normal. Following a drought in 1981 to 1982, 1983 was a recovery year in both regions, strong in the south and moderate in the north. An early and severe drought occurred in 1985 that may have reduced the number of feeding sites sufficiently to cause a decline in the number of nesting pairs in both regions.

If this north–south interregional relationship does occur, then one would expect southern colonies to have been larger in years when colony formation occurred early (good feeding conditions early in the nesting season) than in years of late colony formation (good feeding conditions either did not develop, or developed late). For Corkscrew, the largest southern colony, between 1976 and 1985 the colony was larger when formation was early (November to December formation, mean colony size = 1,850 pairs, range = 1,050–2,300, $n = 3$ years; January to February formation, mean colony size = 1,158 pairs, range = 990–1,475, $n = 3$ years; March formation, mean colony size = 706 pairs, range = 18–1,200, $n = 3$ years; no nesting in 1978). The missing adult storks in the years of late colony formation either moved north to nest or did not nest at all in those years. If they did not nest, they also apparently did not remain in southern Florida, as large numbers of nonbreeding adult storks are rarely detected in the south in spring (March to May) in years when little or no breeding occurs there.

The last year in which a clear majority of the U.S. breeding population nested in the traditionally large southern Florida colonies was 1976. The number of pairs in the south has fluctuated between 0 and 2,600 annually in the years since. The decline in southern Florida nesting is partially due to a reduction in feeding habitat (Kahl 1964; Kushlan et al. 1975; Browder 1978, 1984). For example, the acreage of five important wetland feeding habitats had decreased by 35% from 1900 to 1973 in the area south of Lake Okeechobee (Browder 1976, 1978). Furthermore, the remaining wetlands have changed dramatically, either by impoundment, partial drainage, or manipulation of normal hydrologic periods (Marshall 1971, Robertson and Kushlan 1974, Kushlan et al. 1975, Browder et al. 1976, Kushlan 1987). These managed wetlands may not provide an adequate food base for Wood Storks due to reduced fish production and to the failure of managed wetlands to concentrate fish at the proper water depths, and in the proper seasons (Kahl 1964, Kushlan et al. 1975, Ogden et al. 1976, Ogden and Nesbitt 1979, Kushlan 1986).

The increase in the breeding population in the north has been associated with a large increase in the number of colonies rather than an increase in colony size. Colonies in the north average smaller than colonies in the south. Historically, southern Florida colonies were in much more extensive wetlands than are found in the northern region, where the nesting storks had access to a much more abundant food resource. The implication is that many northern colony sites, drawing on more limited areas of wetlands and more limited food resources, already contain as many storks as the surrounding country will support. As more storks nest in the north, the fact that many are forming new colonies suggests that food availability is operating to limit the size of existing colonies. For example, the Birdsville colony in Georgia has maintained relatively constant size despite overall good reproductive success (Meyers 1984; Coulter 1986a, 1986b). First discovered in 1980, Birdsville contained 100, unknown, 60, 113, 100, and 108 pairs through

1985. During 1981 an unknown number of pairs abandoned early because of dry conditions.

We suspect that the northern colonies have been more successful in recent years because storks in any given colony have relatively more feeding site options than are available to storks in southern Florida. Storks nesting in the north in most cases have a large number of independently functioning small stream systems, lakes, marshes, and farm ponds where they may obtain food. During the full nesting season the storks at any given time apparently have a set of options about where to obtain food, so that if one or more sites do not provide the needed amount, others are available.

In conclusion, nesting populations of Wood Storks in the southeastern United States appear to have stabilized at about 6,000 pairs per year during the mid-1980s. The stabilization is associated with a reduction in the southern Florida breeding population, northward extension of the breeding range, and a pronounced northward shift of the center of breeding. Storks now breed annually in Georgia and South Carolina. The southern Florida region, however, may still be critical to the preservation of the species. The south is important not only as a breeding location for approximately one-third of the population, but also may be an important wintering ground for storks from throughout the U.S. breeding range (J. Ogden, banding records; M. Coulter, pers. comm.). Preservation and improvement of the feeding habitat of storks in the south seems imperative to the maintenance of this species.

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