# PREY SELECTIVITY BY THE WOOD STORK

JOHN C. OGDEN
JAMES A. KUSHLAN
AND
JAMES T. TILMANT

The Wood Stork (*Mycteria americana*) forages by moving its open bill vertically or from side to side in the water until it touches prey. It uses an exceedingly rapid bill-snap reflex to capture prey, a technique that requires no sighting of the prey item (Kahl and Peacock 1963). Kahl (1964), working primarily in the Big Cypress Swamp of southern Florida, discovered that this technique was effective for feeding on fish densely concentrated in shrinking pools during the southern Florida dry season.

Despite Kahl's study, little is known about the kinds of prey taken by Wood Storks, and nothing is known about prey taken in specific habitats. Kahl (1963, 1964) summarized existing information on Wood Stork food and reported the stomach contents of seven individuals from southern Florida. These included four collected along the southwest Florida coast in 1924 and three from the Big Cypress Swamp. All contained only fish, although other kinds of prey were recorded from birds from other areas (Kahl 1963).

We report here on over 3,000 prey items recovered from nestling and adult Wood Storks in Everglades National Park and discuss selectivity of foraging storks in relation to the availability of potential prey. The Everglades population of Wood Storks nests in three colonies located in mangrove swamps along the southern coast (fig. 1). Storks feed in a succession of habitats from the time of their arrival in southern Florida in November to their departure in May or June after the nesting season. This period of residence corresponds to the southern Florida dry season, when most coastal and inland aquatic habitats become dry. Storks go from one habitat to another as each dries in sequence, first feeding in coastal marshes and then moving inland to feed along creeks, streams and pools at the landward edge of mangrove swamps. Later they feed in the extensive inland marshes of the Everglades.

## METHODS

Obtaining information on the food of a species threatened by frequent nesting failure and consequent population decline is difficult in most cases because of potential adverse effects of collecting specimens. In this study we collected food samples either from nestling storks which, like many wading birds, readily regurgitate food when handled, or from adults on the feeding grounds through the use of a helicopter. This technique involved vertical descent in a helicopter from about 100 m to a point 3 to 10 m above actively feeding storks. The helicopter hovered there, moving laterally if necessary, to worry the storks, which often regurgitated immediately, after running a short distance or while taking flight. We collected these regurgitated items after landing.

Sampling food from adults at feeding sites allowed comparison with prey actually available in the same habitat. Available prey was determined from 3 to 8 samples taken with 1-$m^2$ throw traps or portable 1-$m^2$ drop traps (described in Kushlan 1974). These samples were collected sufficiently long after landing so that fish scared by the helicopter appeared to have resumed normal activity. Concurrent observations and quantitative samples indicated that the most densely concentrated and, therefore, most readily available fishes were sampled adequately. Because of low density, larger fish were captured less commonly although it is also possible at some sites that a trap as small as 1-$m^2$ misses some of the large fish. Our assumption is that the failure to trap fish present in the regurgitated samples indicates selectivity by foraging storks.

Animals collected were identified to species, except for some small sunfish. All species of sunfish were combined in most analyses. Total length and dry weight of specimens were measured. Prey density is expressed as animals per square meter. Food samples from foraging storks were combined for analysis according to three habitat types—coastal marsh and mangrove swamp, streams and pools near the inland edge of mangrove swamp, and everglades marsh (fig. 1). The same was done with prey available at feeding sites. Selectivity of foraging Wood Storks for certain species or sizes of prey was calculated using Ivlev's (1961) selectivity index (E):

$$E = (r - p)/(r + p)$$

where "r" is the proportion of a species or length of fish in the food sample and "p" is the proportion of a species or length of fish available to foraging storks. For each feeding habitat, indices were calculated from all adult regurgitation samples and from all trap samples taken in each habitat. The selectivity index ranges from +1 to −1. Prey species or size classes with an index near +1 are consumed selectively in much greater proportion than they are available. Prey species or size classes with an index near zero are consumed in proportion to their


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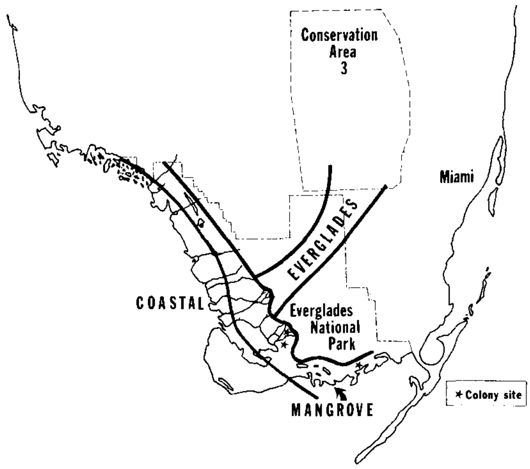


FIGURE 1. Map of southern Florida showing three habitat areas within which food consumed and available prey were sampled.

availability. Those with an index near –1 are consumed well below their relative abundance in the environment. Selectivity, as used in this paper, is defined by this index and implies neither the active searching for certain species nor any other motivation on the part of storks.

## RESULTS

### FOOD OF STORKS

Fish comprised nearly the entire diet of Wood Storks in extreme southern Florida (table 1). Although at least 27 species of fish were represented in our samples, a few kinds made up most of the total. Flagfish, sailfin mollies, marsh killifish, and the several species of sunfish accounted for 83% of the individuals and 72% of the biomass. The yellow bullhead, making up less than 2% of the individuals, comprised 12% of the biomass. Together these five groups of fish included 85% of the number and 84% of the biomass of prey consumed by Wood Storks.

Other prey items were 1 newt, 3 tadpoles, 1 adult frog and 7 freshwater prawns. Prawn density at stork feeding sites averaged 128/m$^2$ but reached 1,242/m$^2$. The average density of prawns was nearly 2.5 times that of the most abundant fish. Thus the low number of prawns in the diet is surprising. As some of these were in the mouths of regurgitated sunfish it seems possible that the prawns were not ingested by storks directly.

### FOOD AVAILABILITY AND CONSUMPTION

Wood Storks consume certain fish in numbers proportionally greater than their relative abundance at feeding sites (fig. 2). The selectivity index (fig. 2c) shows that relatively abundant mosquitofish were under-represented in the diet, whereas other species including the relatively common flagfish, sailfin mollies and marsh killifish and the relatively scarce sunfish were consumed selectively. Species under-represented in the overall diet were under-represented in all habitats. Among the fish most frequently consumed, sunfish and marsh killifish were highly selected in all habitats while the strength of selection for other species important in the diet varied in different habitats (fig. 3).

Wood Storks also chose the larger fish (fig. 4). In each habitat analyzed, the mean length of fish consumed was significantly larger than the mean length of fish available (t-test, $P < .01$). If some larger fish were missed because of the small trap size, as previously suggested, the difference between "available" and "consumed" curves in fig. 4 may be slightly less. The length of fish available in all areas was similar, but storks ate larger fish in the Everglades than in coast or man-

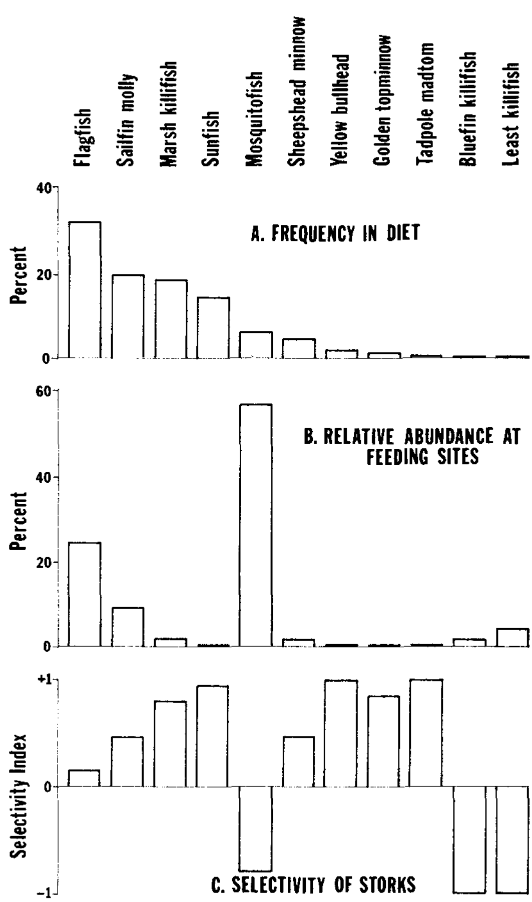


FIGURE 2. Frequency of occurrence of various species of fish in the diet of Wood Storks, the relative abundance of fish species at stork feeding sites, and the selectivity of storks for each species.

TABLE 1. Prey consumed by Wood Storks in southern Florida habitats.[a]

| | | Coastal | Mangrove | Everglades | Madeira Rookery | Lane River Rookery | All Samples |
|---|---|---|---|---|---|---|---|
| Fish | | | | | | | |
| Florida gar | *Lepisosteus platyrhincus* | 0 (0) | 0 (0) | 0.4 (9.2) | 0 (0) | 0.4 (3.2) | 0.2 (2.8) |
| Bowfin | *Amia calva* | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0.1 (0.3) | <0.1 (0.1) |
| Chain pickerel | *Esox niger* | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0.1 (0.3) | <0.1 (0.1) |
| Golden shiner | *Notemigonus crysoleucas* | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0.3 (0.4) | <0.1 (0.2) |
| Taillight shiner | *Notropis maculatus* | 0 (0) | 0.4 (0.2) | 0 (0) | <0.1 (0.1) | 0.4 (<0.1) | 0.2 (<0.1) |
| Yellow bullhead | *Ictalurus natalis* | 0 (0) | 0 (0) | 1.8 (8.5) | 0.8 (11.5) | 4.2 (16.4) | 1.7 (11.8) |
| Tadpole madtom | *Noturus gyrinus* | 0 (0) | 0.4 (0.2) | 0 (0) | 0.3 (0.2) | 0.3 (0.1) | 0.2 (0.1) |
| Sheepshead minnow | *Cyprinodon variegatus* | 18.1 (18.2) | 6.7 (4.8) | 2.0 (1.0) | 0.5 (0.2) | 0.7 (<0.1) | 4.1 (2.7) |
| Golden topminnow | *Fundulus chrysotus* | 0 (0) | 0 (0) | 1.5 (1.6) | 1.7 (1.8) | 1.8 (0.4) | 1.3 (0.8) |
| Marsh killifish | *F. confluentus* | 7.5 (8.9) | 28.0 (31.7) | 25.1 (22.0) | 18.4 (14.9) | 17.4 (5.2) | 18.0 (10.7) |
| Seminole killifish | *F. seminolis* | 2.7 (15.2) | 1.8 (22.6) | 0 (0) | 0.3 (0.8) | 0.1 (0.4) | 0.7 (3.1) |
| Flagfish | *Jordanella floridae* | 0 (0) | 22.7 (9.3) | 46.2 (11.0) | 41.1 (15.6) | 34.0 (4.0) | 32.0 (7.0) |
| Bluefin killifish | *Lucania goodei* | 0 (0) | 0 (0) | 0 (0) | 0.3 (<0.1) | 0 (0) | 0.1 (<0.1) |
| Rainwater killifish | *L. parva* | 0.2 (<0.1) | 4.4 (0.9) | 0 (0) | 0 (0) | 0 (0) | 0.3 (<0.1) |
| Rivulus | *Rivulus marmoratus* | 0.2 (0.1) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | <0.1 (<0.1) |
| Mosquito-fish | *Gambusia affinis* | 16.4 (0.7) | 3.1 (0.5) | 2.8 (0.2) | 4.7 (0.7) | 4.8 (0.4) | 6.3 (0.5) |
| Least killifish | *Heterandria formosa* | 0 (0) | 0 (0) | 1.8 (<0.1) | 0.6 (<0.1) | 0.1 (<0.1) | 0.5 (<0.1) |
| Sailfin molly | *Poecilia latipinna* | 54.4 (50.9) | 23.1 (14.0) | 8.3 (5.4) | 21.4 (12.9) | 1.8 (0.5) | 19.8 (10.6) |
| Brook silverside | *Labidesthes sicculus* | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0.3 (<0.1) | 0.1 (<0.1) |
| Tidewater silverside | *Menidia beryllina* | 0 (0) | 0.4 (0.2) | 0 (0) | 0 (0) | 0 (0) | <0.1 (<0.1) |
| Bluespotted sunfish | *Enneacanthus gloriosus* | 0 (0) | 0 (0) | 0.8 (0.9) | 0.2 (0.3) | 2.2 (1.5) | 0.8 (0.9) |
| Warmouth | *Lepomis gulosus* | 0 (0) | 3.1 (11.6) | 2.5 (21.9) | 2.1 (21.5) | 12.3 (38.8) | 4.8 (27.2) |
| Bluegill | *L. macrochirus* | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 1.1 (1.4) | 0.3 (0.7) |
| Redear sunfish | *L. microlophus* | 0 (0) | 0 (0) | 0 (0) | 0.6 (3.1) | 7.2 (9.4) | 2.3 (5.4) |
| Spotted sunfish | *L. punctatus* | 0 (0) | 0 (0) | 4.5 (17.3) | 0.8 (8.7) | 6.7 (9.3) | 2.8 (8.7) |
| Unidentified sunfish | *Lepomis* spp. | 0 (0) | 4.4 (4.0) | 1.5 (1.0) | 3.4 (2.3) | 2.7 (0.6) | 2.5 (1.0) |
| Total sunfish | | 0 (0) | 7.5 (15.6) | 9.3 (40.2) | 7.1 (35.6) | 32.2 (61.0) | 13.5 (43.9) |

[a] Numbers = percentage of items consumed. Numbers in parentheses = percentage of biomass consumed.

TABLE 1. *Continued.*

| | | Coastal | Mangrove | Everglades | Madeira Rookery | Lane River Rookery | All Samples |
|---|---|---|---|---|---|---|---|
| Largemouth bass | *Micropterus salmoides* | 0 (0) | 0 (0) | 0 (0) | 0.2 (3.6) | 1.0 (7.2) | 0.3 (4.4) |
| White mullet | *Mugil curema* | 0.4 (6.0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0.1 (0.8) |
| Other | | | | | | | |
| Freshwater prawn | *Palaemonetes paludosus* | 0 (0) | 0.4 (<0.1) | 0.2 (<0.1) | 0 (0) | 0.3 (<0.1) | 0.2 (<0.1) |
| Red-spotted newt | *Diemictylus viridescens* | 0 (0) | 0.4 (0.1) | 0 (0) | 0 (0) | 0 (0) | <0.1 (<0.1) |
| Bullfrog | *Rana grylio* | 0 (0) | 0 (0) | 0 (0) | 0.5 (1.7) | 0 (0) | 0.2 (0.4) |
| Total number of prey items or total biomass (g dry wt.) | | 518 (249.4) | 225 (63.2) | 398 (245.2) | 1150 (415.2) | 907 (978.8) | 3198 (1952) |

grove habitats (t-test, $P < .05$). This is accounted for by the high consumption of sunfish in the Everglades (table 1). Storks ate fish larger than 3.5 cm in greater proportion than their relative availability in the feeding sites (fig. 5) with similar patterns holding in each habitat. The mean length of available fish was 2.5 cm (fig. 4).

Wood Storks selected, therefore, certain species of fish and relatively larger fish. Fish of some species are larger than others so it is necessary to resolve the interaction of these two patterns of prey selectivity. Figure 6 shows size selectivity for seven of the most abundant or most frequently eaten fish. In the sailfin molly, increased selectivity with size rises smoothly to a positive selectivity above 4 cm. In the sheepshead minnow only the largest fish, above 5 cm, were eaten. Neither mosquitofish nor flagfish showed a consistent pattern of size selectivity. The pattern for the marsh killifish was also inconsistent but showed that fish larger than 8 cm were highly selected. It appears in general that for most species, larger individuals were selected while in a few species there is little evidence of selectivity by size.

Kahl (1964) found that Wood Storks in the Big Cypress Swamp characteristically fed in locations where fish densities were high, usually because of concentration during the dry season. We found a sharp contrast between fish densities at stork feeding sites and at permanent sampling stations where storks did not feed. Fish densities were significantly higher at feeding sites in both coastal and Everglades habitats (means, 40 vs 16.8 fish/m$^2$ on the coast and 141 vs 10.3 fish/m$^2$ in the Everglades, t-test, $P < .05$). These data quantify and extend Kahl's (1964) findings to everglades and coastal habitats and show that storks feed where fish densities are relatively high. The data also suggest that, if prey density is a critical factor in site selection, it may also be a factor in selectivity of prey.

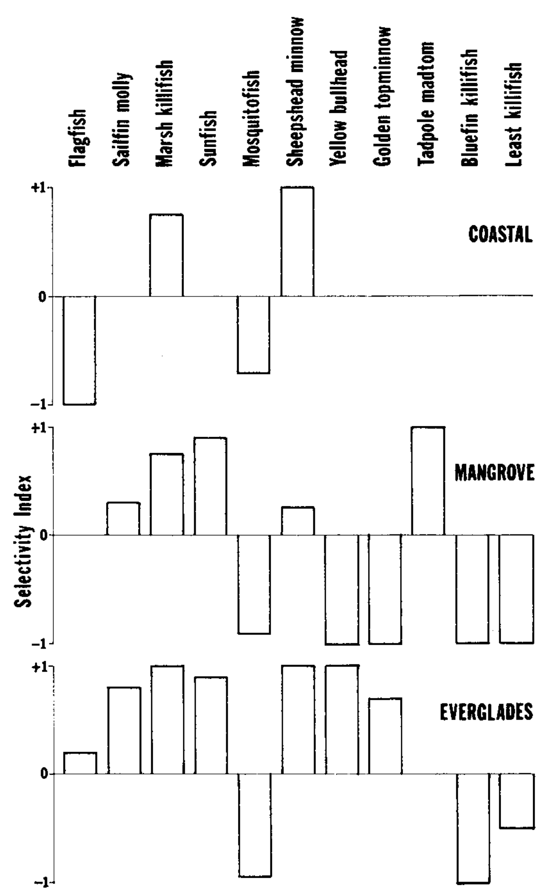


FIGURE 3. Variation in the selectivity of storks for various species of fish in different habitats.

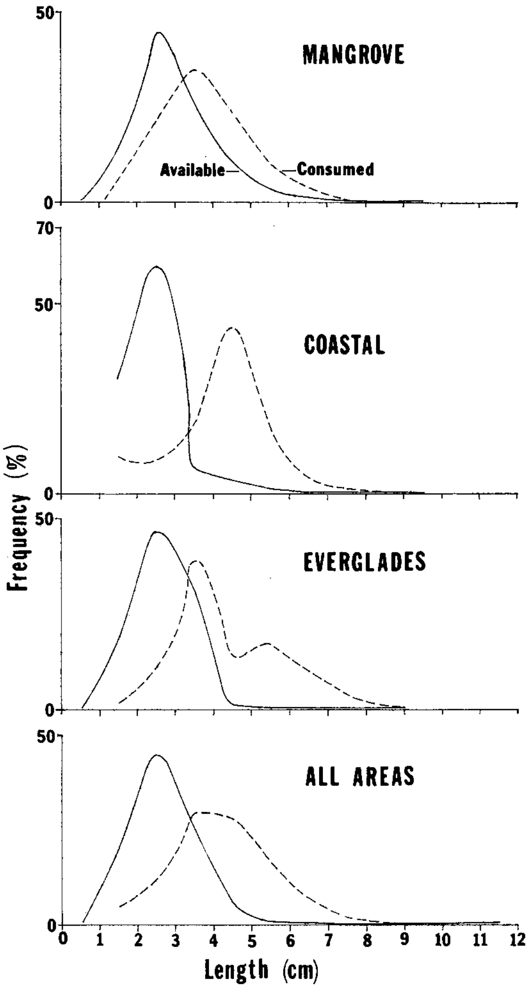


FIGURE 4. Length frequency distribution of fish available to and consumed by Wood Storks in different habitats.

The effect of increasing density on selectivity differed with various species (fig. 7). Higher density increased selectivity only for flagfish and marsh killifish. Selectivity for sheepshead minnows and sailfin mollies declined at higher density. Selectivity for mosquitofish was low irrespective of density.

## DISCUSSION

Any contact a feeding Wood Stork makes with suitable prey should be followed by a capture attempt, and the types of prey actually eaten should depend on such characteristics as abundance, size and behavior of the prey, and on the morphological and physiological constraints imposed by the feeding apparatus of the predator. Wood Storks, whose bill-snap is one of the fastest reflex actions among vertebrates (Kahl and Peacock 1963), are highly adapted to respond to tactile stimulation by potential prey. Selection of prey, however, can be little more than the choice of feeding sites because above-threshold stimulation by fish touching the bill should elicit a capturing reflex. Prey selection, then, is almost a consequence of foraging in places that differ in availability of suitable prey.

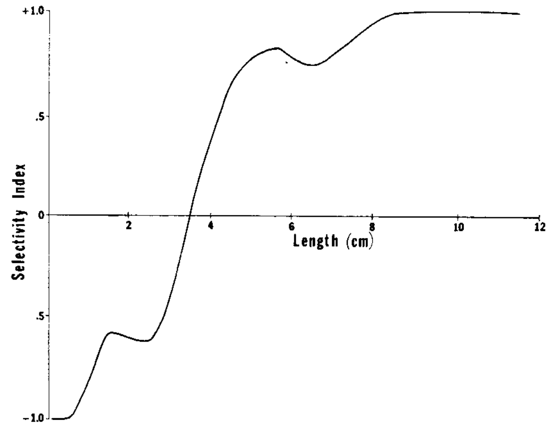


FIGURE 5. Selectivity of Wood Storks for different sizes of prey.

Despite the Wood Stork's nonvisual feeding behavior and generally passive method of

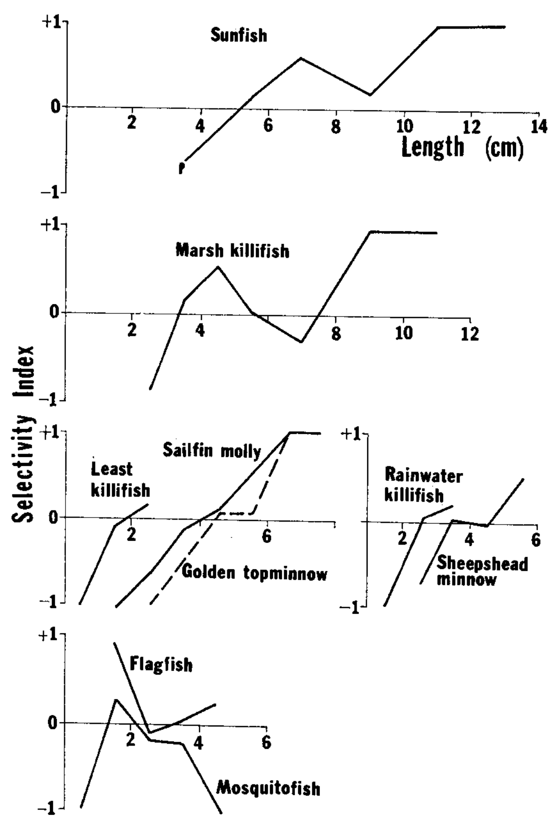


FIGURE 6. Selectivity of Wood Storks for different sizes of various fish species.

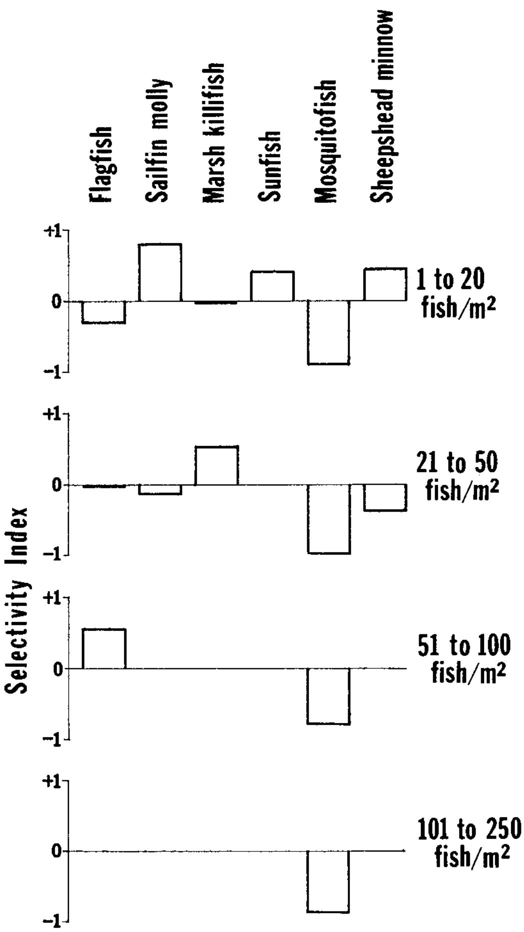


FIGURE 7. Selectivity of Wood Storks for various species of fish at different densities of those species.

prey selection, it has a highly restricted diet, 85% of which is composed of only five kinds of fish. The major determinants of the stork's diet must involve the behavior, size, density or vertical distribution in water of potential prey which determine the vulnerability of various species in complex and differing ways. For example, the flagfish is the most frequent prey item in our study area. It is slightly favored in the Everglades but is under-represented in the diet in coastal habitats (fig. 3). The ability of storks to eat flagfish is apparently a matter of density (fig. 7) rather than size (fig. 6). Overall, it is the second most abundant fish and occurs in extremely high numbers in remnant everglades pools, where storks feed heavily. It is vulnerable under such conditions even though other characteristics such as behavior may make it difficult to capture at low densities. In contrast, sailfin mollies and sheepshead minnows apparently are captured more readily at lower densities (fig. 7). At higher densities, these species may alter their behavior (e.g., schooling in the sheepshead) in such ways as to be less susceptible to predation. Capture of sunfish appears to be primarily a matter of size. In most cases, the relation between selectivity of storks and characteristics of the prey cannot be described adequately because of limited information on fish biology in southern Florida.

The failure of storks to feed extensively on some of the most abundant and densely concentrated but relatively small species (e.g., mosquitofish and the freshwater prawn) eliminates from their diet a considerable segment of the array of available food. Prawns are rarely eaten directly and mosquitofish are under-represented probably because of their small size and perhaps also because of their behavior or distribution in the water. The abundant mosquitofish seems to be a top-water feeder and thus may avoid the submerged, distal one-half of the bill most often used to catch fish. We do not know whether small fish escape capture by avoiding the closing mandibles or whether such fish fail to trigger the bill-snap reflex. The latter is reasonable if, as Kahl and Peacock (1963) postulated, the bill-snap is a myotactic reflex.

Dependence on large and in some cases less abundant species may explain why the Wood Stork is having difficulty adjusting to the rapidly degrading southern Florida environment. The hydrologic conditions that make relatively high concentration of less abundant fish available to foraging Wood Storks may be more complex than those that result in high densities of abundant species such as mosquitofish and prawns. If the larger fish selected by storks are in their second year, the annual production of fish within the highly seasonal hydrological cycle of the Everglades may not provide sufficient food for successful nesting, and the prey available one year may have had to survive exigencies of the previous dry season unnaturally prolonged by water management in south Florida. If large fish are the result of the current year's production, water and food conditions proper for rapid fish development must prevail in the wet season to provide adequate numbers and sizes of prey during the following dry season.

## SUMMARY

The diet of Wood Storks nesting near the Florida Everglades is composed almost en-

tirely of 27 species of fish. Several species of sunfish and four other species made up 85% of the number and 84% of the biomass of over 3,000 prey items collected from adult and nestling storks. Using a helicopter to gather food samples from storks on the feeding grounds permitted comparison of food captured with the prey available at foraging sites. A selectivity index was used to quantify the relation between relative proportion of an item in the diet and its relative proportion in the environment. Storks chose certain species and larger sizes of fish. They also fed where fish were relatively concentrated but the effect of density on selectivity differed in various prey species. The overall diet of storks was highly selective despite the species' nonvisual, groping method of foraging. The major determinant of prey selection appeared to involve characteristics of the prey species, about which more needs to be known. The choice of larger fish raises the problem of the age of these fish and the hydrological and biological factors that permit rapid growth or survival over the dry season prior to consumption.

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*National Audubon Society, Research Department, Tavernier, Florida 33070.* Present address for second author: *Everglades National Park, Homestead, Florida 33030.* Present address for the third author: *Biscayne National Monument, Homestead, Florida 33030.* Accepted for publication 22 April 1975.