WADING BIRD PREDATION IN A SEASONALLY FLUCTUATING POND

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THE vast wetlands of southern Florida are characterized by seasonal rainfall and extensive water level fluctuations, a pattern typical of many tropical ecosystems. When water levels fall in the dry season, aquatic organisms are concentrated within increasingly smaller areas of remaining water where they become readily utilizable patches of food for highly mobile predators, particularly wading birds of the order Ciconiiformes. Concentrations of herons, ibises, and storks feed on the aquatic animals concentrated in these dry season pools throughout the southern Florida wetlands, and because of their numbers and mobility, these birds play an important role in energy movement within the southern Florida ecosystem. However, little information exists on such wading bird feeding assemblages, called aggregations by Morse (1970). Aggregations were apparently even greater in the past (see Audubon 1827, Harper 1926, Bartram 1958). A few comments in the literature (e.g. Lowe-McConnell 1964) suggest that they may be widespread in the tropics as well.

This paper discusses aspects of the ecology of ciconiiform aggregations that utilized a small pond in the Big Cypress Swamp of southern Florida. Particular attention is given to how aggregations form, competitive relations among the predator species, and the impact of predation on prey populations in the pond. The study was conducted from 1969 through 1973. In 1969 observations were made on wading bird behavior and ecology. During 1970–73, data were gathered on changes in fish populations in relation to water level fluctuations. These data permit comment on the impact of wading bird predation because the study covered two comparable dry periods, one with (1973) and one without predation (1970).

STUDY SITE

The study pond is in the southeastern part of the Big Cypress Swamp, Florida, 25° 44′ 50″ N, 80° 56′ 50″ W (Fig. 1). It has a surface area of 1520 m^2 and a maximum depth of 1.50 m during high water. A shallow peripheral zone of emergent grass (1150 m^2), predominantly maidencane (*Panicum hemitomon* and *P. paludivagum*), surrounds a deeper central zone of submerged naiad (*Najas flexilis*). The pond is bordered by shallower swamps of willow (*Salix caroliniana*) and bald cypress (*Taxodium distichum*).

Water level in the pond depends on local rainfall and surface drainage from the Big Cypress Swamp to the north, both of which are seasonally variable. An average

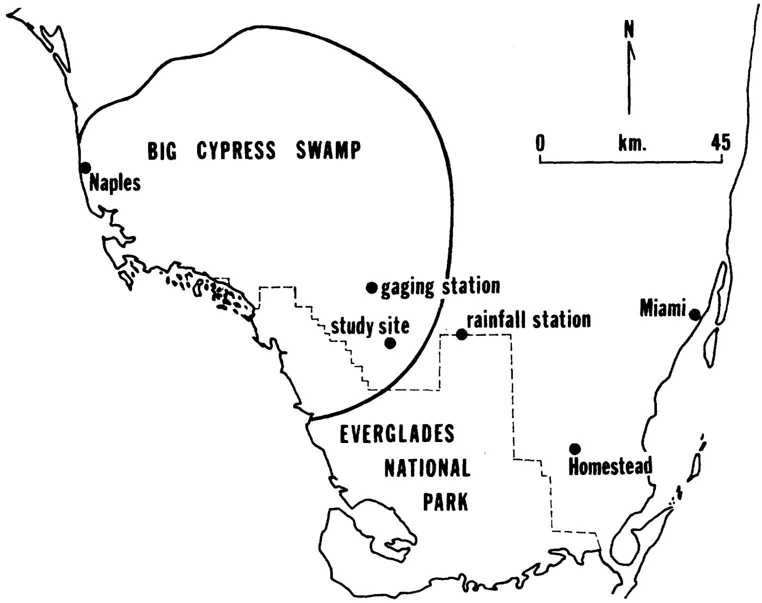

Fig. 1. Map of southern Florida.

of 1350 mm of rain falls in the area of the study site each year, 81% of which occurs in the rainy season from May to October (Fig. 2). During most of the year, water in the pond is confluent with that of surrounding swamps. Water levels begin to fall in early winter, and fall rapidly when transpiration by aquatic plants and evaporation increase in spring. As water levels fall and surface flow decreases, marsh bottom becomes exposed and surface water becomes confined to topographic depressions. Water levels rise again with the onset of the rainy season in May or June.

Methods

Wading birds in the pond were watched from a ground level blind in 1969 and from a blind 4 m above ground in 1970 to 1973. Information on wading bird movements at and near the study site was obtained by aerial surveys. Heron feeding behaviors mentioned are described by Meyerriecks (1960) and Kushlan (1972a).

Prey were sampled using six quantitative sampling devices. Two 1-m^2 drop traps, located in each of the two plant zones, sampled smaller fish, and two 4-m^2 pull-up traps, located in the central zone, sampled larger fish. An average density for the pond in fish per m^2 surface area was computed by determining the average fish density in each plant zone and multiplying by the percentage of the pond each zone occupied. Total numbers of fish in the pond were computed by multiplying the average density in the pond by the surface area. Details of the sampling devices and density calculations are in Kushlan (1974a, 1974b). During the study, 25 species of fish, listed in Kushlan (1972b), were collected in the pond. Also included in prey calculations was the freshwater prawn, *Palaemonetes paludosus*, an important minnow-sized crustacean.

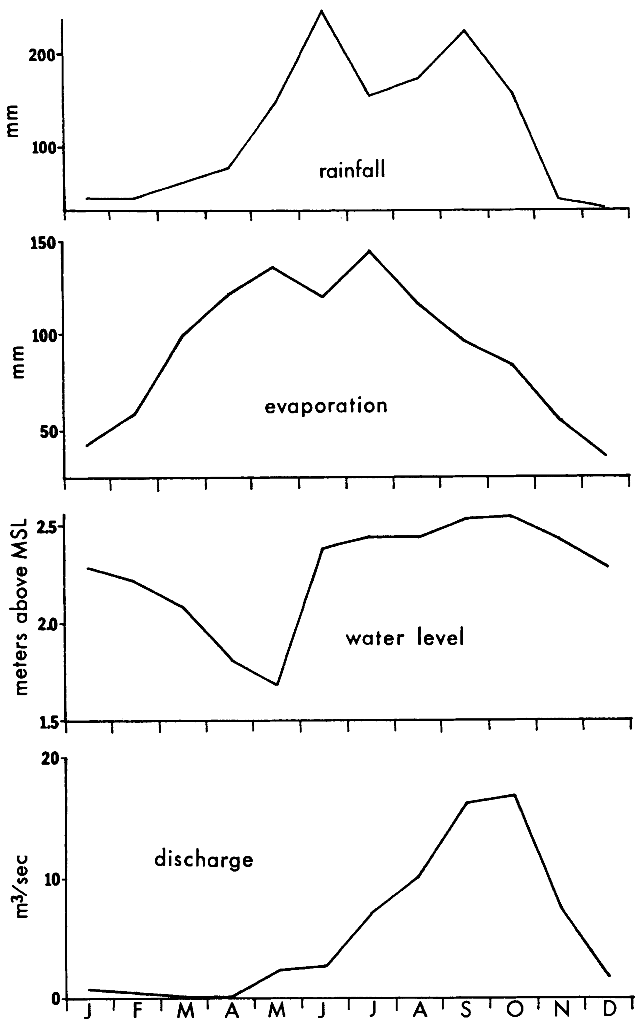

Fig. 2. Mean monthly rainfall, evaporation, water level, and surface discharge in the eastern Big Cypress Swamp. Locations of stations are in Fig. 1.

As water level variation in the pond was similar to that at a U.S. Geological Survey gaging station 13 km northwest of the pond (Kushlan 1972b), data on water level and discharge are taken from that station. Rainfall data were collected at a U.S. Department of Commerce weather station 13 km east of the pond (Fig. 1).

RESULTS

PREY CONCENTRATION

Abundance and biomass of fish and the number of fish species in the pond increased when water levels declined (Fig. 3). The increase was

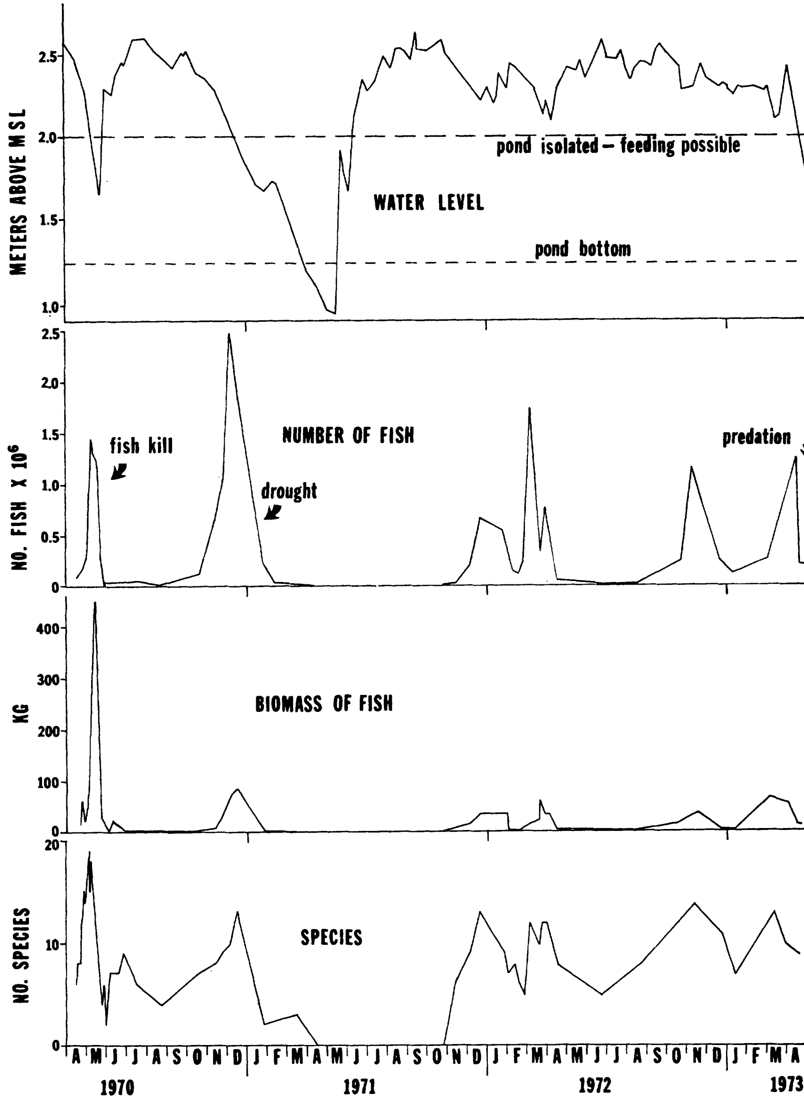

Fig. 3. Change in water level, in the abundance, biomass, and number of species of fish in the pond 1970–73.

due to the emigration of fish from drying swamps surrounding the pond. Fish density in the pond began to increase while surface water still remained in the swamps and generally reached its maximum just prior to the periphery of the pond becoming dry. Fish density then declined from fish kills or predation. Although it is not known how far fish move in response to falling water levels, the pond, being the deepest spot within 0.5 km, probably has a tributary area of about 0.2 km^2.

During the summer rainy season when water levels were high, the standing crop of fish in the pond was generally low. For example, there were 42×10^3 fish of 7 species in the pond in June 1970 as contrasts with a dry season maximum of 1.4×10^6 fish of 19 species during May 1970. High levels in the dry season were due to immigration.

WADING BIRD MOVEMENT

As the Big Cypress Swamp dried, wading birds utilized food resources concentrated in scattered pools by feeding in one such location for a matter of days or weeks and then moving elsewhere. At the study site, utilization of concentrated fish stocks by wading bird aggregations occurred only in March and April when most resident populations were nesting and wintering populations were still active in the region. Episodes of feeding by wading bird aggregations occurred at approximately the same water level on each occasion, suggesting that at a specific water level the pond becomes shallow enough for efficient feeding.

Utilization of the pond by wading birds is therefore predicated on the water level receding to a specific level within a 2-month period in the spring. During the study this occurred only in 1969 and 1973. In 1970 the water level did not reach this point until May; in 1971 it occurred in the winter; in 1972 the level never become low enough (Fig. 3).

Black-crowned Night-Herons (*Nycticorax nycticorax*), Louisiana Herons (*Hydranassa tricolor*) and Little Blue Herons (*Florida caerulea*) were the first to feed in the pond (Fig. 4). The latter two species visited the pond for short periods, tried to feed from the emergent grass, and usually soon left. Later, wading birds fed at the pond more frequently, the duration of their visits increased, and a few Snowy Egrets (*Egretta thula*) and Great Egrets (*Casmerodius albus*) attempted to feed there (Fig. 4). In 1969, maximum use occurred in March and seemed to coincide with the first appearance at the pond of Great Blue Herons (*Ardea heroidias*). During the period of maximum utilization, herons began to feed in the pond soon after dawn but various species arrived at different times (Fig. 5). Maximum concentration of wading birds was achieved around 30 min after dawn. Numbers began to decrease around 0800, 2 h after dawn, although most birds remained at the pond for the entire day.

FEEDING AGGREGATION

Wading birds feeding in the pond were apparently ecologically separated by a combination of size, feeding location, and feeding behavior

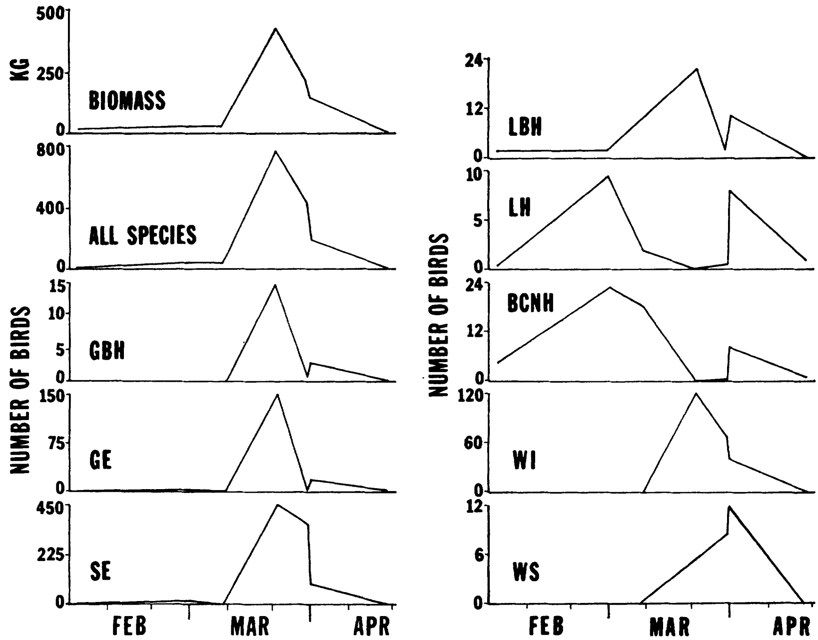

Fig. 4. Changes in number and biomass (live weight) of wading birds feeding in in the pond February–April 1969. Abbreviations are: GBH, Great Blue Heron; GE, Great Egret; SE, Snowy Egret; LBH, Little Blue Heron; LH, Louisiana Heron; BCNH, Black-crowned Night-Heron; WI, White Ibis; WS, Wood Stork.

(Fig. 6). The Great Blue Heron and the Great Egret both fed by stand and wait. Great Blues fed in the central area while Great Egrets fed in the emergent zone. Three similarly sized herons, the Snowy Egret, Little Blue Heron, and Louisiana Heron, all fed in the same location, the emergent zone, but generally used different feeding methods. The Black-crowned Night-Heron, on the basis of this comparison, seems to feed similarly to the other small herons, especially the Snowy Egret, but night-herons were present only in small numbers when other species were numerous (Fig. 4). Wood Storks (*Mycteria americana*) and the White Ibis (*Eudocimus albus*) fed differently from the visually feeding herons.

Changes in feeding behavior and location took place during the morning (Fig. 6), perhaps in response to changing availability of fish (Kushlan 1972a). Active behaviors such as foot dragging by Snowy Egrets and hovering stirring by Louisiana Herons occurred in the open central area after larger birds had vacated it.

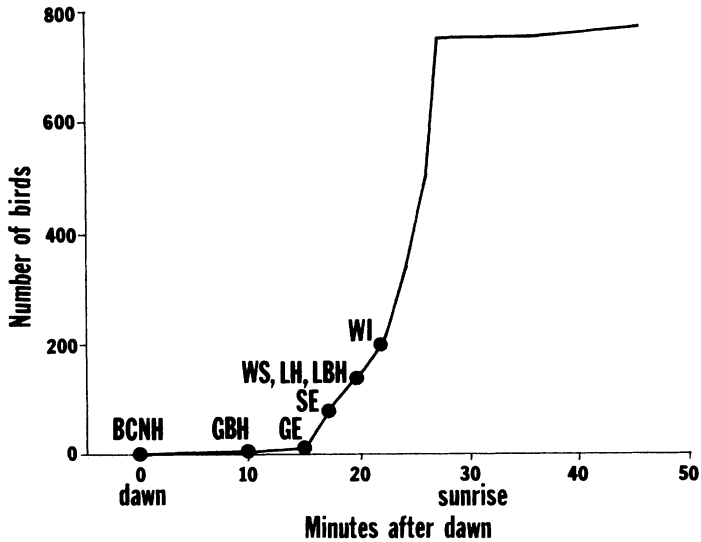

Fig. 5. Increase in number of birds feeding in the pond during the morning. Data collected in April 1969, from 0600 to 0645. Letters show when various species of wading birds entered the pond.

Members of the wading bird aggregation collectively emitted a loud noise while feeding was in progress and the assemblage was undisturbed. When the birds were disturbed, the noises stopped, and they became more attentive to their surroundings. Thus the noise may function as an "all-is-well" signal permitting less attention to be paid to potential danger and more to feeding.

All species except White Ibis, Wood Storks, and Little Blue Herons maintained both inter- and intraspecific feeding territories, i.e. individual

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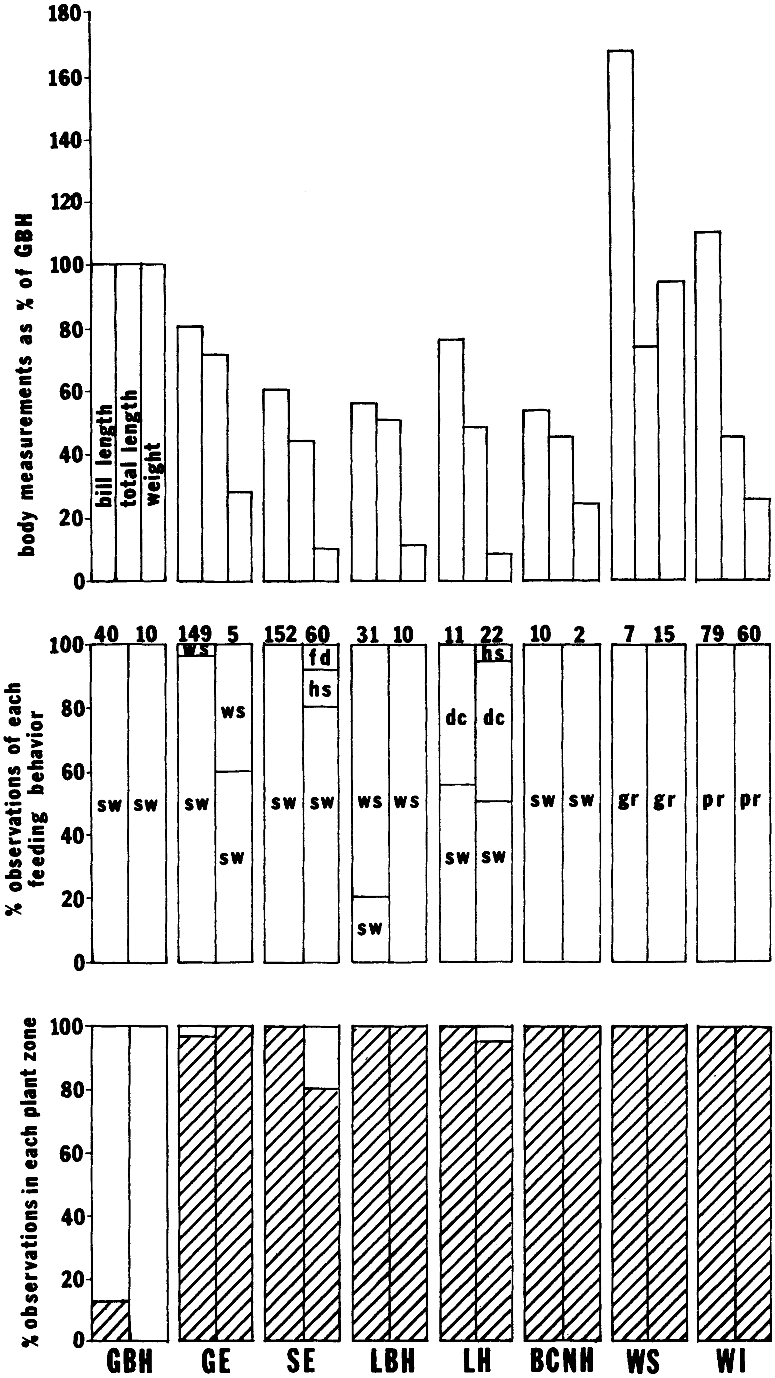
Fig. 6. Feeding behavior and feeding location for species of wading birds utilizing the pond as part of a feeding assemblage, and body measurements of each species expressed as a percentage of the Great Blue Heron. Values are averages for males from Palmer (1962). In the graphs of feeding behavior and feeding location, the first bar for each species represents observations from 0600 to 0700, the second bar, from 0700 to 1000. Number of observations of feeding behavior and location are noted above the middle graph. Symbols for feeding behavior are: sw, stand and wait; ws, wade slowly; pr, probe in mud; gr, grope in water; dc, disturb and chase, a category including several active behaviors; fd, foot dragging; hs, hovering stirring. Percentage of observations of feeding in the shallow emergent plant zone is indicated by hatch lines. Percentage of observations in the deeper more open central area is unshaded.


body measurements as % of GBH
bill length
total length
weight
% observations of each feeding behavior
40 10 149 5 152 60 31 10 11 22 10 2 7 15 79 60
sw ws fd hs dc gr pr
% observations in each plant zone
GBH GE SE LBH LH BCNH WS WI

distances, while feeding in the aggregation. Generally larger birds predominated over smaller ones. Encroachment from the air by similarly sized or larger herons was successful; encroachment on the ground by a similarly sized heron was thwarted. Maintenance of individual distance may have been responsible for the low numbers of Little Blue Herons and the decrease in numbers of Louisiana Herons and Black-crowned Night-Herons feeding in the pond after the assemblage formed (Fig. 4). The walk slowly feeding behavior of the Little Blue Heron and the disturb and chase behavior of Louisiana Herons caused these species to encroach on the feeding territories of still-hunting birds that were able to repel them. Similarly Black-crowned Night-Herons, the only species that apparently overlapped other herons in size, feeding location, and behavior, were excluded by other herons (Kushlan 1973).

IMPACT OF PREDATION

Wading birds fed in aggregations at the pond in 2 of 5 years of the study. Based on the few data available on fish abundance in 1969, I estimated (Kushlan 1972b) that wading bird predation reduced the number of large fish in the pond by 80% and the number of smaller fish by 75%. From 3 to 31 March 1973, wading bird predation accounted for a 76% reduction in the biomass and a 77% reduction in the numbers of fish in the pond (Fig. 3).

LACK OF PREDATION

A comparison of the events of 1970 and 1973 demonstrated what happened to fish density in the absence of predation. In May and December 1970, water levels fell to the point at which the aggregation would be expected to form. In both cases wading birds were not in the area of the pond at the time fish became accessible, and in both cases fish began to die. In early 1971, the pond dried completely and all fish died. In the spring 1970 dry season, however, the pond didn't dry and a fish kill that occurred from 14 to 24 May eliminated 93% of the biomass and 99.4% of the number of fish present in the pond (Fig. 3). This fish kill was caused directly by factors associated with crowded conditions in the pond, especially a progressive decline in oxygen levels prior to the fish kill (Kushlan 1974b).

The 93% loss of fish stock during the fish kill of 1970 contrasts with the 76% reduction caused by predation during the comparable dry season of 1973 and suggests that wading bird predation may function to provide a compensatory mortality for more extensive losses of a fish kill. Additionally, in the 2 years when predation occurred no species of fish was eliminated from the pond, although some became so scarce that they were caught only by qualitative trapping. In contrast only six species of fish survived the fish kill of 1970. Wading bird predation may therefore function to permit the survival of prey populations during the dry season, provided, of course, that it is not severe enough to dry the pond entirely.

Discussion

The ecology of the Big Cypress Swamp is characterized by the seasonality of its hydrology, a factor that has created an ecosystem adapted to extreme fluctuations in the surface water level. When water levels recede during the dry season, large expanses of shallow marsh and swamplands dry. As the drying occurs, the immigration of fish into remnant pools provides a highly concentrated and readily harvestable energy source for wading birds. As different parts of the southern Florida wetlands dry at different times, feeding locations become available in a temporal and spatial sequence. The pattern of regional drying, at least prior to artificial drainage, was generally predictable, although the availability of food in local patches within each region was probably somewhat unpredictable and is even more so under present conditions.

It is significant therefore that the dominant predators are not only capable of long-distance movements but nest and roost colonially during the period when the wetlands dry, a strategy advantageous where resources are clumped and unpredictably distributed (Horn 1968). Ward and Zahavi (1973) have provided a detailed review of the evidence that communal roosting and nesting is advantageous to species feeding in flocks. It is also advantageous for the mixed species assemblages discussed in this paper that feed at seasonally variable food patches that may be located, in the case of the Wood Stork, up to 130 km from the colony site. It might be noted that the Great Blue Heron, which feeds more solitarily at other times of the year, feeds in aggregations during the dry season. The feeding dispersion of Great Blue Herons is a matter of prey density. It feeds solitarily when prey density is low but in aggregations when prey density is high.

The advantage to all species of feeding in an aggregation is the increased ability to locate utilizable patches of food and conversely a decreased searching time to find such patches. Both seasonal (Fig. 4) and daily (Fig. 5) increases in the number of birds feeding at the pond seem to be the result of local enhancement (Hinde 1961), i.e. increasing utilization by the attraction of searching birds to actively foraging ones. In southern Florida locating ciconiiform aggregations is undoubtedly aided by the white plumage of several species, which is highly visible to humans from the air and which probably, in this case, functions in "social food signalling" as suggested by Armstrong (1971).

Two groups of wading birds utilize the food resources of southern Florida. Most populations usually nest during the drying season, as Kahl (1964) showed for the Wood Stork. Other populations utilizing this food for part of the dry season are winter residents that breed elsewhere (Palmer 1962). The food sources made available by low water levels in southern Florida are therefore important to wading bird populations nesting over much of eastern and southern North America.

Utilization by aggregations can occur only when fish density is high, when wading birds are in the area, and at a specific water level where feeding becomes physically possible. Formation of a feeding aggregation apparently is initiated through trial-and-error feeding by individual birds that feed for longer periods as fish densities increase and water levels drop.

Within the aggregation, species, with one exception, differ by a combination of size, feeding location, and feeding behavior (Fig. 6). Differences in these three dimensions of niche breadth suggest that available food is divided among species in a nonoverlapping fashion, although more data on actual food consumption are desirable. Food is apparently apportioned within the aggregation by a combination of two predominant types of niche specificity, behavioral interaction resulting in spatial segregation and structural differences resulting in both resource segregation (small birds—small fish) and spatial segregation (large birds—deeper water). Several species are apparently restricted in their utilization of food resources while the aggregation is feeding in the pond because their active foraging behavior is incompatible with the individual distances maintained by the more abundant species. This results in a second level of spatial segregation, some birds are able to feed in the pond with the aggregation while other birds are restricted to feeding elsewhere.

The dry season immigration of fish into progressively smaller pools of deeper water results in their being exposed to increasingly stressful conditions because of high densities and lowered water quality. Whereas wading bird predation reduced fish biomass in the study pond by 76% without loss of species richness, a fish kill, which occurred in a year when wading birds did not utilize the pond, eliminated 93% of the fish biomass and all but six species of fish. In years when ponds do not dry entirely, the usual case under natural conditions, wading bird predation may serve an important function by preserving fish species richness and cropping fish stocks to levels compatible with their survival during the dry season.

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SUMMARY

This paper discusses aspects of the ecology of wading bird predation in a small pond in the Big Cypress Swamp of southern Florida, a region characterized by seasonal rainfall and water level fluctuation. When water levels receded and shallow swamps dried, fish migrated into deeper areas finally becoming concentrated in remnant pools, thereby serving as patches of highly concentrated and easily obtainable food for highly mobile wading bird predators. Utilization of the fish concentrated in the study pond occurred only in the spring if fish density was high and if the water became shallow enough for efficient feeding.

As the water level dropped the number of wading birds feeding at the pond increased through local enhancement, probably aided by the white plumage of several species. Species comprising the wading bird aggregation apparently divided food resources by a combination of spatial and resource segregation. In 1973, wading birds decreased the biomass standing crop of fish by 76%. In a comparable year when predation did not occur, a fish kill decreased fish biomass by 93%. Wading bird predation may therefore function to reduce fish stocks to levels compatible with their survival during the dry season.

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