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Responses of Wading Birds to Seasonally Fluctuating Water Levels: Strategies and Their Limits

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Abstract.—Wading birds (Ciconiiformes) may use diverse strategies to cope with the seasonal fluctuations of water levels characteristic of large tropical wetlands. Drawing on studies of two species in the Florida Everglades, in this paper I discuss such accommodations to hydrologic variability as foraging tactics, population movements, breeding seasonality, colony site selection, and colony site tenacity. Wood Storks (*Mycteria americana*) and White Ibises (*Eudocimus albus*) show both similarities and differences in their use of the Everglades wetland. The accommodative limits to life in fluctuating-water wetlands may be exceeded by water management practices, which in the Everglades involve increasing seasonal water depths and decreasing dry season recession rates. The White Ibis appears to have responded to these alterations by abandoning large-scale nesting in the southern Everglades, whereas the Wood Stork has shifted time of nest initiation. The resulting nesting failure and consequent decrease of the Wood Stork population suggest that its limits of accommodation have been surpassed. Thus rather subtle manipulations can have profound effects on population stability of wading birds using fluctuating wetlands, which in turn may affect energy flow and ecosystem functioning.

Key words.—Ciconiiformes, environmental variability, Everglades, evolutionary strategies, Florida, marsh ecology, wading birds, wetlands, White Ibis, Wood Stork.

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Wetlands are not easy places to live. Although productivity may be high, obtaining it can be difficult. This is especially so in tropical wetlands where water depths fluctuate seasonally and the frequency and magnitude of such fluctuations may severely constrain the ability of organisms to survive there. In the Florida Everglades, for example, water depth fluctuation appears to be the primary factor influencing ecosystem composition and functioning (Kushlan 1976a) and maintaining appropriate patterns of water fluctuation is essential to the management of such wetlands (Johnsgard 1956, Weller 1978, Weller and Fredrickson 1974, Kushlan 1986). Thus the strategies by which birds are able to use fluctuating wetlands can reveal much about their evolutionary ecology. Furthermore from an understanding of such strategies and their limits, in relation to the natural functioning of wetlands ecosystems, it may be possible to infer appropriate management strategies.

In this paper I expand on these assertions through review of studies that have revealed aspects of the adaptations possessed by two species of wading birds using the Florida Everglades, the White Ibis (*Eudocimus albus*) and the Wood Stork (*Mycteria americana*). I then discuss how modification of the critical pattern of water fluctuation in the Everglades has in some cases exceeded the limits of their ability to accommodate, thus providing a cautionary example for the management of fluctuating wetlands and their constituent bird species.

STUDY AREA

The studies reviewed here were conducted in the southern Florida Everglades, a fluctuating-water marshland that historically covered 9300 km^2 extending from Lake Okeechobee to the Gulf of Mexico (Fig. 1). Surface water averages less than one meter deep and flows south and southwestward over a gradient of about 4 cm/km. The predominant vegetation is a herbaceous marsh community. Scattered ponds maintained by the activities of the American alligator (*Alligator mississippiensis*) constitute the deepest-water habitats (Kushlan 1974).

The water level in the Everglades fluctuates seasonally because of variation in rainfall. On the average 85% of the 1250 mm annual total rain is concentrated in half of the year, June through December (Fig. 2). During the winter, reduced rainfall leads to a recession of surface waters, a process accelerated by increasing evaporation in the spring (Fig. 2). The lowest water levels occur in spring, when surface water may be contracted into the deeper marshes and alligator ponds.

Water conditions in the Everglades basin are strongly influenced by human modifications to the system, drainage and water manipulation. Drainage has eliminated the wetland character of 65% of the original Everglades, the upper reaches of the Everglades immediately south of Lake Okeechobee having been completely converted to agricultural use

Figure 1. Map of southern Florida showing the land uses of the Everglades basin, south of Lake Okeechobee, including the Everglades Agricultural Area, the Water Conservation Areas, and Everglades National Park.

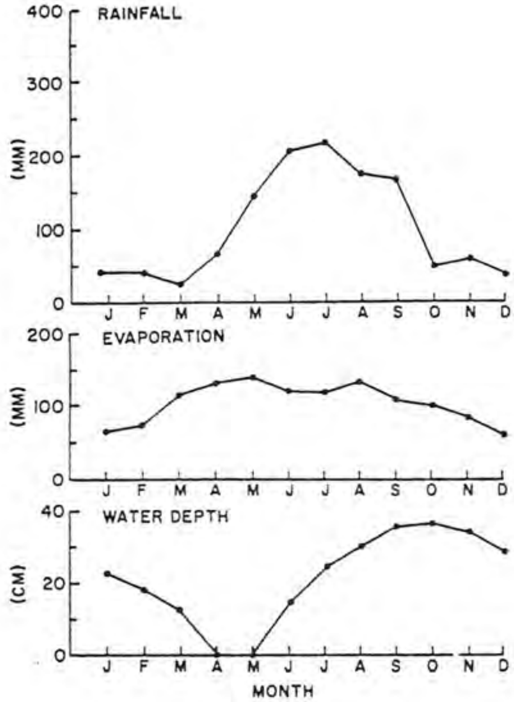

Figure 2. Seasonal changes in rainfall, evaporation, and water depth in the southern Everglades.

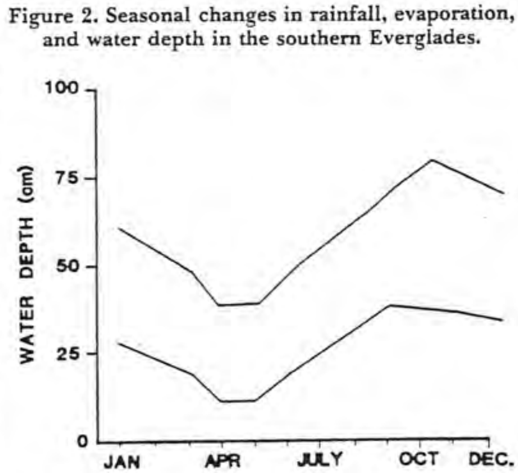

Figure 3. Water depths in two nearby locations in the Everglades. Top is behind a levee that impounds surface water flow. Bottom is 20 km south of the levee.

(Fig. 1). Other Everglades areas near the developed east coast have also been reclaimed. The remaining Everglades has been partitioned into three shallow-water reservoirs managed by a state agency and Everglades National Park, the latter containing only 6% of the original Everglades marsh. Most of the Everglades is encompassed within the three reservoirs, the Water Conservation Areas, of 3600 km^2 (Fig. 1). These Conservation Areas are nearly entirely surrounded by levees, and water levels are manipulated for purposes of flood control and water supply for municipal and agricultural use.

The physical compartmentalization of the Everglades by levees and canals has caused substantial changes in the patterns and timing of water level fluctuations (Kushlan 1986). Water depths in some areas are now higher than they were historically, and others are drier. Under both conditions the timing of water level fluctuations has been altered. For example, Figure 3 shows the average seasonal water level fluctuation in locations fewer than 20 km apart. The differences in depths are attributable surface water impounding behind levees, as shown by the top graph.

RESULTS

Use of wetlands by wading birds involves such characteristics as foraging tactics, movement patterns, breeding seasonality, colony site selection, and site tenacity. White Ibises and Wood Storks show both similarities and differences in their use of the Everglades wetlands.

Foraging

White Ibis and Wood Storks are both tactile foragers, but they feed differently in the Everglades (Kushlan 1979 a). The

White Ibis probes by repeatedly inserting the tip of its bill into the bottom sediment of the marsh. The Wood Stork gropes by placing its bill in the water and holding that posture for many seconds. In both cases they respond to touching a potential prey item by snapping their bill shut (Kahl and Peacock 1963).

The ibis obtains relatively small and poorly mobile prey items. In the Everglades marsh, crayfish comprise 66% of the diet by energy content, with an additional 25% being composed of other invertebrates (Kushlan 1979 b). This diet contrasts markedly with the exclusively fish diet of the Wood Stork (Ogden et al. 1976). By placing its bill in the water column rather than in the sediment, the Wood Stork obtains mobile species that swim through the water and contact its bill.

The differences in diet reflect fundamentally divergent foraging strategies. An evaluation of the availability of various prey items with respect to their use reveals that the Wood Stork "selects" the relatively larger fishes of those available, and the White Ibis "selects" crayfish and some aquatic insects (Ogden et al. 1976 and Kushlan 1979 b). These evaluations indicate that the differences in diet are not due to the relative abundances of various prey types but to differences in foraging abilities of the two species. Owing to the dominance of a single prey type, the White Ibis' feeding niche breadth (2.12) is half of that of the Wood Stork (4.08) (Levins 1968, data in Kushlan 1978 b and Ogden et al. 1976); and prey overlap among the two birds in the Everglades marshes is minimal.

The prey preferences result in the two species using the wetlands in different ways. In the Everglades, as in most such wetlands, falling water levels result in the drying of the marsh and concentration of remaining surface water in the relatively deep pools, such as ponds (Kushlan 1976 b). Fishes and other natant species migrate into these pools where their densities increase as water levels fall (Fig. 4). Wood Storks feed on the densely concentrated prey and choose feeding sites where such concentrations occur (Kahl 1964, Ogden et al. 1976). In the Everglades, foraging patches chosen by storks had fish concentrations that averaged 141 fish/m^2, contrasted with unused control sites that averaged 10.3 fish/m^2 (t-test, $p<0.05$).

The principal prey of the White Ibis, crayfish (*Procambarus alleni*) do not concentrate but rather faculatively burrow, surviving the dry season by tunneling in the marsh rather than by migrating into residual pools (Kushlan and Kushlan 1979). Crayfish achieve maximum density of about 1.6 kcal/m^2 in the marsh at a water depth of about 25 cm (Fig. 4).

These patterns of prey availability require that ibises and storks choose rather different feeding situations within the drying marshes. Storks feed where fish are densely concentrated, such as deep marshes and ponds and are capable of feeding in up to 40 cm of water. Ibises feed in water less than 30 cm and usually 5-10 cm deep and therefore are confined to shallow water marsh sites.

Population Movements

To locate and use the patches of available prey, both storks and ibises undertake seasonal movements within the southern Florida wetlands. The details may differ from one year to the next, depending on local water level fluctuations and more importantly the number of birds that happen to be residing in southern Florida that year. However year to year differences in the pattern of use are relatively inconsequential. Figure 5 shows the distribution of foraging White Ibises and Wood Storks in several months of the drying period.

The movements of both populations corresponded to the geographical pattern by which the southern Everglades dries in the spring (Fig. 6). The Everglades dries toward its center, the higher peripheral

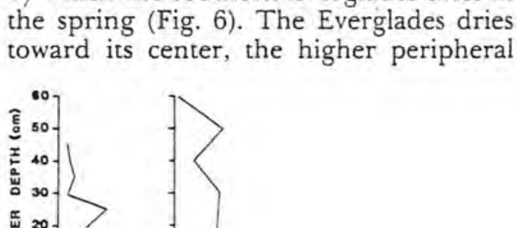

Figure 4. Changes in the energy density of crayfish in the Everglades marsh (left) and fishes in an Everglades pond (right) during the drying season. Graphs show energy available when the water reaches various depths.

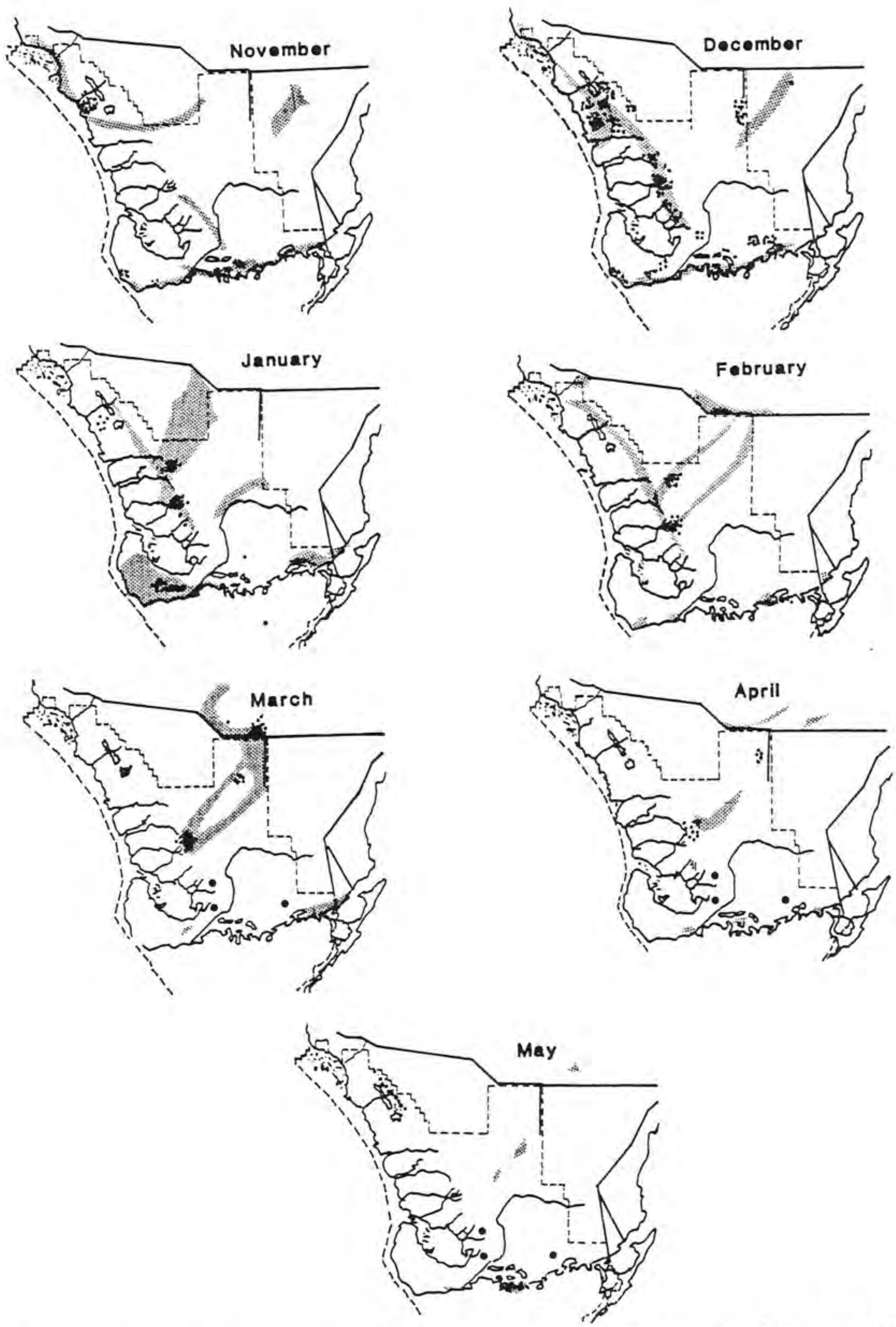

Figure 5. Distribution of foraging White Ibises (shading) and Wood Storks (stippling) during the drying season in southern Florida. Wood Stork colony sites are shown as large dots.

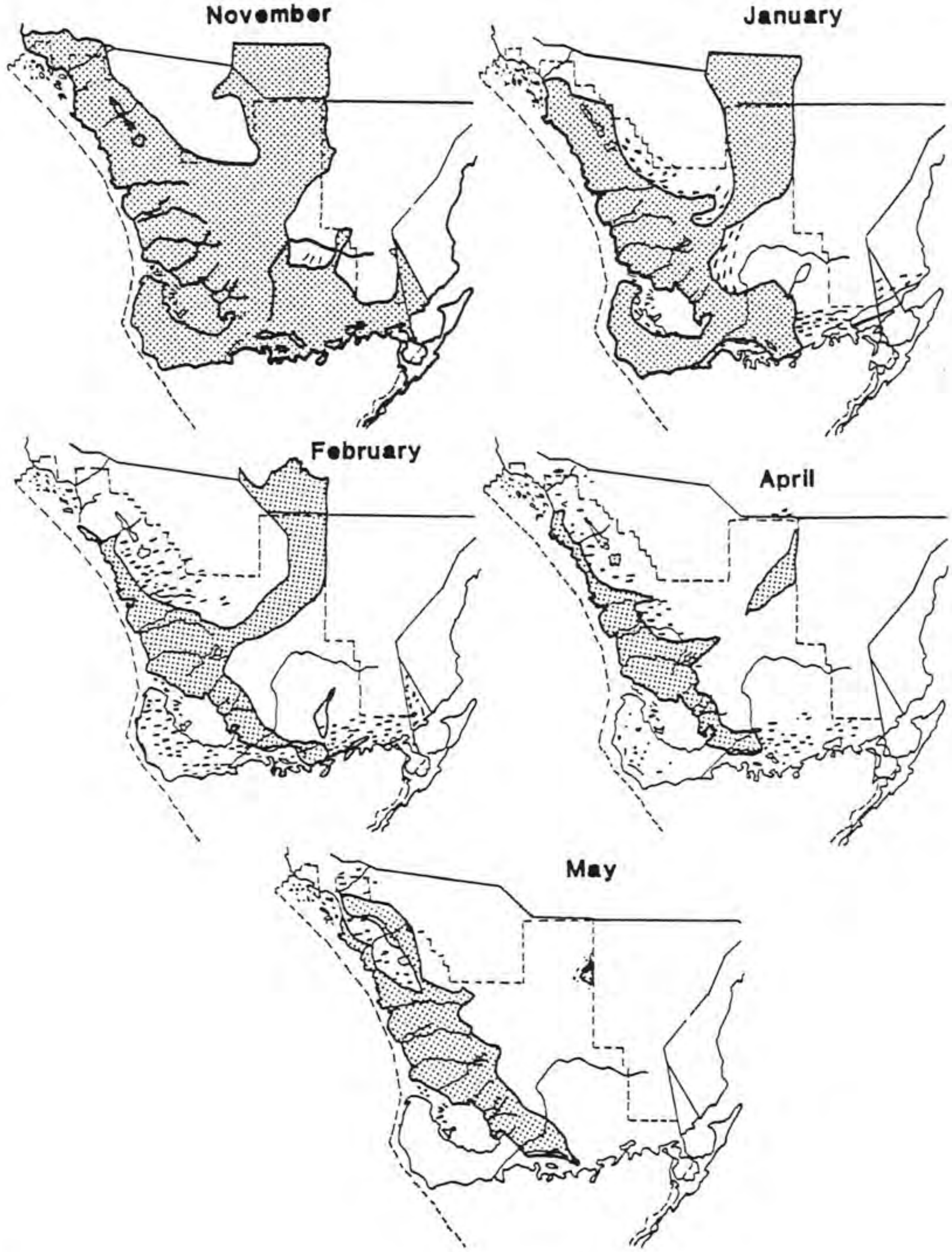

Figure 6. Pattern of drying in the southern Everglades marsh. Shading indicates standing surface water.

marshes drying first. Wood Storks concentrate their foraging sites in locations where concentrations of fishes occur. The White Ibis follow the drying pattern more broadly because they forage in marsh habitat just inside the drying edge. The strategy of seasonal movement allows both species to use the resources available over the entirety of the Everglades wetlands during the course of the drying season.

Breeding Seasonality

Historically, Wood Storks began nesting in fall and early winter, from October to December. However after 1962 the start of nesting shifted later, to December through March (Fig. 7). The late initiation of nesting has caused the repeated nesting failure in the southern Everglades because of insufficient time in which to complete nesting before the rainy season begins in May. The timing of nesting of Wood Storks is intimately tied to the seasonal fluctuation in water level, initiation time being highly predictable and correlated with the rate at which the water level recedes (Kushlan et al. 1975). The slower the Everglades dries, the later Wood Storks initiate their nesting season, with severe consequences to reproductive success.

White Ibises usually begin to nest in March in southern Florida. Their gonadal cycle corresponds to the usual period of water level recession (Fig. 2). The proximal stimulus is undoubtedly photoperiod, in that captive birds develop breeding coloration at the appropriate season (pers. obs.). Prey availability may influence the expression of breeding activity however. The White Ibis has nested successfully in southern Florida as late as fall, under appropriate water conditions. The ability to initiate nesting any time after spring provides ibises more breeding flexibility than is found in storks. Ibises can complete nesting within 60 days and can forage on both rising and falling water levels.

Colony Site Selection

The physical site of nesting colonies is not limiting in southern Florida as

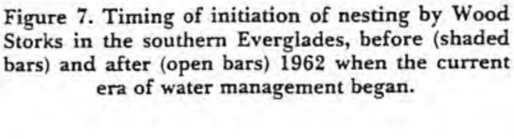

Figure 7. Timing of initiation of nesting by Wood Storks in the southern Everglades, before (shaded bars) and after (open bars) 1962 when the current era of water management began.

thousands of suitable tree-covered islands exist throughout the Everglades and nearby estuarine swamps. Nonetheless, the locations chosen for colonies and the tenacity of their use reveals much about the strategies of the two species.

The Wood Stork is extremely traditional in its use of nesting sites. The colony sites used in the southern Everglades (Fig. 5) have been occupied for decades (Kushlan and Frohring 1986). Requiring 4 months to nest, the Wood Stork, it seems, must repair to colony sites soon after arriving in southern Florida in early winter. Wood Storks can travel over 80 km from the nest site to foraging sites and thus have the capability of using food resources scattered over a wide area of marsh and made available over the several months of their nesting season (pers. obs.).

The White Ibis appears to have the opposite strategy of colony site use. It is nearly nomadic, seldom using the same site for more than a couple of years in succession. The ibis is capable of flying up to 60 km to feeding sites, but it seldom does so (pers. obs.). Rather in the Everglades it responds to localized conditions by establishing colonies near current food supplies, which need only to last for the relatively short nesting season. Colony site selection depends on the availability of foraging habitat, and birds relocate when conditions change from one year to the next (Kushlan 1976 c).

Discussion

The naturally fluctuating water conditions of the Everglades clearly present potentially severe constraints on wading birds attempting to feed and nest there. The suites of adaptations possessed by White Ibises and Wood Storks, which have permitted their existance in the Everglades, differ in several respects. Common to both are tactile foraging while wading, dry season nesting, and intraregional population movements. The long nesting season of the Wood Stork, a result of its relatively large size, restricts its nesting season. Because nesting must be completed before the end of the drying period, early nesting is crucial to its eventual success. In contrast the White Ibis, requiring a relatively short nesting season, can be more flexible in

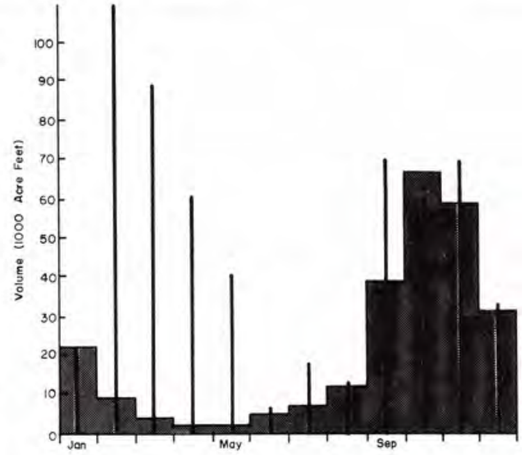

Figure 8. An example of unseasonality of discharge into the southern Everglades. Lines are actual discharge, contrasted with the bars that are historic median flows.

nesting timing. Although differing, both species have the ability to accommodate to the natural variability that characterizes fluctuating water wetlands.

However the Wood Stork population has nested successfully in only three years from 1962 to 1982, as a direct result of which the nesting population in Everglades National Park decreased from 2000 pairs in 1967 to 670 in 1982 (Kushlan and Frohring 1986). The White Ibis last nested in large numbers in the southern Everglades in 1973. Thus it has tended to abandon nesting in Everglades National Park, shifting its colonies to sites in the northern Everglades and elsewhere. These responses suggest that ecological conditions in the southern Everglades marsh have ceased to be appropriate for successful nesting by these species in most years.

Considering the demonstrated importance of water level fluctuations in determining ecological relationships in the Everglades, it is reasonable to expect that some alteration in these fluctuations has occurred, probably related to water management procedures. Such alterations may be either in the spatial pattern of water depth change or in its rate of recession. The levee system partitioning the Everglades has caused excessively high water upstream from the levees transversing the drainageway (Fig. 3), and management procedures have altered the pattern and timing of drying substantially (Kushlan 1986).

The rate of water level decline is critical for Wood Storks, although not for White Ibis. The relationship between the rapidity of recession and the timing of Wood Stork nesting together with the late start of recent nesting attempts strongly implies that the limits of appropriate water level recession have been exceeded. A slowed recession rate results from the management of surface water discharge into Everglades National Park. Figure 8 shows an example of how the monthly amounts of discharge into the park has been artificially increased in the dry season recent years. Such excessive discharges, especially in the dry season, will affect drying rates and therefore the timing and success of Wood Stork nesting.

The predominant role of hydrological variability in some natural wetlands apparently requires specific accommodative adaptations on the part of aquatic organisms, such as wading birds. An important aspect of this variability must be an inherent long-term predictability within the annual hydrological cycle. If this were not so, it is unlikely that suitable accommodations would be possible over the long term. The existence of an inherent predictability in water level fluctuation suggests that the variability is explainable in a statistical sense on the basis of antecedent conditions to which the wading birds can respond. Such a relationship has been documented in the Everglades for alligators (Kushlan and Jacobsen in prep.). Inappropriate management of man-modified wetlands may ultimately result from disruption of the natural predictability of the fluctuating water system.

The modification of wetlands may be dramatic, such as that accomplished by drainage or creation of relatively deep reservoirs upstream of levees. However, modification may also be considerably more subtle. It can result from a relatively slight delay in the downstream flow of surface water derived from a rainfall event or from the trickling of water into a marsh during the normal drying season. Such manipulations will increase water levels over what would have occurred naturally and retard the rates of recession.

These seemingly minor modifications, and the disruption to nesting wading bird populations they may cause, would not necessarily be as obvious as draining a wetland or permanently flooding it. Nevertheless wetland managers need to be concerned not only with massive dislocations of wetlands but also more subtle effects of water manipulation that can change the fundamental functioning of the wetland ecosystem by altering the water level fluctuation on which that functioning depends.

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