RELATION OF WATER LEVEL AND
FISH AVAILABILITY TO WOOD STORK REPRODUCTION
IN THE SOUTHERN EVERGLADES, FLORIDA

OPEN-FILE REPORT 75-434

Prepared in cooperation with the
U.S. NATIONAL PARK SERVICE

Tallahassee, Florida
1975
RELATION OF WATER LEVEL AND
FISH AVAILABILITY TO WOOD STORK REPRODUCTION
IN THE SOUTHERN EVERGLADES, FLORIDA

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ABSTRACT

The wood stork is a species of colonial wading bird in the Everglades that is most sensitive to changes in the availability of food. Previous studies have shown that the initiation and success of wood stork nesting depends on high densities of fish concentrated in ponds and other catchment basins during the dry season. The extreme dependence of the wood stork on the cyclic hydrologic regime of the southern Florida wetlands makes it an indicator of the well-being and ecological stability of the Everglades.

The wood stork has declined in numbers over the last 25 years. One reason for the decline in the wood stork population was the change in the hydrologic regimen of the Everglades which affected the feeding habitat and the food production.
The fish on which the wood stork feeds increase in density during the dry season as water levels fall. In the Everglades marsh, densities were highest in front of the drying edge of surface water at a depth of about 0.3 m. Dry-season densities were greatest when a drought occurred the previous year.

Historically wood stork nesting success was associated with high summer water levels, high rates of surface-water discharge and high rates of drying. Before the closure of the south side of Conservation Area 3 in 1962, years of successful and unsuccessful nesting were characterized by different patterns of drying. These patterns changed after 1962 and generally the predictability of successful nesting breaks down thereafter. Only two nesting years after 1962 were successful and in only one of these was the drying rate similar to years of successful nesting before 1962. Two other potentially successful years failed after 1962. This suggests that further changes in the hydrobiological relations occurred within the Everglades after 1962.

Lack of successful nesting after 1962 can be attributed in large part to late colony formation and the interruption of nesting by winter rainfall. In this period (1962-72), colonies formed earlier in years of high early drying rates than in years of low early drying.
rates. Delay of colony formation is ultimately the result of inability to attain a suitable nutritional state since food supply is the primary factor in the initiation of nesting. Many of the complex food associations of the wood stork remain to be explained.
INTRODUCTION

The Florida Everglades is a vast, shallow marshland which in its natural state encompassed nearly 10,000 km² stretching from the south shore of Lake Okeechobee to the mangrove swamps of southwest Florida, 160 km to the south. A sheet of surface water generally less than 1 m deep flowed southward with a gradient averaging about 5 cm/km (Leach, Klein and Hampton, 1972). Near the latitude of Miami, the principal Everglades drainage, called the Shark River Slough, is constricted by a higher marshland to the east and west and funnels into a series of dendritic streams which enter coastal mangrove swamps. These streams coalesce into mangrove-lined rivers.

The Everglades can be divided into three distinct regions (fig. 1): agricultural lands directly south of Lake Okeechobee, three water conservation areas established as water-management impoundments, and Everglades National Park including within its boundaries the southernmost part of the Everglades.
Figure 1.--Physiographic features and geographical locations in southern Florida. Aerial photography by Earth Resources Technology Satellite.
The present paper reports on studies made in 1965-73 by the Geological Survey and the National Park Service to relate variation in water level to the production of aquatic animals and the reproductive success of the wading birds, particularly the wood stork, that breed in Everglades National Park.

Water level is critical to the colonial nesting wading birds (order Ciconiiformes: herons, ibises, storks) that breed during the dry season when inundated areas are reduced to isolated pools and fish become concentrated by falling water levels. The wood stork (Mycteria americana) is the species most sensitive to variations in food availability because, unlike visually hunting species of herons, the stork feeds exclusively by non-visual, tactile methods and its feeding efficiency is directly related to fish density (Kahl, 1964). Kahl also found that in southern Florida this species requires the high densities of aquatic organisms concentrated by falling water level to trigger and sustain nesting. Historically, when wood storks nested successfully so did other species of wading birds, although wood storks failed in some years when other wading birds were successful.

Since wading birds are dominant predators in the ecosystem and
adapted to the naturally fluctuating water conditions of the Everglades, the wood stork is in many respects an indicator of the natural functioning and general well-being of the Everglades ecosystem. For this reason the biology of the wood stork has been emphasized in this paper.
ACKNOWLEDGMENTS

We acknowledge the contributions of two colleagues who initiated this study and saw it through its early stages -- W. B. Robertson, Jr. and M. C. Kolipinski. Dr. Robertson was responsible for beginning the study of wood storks in Everglades National Park and has contributed his hard-earned data, valuable suggestions and interest to the continuing study. Dr. Kolipinski was responsible for setting up the fish sampling program and establishing preliminary methods of data analysis. We thank Messrs. G. E. Davis, R. Hermance, H. Klein, B. F. McPherson, F. N. Nix, O. T. Owre, T. A. Schmidt, L. L. Purkerson, W. B. Robertson, and J. T. Tilmant for their most helpful and constructive criticism of this and earlier drafts of this paper. We also wish to thank the ranger division of Everglades National Park for supplying logistical support under various adverse circumstances.
STUDY AREA

The study area was the Everglades drainage system south of U. S. Highway 41 (fig. 2). The study was concentrated in the Shark River Slough which originates in the marshes north of U. S. Highway 41 in what is now Water Conservation Area 3 and extends to the southwest coast (fig. 2). South of U. S. 41, the slough covers 791 km². However 214 km², lies east of Everglades National Park and are cut off from the rest of the southern Everglades by Levee 67 extension (fig. 2).

Vegetation of the Everglades is dominated by four plant associations described in detail by Davis (1943), Loveless (1959) and Craighead (1971). Saw grass marsh, composed of almost pure stands of Cladium jamaicensis, is the predominant community. Mixed marshes or prairies of Eleocharis cellulosa and Rhynchospora tracyi occur at slightly lower elevation than saw grass marshes. Tree islands are raised slightly above the surrounding marshes and vegetated by hardwood communities. In the lower part of the slough, dendritic streams are lined by river-bank forest, primarily of mangroves (Rhizophora mangle). Inland, river-bank forest is replaced by saw grass.
Figure 2.—Location map of the southern Everglades showing an expanded longitudinal profile of ground level.
Shark River Slough is the southern part of the Kissimmee-Okeechobee-Everglades drainage system. Through the years the system has been modified by canal drainage, water control and water-management practices, and urban and agricultural growth. One of the management works was the completion of a levee along the south side of Conservation Area 3 which changed the pattern of southward flow to the Shark River Slough. The history and some of the consequences of these developments on the total system have been reviewed by Leach and others (1972).
METHODS

Water level was recorded continuously at gaging station P-33 (fig. 2). Station P-33 is located in saw grass marsh in Central Shark River Slough at land elevation 1.6 m above msl (mean sea level). Data from P-33, from 1953 through 1972, were used as an indicator of water conditions of the southern Everglades and generally of water conditions in southern Florida. High water years are those in which water level at P-33 exceeded 2.0 m above msl during January. The rate of water level decline was quantified by calculating an early and late drying rate for the hydrobiological year, June through May. The early drying rate is the net rate of change from the highest water level in November of the previous calendar year to the highest level the following January. The late drying rate is the net rate of change from the highest water level in January to the highest level in March.

Surface-water flow was measured at culverts and water control structures along U. S. Highway 41 and divided for analysis into three discharge segments as shown in Fig. 2. (Flows from Water Conservation Area 3 are controlled whereas flows from the eastern Big Cypress are uncontrolled.) Years of low discharge are those in which flow through the two sections across the Shark River Slough was less than $320 \times 10^6 \text{ m}^3$ during the June-May annual cycle.
Density of aquatic organisms in number per unit area was determined by samples obtained with Higer pull-up traps. The traps consisted of a sheet of 3-mm mesh nylon netting on a 1.5 x 3.0 m frame which rests on the bottom of the marsh and is pulled up by two operators standing 15 m away. This device has been described and discussed by Higer and Kolipinski (1967) and Kushlan (1974). Specimens were fixed in 10 percent formalin in the field and later identified, counted and weighed to 0.001 gm after being blotted dry. Computer programs were used to calculate the average density of organisms per square meter of surface area for such sample period.

Ten traps were installed in 1965 in the central part of Shark River Slough (fig. 2): 5 in saw grass marsh and 5 in Eleocharis-Rhynchospora marsh. Samples were generally collected during 1 week of each month; each trap was sampled on 2 consecutive nights whenever possible. Because variation between samples from the 2 communities was within the range of variation within each community, data from all trap sites were averaged to find the mean density of all fish and prawns for the period.

Population, movements, and feeding areas of wood storks from 1965 to 1972 were determined by regular, generally monthly, aerial surveys. The total population within the southern Everglades was
censused during the winter-spring breeding season. Nesting numbers and success were determined by aerial observation and photography. Information on colony formation and nesting success from 1953 to 1965 was obtained from W. B. Robertson, Jr. (National Park Service, pers. comm. 1972). A breeding season was considered successful if the number of young produced was great enough to sustain a stable total population through the next breeding season. R. P. Allen's estimates of annual mortality (in Palmer, 1962) were used in calculating population trends.
RESULTS

Hydrology

Variation in rainfall, evapotranspiration and overland flow from the water conservation areas results in seasonal changes in the quantity of water in the southern Everglades. Water levels begin to rise in May or June to a peak in October; thereafter levels decline, slowly and irregularly at first, but accelerate in the spring and continue to decline until the next rainy season starts. This temporal pattern of water-level fluctuation causes a spatial variation in the distribution of surface water. As the dry season progresses, evapotranspiration causes a decline of water level throughout the southern Everglades, surface flow decreases and finally ceases, marsh bottom becomes increasingly exposed along the higher land to the east and west, and drying progresses inward from the lateral edges and longitudinally from both the north and the south. Dry season discharge from Water Conservation Area 3 sustains inundation southwest of Levee 67 longer than would otherwise occur.

After completion of the levee on the south side of Conservation Area 3 in 1962 water-levels in and flows to the Shark
River Slough were further altered by operation of the control structures (fig. 2). Graphs of surface flows through the eastern Big Cypress Swamp and flows into the eastern and central parts of the Shark River Slough for 1940-72 are shown in fig. 3. Until 1962, the Big Cypress and Shark River flows were comparable. Thereafter, there occurred a change in the pattern of flow to the Slough as compared to the flow through the eastern Big Cypress.

To determine the significance of these changes of surface flow patterns, a comparison was made between recent controlled flow to the Shark River Slough and uncontrolled flows in the Big Cypress Swamp. This can be done because of the comparability of annual flow through the eastern Big Cypress Swamp with flow into the southern Everglades \( r \) (correlation) = 0.93, \( p \) (probability) < 0.01. For the interval 1940 to 1961 (uncontrolled), the ratio of Everglades to Big Cypress flow was 0.58 (Standard Deviation = 0.17) for the central slough and 1.07 (SD = 0.88) for the eastern slough.

The surface-water flow into the central slough expressed in terms of this ratio is shown in figure 4. Although flow was reduced in 1962-65, these were dry years, and the index of surface flow into the Everglades relative to the Big Cypress Swamp was similar to
Figure 3: Surface water flow into two sections of Shark River Slough and through the eastern Big Cypress Swamp.

DISCHARGE, IN CUBIC FEET PER SECOND

1970 1960 1950 1940

0 0 0 0

EASTERN BIG CYPRESS

LEVEES COMPLETED

CENTRAL SHARK RIVER SLough

DISCHARGE, IN CUBIC METRES PER SECOND

0 0 0 0

0.0 0.0 0.0 0.0

Squares from L. 24
Figure 4.--Deviation from natural flow in the southern Everglades 1962-72 based upon water flow index (discharge into the central part of the slough/discharge eastern Big Cypress Swamp). The average index for 1953-61 (0.58) is indicated by a solid line the standard deviation (± 0.17) is indicated by dashed lines.
values before 1962. After 1965, however, surface flow into the central slough for the five years, 1966, 1968, 1969, 1970 and 1972, was greater than what the flow would have been (t-tests, p < 0.05).

Water that under natural conditions would have flowed into the entire slough was directed into the center of the slough, while discharge into the eastern slough consisted only of seepage. The increased flow diverted into the center of the slough can maintain high levels there for prolonged periods.
Wood Stork Population

The southern Everglades wood stork population, referred to by Kahl (1964) as the "Everglades-mangrove population," consists of those birds nesting in colonies at the margin of the southern Everglades. Information on this population before Everglades National Park was formed in 1947 is scattered and incomplete, but Holt (1933) reported 50,000 storks in a single colony in 1933. By 1960, the population stood at 6,200 and a further decline occurred during the 1960's. By 1972 the southern Everglades population had declined to 1,800.

Under natural conditions, storks nested successfully in most years. Storks were successful in 6 of 9 years from 1953 to 1961 but in only 2 of 12 years from 1962 to 1973 (Table 1). During 1965-72, the period of fish monitoring, nesting was successful only in 1967.

Wood storks disperse northward in summer and return to south Florida in fall, generally November (Palmer, 1962, Kahl, 1964). On returning, they feed in a predictable sequence of locations first utilizing drying ponds and marshes within the coastal mangrove zone, remaining there through December. Feeding storks then move to the drying lower part of Shark River Slough in and near the mangroves. Later, in early spring, they feed along the drying lateral edges of the
Table 1.--Water conditions and nesting success of wood storks in the southern Everglades 1953-73.

<table>
<thead>
<tr>
<th>Year of Nesting</th>
<th>Nesting Success</th>
<th>Water Level</th>
<th>Discharge</th>
</tr>
</thead>
<tbody>
<tr>
<td>1953</td>
<td>+</td>
<td>High</td>
<td>High</td>
</tr>
<tr>
<td>1954</td>
<td>+</td>
<td>High</td>
<td>High</td>
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<tr>
<td>1955</td>
<td>+</td>
<td>High</td>
<td>High</td>
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<tr>
<td>1956</td>
<td>-</td>
<td>Low</td>
<td>Low</td>
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<td>1971</td>
<td>-</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>1972</td>
<td>-</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>1973</td>
<td>-</td>
<td>High</td>
<td>High</td>
</tr>
</tbody>
</table>

1/  + = successful nesting season, - = unsuccessful nesting season
slough, a residual pool north in the middle of the slough and, in recent years, along the south side of Water Conservation Area 3A.

Nesting in the southern Everglades takes place in the winter and spring. Before 1962, colonies formed primarily in November and December, but after 1963, the time of colony formation became increasingly irregular ranging from December to as late as March (fig. 5). Through 1973, no year in which colonies formed as late as January has been successful. During years when colonies formed in December, successful nesting occurred about half the time (fig. 5).
Figure 5.--Month when wood stork colonies formed in the southern Everglades 1953-1973. Years of successful nesting are stippled. No wood stork colonies formed in 1962.
Wood Storks and Water Conditions

Since the nesting success of wood storks is apparently predicated on colonies forming from November through January (Fig. 5), it is important to determine whether hydrologic conditions affect the timing of colony formation. Wood storks begin nesting in the Big Cypress Swamp when the water level falls to a specific point (Kahl, 1964). Wood storks nesting in the Everglades show no such correlation. As demonstrated in figure 6, water level at the reference station in the central slough varied 0.7 m (2.29 m to 1.59 m) during the times of colony formation. It is reasonable to suspect that the timing of colony formation may be related to the rate of water-level decline during the dry season. There is no such correlation before 1962 since colonies formed in November or December irrespective of drying rate. After 1962, the early drying rate was significantly higher in years when colonies formed in December than in years when colonies formed later \((r -0.87, p < 0.01)\) (Fig. 7). If this correlation between the rate of drying and time of colony formation is meaningful, it may be related to changes in the surface flow system after 1962.

Desertion of colonies by nesting wood storks is apparently also related to water conditions. This is important because only one of 7 attempts at renesting after desertion succeeded. Desertion was, in all cases for which information is adequate, correlated with rises...
Figure 6. Water level at P-33 in southern Everglades at the initial formation of wood stork colonies.

METRES ABOVE MEAN SEA LEVEL

FEET ABOVE MEAN SEA LEVEL

YEAR

1953

0

2.0

2.5

3.0

3.5

4.0

4.5

5.0

5.5

6.0

6.5

7.0

7.5

8.0
Figure 7. -- Relation of early drying rate and time of nesting showing the high correlation \( r = -0.87 \) after 1962 (dots). The regression \( \log Y = \log a + b \log x \) where \( \log a = 6.8459 \) and \( b = -152 \) is significant at \( P < 0.01 \). The transformation of the equation is \( Y = a x^b \). There is no significant relation before 1962. These data are shown in crosses and have a non significant correlation \( r = -0.13 \)
in water level of 3 cm or more (table 2). However, desertion in response to such water level rises occurred only within the first 2 months of nesting. After 2 months, nesting storks apparently continue to nest for as long as they can locate food sources. The desertion of nesting colonies due to relatively small rises in water level suggests why colonies that formed after December have failed. Wood storks require approximately 4 months to fledge young and colonies formed late have insufficient time for development prior to the onset of the rainy season which raises water levels and causes desertion. It seems possible that colonies formed as late as late January could succeed prior to the rainy season, but until 1973 none has.

In that colony desertion and, after 1962, colony formation are correlated with hydrologic conditions, it seems probable that wood stork nesting success may also be related to water conditions in the southern Everglades. In an attempt to discern such a relation, 3 parameters were used to describe the temporal variation in water level: discharge into Shark River Slough, altitude of winter water levels which relates to water depth, and the rate of winter-spring drying. Table 1 shows the correlation of the first two parameters with wood stork nesting. Before 1962, this relation was straightforward: stork nesting failed in low water years but generally was successful in
Table 2.—Effect of short-term rises in water level on wood stork nesting 1953-73.

<table>
<thead>
<tr>
<th>Magnitude of the short-term rise</th>
<th>Reaction of nesting storks</th>
<th>Number of short-term water-level rises occurring in the:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>First month of nesting</td>
</tr>
<tr>
<td>desertion</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Less than 3 cm</td>
<td>no desertion</td>
<td>4</td>
</tr>
<tr>
<td>Greater than or equal to 3 cm</td>
<td>no desertion</td>
<td>0</td>
</tr>
</tbody>
</table>
years of high winter water levels and high discharge. The latter relation was first noted by Robertson (1964). After 1962, however, this relation broke down: storks failed in the three years having both high water level and high discharge and they successfully nested in two years of low water conditions. This strongly suggests that the hydrobiological system supporting Everglades wood storks underwent changes that apparently coincided with the alteration of the patterns of flow to the slough after the levee was built.

Analysis of the parameter, rate of winter-spring drying, describing water-level fluctuations is more complex. An analysis is shown in figure 8 where the late drying rate is plotted against the early drying rate for each year of record. Plots of successful and unsuccessful years before 1962 form 2 distinct clusters, shown as shaded polygons, which differ in mean late drying rate (t-test, p < 0.05). (The single exception to the pattern, 1959, which is not included in the successful polygon because its position is the result of a lowered late drying rate due to a rise in water level after young storks had already fledged).

Comparison of later years to base line data from before 1962 shows that the drying rates of most unsuccessful years continued to fall within or close to the cluster for unsuccessful years before 1962.
Figure 8.--The relation between early and late drying rates in the southern Everglades. The derivation of these rates is explained in the text. Drying rates in years of successful wood stork nesting are shown in circles, years of unsuccessful nesting as squares. Open symbols are those for the years 1953-61, prior to completion of levees. Closed symbols are those for the years 1962-73. The averages for each group before 1962 are shown in double symbols. The shaded polygons represent the range of variation of successful and unsuccessful year before 1962.
However, 4 years are anomalous. The unsuccessful year of 1969 was considerably deviant from other years. Drying rates for 1962 and 1971 were similar to pre-1962 successful years, but in both these years wood storks failed. Drying rates in 1967 were different from all other successful years (t-test, $p < 0.05$) but produced successful nesting. Only in 1963 were drying rates similar to those of pre-1962 successful years. However, before 1962 such rates were produced in high water years whereas 1963 was a low water year.

These results show that successful and unsuccessful years before 1962 can be characterized by how fast water levels dropped in the nesting season in addition to being characterized by water level and discharge parameters. However, the results since 1963 do not conform to these indices.
The density of fish in Shark River Slough is related to water depth (fig. 9). As water levels fell, density of fish at the trap sites increased to a peak in January and then declined as water level declined further. The occurrence of peak fish densities during moderately low water levels is apparently caused by the movement of small fish to deeper areas well in advance of the drying edge of the marsh. Such peak densities occurred when water depth in the marshes reached about 0.3 m (table 3). This wave of densely concentrated fish apparently moves across the southern part of the Everglades until fish finally become concentrated in localized depressions. Such movement of fish during periods of drying was shown previously by Kushlan (1972) for a pond in the Big Cypress Swamp, but those movements were more limited.

To analyze how water level correlates with changes in fish density, it is necessary to first examine the water level fluctuations at station P-33 (fig. 10). Droughts occurred in 1965 (prior to the study), 1967, 1971, and 1972. From the summer of 1968 through 1970 water levels were continuously high due to high-surface water discharge discussed earlier (fig. 3). Both the prolonged wet period and the drought affected fish populations during the study (fig. 10).
Figure 9.—Relation between fish density in the marshes of Shark River Slough and water level, October 1966 to April 1967. Numbers at data points indicate month of datum.
Table 3.--Water depth at peak fish density in southern Everglades marshes.

<table>
<thead>
<tr>
<th>Date</th>
<th>Depth at Trap site (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>11 Jan 1967</td>
<td>0.24</td>
</tr>
<tr>
<td>7 Dec 1967</td>
<td>0.28</td>
</tr>
<tr>
<td>6 Feb 1969</td>
<td>0.31</td>
</tr>
<tr>
<td>24 Feb 1971</td>
<td>0.27</td>
</tr>
<tr>
<td>22 Feb 1972</td>
<td>0.28</td>
</tr>
<tr>
<td>Mean</td>
<td>0.28</td>
</tr>
</tbody>
</table>
Figure 10.--Fluctuations of water level at P-33 and density of fish in Shark River Slough.
Since fish density varied with both water level and time of year, density at different times can be compared directly only if the data are for the same time of year, at approximately the same water level, and at a time when water levels are changing at similar rates in the same direction. These criteria were met in August of several years (fig. 10). Fish densities were relatively high during the summer of 1966 and 1968 (both after droughts), but during the continuously wet period from 1968 through 1970, summer fish density declined by 47 percent from the first (1968) to the third (1970) summer (Table 4). Additional evidence of a decline in the fish population during extended high water is shown in the dry period of 1971. Samples taken near what should have been peak fish density showed a moderate rather than a high density (fig. 10). This is in contrast to the high densities in 1972 which, following the 1971 drought, reflected the return of typical conditions. These data indicate that the abundance of fish declines during continuous high-water periods and increases after droughts.
Table 4. -- Density of fish in southern Everglades during summers of similar water depth.

<table>
<thead>
<tr>
<th>Summer</th>
<th>Water Depth at traps (m)</th>
<th>Density (fish/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aug 1966</td>
<td>0.68</td>
<td>8.9</td>
</tr>
<tr>
<td>Aug 1968</td>
<td>0.78</td>
<td>7.6</td>
</tr>
<tr>
<td>Aug 1969</td>
<td>0.73</td>
<td>5.9</td>
</tr>
<tr>
<td>Aug 1970</td>
<td>0.63</td>
<td>4.0</td>
</tr>
</tbody>
</table>
Wood Storks and Fish Availability

Of the several feeding areas used by wood storks, information on the fish populations is available only for the Shark River Slough. However, this is perhaps the most critical area because storks feed there when securing food for young in the nest, the period of highest energy demand. Wood storks feed during periods of falling water levels when fish densities are increasing (fig. 10), and usually at a water depth of about 0.3 m, where fish are concentrated (Table 4). Storks probably feed on the dense wave of fish while the slough dries and continue to do so as remnant fish stocks become concentrated within topographic depressions. The result of this pattern of fish concentration is that highly concentrated food supplies are generally available to storks feeding in the slough throughout the mid-nesting period.

The prolonged wet period from 1968 to 1970 resulted in a 47 percent decrease in the standing crop of fish in central Shark River Slough (Table 4). Because the analysis of drying rates (fig. 8) suggested that 1971 probably should have produced successful wood stork nesting, the failure may have been caused in part by lack of food. If so, it was probably due to the
combined effects of high water from 1968 to 1971 and the reduced inflow of fish into Shark River Slough from the northern Everglades and previous tributary areas to the east.
DISCUSSION

Requirements for Successful Nesting

Wood stork colonies in Everglades National Park are fully protected and thus nesting failure is not caused by disturbance. Nor does the species' movements or residence during the non-breeding season appear to be a source of high mortality because the population returns to south Florida each year in numbers which correspond to the previous seasons' reproductive output. It is possible, however, that the nutritional condition of returning storks may be poorer than in previous years. Furthermore, unlike storks nesting in the Big Cypress Swamp (Kahl, 1964), there is no evidence that Everglades colonies have failed due to high winds or cold weather (W. B. Robertson, Jr., National Park Service, oral commun., 1972). Nesting success or failure, in most cases, is probably related to the abundance and availability of food in the supporting system.

The well documented dependence of southern Florida wood storks on concentrated food supplies (Kahl, 1964) means that feeding success requires a water depth shallow enough for
wading and a relatively high density of fish. Feeding sites are located where these two conditions are met. Thus storks move to a succession of feeding areas during the winter and spring as suitable feeding conditions become available. Storks first use coastal feeding sites in early winter when water in the Everglades is too deep for feeding. Later movements to inland sites and within the Everglades follow the pattern of drying.

The pattern of food utilization and availability in the Everglades suggests why drying rates might be important in relation to nesting success. Fish must be available in high densities in Shark River Slough over several months. This necessitates continual concentration along drying edges and, ultimately, concentration in residual pools. Such a process may require a drying rate sufficient to maintain a wave of concentrated fish over a relatively long period of time. High water-level conditions, whether caused by short term rainfall (Table 2), beginning of the rainy season, or increased overland flow due to surface-water discharge, reduces fish density by dispersing concentrated fish and, as a consequence, decreases feeding efficiency of storks.

During the 1950's, wood stork nesting was generally successful
in high water years and unsuccessful in low water years. Successful years were also characterized by high discharge and high late drying rate. Changes in the manner and extent of surface water flow into the southern Everglades after 1961 (fig. 3, 4), discussed in the next section, have adversely affected wood stork nesting success. In the 12-year period after 1961, wood storks bred successfully only twice and in only one of these years were drying rates similar to successful years before 1962. Also, in two unsuccessful years, drying rates were similar to those of earlier successful years. Thus after 1962, the relationship between stork reproduction and drying rates differed from the relationship that held before 1962. This can also be seen in the relationship between drying rates and time of colony formation (fig. 7). After 1962, higher early drying rates correlated with early nesting. Before 1962 this relationship did not hold.

Thus whereas water conditions which produced successful wood stork nesting before 1962 were relatively straightforward, conditions producing successful nesting thereafter are not. In fact the pattern may be completely reversed in that after 1962 nesting succeeded only in a low water year.

Figure 5 suggests that nesting failure after 1962 was in part
associated with late colony formation that did not allow sufficient
time to complete nesting before the rainy season. A major re-
quirement for successful wood stork nesting is, therefore, early
colony formation. Historically no nesting that began after December
succeeded although colonies forming as late as the end of January
could theoretically succeed. Factors affecting early nesting are
not known, but the correlation between high early drying rates in
Shark River Slough and early nesting (fig. 7) is compelling. This
relation is meaningful only insofar as the data from the slough re-
fect conditions throughout southern Florida, since storks are not
utilizing the slough through most of the period measured by early
drying rates. However it is not an unreasonable assumption that
water conditions in southern Florida can be approximated by
conditions in the southern Everglades.

Delay in colony formation is probably due to failure to attain
a suitable nutritional state if food is the proximate stimulus in
initiating nesting as Kahl (1964) suggests. If colonies are to form
as early as December, storks must begin nesting soon after they
arrive in southern Florida. Either a suboptimal nutritional state
on arrival, failure to obtain enough food in November-January, or
both, are the proximate causes of delayed nesting. More information on the food ecology of wood storks on their summering grounds and immediately after arrival in southern Florida is clearly needed.
Relation of Wood Storks to Water Supplies

During 1962-65, flows to the Park were primarily affected by below normal rainfall and resultant low storage in Conservation Area 3. Flows during the early 1960's were reminiscent of those during early and middle 1940's. In fact, wood storks bred successfully in one of these dry years (1963). Discharge to the Shark River Slough increased after 1965. However the distribution of flow differed from previous years because surface water was diverted into the central part of the Shark River Slough (fig. 3) rather than through the total flow section. In 1966, 1968, 1969, 1970, and 1973 this flow exceeded what would have occurred under natural conditions (fig. 4), and in each of these years wood stork nesting failed. Wood stork nesting succeeded in 1967 and had low production in 1971 and 1972. The annual surface flow in each of these three years was similar to what would have been expected under noncontrolled conditions (fig. 4).

The correlation of high drying rates to wood stork nesting success suggests the importance of the timing of discharge as well as amount. Decreased drying rates can be caused by the continuation of excess flow into the dry season when water levels would otherwise be dropping.
That the rate of water-level recession and not absolute water level is important in the Everglades is somewhat unexpected in light of the findings of Kahl (1964) and Kushlan (1972) that, in the Big Cypress Swamp, wood stork nesting and feeding of wading birds on concentrated fish stocks both occur at specific water levels. The difference between the Everglades and Big Cypress Swamp is probably due to the nature of fish concentration in the two areas. In the Big Cypress Swamp, fish become concentrated in highly localized and relatively small depressions where feeding depends on water becoming shallow enough for wading. In the Everglades, fish are apparently concentrated along a drying edge in broad gently sloping marshes making a continual supply of food available along a gradient over a range of falling water levels.

An additional aspect of water supply is its effect on the important intermediate links in the Everglades food chain. The extended high-water period from 1968 through 1970 (fig. 10) which led to a 47-percent decline in fish abundance from the first to the third summer (table 4), may have contributed to the nesting failure of 1971.
Wood Stork as an Indicator of Ecological Stability

Since the early 1960's, the population of wood storks breeding in the southern Everglades has experienced lowered nesting success and, as a result, a marked decrease in numbers. It is necessary to understand the factors involved in successful reproduction of wood storks not only because the species is endangered in southern Florida but because its dependence on concentrated fish and falling water levels makes it an indicator of the ecological stability and natural functioning of the southern Everglades. The stork's dependence on specific water level and food relations is greater only by degree than that of several other once-abundant species of ciconiiforms, such as the snowy egret, common egret, and white ibis, which comprise an important segment of the dominant carnivore trophic level in the Everglades and are essential to the proper functioning of the unique wetland ecosystems of southern Florida.

Analysis of the factors leading to failure of wood stork nesting in the southern Everglades is complicated because the population decline coincided with a sequence of uncontrolled drainage, water control, urban expansion into peripheral wetlands and, finally, water management, all of which probably impelled the population decline.
of all wading birds in southern Florida after the 1930's when nesting colonies exceeded 1 million birds. It is this loss of habitat that also makes management of present wetlands for remnant populations of these dominant carnivores exceedingly difficult. Loss of peripheral, higher marshes, particularly along the developed Florida east coast (fig. 1) decreased feeding areas that were utilizable when water levels in the Everglades are too high for effective feeding and also decreased the tributary area of regions such as Shark River Slough, thus decreasing the food available during the dry season.

Loss of habitat from lowered water levels and urban encroachment has irrevocably altered the natural system to which the wood stork was adapted. Management, especially water management, in an attempt to replicate habitat conditions for the most sensitive of the wading birds would be ecologically sensible. More detailed study would be needed to determine whether supplying specific water conditions might be sufficient to bring about successful nesting.
LITERATURE CITED


