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"Importance of Landscape Heterogeneity to Wood Storks in Florida Everglades"

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Importance of Landscape Heterogeneity to Wood Storks in Florida Everglades

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ABSTRACT / Declines in populations of and reproductive success of wood storks and other wading birds have occurred in the Florida Everglades over the past several decades. These declines have been concurrent with major changes in the Everglades' landscape characteristics. Among the plausible hypotheses that relate to landscape change are the following: (1) general loss of habitat; (2) heavy loss of specific habitat, namely, short-hydroperiod wetlands that provide high prey availability early in the breeding season; and (3) an increase in frequency of major drying out of the central slough areas, which can affect prey availability late in the breeding season.

These three hypotheses were compared using an individual-based model of wood stork (*Mycteria americana*) reproduction. This model simulated the behavior and energetics of each individual wood stork in a breeding colony on 15-min time intervals. Changes in water depth and prey availability occurred on daily time steps. Simulation results showed a threshold response in reproductive success to reduction of wetland heterogeneity. Model comparisons in which (1) only short-hydroperiod wetlands were removed and (2) wetlands of both long and short hydroperiods were removed showed that, for the same loss of total area, the specific habitat removal caused a much greater reduction in wood stork reproduction, indicating hypothesis 2 may be a more likely explanation than hypothesis 1. Reduction of initial prey availability in the central slough areas (simulating frequent drying; hypothesis 3) reduced fledging success by an average of more than 90% in the model.

Changes in the trophic structure and dynamics of native animal assemblages that occur when natural landscape patterns are altered frequently result in a loss of biodiversity (Craighead 1968). For example, undisturbed natural areas such as the historical Everglades once supported large populations of top-level carnivores (Lovelass 1959, Craighead 1968, Robertson and Kushlan 1974, Kushlan and Frohring 1986, Fleming and others 1994 a,b). Such species, however, are often vulnerable to changes that alter the natural landscape (Wright and Hubbell 1983, Harris 1984, Lovejoy and others 1984, Quinn and others 1985, Noss 1987, Wilcove 1987, White 1987, Pimm and Gilpin 1989).

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Declines in top carnivore populations have occurred in the Everglades concurrently with major changes in the system's landscape during the last several decades. Reduction in the system's areal extent, resulting changes in landscape composition or terrain patterns, and alteration of the seasonal hydrologic regime have resulted from drainage and water management for agriculture, flood control, urban development, and aquifer recharge (Parker and others 1955, Parker 1974, Wagner and Rosendahl 1985, Smith and others 1989, Johnson and others 1994, Fennema and others 1994). Severe population declines in the Florida panther, *Felis concolor coryi*, colonial wading birds, the American alligator, *Alligator mississippiensis*, and the snail kite, *Rostramus sociabilis* have occurred (Craighead 1968, Robertson and Kushlan 1974, Sykes 1984, Bennetts and others 1994, Ogden 1994, Smith and Bass 1994).

Because of their large numbers and the seasonal shift in their feeding areas, colonial wading birds are

an important predator in the system, influencing both freshwater and estuarine prey communities. During the past several decades, however, there has been a drastic reduction in the reproductive success of wading bird species in the southern Everglades (Robertson and Kushlan 1974, Kushlan and White 1977, Ogden 1978, Ogden and Patty 1981, Kushlan and others 1984, Kushlan and Frohring 1986, Collopy and Frederick 1986, Powell 1987, Frederick and Collopy 1988, Powell and others 1989, Bancroft 1989).

Although declines in wading birds have received attention, the causes for the declines have not been investigated in a rigorous fashion. Several hypotheses have been proposed to explain the reductions in reproductive success. Because experimental manipulations of the type necessary to test these hypotheses are not practical, we propose to use computer modeling as a surrogate and study the feasibility of three of these hypotheses that can be explored on the basis of current knowledge.

Some of the hypotheses suggested involve various effects caused by changes in characteristic features of the Everglades landscape. We will use the term "landscape" here in the sense that it is commonly used in the field of landscape ecology (e.g., Forman and Godron 1981). In this sense, the landscape is a mosaic of habitat patches covering a region occupied by an ecological population or community of interest. The size of the landscape size depends on the questions being asked and will be described below.

The historical predrainage hydrology of south Florida was characterized by: (1) uninterrupted sheet flow of water during the wet season that resulted in (2) the annual inundation of extensive high elevation wetlands peripheral to the central drainage basin, (3) attenuated (i.e., slowed or buffered) changes in seasonal marsh water depths in the interior wetlands and central sloughs of the basin, (4) long intervals between major drydown events (periods of a complete drying out during the dry season) in these long hydroperiod wetlands, and (5) substantial dry season flows through the central sloughs or major flow-ways into downstream estuaries and Florida Bay (Parker and others 1955, Parker 1974, Wagner and Rosendahl 1985, Smith and others 1989, Johnson and others 1994, Fennema and others 1994).

In contrast to this historical scenario, the present postdrainage hydrology has led to a disproportionate loss in high elevation short-hydroperiod wetlands (Figure 1); that is, wetlands covered with shallow water for a relatively short duration within the year due to their relatively high elevation. Furthermore, instead of attenuated seasonal changes in marsh water
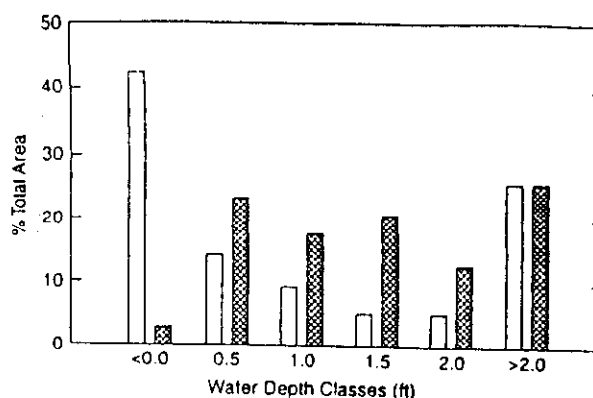

Figure 1. Comparison of early dry season surface water proportions between predrainage (white bars) and postdrainage (hatched bars) Everglades landscape, showing the disproportionate loss of the shallow, short-hydroperiod wetlands.

depths within the low-elevation interior wetlands and central sloughs, water levels now show pronounced fluctuations. Major drydown events in the interior wetlands and central sloughs are now more frequent and dry season freshwater flows into the downstream estuaries are reduced. Rather than experiencing uninterrupted sheet flow during the wet season as under the predrainage conditions, the wetlands in the northern reaches of the Everglades catchment area are now impounded and the remaining peripheral short-hydroperiod wetlands and central sloughs in the southern reaches are overdrained, or altered so that water drains off faster than under natural circumstances (Parker and others 1955, Parker 1974, Wagner and Rosendahl 1985, Smith and others 1989, Johnson and others 1994, Fennema and others 1994).

Change in colonial wading bird populations, possibly in response to these alterations, has been dramatic. During the past 30+ years there have been declines in the total number of wading birds across all feeding guilds (Fleming and others 1994b, Ogden 1994). Fewer birds now attempt to nest, with declining rates of reproduction per nesting pair. For example, the numbers of nesting pairs at traditional colony sites within the southern Everglades has declined 90% in the recent past (Ogden 1994).

The starting dates of colony formation and the nesting success rate have been highly variable and strongly correlated (Kushlan and others 1975, Ogden and others 1980, Kushlan and Frohring 1986, Frederick and Collopy 1988, Powell and others 1989, Bancroft and others 1991). This correlation has been interpreted in the following way. The fledging of young

wading birds in the Everglades takes up to 16 weeks and must be completed during the dry season before the onset of spring rains in May or June, because, by raising water levels, the spring rains dilute the concentration of prey and hence decrease foraging success. Therefore, environmental conditions that delay the start of nesting may lead to reproductive failure of entire colonies.

Delays in the start of nesting may be related to postdrainage changes in the Everglades landscape mentioned above. Wading birds typically forage over large areas during their seasonal cycle. During the wet season, they generally feed in the shallow water of the short-hydroperiod wetlands and in coastal habitats during low tides. During the dry season, wading bird foraging concentrations shift to longer hydroperiod, interior wetlands as these progressively dry down (although usually retaining some surface water through the dry season). These changes in feeding location are necessary because the birds require shallow water depths and concentrated prey, primarily fish and macroinvertebrates, to forage efficiently.

On a daily basis, wading birds move between their feeding areas and their roosting or nesting sites. Landscape characteristics that affect the spatial distribution of available prey affect the flying distances to and from the colony and the time spent by wading birds in searching for prey. These prey parameters thus influence wading bird foraging efficiency and related timing of colony formation, as well as create constraints on the time and energy budgets of nesting pairs (Orians and Pearson 1979), affecting their subsequent reproductive performance. Alterations in the predrainage Everglades landscape appear to have altered these prey parameters, as suggested by the decline in wading birds numbers and in their reproductive success.

Several specific hypotheses have been proposed linking these observed declines in wading birds and in their reproductive success to changes in landscape characteristics of the Everglades:

1. General habitat loss. The reduction in total size of the Everglades because of development and/or drainage, resulting in general habitat loss, has caused the overall decline of wading bird numbers within the system (Robertson and Kushlan 1974).

2. Reduction in prey availability and/or productivity in estuaries. Traditional wading bird colony sites were located in the headwater regions of downstream estuaries of the Everglades catchment basin. Recent sea level rise and related hypersaline conditions are thought to have decreased productivity and/or prey availability within the estuaries, depriving the wading

birds of their food source (Powell and others 1989). During the dry season the sea level drops about 30 cm, which should allow estuarine water levels to recede, creating shallow water foraging sites for wading birds. In the past 60 years, however, mean sea level has risen at a rate of approximately 20–40 cm per hundred years (Hoffman and others 1983), possibly affecting water level recession rates in the estuaries and prey availability. Simultaneously, freshwater flows from the upstream reaches of the catchment basin into the estuaries were reduced by water management practices, fostering more hypersaline conditions in the estuarine waters (Tabb and others 1962, Craighead 1968, Browder 1985).

3. Alteration of drying rates. High flow volumes to the downstream reaches of the Everglades occurred in the mid- to late 1970s during the late wet and early dry season. This resulted in slower marsh water level recession rates within the southern Everglades and thus in lower prey availabilities. Wading birds at traditional colony sites in the estuaries are hypothesized to have responded by delaying colony formation or not forming nesting colonies at all. Late nesting left insufficient time for nesting pairs to raise young before the advent of spring rains, which cause a rising of marsh levels and a dispersion of preys. Kushlan (1979) hypothesized that high drying rates during the early dry season months are needed to trigger early wading bird colony formation. Early colony formation allows pairs sufficient time to raise their young during the dry season, that is, between successive wet seasons.

4. Specific habitat loss. The timing of colony formation at traditional sites located in the southern Everglades is associated with the areal extent of shallow water within a core foraging area (Fleming and others 1994b). Under predrainage conditions, high drying rates were not required for shallow water areas to exist during the early dry season (the prenesting period). Late wet season inundation of peripheral short-hydroperiod wetlands provided extensive shallow water areas before regional water levels began to recede in the dry season. These extensive peripheral short-hydroperiod wetlands provided extensive (shallow water) foraging habitat during the late wet/early dry season, the prenesting period. The disproportionate reduction (85%) of this specific habitat known to have occurred due to loss from development and/or degradation (overdrainage) has been proposed as a major cause of late colony formation of wading birds at traditional colony sites located in the headwater region of downstream estuaries of the Everglades catchment budget (Fleming and others 1994b).

5. Increase in major drydown frequency. Major dry-

down events severely reduce the next few year's prey standing stocks. The increased frequency with which these major drydown events occur now leaves insufficient time for prey populations to recover (Loftus and Ecklund 1994). In addition to late colony formation, such interannual effects are thought to have further reduced the reproductive performance of wading birds (Fleming and others 1994b).

6. *Bioaccumulation of mercury.* Mercury that has accumulated in aquatic food webs in the Everglades has been hypothesized to affect the motor coordination of adult wading birds and their subsequent foraging capabilities.

7. *Eutrophication effects.* Sites of eutrophication, related to water-quality problems in those areas, support endemic populations of nematodes that infect local fish populations. Fish captured at these sites and then transported as food items by adult wading birds to nestlings cause mortality related to an increasing parasitic load or internal damage; for example, hemorrhaging, physical obstruction of the abdominal cavity.

8. *Distant magnets.* Declines in the number of migratory colonial wading birds that regulatory overwinter in south Florida have also occurred concurrent with population increases in these species in more northern parts of their geographic ranges. A shift in migratory patterns to account for these changes has been proposed as one possible explanation for the decrease in wading bird total numbers in the Everglades during the recent past (Walters and others 1992).

9. *Alteration in frequency of major hurricanes and related effects on the system's aquatic productivity.* Nutrient pulses into the system resulting from litter deposition through defoliation and downed vegetation as well as sediment disturbance due to wind forces may increase both primary and secondary production; for example, the abundance of aquatic organisms as important food resources for wading birds. The absence of major hurricanes over the past 30 years, therefore, has resulted in a decrease in the system's overall productivity and standing stocks of aquatic prey for wading birds, adversely affecting their reproductive success.

These nine hypotheses make different predictions concerning what stage or time period in the nesting cycle of the birds is affected, as well as on how large the effect will be on population numbers of adult birds and their reproductive success. Some of these hypotheses are not fully consistent with observations and can be eliminated from urgent consideration on the basis of what is currently known.

Hypothesis 2—decline of wading bird reproductive performance in relation to decline in estuarine productivity and/or prey availability—appears to be contradicted by the fact that in the 1970s water management practices significantly increased relative flow volumes to the downstream reaches of the Everglades catchment basin during the late wet and early dry season. Despite these increased freshwater flows into the hypersaline estuaries, traditional colony sites continued to decline at an accelerated rate. It is not established, moreover, that estuary production, by itself, could have supported the large wading bird numbers observed in the past. Prey in the lower reaches of the estuaries would be available only during low tides each day and the available feeding area in the headwaters would be limited. This hypothesis also fails to address the observed annual variability in the timing of colony formation and related wading bird reproductive success.

According to the "alteration of drying rates" hypothesis (3), rapid drying of the marshes is required for successful nesting and the interference with this rapid drying has led to reproductive declines. A problem with this is that high initial drying rates during the early dry season also often lead to major drydown events in the low elevation central sloughs as well. Prey standing stocks are then significantly reduced systemwide and require several years to recover (Loftus and Ecklund 1994). Due to interannual effects, drydown events with a mean period of occurrence of less than three or four years can keep the prey base at continuously low levels (Loftus and Ecklund 1994) adversely affecting the reproductive performance of nesting pairs in subsequent years. Such rapid drying conditions, therefore, if repeated each year, would soon reduce the prey base required for successful nesting.

Although hypothesis 6—bioaccumulation of mercury—may provide a causal explanation for a declining trend in wading bird performance, it, like the above hypothesis, does not account for the interannual variation in colony formation dates and the resulting variability in reproductive performance of nesting pairs. Declines in local population levels of migratory species concurrent with population increases in these species in other parts of the range, as a result of changes in migratory patterns, the distant magnets hypothesis (8), does not explain the decline in wading bird numbers in the Everglades across all species and feeding guilds, nor does it address their highly variable reproductive success in present postdrainage conditions. The alteration in hurricane frequency hypothesis (9) also does not address the observed annual variability in the timing of colony formation and related reproductive success. Increases

in prey abundance alone do not increase prey availability during the early dry season months of the critical prenesting season when required shallow water foraging areas are limited in the present postdrainage landscape.

None of the hypotheses can be eliminated from consideration, but we will focus on comparing those that appear to us to be the strongest candidates: general habitat loss (1), specific habitat loss (4), and the increase in the frequency of major drydowns (5). We also focus on these because they are amenable to testing with our landscape model and because we lack specific information that would allow us to study other hypotheses, such as the eutrophication hypothesis. This study should be seen as an examination of the feasibility rather than a rigorous test of hypotheses.

Methods

Empirical testing of the three hypotheses would involve the performance of long-term trials or experiments in water delivery and flow, which are both impractical and potentially destructive. However, computer simulation modeling provides a means for performing a very large number of numerical "experiments" using different assumptions.

To realistically test the particular hypotheses regarding the reproductive failure of wading birds, the model must satisfy several conditions. First, it must account for both spatial extent and landscape heterogeneity, because these are explicitly involved in the hypotheses. Second, because changes in the environment (e.g., water level, food availability) may change appreciably on a time scale of days during the reproductive period, the simulation model must operate on this time scale. Third, because chance happenings, such as rainfall events during the nesting period (dry season) can be crucial, the model must incorporate some stochasticity. Fourth, it is doubtful that merely simulating an average pair of wading birds will be sufficient, since there may be a broad spectrum of degrees of success among pairs in the colony. Therefore, it is necessary to consider in the model either all or a large sampling of the nesting pairs in the colony. Fifth, because a nesting colony may have a significant impact on its supply of potential prey, the feedback effects of the foraging birds on prey biomass should be taken into account.

An Individual-Based Model of Wood Stork Nesting Colony

The type of modeling approach employed in the present paper is designed to meet the above condi-

tions and is an example of what is commonly referred to as an individual-based approach. This approach has been discussed in general by Huston and others (1988) and DeAngelis and Gross (1992). In this type of model all or a representative fraction of the members of a population are simulated simultaneously. The experiences of each individual, its movements on a landscape, success in gathering food, and reproductive success can differ. Decision making by the individual organism, which can depend in a complex way on day-to-day, or even minute-to-minute circumstances is included.

The individual-based model simulated a colony of wood storks (*Mycteria americana*) for a period of time immediately preceding the formation of a nesting colony and then the whole of the nesting season. This model is described in detail by Wolff (1994), who also gives the sources for all of the assumptions that are built into the model. In this model each of the adult nesting birds as well as each of the offspring of these adults were modeled as individuals.

The model consists of the following parts (Figure 2): (1) a submodel of the heterogeneous landscape, on which changing water depth is the key variable; (2) a submodel for the prey population, which varies spatially and temporally across the landscape; (3) a set of submodels for the behavior and energetics of each potentially nesting adult; and (4) a set of submodels for the energetics and growth of each nestling, until the nestling is fledged or dies.

Landscape Submodel

The importance of spatial heterogeneity of the environment surrounding the colony requires that heterogeneity be taken into account, which was done through division of the potential foraging area into 25,600 contiguous square cells, each 1/4 km × 1/4 km. Each cell had its own mean elevation, so that the whole set of cells described the typical topography of the central part of the southern Everglades (shown schematically in Figure 3). As the general water level receded during the dry season, the average water depth in each of the cells went down until either the cell dried out or rainfall from the new rainy season started raising its level again. Rainfall events could also occur during the dry season and cause temporary reversals to this general decline. Water depth in the spatial cells changed on daily time steps.

Prey-Based Submodel

The prey for the wood storks consisted of small fish and macroinvertebrates. For convenience, all prey in the model that were consumed by the foraging
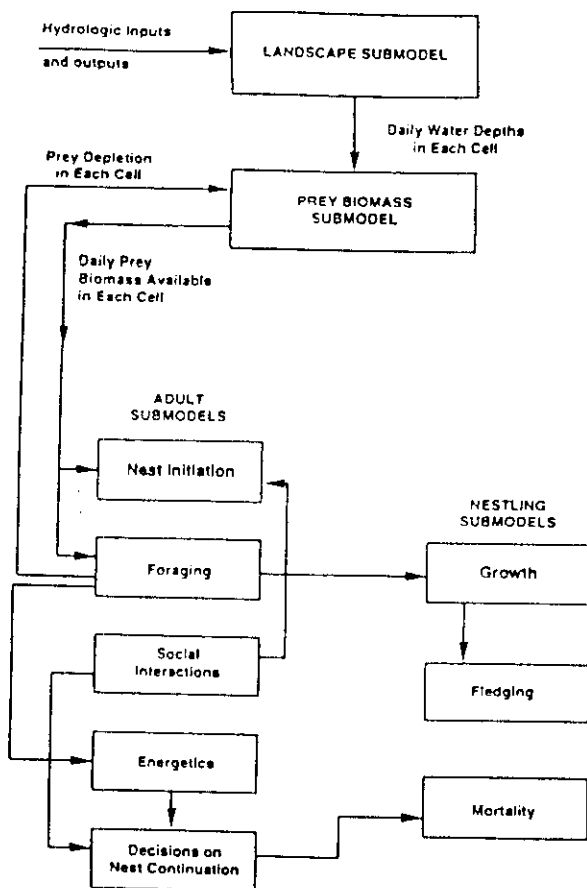
Figure 2. Schematic of individual-oriented model of wading bird reproduction showing the major components of the model.

Figure 3. Schematic representation of the landscape around a traditional wading bird colony located in the estuarine headwater region of the southern Everglades: A long hydroperiod central slough upstream of the colony site bordered by short-hydroperiod peripheral wetlands on both sides.

birds were assumed to occur in the form of cyprinodontoid and centrarchid fishes, with an average weight of 1.73 g (Ogden and others 1980). However, seasonal fish densities in the Everglades are variable from year to year, depending upon antecedent surface water conditions (drying and inundation rates, etc.). Typical late wet season densities range from 50 (±25) fish/m^2 in long-hydroperiod sites to 10 (±8) fish/m^2 in short-hydroperiod wetlands (Loftus and Eklund 1994), where the standard deviations are in parentheses. A simulation started near the end of a wet season, with prey assigned densities across the landscape that are typical for the hydrologic conditions being simulated. The prey in a given cell were assumed to be available to the wood storks using the cell only when the average water level of the cell is within a certain range (10–40 cm for wood storks). In reality, only part of a cell can be expected to consist of an o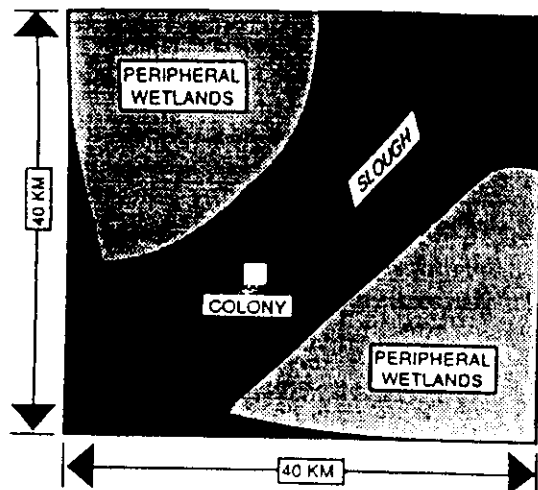pen area suitable for wood stork feeding. It was assumed that only 10% of the area of each cell, and thus of the prey in the cell, was available to the wood storks. This assumption of 10% prey availability may be thought of as reflecting not only the unfavorability of much of the cell for wood stork feeding, but also the effects of other wading birds that compete with the wood storks. As a consequence, an average of 108 kg prey/cell were assumed available to the wood storks.

In the model simulations, a standard deviation of 56% of the mean was used and the total available prey in a given cell was chosen from a normal distribution. The wood storks could feed on the fish in that cell and in so doing they reduced the fish biomass of the cell. (Movements of fish from one cell to the next or fish reproduction in the cell during the dry season were not represented in the model.) Prey densities changed due to wading bird foraging on 15-min time steps. The foraging efficiency of wood storks in a given spatial cell was proportional to the number of prey in the cell, so as prey biomass goes down, the feeding success of the birds in the cell also decreases. The birds also tended to stay for longer periods of time in cells with high prey density.

Behavior and Energetics Submodels of Potential Nesting Adults

The nesting adult wood storks were described by a set of rules that governed their behaviors from one

time interval to the next. The time unit chosen to describe the behaviors of the adult birds was 15 min. This time unit was chosen because many discrete activities of wood storks, such as carrying food back to the nest, take time intervals as short as 15 min. Note that this characteristic time differs from the daily time step changes of cell water depth.

The first choices made by adult pairs during this prenesting season were if and when to start nesting. The rule that was followed in the model was that, if the female could obtain 20% more than its food needs for several consecutive days during the time period after the end of the rainy season, she would start nesting. Usually three or four eggs were produced asynchronously per pair and hatching took place in about three weeks.

After the start of nesting the decisions made by the adults were guided by various constraints. Each adult had to meet a maintenance energy demand each day. To meet this demand the adult used the first part of the food it collected in a given day for itself. The individual birds usually foraged between 1000 and 1600 h each day, with each bird deciding when to start and whether to follow others or to go by itself. The location chosen by an individual for foraging was based on its partial information concerning the system. It was assumed that each wood stork had some knowledge, perhaps obtained from visual cues when flying or soaring, concerning the water depth of various locations (cells in the model) in its foraging area, but a wood stork was not assumed to know the prey density in a given cell until it had sampled it for some time (15 min). The wood stork could select a cell in the appropriate water depth range, but randomly otherwise, and forage for food in that cell. Alternatively, it could decide to join one of several flocks of birds from the colony that were already feeding. Although each capture of prey by a bird was a stochastic event, the rate of prey captures depended on the current fish density of the cell. Because the wood stork is a tactile forager, its foraging efficiency should be roughly proportional to the (mean) density of prey within a cell.

If the wood stork found no prey during a 15-min interval, it moved to another cell, either one nearby or at some distance, although there were greater costs in travel time in flying to a more distant foraging site. Again, it may choose to feed solitarily or join a flock. Probabilities for such choices can be assigned in the model. It should be noted that the presence of a flock will usually indicate high food density, although it may have been depleted already by the birds foraging there.
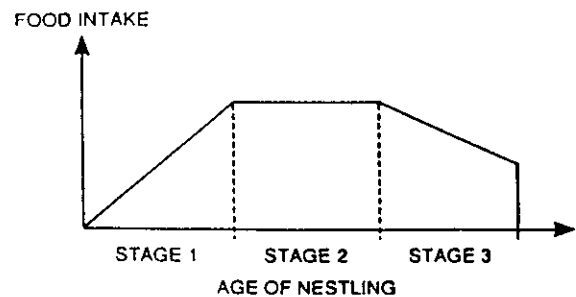

Figure 4. Simplified pattern of maximum daily food intake of nestling wood storks over the nestling period.

Energetics and Growth Submodels of Nestlings

After obtaining sufficient food for itself, the model wood stork would continue to forage for its offspring, and it would decide at some point to bring food back to its nestlings, either all the food that it could carry or all that it was able to gather during the time it foraged. The adult regurgitated its food inside the nest, and there was "scramble competition" among the nestlings for the food. According to the rule used in the model, a greater proportion of the food was taken by the largest nestling, the next greatest amount by the second largest and so forth, until all food was distributed.

The daily growth of the nestlings was computed on the basis of the energetic value of the daily ration of food brought by their parents. Depending on their age in days since hatching, there is some maximum that an individual nestling can consume (Kahl 1962). This maximum increases linearly at first, then levels off and finally declines as the nestling approaches fledging (see Figure 4). From experimental measurements (Kahl 1962), it is known that a nestling must attain some threshold level of accumulated food (taken here as 14 kg) in order to fledge. If the nestling does not receive this amount of food before the rainy season begins and adult foraging capability decreases, the model nestling will usually die, because the parents will no longer be able to provide food at a rate sufficient for its survival. Furthermore, if over any five-day time period during the nesting season a nestling receives less than a certain percentage of its cumulative food needs, it will die. If the parents cannot find enough food to meet their own energetic demands, they will abandon their nest and the nestlings will perish.

Experimental Design to Test Selected Hypotheses

Model experiments were carried out to compare the three hypotheses under consideration: general habitat loss, specific habitat loss, and increase in the

frequency of major drydown frequency. The landscape used in the simulation represents the typical core foraging area of a traditional wood stork colony located in the estuarine headwater region of the southern Everglades. In rough terms, the area consists of a long-hydroperiod central slough upstream of the colony site that is bordered by short-hydroperiod wetlands on both sides (Figure 3).

Baseline Hydrologic Scenario

For purposes of comparison, a baseline simulation that approximates the predrainage landscape was performed first. In this simulation, all peripheral short-hydroperiod wetlands were present and contained an initial low prey density (10 fish/m^2) but widespread distribution of prey (prey occurred in 80% of model peripheral short-hydroperiod wetland cells), indicative of sufficient inundation during the preceding wet season. Initial prey densities were high (50 fish/m^2) throughout all long-hydroperiod central slough cells. Colonies of 50 and 250 pairs of wood storks were simulated in this landscape.

Each pair produced three nestlings. There was no mortality of adults over the reproductive period, and the only potential source of mortality of the offspring included was the possibility of starvation.

Alternative Hydrologic Scenarios

The hypothesis of specific habitat loss states that the removal of a large fraction of the original peripheral short-hydroperiod wetlands led to a decline in wading bird reproductive success. For the smaller colony with 50 pairs, the model was used to examine removals of 10%, 20%, 30%, 40%, 50%, 60%, 70%, and 80% of the peripheral short-hydroperiod wetland areas shown in Figure 3 (equivalent to removing those percentages of peripheral short-hydroperiod wetland cells in the model). These correspond to 5%, 10%, 15%, 20%, 25%, 30%, 35%, and 40% of the total area, since the short-hydroperiod wetlands and central slough were each assumed to occupy half of the total area. The larger colony with 250 pairs was simulated for removals of 5%, 10%, and 15% of the short-hydroperiod wetlands (corresponding to 2.5%, 5%, and 7.5% of the total area). To determine whether the short-hydroperiod wetlands have special importance, these removals can be compared with removals purely of central slough marshes. To compare the above hypothesis with the general habitat loss hypothesis, random mixtures of area, half from the peripheral short-hydroperiod wetlands and half from central slough, were removed.

The hypothesis of an increase in the frequency of major drydown frequency states that the reproductive decline is a result of low prey availability in the long-hydroperiod wetlands (that is, the interior wetlands and central sloughs) because of too frequent drydowns. To test this, we used scenarios in which the initial prey base in the central slough cells was decreased to 10% of their baseline level (Loftus, personal communication). However, prey densities in the short-hydroperiod wetland areas remained the same as in the previous scenarios, as the highly eroded landscape of these marshes provides numerous drought refugia, allowing for greater fish survival in the short-hydroperiod than in the long-hydroperiod wetlands following major drydowns and, therefore, a more rapid recovery of standing stocks during the following wet season months (Loftus and others 1992). Compared to the baseline situation, these alternative scenarios together approximate the present postdrainage conditions.

Results

Baseline Simulation Results

The baseline scenario represents a favorable dry season, in which the drydown is at a steady rate with no reversals in water depth decline, which could cause nest desertion. For this scenario, the simulation results show the same basic pattern for both colony sizes: early colony formation within 30 days after the start of the simulation and a successful breeding season with high reproduction. The results of a typical run of the 50-pair colony are shown in Figure 5. Nesting started early (on day 5) and was over before the wet season began around day 150. Each nesting pair produced three eggs, all of which hatched, and the number of nestings rose rapidly after about three weeks after the first egg-laying (Figure 5A). Food availability was high in this scenario, and all nestlings survived. Around day 105 nestlings started to fledge (Figure 5B). All nestlings received more than the 14 kg they required to fledge, as shown in Figure 5C.

The results of this simulation should not be thought of as representative of every year in the predrainage Everglades. Even under natural conditions, hydrologic conditions are variable and can lead to nesting failures.

Alternative Hydrologic Scenarios as a Test of Specific Habitat Loss Hypothesis

When the peripheral short-hydroperiod wetlands were reduced to 60% of their baseline area (that is,
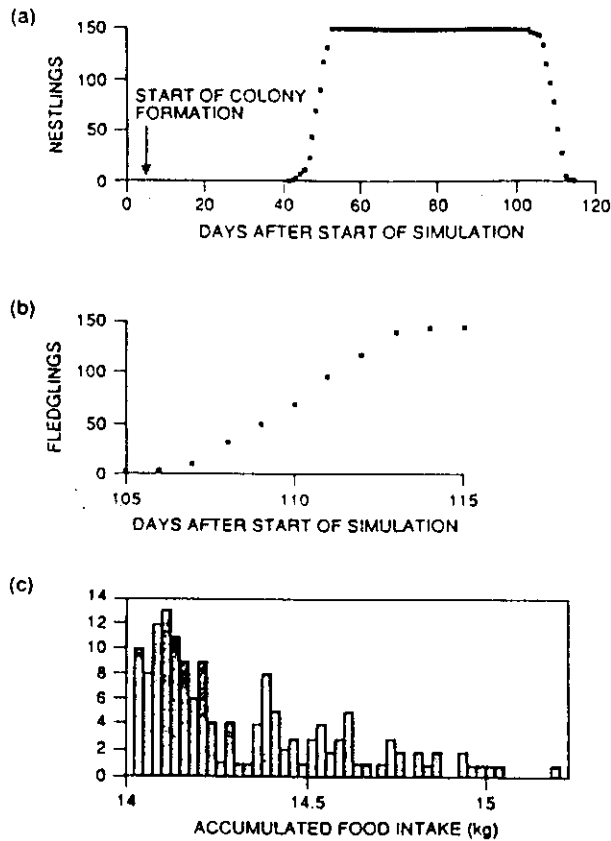
Figure 5. (a) The number of nestlings in the 50-pair colony during the entire breeding season. The first nestling appears on day 42 and the last one fledges after 115 days. (b) The cumulative number of fledglings in the colony. (c) Distribution of total food intake of the nestlings at the time of their fledging.

40% reduction), the colony with 50 pairs was still quite successful. Colony formation was delayed by not more than three weeks and, on average, each pair produced more than two fledglings (Table 1). When 60% of the short-hydroperiod wetlands were removed, the situation changed completely. A typical result (Figure 6A) shows that nesting was delayed by approximately 100 days, because nesting adults could only forage efficiently when water levels were low enough at the edges and upper portions of the central slough. The wet season with its water level reversal began around the middle of the nesting period. Then adults could not obtain enough food for their young and all the nestlings starved, with a very rapid die-off beginning about 20 days after the start of the rains (Figure 6B).

For a colony of 250 pairs, the results were different (Table 2), because a colony this size could have a significant effect on the prey density. The baseline sce-

nario led to early colony formation and successful reproduction. A 5% reduction in the areal extent of peripheral short-hydroperiod wetlands did not change the overall pattern, but increased the variability in the timing of colony formation and fledging success between different simulation runs (Table 2). The 10% loss scenario produced highly irregular and unpredictable results (large standard deviation). On average, colony formation was delayed by about 60 days, but could start anywhere from 30 to 100 days after the simulation started. The date of colony formation changed with the number of pairs in the colony that attempted to nest. If many pairs nested, the date of colony formation was usually late (about 80–90 days after the start of the simulation run) and reproductive success was low, because the wet season set in before nesting was completed. If only a few of the pairs in the colony attempted to nest, colony formation usually started early (about 30–40 days after the start of the simulation) and most of the nestlings that were produced were able to fledge.

The 15% loss scenario led to similar results as the 60% loss scenario for the smaller colony with 50 pairs. Most of the simulation runs led to colony failures. Nesting was delayed by more than 90 days, with only 40% of the pairs attempting to nest. Consequently, reproductive success was low. The pairs that did nest, however, were generally able to produce one fledgling each. Late nesting and low reproduction was partly due to the nonnesting pairs that did not contribute to reproduction but represented a sink of prey resources in addition to the background competition by other wading bird species.

Results of removals of purely central slough cells for the 50-pair colonies are shown in Table 3. Removals of central slough habitat area above 40% had a major effect on surviving fledglings. However, comparison of the day of colony formation in Table 1 and Table 3 shows that the reasons are quite different. Removal of the central slough area did not cause much of a delay in the start of nesting or much reduction in nesters. However, it reduced the amount of prey available to the wood storks late in the dry season, at which time mass starvation took place. Table 4 shows the results of removals of 5%, 10%, 15%, 20%, 25%, and 30% of central slough areas for a 250-pair colony. For the 250-pair colony, the effect of central slough removal is much less drastic than reduction in short-hydroperiod wetlands, requiring over 30% removal to have the same effect as a 15% removal of the latter.

Finally reductions of the total area of 5%, 7.5%, 10%, 12.5%, and 15% were performed through ran-

9.

Table 1.   Results of computer simulations (based on 50 runs) of removal of different percentages of peripheral short-hydroperiod wetland area: Day of colony formation (measured from the start of the simulation at end of wet season), percentage of pairs that nest, and reproductive success for a colony with 50 pairs

% reduction short-hydro. wetland area (total area)	Day of colony formation (SD)	Percentage of pairs nesting (SD)	Number of fledglings (SD)[a]
0 (0)	9 (2)	100	148 (2)
10 (5)	8 (3)	99 (1)	147 (4)
20 (10)	13 (4)	96 (4)	144 (3)
30 (15)	15 (4)	92 (7)	131 (6)
40 (20)	19 (8)	87 (12)	112 (21)
50 (25)	35 (14)	67 (37)	43 (35)
60 (30)	98 (21)	34 (19)	6 (5)
70 (35)	103 (25)	19 (17)	2 (2)
80 (40)		no nesting in all runs	

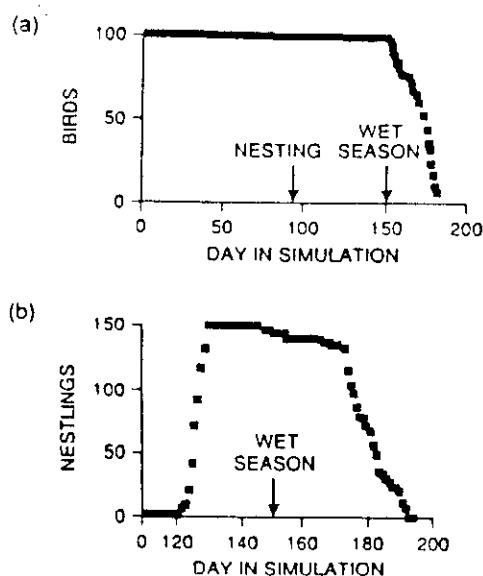[a]The maximum possible number of fledglings is 150.

Figure 6. A typical simulation for a colony with 50 pairs when 60% of the peripheral short-hydroperiod wetlands were removed. (a) The number of adult birds; (b) the number of nestlings in the colony.

dom removals of cells from both areas, so that roughly equal amounts of area were lost. This is general habitat reduction as opposed to specific habitat reduction. The results of these removals are shown in Table 5. In comparing these results with specific habitat removal, recall that a 5% removal of one specific habitat corresponds to 2.5% reduction in total area. Clearly, the effect of the general habitat reduction lies between that of the two specific habitat reductions that affected the same total area. The reduction of short-hydroperiod wetlands has a far more severe effect than either equivalent reduction in general area or long-hydroperiod wetlands.

Data on wading bird reproduction in the post-drainage southern Everglades lends indirect support to some model predictions. Figure 7A shows the percentage of wading bird breeding colonies in which early nest initiation occurred and in which successful nesting occurred. A greater percentage of early nesting took place under low surface water conditions (which occurred in 1989). The reason for the early nesting under these circumstances is that in the post-drainage Everglades, in the absence of high-elevation short-hydroperiod wetlands, shallow water (i.e., available prey) exists early in the nesting season only when initial dry season water levels are so low that the normally long-hydroperiod central slough areas start to dry out early. If surface water conditions were normal, as in the model simulations, nesting would have been greatly delayed. Only a small percentage of the nests started under low initial surface water conditions successfully produced fledglings (Figure 7). The reason is that under low initial water level conditions, the system usually dries out before the nestlings are fledged, so there is reproductive failure. This is essentially the story that the model tells.

Alternative Hydrologic Scenario as a Test of Increase in Frequency of Major Drydown Frequency Hypothesis

A test of the feasibility of this hypothesis requires lowering of prey numbers in the long-hydroperiod wetlands in order to model the effects of reduced prey availability resulting from a major drydown during the previous year. In the model simulations, prey biomass in the central slough was decreased to one tenth of the baseline value, but was kept at the same level in the peripheral short-hydroperiod wetlands. Figure 8 shows a typical result. Nesting was delayed

Table 2.   Results of computer simulations (based on 50 runs) of removal of different percentages of peripheral short-hydroperiod wetland area: Day of colony formation (measured from the start of the simulation at end of wet season), percentage of pairs that nest, and reproductive success for a colony with 250 pairs

% reduction peripheral wetland area (total area)	Day of colony formation (SD)	Percentage of pairs nesting (SD)	Number of fledglings (SD)[a]
0 (0)	10 (2)	100	742 (7)
5 (2.5)	13 (7)	95 (2)	724 (28)
10 (5)	63 (38)	62 (33)	162 (81)
15 (7.5)	95 (18)	39 (16)	21 (15)

[a] The maximum possible number of fledglings is 750.

Table 3.   Results of computer simulations (based on 50 runs) of removal of different percentages of central slough area: Day of colony formation (measured from the start of the simulation at end of wet season), percentage of pairs that nest, and reproductive success for a colony with 50 pairs

% reduction central slough area (total area)	Day of colony formation (SD)	Percentage of pairs nesting (SD)	Number of fledglings (SD)[a]
0 (0)	7 (2)	100	147 (2)
10 (5)	9 (5)	97 (1)	144 (3)
20 (10)	11 (5)	92 (2)	127 (4)
30 (15)	13 (7)	94 (4)	128 (12)
40 (20)	17 (9)	89 (5)	102 (32)
50 (25)	16 (7)	88 (3)	15 (11)
60 (30)	21 (12)	85 (9)	2 (1)
70 (35)	23 (14)	81 (10)	0

[a] The maximum possible number of fledglings is 150.

Table 4.   Results of computer simulations (based on 50 runs) of removal of different fractions of central slough area: Day of colony formation (measured from the start of the simulation at end of wet season), percentage of pairs that nest, and reproductive success for a colony with 250 pairs

% reduction central slough area (total area)	Day of colony formation (SD)	Percentage of pairs nesting (SD)	Number of fledglings (SD)[a]
0 (0)	10 (2)	100	742 (7)
5 (2.5)	13 (8)	97 (1)	721 (26)
10 (5)	14 (9)	96 (2)	711 (29)
15 (7.5)	15 (11)	95 (4)	687 (178)
20 (10)	12 (9)	97 (3)	159 (157)
25 (12.5)	13 (7)	94 (3)	102 (55)
30 (15)	16 (8)	95 (4)	32 (12)

[a] The maximum possible number of fledglings is 750.

and began around day 30 of the simulation. During the first 70 days, when adults could utilize the short-hydroperiod wetlands, enough prey was available. However, prey availability in the central slough was not high enough to supply sufficient food through the entire breeding season. Most nests were subsequently deserted, partly because adults could not satisfy their own energy requirements and partly because all nestlings in a nest had starved. However, some of the broods were reduced to one nestling each, and 10 nestlings managed to fledge.

This basic pattern occurred in all 50 simulations of this scenario. Initially the colony showed the same behavior as in the baseline scenario case, because prey biomass in the peripheral short-hydroperiod wetlands was not changed. Foraging success started to decrease as soon as the short-hydroperiod wetlands become dry and adults were forced to forage in the central slough. Then brood reduction occurred in almost all nests, immediately followed by a rapid and almost complete collapse of the colony, reflecting the inability of the adults to find enough food. Although a few

Table 5. Results of computer simulations (based on 50 simulations) of removal of different percentages of non-specific area: Day of colony formation (measured from the start of the simulation at end of wet season), percentage of pairs that nest, and reproductive success for a colony with 250 pairs

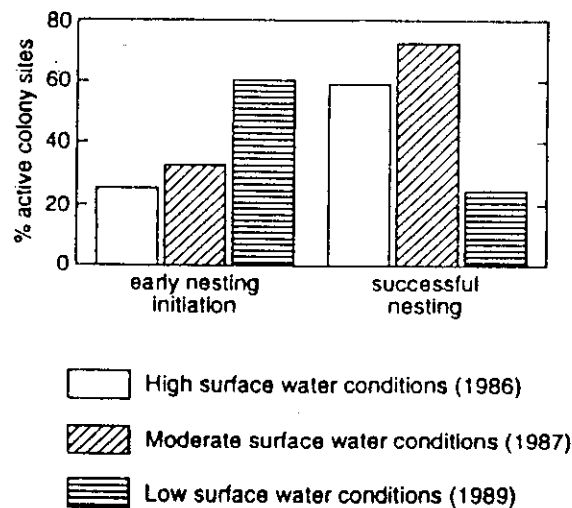| % reduction total area	Day of colony formation (SD)	Percentage of pairs nesting (SD)	Number of fledglings (SD)[a]
0	10 (2)	100	742 (7)
5	12 (6)	93 (2)	743 (3)
7.5	23 (6)	92 (3)	621 (49)
10	53 (34)	66 (4)	154 (33)
12.5	75 (4)	62 (7)	22 (21)
15	89 (18)	37 (2)	4 (2)

[a] The maximum possible number of fledglings is 750.

Figure 7. Empirical data from the southern Everglades on the percentage of wading bird colonies in which the nesting is initiated early in the dry season, and in which the nesting is successful, as a function of the initial water conditions.

pairs [7 (SD = 3); 50 runs] managed to support one of their nestlings through the entire breeding season, their remaining chick was often too small to fledge successfully at the end of the nesting period.

Discussion and Conclusions

Model simulations are always highly artificial compared with what happens in real ecological systems, because of the way the model simplifies the environment and the biology of the organisms. Even the highly detailed individual-based simulation model used in this study is a highly simplified picture of a wood stork breeding colony. For this reason we do not claim that the simulation studies were rigorous tests of the hypotheses. What the model does, however, is reveal some patterns that signify the importance of a
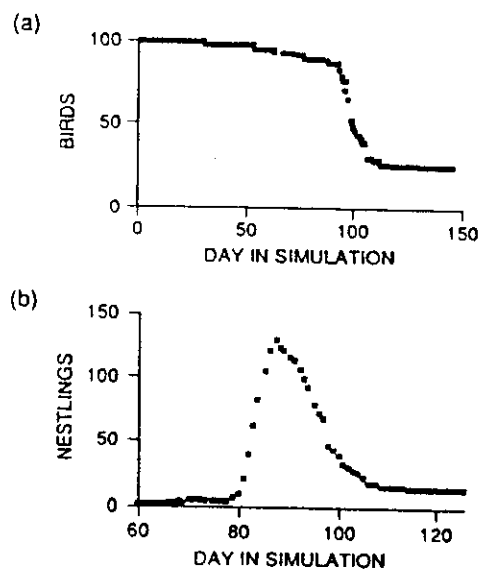

Figure 8. A typical simulation for a colony with 50 pairs when the prey availability in the central slough was reduced by 90%. (a) The number of adult birds; (b) the number of nestlings in the colony. The colony collapses when the peripheral short-hydroperiod wetlands become dry and the birds are forced to forage in the central slough.

heterogeneous landscape for the wood storks. The wood storks require not only that their foraging area contains sufficient prey biomass, but also that this biomass be available at the right times. Under ideal conditions, early in the nesting season, the short-hydroperiod wetlands supply most of the energy, whereas later the long-hydroperiod wetlands supply the energy needed to successfully fledge the offspring. A major loss or disruption of either specific habitat could cause reproductive failure. The simulations thus indicate that both spatial extent and spatial heterogeneity are landscape characteristics that must be taken into account in describing a population.

12.

Wood storks are highly mobile and individuals can move from one place to another on the landscape as their needs change or as the landscape itself changes; that is, as one area of the landscape becomes unfavorable from the point of view of food availability or the presence of predators or competitors. Only by having a large spatial area available are individual wood storks able to meet their demands for food, and especially the demands of offspring, over an entire yearly cycle. These considerations led to the hypothesis that specific habitat loss has resulted in the decline of wood stork reproductive success during the past few decades in the Everglades. In particular, it was hypothesized that loss of a great amount (85%) of the historical short-hydroperiod wetlands resulted in a decrease in available prey in the early part of the dry season, the time that the wood storks are preparing to begin nesting. The lack of significant foraging area in the landscape forces the birds to postpone nesting until later in the dry season, when water levels in the long-hydroperiod wetlands have declined sufficiently that feeding is possible in them.

The results of model analysis reported here support the hypothesis of specific habitat loss in the Everglades. The deficiency of wetlands with water in depth ranges appropriate for feeding until February or March in the 60% peripheral short-hydroperiod wetland loss scenario caused a delay of several weeks in the initiation of colonial nesting, even for a small colony of 50 pairs. As a result, few or none of the nestlings reached the fledgling stage before the rainy reason began, at which point prey availability decreased and nestlings starved or nests were abandoned.

This reduction of a specific habitat type required by the birds on a seasonal basis for successful reproduction, and their resulting inability to nest successfully as a result, may be referred to as a habitat bottleneck. The reduction of prey resources in all habitats for several years following a major drydown also creates a resource bottleneck for nesting pairs in subsequent years. These habitat and resource bottlenecks represent alterations in the spatial heterogeneity and temporal variability of the landscape, respectively. Without both the short-hydroperiod wetlands to influence proper timing of nest initiation and the long-hydroperiod wetlands to provide available prey to sustain adults and nestlings through the latter part of the nesting period, reproduction cannot be successful.

Drainage and the initiation of water management regulation have changed the spatiotemporal landscape characteristics of the Everglades, leading to a decrease in spatial heterogeneity. The lessons learned from the model suggest that this spatial heterogeneity must be restored if wood stork populations are to return to their historical levels. We specifically recommend restoration of at least someof the short-hydroperiod wetlands that were removed on the eastern edge of the historical Everglades. Because these eastern short-hydroperiod wetlands are rich in limestone solution holes that can serve as refugia for fish during the dry season, they could be expected to maintain high populations of fish and aquatic macroinvertebrates that can serve as prey for the wood storks.

Acknowledgments

Literature Cited

Bancroft, G. T. 1989. Status and conservation of wading birds in the Everglades. *American Birds* 43:1258–1265.

Bancroft, G. T., S. D. Jewell, and A. M. Strong. 1991. Foraging and nesting ecology of herons in the lower Everglades in relation to water conditions. Final report, N.A.S., Contract #202-M86-0254-R, South Florida Water Management District. West Palm Beach, Florida.

Bennetts, R. E., M. W. Collopy, and J. A. Rodgers, Jr. 1994. The snail kite in the Florida Everglades: A food specialist in a changing environment. *In* S. Davis and J. Ogden (eds.), Everglades: The ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida (in press).

Browder, J. 1985. Relationship between pink shrimp production on the Tortugas grounds and water flow patterns in the Florida Everglades. *Bulletin of Marine Science* 37:839–856.

Craighead, F. C. 1968. The role of the alligator in shaping plant communities and maintaining wildlife in the southern Everglades. *Florida Nature* 41(1 and 2):2–7, 69–74, 94.

Collopy, N. W., and P. C. Frederick. 1986. Wading bird nesting success and foraging dispersion in Water Conservation Area 3A and Everglades National Park. 1986 Interim Report to US Army Corps of Engineers, Jacksonville, Florida.

DeAngelis, D. L., and L. J. Gross (eds.). 1992. Individual-based models and concepts in ecology. Routledge, Chapman and Hall, New York.

Fennema, R. J., C. C. Neidrauer, R. A. Johnson, W. A. Perkins, and T. K. MacVicar. 1994. A computer model to simulate natural south Florida hydrology. *In* S. Davis and J. Ogden (eds.), Everglades: The ecosystem and its

restoration. St. Lucie Press. Delray Beach, Florida (in press).

Fleming, D. M., J. Schortemeyer, W. Hoffman, and D. L. DeAngelis. 1994a. Colonial wading bird distribution and abundance in the pre- and post-drainage landscapes of the Everglades *Oecologia* (in review).

Fleming, D. M., J. Shortemeyer, W. Hoffman, and D. L. DeAngelis. 1994b. Colonial wading bird reproduction in the pre- and post-drainage landscapes of the Everglades *Oecologia* (in review).

Forman, R. T. T., and M. Godron. 1981. Patches and structural components for a landscape ecology. *BioScience* 31: 733–740.

Frederick, P. C., and M. W. Collopy. 1988. Reproductive ecology of wading birds in relation to water conditions in the Florida Everglades. Florida Cooperative Fish and Wildlife Research Unit, School of Forestry Research and Conservation, University of Florida Technical Report No. 30, Gainesville, Florida.

Harris, L. D. 1984. The fragmented forest: Island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago, 211 pp.

Hoffman, J. S., D. Keyes, and J. G. Titus. 1983. Projecting future sea level rise. US Environmental Protection Agency, Washington, DC. EPA-230-09-007, 121 pp.

Huston, M. A., D. L. DeAngelis, and W. M. Post. 1988. New computer models unify ecological theory. *BioScience* 38: 682–691.

Johnson, R. A., S. J. Connors, and J. Veriel. 1994. A review of the hydrologic changes in the southern Everglades from 1940 through 1992. National Park Service report, South Florida Natural Resources Center, Everglades National Park, Homestead, Florida (in preparation).

Kahl, M. P. 1962. Bioenergetics and growth of nestling wood storks. *Condor* 64:169–183.

Kushlan, J. A. 1979. Design and management of continental wildlife preserves: Lessons from the Everglades. *Biological Conservation* 15:281–290.

Kushlan, J. A., and P. C. Frohring. 1986. The history of the southern Florida wood stork population. *Wilson Bulletin* 98:368–386.

Kushlan, J. A., and D. A. White. 1977. Nesting wading bird populations in southern Florida. *Florida Scientist* 40: 65–72.

Kushlan, J. A., J. C. Ogden, and J. L. Tilmont. 1975. Relation of water level and fish availability to Wood Stork reproduction in the southern Everglades. US Geological Survey Open File Report 75-434, Tallahassee, Florida.

Kushlan, J. A., P. C. Frohring, and D. Voorhees. 1984. History and status of wading birds in Everglades National Park. National Park Service report, South Florida Research Center, Everglades National Park, Homestead, Florida.

Loftus, W. F., and A. M. Ecklund. 1994. Long-term dynamics of an Everglades small-fish assemblage. *In* S. Davis and J. Ogden (eds.), Everglades: The ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida (in press).

Loftus, W. F., R. A. Johnson, and G. H. Anderson. 1992. Ecological impacts of the reduction of groundwater levels

in short-hydroperiod marshes of the Everglades. Pages 199–208 *in* J. A. Standford and J. J. Simons (eds). First international conference on ground water ecology. US Environmental Protection Agency. American Water Resources Association. Tampa, Florida.

Lovelass, C. M. 1959. The Everglades deer herd, life history and management. Technical Bulletin No. 6, Florida Game and Fresh Water Fish Commission, Tallahassee. 104 pp.

Lovejoy, T. E., J. M. Rankin, R. O. Bierregaard, Jr., K. S. Brown, Jr., L. H. Emmoms, and M. E. Van der Voort. 1984. Ecosystem decay and Amazon forest remnants. Pages 69–117 *in* M. H. Nitecki (ed.), Extinctions. The University of Chicago Press, Chicago.

Noss, R. F. 1987. Protecting natural areas in fragmented landscapes. *National Area Journal* 7:2–13.

Ogden, J. C. 1978. Recent population trends of colonial wading birds on the Atlantic and Gulf coastal plains. Pages 135–153 *in* A. Sprunt, IV, J. C. Ogden, and S. Winckler, (eds.), Wading birds. National Audobon Society Research Report 7, Tavernier, Florida.

Ogden, J. C. 1994. A comparison of wading bird nesting colony dynamics, 1931–1948 and 1974–1989, as an indication of changes in ecosystem conditions in the southern Everglades. *In* S. Davis and J. C. Ogden, Everglades: The ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida (in press).

Ogden, J. C., and B. W. Patty. 1981. The recent status of the Wood Stork in Florida and Georgia. *In* R. R. Odom and J. W. Guthrie (eds), Proceedings of the nongame and endangered wildlife symposium. Georgia Department of Natural Resource, Fish and Game Division. Technical Bulletin, WL 5, Atlanta, Georgia.

Ogden, J. C., H. K. Kale, III, and S. A. Nesbitt. 1980. The influence of annual variation in rainfall and water levels on nesting by Florida populations of wading birds. *Transactions of the Linnean Society NY* 9:115–126.

Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pages 155–177 *in* D. J. Horns, G. R. Stairs, and R. Mitchell (eds.), Analysis of ecological systems. Ohio State University Press, Columbus.

Parker, G. G. 1974. Hydrology of the pre-drainage system of the Everglades in southern Florida. Pages 18–27 *in* P. J. Gleason (ed.), Environments of south Florida: Present and past. Miami Geological Society Memoirs 2. Miami.

Parker, G. G., G. E. Ferguson, and S. K. Love. 1955. Water resources of southeastern Florida, with special reference to the geology and ground water of the Miami area. US Geological Survey Water Supply Paper 1255. US Government Printing Office, Washington, DC.

Pimm, S. L., and M. E. Gilpin. 1989. Theoretical issues in conservation biology. Pages 287–305 *in* J. Roughgarden, R. M. May, and S. A. Levin (eds.), Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey.

Powell, G. V. N. 1987. Habitat use by wading birds in a subtropical estuary: Implications of hydrography. *Auk* 104:740–749.

Powell, G. V. N., R. D. Bjork, J. C. Ogden, R. T. Paul, W. B. Robertson, Jr., and A. H. Powell. 1989. An analysis of

/14.

population trends in some Florida Bay wading birds. *Wilson Bulletin* 101:436–457.

Quinn, J. F., C. van Riper, III, R. Karban, G. Robinson, and S. P. Harrison. 1985. Conservation strategies: Island biogeography and the design of nature reserves. *Park Science* 6:6–9.

Robertson, W. B., Jr., and J. A. Kushlan. 1974. The south Florida avifauna. Pages 414–452 *in* P. J. Gleason (ed.), Environments of South Florida: Present and past. Miami Geological Society Memoirs 2, Miami.

Smith, T. and O. L. Bass. 1994. Landscape, white-tailed deer, and the distribution of Florida panthers in the Everglades. *In* S. Davis and J. Ogden (eds.), Everglades: The ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida (in press).

Smith, T. J., III, J. H. Hudson, M. B. Robblee, G. V. N. Powell, and P. J. Isdale. 1989. Freshwater flow from the Everglades to Florida Bay: An historical reconstruction based on fluorescent banding in the coral *Solenastrea bournoni*. *Bulletin of Marine Science* 44:274–290.

Sykes, P. W. Jr. 1984. The range of the snail kite and its history in Florida. *Bulletin of the Florida State Museum, Biological Science* 29:211–264.

Tabb, D. C., D. L. Dubrow, and R. B. Manning. 1962. The ecology of northern Florida Bay and adjacent estuaries. *Florida State Board of Conservation, Technical Series* 39:1–79.

Wagner, J., and P. C. Rosendahl. 1985. An historical review and assessment of surface water delivery to the Shark River slough, Everglades National Park, 1940–1980. South Florida Research Center Draft Technical Report. Homestead, Florida.

Walters, C. J., L. H. Gunderson, and C. S. Holling. 1992. Experimental policies for water management in the Everglades. *Ecological Applications* 2:189–202.

White, P. S. 1987. Natural disturbance, patch dynamics, and landscape pattern in natural areas. *Natural Areas Journal* 7:14–22.

Wilcove, D. S. 1987. From fragmentation to extinction. *Natural Areas Journal* 7:23–29.

Wolff, W. F. 1994. An individual-oriented model of a wading bird nesting colony. *Ecological Modeling* (in press).

Wright, S. J., and S. P. Hubbell. 1983. Stochastic extinction and reserve size: A focal species approach. *Oikos* 41:466–476.

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