PREY CHOICE BY TACTILE-FORAGING WADING BIRDS

James A. Kushlan

U.S. National Park Service
South Florida Research Center
Everglades National Park
Homestead, Florida 33030

Tactile foraging has developed several times among ciconiiform wading birds. The tactile techniques of groping, probing and head-swinging are exemplified by wood storks, ibises and spoonbills respectively (Kushlan 1978). Species specializing in 2 of these tactile techniques, the White Ibis (*Eudocimus albus*) and the Wood Stork (*Mycteria americana*), occur together in southern Florida. This circumstance permits the comparison of adaptive strategies associated with tactile foraging through analysis of prey choices made by these species in response to the same overall regional pattern of prey availability.

Such a comparison is possible because the foraging ecology and population biology of these species have been well documented (Kahl and Peacock 1963, Kahl 1964, Kushlan, Ogden and Higer 1975, Ogden, Kushlan and Tilmant 1976, Kushlan 1977a,b, 1979a). In southern Florida, both species usually nest in winter and spring during the drying season and both forage nonvisually by placing their bill in the water and catching prey they encounter. The purpose of this paper is to compare prey choice strategies resulting from differences and similarities between these tactile foraging birds.

METHODS

I compared prey choice of ibis and storks foraging immediately before or during nesting in coastal habitats and in the freshwater Everglades marshes of southern Florida. Data for storks are from 1974 (Ogden, Kushlan and Tilmant 1976). Data for ibis are from birds nesting in 1972 (Kushlan 1980). Because energy consumption is undoubtedly a critical factor in foraging, food data were expressed in terms of the energy content (Kcal) of the diet consumed in each habitat. In this paper I analyze the proportions each prey type comprised of the total energy content of prey consumed. The energy available (Kcal/m^2) as potential prey was measured using 1-m^2 throw and drop traps in the feeding locations used by each species. See Kushlan (1979a) and Ogden et al. (1976) for sampling and analytical procedures.

Food diversity was calculated for each species (i) in each habitat by Levin's (1968) niche breadth equation,

$$B_i = 1/\Sigma_h p_{ih}^2,$$

where "B" is niche breadth and "P_h" is the proportion of a particular item "h" in the diet of the species.

Food niche overlap between species or habitats was calculated by Pianka's normalized overlap equation,

Proc. Colonial
Waterbird Group, 1979.
Vol. 3: 133-142.

$$\alpha_{ij} = \Sigma_h P_{ih} P_{jh} / \left[(\Sigma P^2_{ih})(\Sigma P^2_{jh})\right]^{1/2}$$

where α_{ij} is the similarity in prey types of predator species "i" relative to species "j" for all "h" prey items (May 1975).

Prey selectivity is calculated by the expression,

$$E_i = \Sigma_h (P_{ih} - n_{ih})/(P_{ih} + n_{ih})$$

where "E_i" is the electivity index for species "i", and "n_{ih}" is the proportion of prey type "h" present in the feeding locations chosen by species "i" (Ivlev 1961). The array of potential prey types used in calculations were those that occurred in the total regional diet of each species. The electivity index is a measure of relative proportions and does not imply a purposeful choice or avoidance of a prey types. It may represent either passive or active selection by a predator.

RESULTS

Food habits of White Ibis and Wood Storks foraging in the Everglades and in coastal habitats are shown in Table 1. Summary statistics show that White Ibis had a smaller niche breadth in the Everglades than in coastal habitats (Table 2). The smaller niche breadth was due to the smaller number of prey types consumed there (8) and the dominance of crayfish in the diet (Table 1). Prey taken by White Ibis along the coast were more diverse, including both freshwater (e.g. crayfish, snails, mussels, newts) and estuarine (e.g. crabs, isopods, rivulus) prey as well as both aquatic and terrestrial insects and crustaceans. Everglades-foraging ibis fed only in freshwater marshes and at the edge of ponds, whereas those foraging on the coast used streams, ponds, prairies, mangrove swamps, and tidal mud flats (Kushlan and Kushlan 1975). Thus the greater niche breadth on the coast may be associated with a greater diversity of prey available in each habitat, or, very likely, with the greater diversity of habitats used there.

In both areas, Wood Storks ate fish almost exclusively, and fed only in drying ponds and streams. The restricted habitat used probably affected prey diversity. Food niche breadth, although greater in the Everglades, was not very different in the 2 areas.

Diets of both species differed markedly between habitats. Diet overlaps between areas were only 0.23 for storks and 0.50 for ibis (with all fish prey combined for coastal habitats). This is, in part, because different prey were available. But the fact that the birds can take different prey types or different proportions of prey types demonstrates considerable flexibility in responding to variations in prey availability.

In the Everglades, White Ibis preyed primarily on invertebrates and there was little overlap with the predominantly piscivorous diet of the Wood Stork (Table 1). The only potential overlap was between the few unidentifiable fish caught by White Ibis and, perhaps, one or more of the species of fishes caught by Wood Storks. In coastal habitats, diet similarity between the 2 species increased somewhat to 0.58, because of the greater importance of fish in the White Ibis' coastal diet. The overlap still was not great, and the 2 species had rather different diets, despite gross similarities in foraging technique.

The elctivity index (selectivity) is a measure of how consumption deviates from proportional abundance. In general, the prey types most important, in terms of total energy content of the diet, were selectivity consumed (Table 3). Considering only the 4 most important prey, positively

Table 1. Prey consumption of White Ibis and Wood Storks in Everglades and Coastal habitats. Data are expressed as the percentage of total energy content (K cal) of the diet consumed in each habitat.

Prey Type	White Ibis Everglades	White Ibis Coastal	Wood Stork Everglades	Wood Stork Coastal
Prawn (Palaemonetes paludosus)		5.8	0.01	
Crayfish (Procambarus)	66.4	12.1		
Crab (Uca)		10.6		
Isopod (Ligia)		0.8		
Millipede (Diplopoda)		0.08		
Spider (Arachnida)		0.03		
Dragonfly larva (Odonata)	15.8	1.6		
Cockroach (Periplanata)		0.3		
Bug (Belostomidae)	5.7	4.1		
Beetle (Hydrophidae, Dytiscidae)	2.8	1.6		
Horsefly larva (Tabanus)		3.5		
Unidentifiable Insects		0.09		
Snail (Pomacea, Helisoma)	1.1	0.03		
Mussel (Unionidae)		0.02		
Florida gar (Lepisosteus platyrhincus)			8.2	
Yellow bullhead (Ictalurus natalis)			7.8	
Sheepshead minnow (Cyprinodon variegatus)		25.1	0.9	16.2
Golden topminnow (Fundulus chrysotus)			1.6	
Marsh killifish (Fundulus confluentus)		2.0	22.4	8.6
Seminole killifish (Fundulus seminolis)				14.5
Flagfish (Jordanella floridae)		1.1	10.9	
Rainwater killifish (Lucania parva)				.0001
Rivulus (Rivulus marmoratus)		0.1		0.1
Mosquitofish (Gambusia affinis)		9.1	2.2	0.7
Least killifish (Heterandria formosa)		0.9	0.1	
Sailfin molly (Poecilia latipinna)		18.8	5.3	53.4
Sunfish (Lepomis spp.)			40.7	
White mullet (Mugil curema)				6.3
Unidentifiable fish	2.1			
Newt (Notophthalmus viridescens)	3.9	1.1		
Frog (Rana sp.)	1.9			
Anole (Anolis carolinensis)		1.0		

* * * * * * * * * * * * * * * *

Table 2. Food niche breadth of White Ibis and Wood Storks foraging in the Everglades and in coastal habitats.

Species	Habitat	Food niche breadth	Total Prey types
White Ibis	Everglades	2.12	8
White Ibis	Coastal	7.75	23
Wood Stork	Everglades	4.08	11
Wood Stork	Coastal	2.91	8

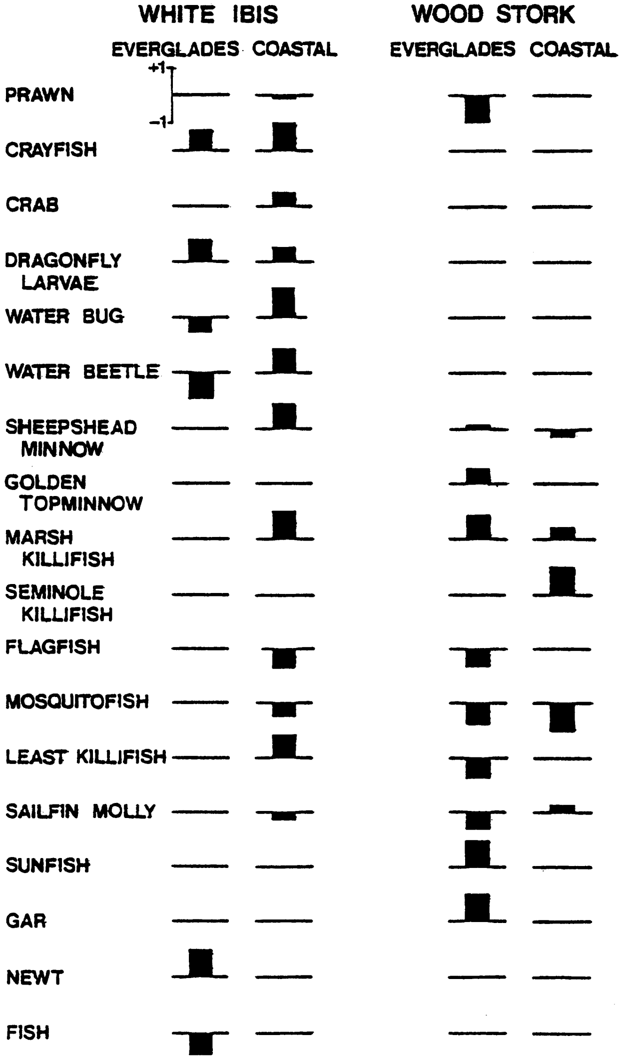

Figure 1. Selectivity of White Ibis and Wood Storks for prey types in coastal habitats and in the Everglades. This selectivity index varies from +1 to -1, from high selectivity to low selectivity.

Table 3. Selective consumption of the four most important prey of White Ibis and Wood Storks.

White Ibis				Wood Stork			
Everglades		Coastal		Everglades		Coastal	
crayfish	+[1]	crayfish	+	sunfish	+	sailfin molly	+
dragonfly larvae	+	crab	+	marsh killfish	+	marsh killifish	+
water bug	-	sailfin molly	+	flagfish	-	seminole killifish	+
newt	+	sheepshead minnow	+	gar	+	sheepshead minnow	-
Percentage of diet[2]	86		67		71		77

[1] + = electivity 0 to +1.0, - = electivity 0 to -1.0
[2] Percentage of the diet composed of the species listed having positive electivity.

selected prey represented 67 to 86% of the total diets. Thus for these predators most of the diet was composed of highly selected prey. That some important prey were not highly selected is also of considerable interest in understanding prey choice. Thus it is useful to examine some individual prey types to search for general patterns of prey selections (Fig. 1).

Prawns were taken by White Ibis on the coast and in very small numbers by Wood Storks in the Everglades. In both cases, prawns were caught less frequently than expected based on their relative availability, which can be extremely high in drying ponds. Size and behavior may account for the absence of prawns from diet of the birds. Their small size probably reduces the probability of capture by storks, which have been shown to select large prey (Ogden, Kushlan and Tilmant 1976), and its active swimming behavior probably allowed it to avoid the probes of ibises.

Crayfish were taken only by ibis and made up a predominance of the diet in the Everglades. Both crayfish and crabs were highly selected by ibis. Storks, in this study, did not take either of these prey. The differential importance of these crustaceans to storks and ibis must reflect basic differences in foraging of the 2 predators. In a similar way, dragonfly larvae were highly selected by ibis in both habitats but were never taken by storks. All of these prey are demersal or burrowing animals that apparently were taken by probing ibis but were not available to Wood Storks.

Water bugs and water beetles were relatively important to the ibis diet in both habitats. They were selectively consumed on the coast but not in the Everglades and were not taken by Wood Storks. These species generally remain close to vegetation.

Among fishes, sheepshead minnows were relatively important to both White Ibis and Wood Storks in coastal habitats, comprising 25 and 16% of the diet, respectively. This species was either selectively consumed or was taken near its proportional availability and apparently was susceptible to capture by either predator. To the contrary, flagfish, abundanct in foraging habitats and moderately important to Everglades storks, were not selectively taken by either storks or ibis. Presumably some aspect of this fish's behavior or morphology decreases its likelihood of capture. These 2 fishes are of similar size and shape, and it is not clear what behavioral or morphological feature affects their susceptibility to capture.

The marsh killifish was also an important prey, especially for storks in the Everglades where it made up 22% of the diet. This fish was selectively consumed by both ibis and storks wherever it was taken. Similarly, the seminole killifish was selectively taken by storks in the Everglades. Probably the tendency of these species to remain at or buried in the bottom mud rendered them susceptible to capture by storks. The mosquitofish, the most abundant fish in the Everglades, was not selectively consumed. Probably its small size and its habit of remaining on the surface of the water interfered with capture by either species. The least killifish was seldom taken by Wood Storks, probably because of its small size. Its tendency to remain still close to vegetation may have made it available to White Ibis. The sailfin molly was an important prey in coastal habitats, especially for Wood Storks. It was more highly selected by storks than by ibis in this habitat, but it was not selected in the Everglades. Reasons for the differences in selectivity are not clear.

Sunfish are relatively large fishes and made up an exceptionally high proportion of the diet of Wood Storks. They were highly selected by storks. Probably their large size and swimming behavior rendered them susceptible to capture by the grope-feeding technique of Wood Storks. The same characteristics may have limited their being caught by ibis.

Although the reasons for the selectivity patterns for some prey, such as sheepshead minnows, flagfish, water bugs and beetles, are unclear, for other prey it appears that morphology and behavior may explain their susceptibility to predation (Table 4). In general, small size and active swimming behavior especially near the surface reduces likelihood of predation by both birds. Prey that are small and also demersal, or burrowing, or that hide in vegetation are susceptible to capture by White Ibis but not Wood Storks. Medium-sized prey are susceptible to Wood Storks and to White Ibis, if primarily bottom dwellers. Large-sized prey are susceptible to Wood Storks.

Table 4. The relation of prey characteristics to susceptibility to capture by White Ibis and Wood Storks.

Selectivity: White Ibis	Selectivity: Wood Stork	Prey characteristics: Size[1]	Prey characteristics: Behavior	Examples of prey types
-	-	small	swimming, especially near surface	prawn, mosquitofish
+	X[2]	small	demersal, burrowing	crayfish, crab, dragonfly larvae
+	-	small	in vegetation	least killifish
+	+	medium	near bottom	marsh killifish
X	+	large	swimming	sunfish, gar

[1]Small < 2 cm, medium 2-6 cm, large > 6 cm long for most specimens taken

[2]X Indicates prey not taken.

DISCUSSION

White Ibis and Wood Storks feed similarly in foraging by tactile methods in shallow marshes. In south Florida during this study, they both nested during the seasonal period of water level decline. They had available the same habitat from which to choose foraging sites and, as a result, an overall similar pattern of prey availability. Foraging differences between the 2 species were, however, sufficient to result in generally low overlap among prey, different characteristics of prey types taken (Table 2,4), and correlative differences in adaptive strategies. These strategies are expressed by the ecological and life history characteristics compared in Table 5.

Table 5. Comparision of ecological and life history characteristics of White Ibis and Wood Storks in southern Florida.

Characteristic	White Ibis	Wood Stork	References
Size	1 kg	2.5 kg	1
Daily energy requirements	165 kcal/day	570 kcal/day	1, 2
Maximum regional nesting population	62,000	5,800	1
Minimum nesting period	61 d	120 d	1, 3
Population energy requirements for nesting	9.3×10^8 kcal	6.4×10^8 kcal	1
Feeding area selection	intraregional movements	intraregional movements	4
Feeding site selection	local enhancement	local enhancement	5
Feeding technique	tactile probe	tactile grope	6
Prey capture	locate by touch	swim into bill	7, 8
Prey location	demersal	natant	9, 10
Prey density	variable	high	4, 10
Prey size	small	larger	4, 10

1. Kushlan 1977a; 2. Kahl 1964; 3. Kushlan, Ogden, and Higer 1975; 4. Kushlan 1980; 5. Kushlan 1977c; 6. Kushlan 1978; 7. Kushlan 1977b; 8. Kahl and Peacock 1963; 9. Kushlan and Kushlan 1975; 10. Ogden, Kushlan, and Tilmant 1976.

An adult stork is over twice the size of a White Ibis. This means that its energy requirements are substantially greater, on both a daily and annual basis. The maximum regional nesting population of the White Ibis is over 10 times that of the Wood Stork, yet the total energy required for each population to nest is of similar magnitude, because of the lower requirements for adult maintenance and for growth of juvenile White Ibis over a shorter nesting period. As a result, the Wood Stork must obtain more food than the White Ibis, and its foraging tactics must accomodate this requirement.

Both species locate suitable foraging areas through intraregional movements, whereby the populations shift from area to area as regional drying occurs and occupy a succession of foraging sites. The White Ibis movement pattern is more extensive than the Wood Stork's, covering more of southern Florida (Ogden, Kushland and Tilmant 1978, Kushlan 1980). Also, both species choose feeding sites by local enhancement, the attraction of searching birds to birds already foraging in a suitable patch.

A primary difference between the 2 species in foraging involves details of their non-visual foraging techniques. The White Ibis probe is rapid and frequently repreated. The bill is placed in vegetation or in the bottom, and if nothing is caught it is then inserted again a short distance away. Thus prey are located and captured by touch and must be slow-moving enough not to be able to avoid capture after contact. The Wood Stork's grope depends on prey initiating contact with the submerged bill, while the stork foot-pumps and wing-flashes. These activities presumably cause prey to swim away from the disturbance and be captured by the bill-closure reflex (Kahl and Peacock 1963).

As a result of these behaviors, different types of prey are taken by the 2 predators. Ibis consume mostly species that are demersal, slow swimming or depend on hiding in mud or vegetation, rather than rapid swimming to avoid capture (Table 4). Many of these prey, especially crayfish, crabs, and insect larvae, are selectively caught by the ibis' non-visual technique. Wood Storks almost entirely take large fish that respond to the storks actions by swimming into the gaping bill (Table 4).

These prey choice patterns are associated with other differences in foraging strategy between storks and ibises. High prey density is crucial for Wood Stork, but the ibis, with lower energy requirements, can rely on less concentrated prey. Furthermore, the ibis consumes smaller prey than the Wood Stork. For the White Ibis, fish prey averaged 2.2 cm long contrasted with averages of 4.2 and 4.5 cm for Wood Storks in the 2 habitats. This is a reflection of both the physical ability of each species to catch prey of different sizes and the need for Wood Storks to obtain energy in large packages for effective foraging. The small sedentary prey consumed by White Ibis are more widely dispersed and probably are, overall, more abundant than the large prey of Wood Storks.

The diets of both storks and ibis vary somewhat in the different areas (Table 2), probably in response to changing prey availability. Ibis feeding in coastal habitats consume a wider variety of prey than those in the Everglades. In habitats where both predators took fish, many species taken were similar (Table 1). Thus of the 7 fishes caught by ibis and 8 caught by storks, the 5 species caught by both accounted for 97 and 85%, respectively, of the fish eaten. Thus overlap was higher among the fish prey than between the 2 coastal diets as a whole. Prey selectivity for some fish species was similar between ibis and storks (Fig. 1). It would appear that such fishes have characteristics that either permit capture or aid in avoiding capture by a tactile-foraging bird.

It is instructive to contrast 2 fish that differed in selection between the 2 predators, least killifish and sunfish (Fig. 1). These prey demonstrate how prey size and behavior affect prey selection. Wood Storks take larger prey than White Ibis, and selectively consume the larger individuals of those prey available (Ogden, Kushland and Tilmant 1977). Sunfish are probably too large and fast for ibis to take frequently, but their size and behavior render them particularly susceptible to stork rpedation. Least killifish are probably too small for storks to capture, but their habit of remaining close to vegetation might render them susceptible to ibises. It appears then that the size and behavior of each potential prey item affects its susceptibility to capture.

For each species, tactile foraging appears to be the basis of an effective foraging strategy providing prey conditions are suitable. These prey availability requirements are less severe for the White Ibis than for the Wood Stork, for which reliance on large amounts of large prey of a few species in high concentrations over a relatively long nesting season provides multiple ways for inadequate prey conditions to result in nesting failure. Thus environmental conditions required for successful nesting are more exacting for Wood Storks. Factors that decrease predictability would differentially affect these species -- the Wood Stork more adversely, as has been seen in the recent history of the 2 species in south Florida (Kushlan 1979b).

Tactile foraging has rendered each species differentially susceptible to changes in their support system. For the Wood Stork, tactile foraging, associated with large body size, has entrained its possible responses to changing environmental conditions. For the White Ibis, tactile foraging is correlated with a successful strategy for coping with environmental unpredictability. Thus, grossly similar tactile foraging techniques are associated with very different, and in many cases opposing, adaptive correlates.

SUMMARY

The Wood Stork and White Ibis forage in superficially similar ways by tactile probing or groping. However, there is little overlap in prey taken between the 2 species. Their diet can be understood by examining how the behavior and morphology of potential prey types render each differentially susceptible to capture. The prey choices of each species are part of a suite of life-history characteristics that differ significantly between the species. In general, the White Ibis' strategy is to feed on small, abundant but dispersed, demersal or burrowing prey that do not rely on rapid swimming through the water column to escape from disturbance. The ibis' small size correlates with a relatively low energy expenditure, a rapid nesting cycle, and energy demands that can be met through relatively abundant smaller prey. The Wood Stork's strategy is to feed on relatively large, densely concentrated prey that respond to the stork's disturbance by swimming into waiting open mandibles. It has relatively high energy requirements over a long nesting cycle, demanding a continuous supply of large, easily-available fish. Grossly similar foraging techniques are therefore correlated with very different adaptive strategies in these 2 species, emphasizing that the understanding of foraging strategy must be placed in context with broader life history characteristics.

ACKNOWLEDGMENTS

I thank John C. Ogden and William B. Robertson, Jr. for reviewing this paper.

LITERATURE CITED

IVLEV, V.S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Conn. 302 pp.

KAHL, M.P. 1964. Food ecology of the Wood Stork (*Mycteria americana*) in Florida. Ecol. Monogr. 34: 97-117.

--------, and L.J. PEACOCK. 1963. The bill-snap reflex: A feeding mechanism in the American Wood Stork. Nature 199: 505-506.

KUSHLAN, J.A. 1977a. Population energetics of the White Ibis. Auk 94: 114-122.

---------. 1977b. Foraging behavior of the White Ibis. Wilson Bull. 89: 342-345.

---------. 1977c. The significance of plumage colour in the formation of feeding aggregations of ciconiiforms. Ibis 119: 361-364.

---------. 1978. Feeding ecology of wading birds. pp. 249-296. In A. Sprunt IV, J.C. Ogden, and S. Winkler (eds.) Wading Birds. Natl. Aud. Soc., New York.

---------. 1979a. Foraging ecology and prey selection in the White Ibis. Condor 81: 376-389.

---------. 1979b. Design and management of continental wildlife reserves: Lessons from the Everglades. Biol. Conserv. 15: 281-290.

--------, J.C. OGDEN and A.L. HIGER. 1975. Relation of water level and fish availability to Wood Stork production in southern Everglades Florida. Open-file Rpt. U.S. Geological Survey, Tallahassee, FL. 56 pp.

LEVINS, R. 1968. Evolution in changing environments: Some theoretical explorations. Princeton Univ. Press. Princeton, N.J. 120 pp.

MAY, R.H. 1975. Some notes on estimating the competition matrix. Ecology 56: 737-741.

OGDEN, J.C., J.A. KUSHLAN and J.T. TILMANT. 1976. Prey selectivity by the Wood Stork. Condor 78: 324-330.