

FEEDING ECOLOGY AND PREY SELECTION IN THE WHITE IBIS

JAMES A. KUSHLAN

Prey selection is constrained by a predator's behavior and morphology and by the availability of suitable prey. Although a number of investigators (Tinbergen 1960, Ivlev 1961, Gibb 1962, Holling 1965, and Royama 1970) have studied predation tactics and have developed hypotheses to account for their empirical data, much remains to be learned about the relationship between the availability of prey in natural systems and its consumption by predators. Particularly important is the question of how prey availability influences prey consumption within the areal range of foraging patches used by a predator. Differences in density, type, distribution and quality of prey may all influence what a predator consumes. This question becomes most interesting, and most difficult to resolve, in mobile, wide-ranging animals such as large birds, whose selection of prey may be expected to vary from habitat to habitat within a region.

In this paper, I examine prey selection of the White Ibis (*Eudocimus albus*), a wide-ranging wading bird. I have attempted to determine the energetic relationships of prey selection on a region-wide basis in order to elucidate the tactics used by such a species in meeting its annual energy requirements. Most work on predation ecology has concerned visually-foraging predators. However, many predators, such as the White Ibis, are tactile, nonvisual foragers (Kushlan 1978a) and are limited in their ability to choose among potential prey. Such choice is required by most theoretical considerations of predation. Nonvisual foraging behavior should affect patterns of prey selection and may differ in crucial detail from better-understood visual techniques. In this study I examine those differences.

METHODS

The study was conducted from 1971 through 1973 in southern Florida, U.S.A. Much of the southern Florida peninsula is swamp and marsh. Mangrove swamps line the coast, and the interior includes the vast Everglades marsh and Big Cypress Swamp (Fig. 1). The northern Everglades is enclosed by levees and is divided into three shallow reservoirs called Water Conservation Areas 1, 2 and 3 (Fig. 1). The southern Everglades is mostly included in Everglades National Park. South Florida has a typical subtropical rainfall regime of alternating rainy and dry seasons. The typical dry season extends from December through May, with water

levels rising extensively at the beginning of the wet season.

Areas and habitats used by foraging ibis were located by fixed-wing airplane reconnaissance conducted on at least a monthly basis. During the study, the maximum southern Florida nesting population was about 60,000 birds, which are joined seasonally by additional winter residents (Kushlan 1977a, Kushlan and White 1977). Ibis constitute the largest population of wading birds in southern Florida, an area characterized by long-term declines in wading bird populations (Robertson and Kushlan 1974). Water conditions over the survey area were assessed by visual analysis of satellite false color infrared imagery (Landsat) in which dry marsh can be distinguished from marsh covered by surface water.

Data on the time required to consume prey after capture (handling time) were from captive birds. Different sized sardines (*Harengula*) were presented to an adult ibis and handling time was recorded. Food samples were obtained outside the breeding season by collecting adults on their feeding grounds and during nesting by collecting regurgitated food samples from nestlings in colonies. Food samples were separated to species and dried to constant weight at 60°C. Prey availability was determined using 1 m² drop-and-throw traps with at least 10 trappings per feeding area. Use of such traps has been discussed by Kushlan (1974) and Ogden et al. (1976). Energy content was calculated by multiplying the dry weight of food types by their caloric content (ash included) determined with a Parr adiabatic calorimeter. Kushlan and Kushlan (1975) discussed the species of prey eaten by White Ibis in southern Florida, and in this paper I concentrate on the most important prey types and larger taxonomic units. Prey consumption was related to prey present in the environment (availability) by the selectivity index $E = (r_i - P_i)/(r_i + P_i)$, where P_i is the proportion of the total prey energy available in the environment composed of prey type i , and r_i is the proportion of total energy consumed composed of prey type i . This measure varies from near +1, when a food is taken in proportions well above its abundance in the environment, to near -1, when a food is taken well below its relative abundance in the environment (Ivlev 1961). Values near 0 indicate that a prey was taken in direct proportion to its abundance. High selectivity, as revealed by a positive selectivity value, need not imply that the predator actively sought out and chose a certain prey type, only that the end result was the consumption of a prey type in proportionately greater amounts than it occurs in the environment. This result could be caused by behavior of prey or of predator as well as active choice. Overlap in food consumption and foraging habitat was measured by the index $c = (2 \sum x_i y_i) / (\sum x_i^2 + \sum y_i^2)$, where x_i and y_i are the proportion of the total energy consumed at colonies x and y composed of food item i (Horn 1966).

RESULTS

FORAGING TACTICS

The basic feeding technique of the White Ibis is probing into the water or soil with the bill held 1-2 cm agape at the tip (Kushlan 1977b). Although vision is used to find

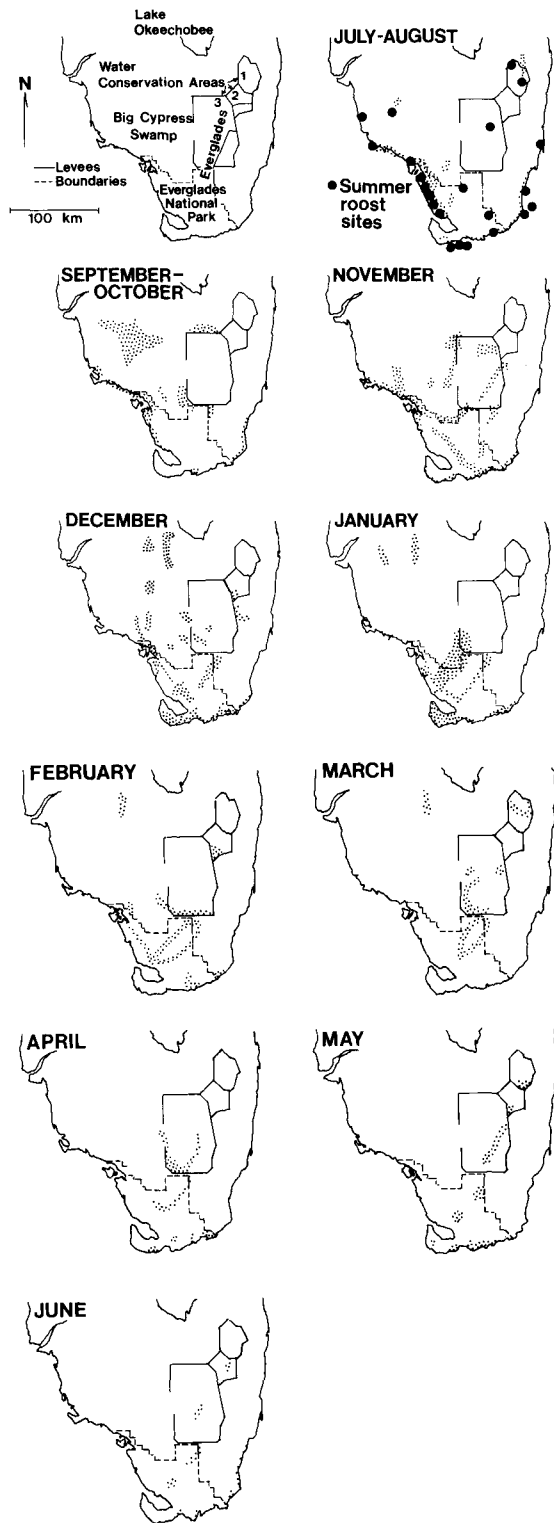


FIGURE 1. Changes in the distribution of concentrations of foraging White Ibis in southern Florida in 1972 and 1973. Concentrations of feeding ibis are shown by stippling. Geographic locations and summer roost sites also are shown.

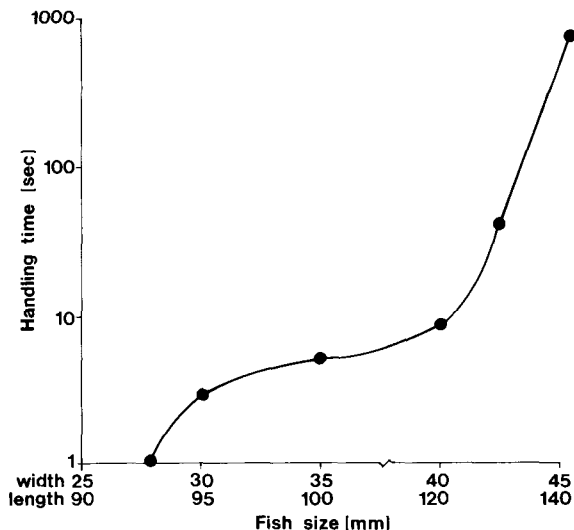


FIGURE 2. Handling time of captive White Ibis for different size fish. Fish size was measured as both maximum width and total length (n = 5 per size class).

foraging sites and is sometimes used on land and rarely in water to locate a prey item prior to probing for it, tactile probing is the primary foraging technique used. Pursuit time is non-existent in that the first contact with the prey is also the instant of its capture or miss. The White Ibis preys almost entirely by searching and attempts to contact prey using a limited foraging repertoire.

White Ibises may form feeding aggregations of 5,000 or more birds in suitable habitat. They were present in over 70% of the aggregations I censused in southern Florida in 1975 (n = 209). They are a core species, initiating the formation of mixed-species foraging aggregations of wading birds, and they are also attracted to feeding areas by the presence of white birds, including other White Ibis (Kushlan 1977c). The species is important within mixed-species aggregations and other wading birds feed commensally with it (Kushlan 1978b).

Flocking and aggregation feeding influenced prey intake. Handling time, in captivity, rose exponentially with prey size because of the need to break large food items into pieces (Fig. 2). In the wild, the increase in handling time rendered ibis with large prey items vulnerable to loss through stealing by other birds, including herons, egrets and grackles, which often concentrated their robbing attack on ibis. Ninety percent of prey longer than 10 cm being handled by White Ibis feeding in aggregations were stolen (n = 20). Such robbing was averted by the ibis flying out of the feeding area, a maneuver that further increased handling

time. The difficulty of successfully handling larger prey apparently restricted the items taken while feeding in an aggregation. In 11 instances I saw ibis that were feeding in an aggregation drop a large prey and resume foraging rather than try to eat it. Although a few small prey with hard shells were broken before swallowing, most did not require handling. In the wild, ibis fed mostly on prey small enough to be consumed almost instantaneously after capture. Such fish and crustaceans were only about 2 cm long (fish $\bar{x} = 2.0 \pm 0.4$ cm, $n = 341$; crustaceans, $\bar{x} = 2.2 \pm 0.6$ cm, $n = 62$).

MOVEMENT AND HABITAT USE

White Ibis foraged in different parts of southern Florida at different times of the year (Fig. 1). During the summer, the inland marshes were deeply flooded and most ibis roosted and foraged along the coast in tidal flats, mangrove swamps, and estuarine marshes. Surveys showed 33,000 ibis foraged along the west (Gulf of Mexico) coast in summer. Some ibis continued to use coastal marshes throughout the year, although less foraging habitat was available during the spring. Ibis that remained inland during the summer fed in flooded fields and in available shallow marshes, especially west of the Everglades. In fall, coastal segments of the population shifted their foraging to more interior marshes and swamplands (Fig. 1). The Big Cypress Swamp and marshes along the edges of the Water Conservation Areas of the northern Everglades (Fig. 1) became important feeding areas in September and October. By November, ibis increased their use of areas along the landward edge of the coastal mangrove swamps. By January, they had abandoned most of the Big Cypress Swamp for habitats on both sides of the southern Everglades. Through March, feeding areas contracted in the southern Everglades and expanded within the levee system surrounding the northern Everglades. From April through June, during the usual nesting period, feeding became further restricted to the central areas of the Everglades. Population segments that nested north of the Everglades also moved around, but monthly surveys were not conducted in this area.

Water levels in the interior and coastal wetlands fluctuated seasonally, and areas of shallow marsh and swamplands lost surface water during the dry season, from January to May. To examine the relationship of drying to habitat choice, I compared the ibis' use of habitat with water conditions re-



FIGURE 3. Distribution of White Ibis in relation to surface water, based on satellite imagery of southern Florida taken 22 March 1973. Marsh covered with surface water, which appears darker in this imagery, is enclosed by lines. The stippling shows distribution of foraging ibis as determined by aerial surveys.

vealed by Landsat imagery. On 22 March 1973, for example, birds were concentrated within, and primarily near the edge of, remaining flooded areas (Fig. 3). Patterns of ibis concentration in other months (Fig. 1), and consequently their movement within the region corresponded similarly to the pattern of drying throughout south Florida. Thus, in fall ibis moved to higher land in the Big Cypress Swamp and to early-drying coastal marshes, then progressively inland to lower-lying marshes adjacent to and finally into the Everglades. As the Everglades dried, they progressed to lower sites and ultimately to the deepest sloughs and ponds. Ibis along the coast also shifted feeding areas as high coastal marshes dried locally, but they used tidal sites throughout the year.

Whereas some wading bird species such as the Wood Stork (*Mycteria americana*) depend almost totally on lowering water levels to concentrate aquatic prey (Kushlan et al. 1975, Ogden et al. 1978), White Ibis can feed when water levels drop or rise. Although ibis generally fed near the edge of pools that were drying-up, if rainfall increased the water level slightly, they moved to reflooded areas. Extreme increases in water level, such as occur at the beginning of the rainy season, force ibis from the inland marshes. It would appear in general

TABLE 1. Habitat selection by foraging ibis during the nesting season. Data are expressed as the percentage of the number of flocks observed on aerial surveys in each of three nesting and foraging areas.

Lake area		Everglades		Coastal	
Habitat	Percent occurrence (n = 63)	Habitat	Percent occurrence (n = 75)	Habitat	Percent occurrence (n = 108)
Marsh prairie	22	Sawgrass marsh	4	Dwarf mangrove swamp	3
Pasture	56	Marsh prairie	47	Mangrove-lined stream	30
Ditches	3	Sawgrass-lined pond	29	Mangrove-lined pond	31
Lake-edge marsh	19	Willow-lined pond	15	Marl prairie	19
		Canal-edge marsh	5	Tidal mangrove swamp	14
				Tidal shoal	2

that water depth was more important than direction of water level change in determining seasonal foraging patterns of the White Ibis.

Ibis nested primarily in three areas: near south-central Florida lakes, along the coast, and in the Everglades. Nesting usually occurred in spring (March–June) with timing and colony locations determined by water conditions and the availability of nearby foraging areas (Kushlan 1976a). Nesting at inland sites occurred during the dry season or when localized drying occurred at other times of year (Kushlan 1976a). Based on a maximum of about 60,000 potentially nesting White Ibis, the percentage of the population nesting each year was: 1971, 3%; 1972, 100%; 1973, 69%; 1974–75, 90% (Kushlan 1977a, Kushlan and White 1977).

Foraging habitat used by nesting birds differed in the three areas (Table 1). Birds nesting on islands in central Florida lakes foraged in pastures, marsh prairies, and lake-edge marshes. Birds nesting on tree islands in the Everglades fed in marsh prairies and along the edges of ponds. Birds nesting on coastal islands fed along mangrove-lined ponds and streams and on coastal prairies.

PREY CONSUMPTION

White Ibis fed on different prey in different areas, outside the nesting season (Fig. 4). For example those in Everglades and in cypress swamp habitats primarily ate crayfish (Fig. 4b, c, d), those feeding in willow ponds primarily ate fish (Fig. 4a) while those feeding in mangrove swamps ate crabs (Fig. 4e). Foraging habitats used by ibis outside of the nesting season differed in their energetic value, as measured by the energy content of food consumed in each habitat. The highest energy content was in willow ponds (Fig. 4a) immediately before nesting ($5.09 \pm .06$ Kcal/g, $n = 2$). This is greater than the energy content of food con-

sumed at other sites outside nesting (Mann-Whitney U -test, $P < .01$). Sites other than willow ponds averaged 2.85 ± 1.0 Kcal/g ($n = 15$).

Figure 5 shows the food consumed by, and prey available to, White Ibis nesting under typical conditions in four major colonies. On the coast crayfish and especially fish, which made up 56% of available energy, dominated the diet. At lake colonies, crayfish made up 72% of the total energy consumption even though fish and insects were the primary prey available. At the two Everglades colonies, crayfish accounted for 60% of the energy consumed even though fish and prawns, which together comprised 84% of available energy, were the primary prey items available. These results show that ibises from the two Everglades colonies took similar types of prey, but that ibises from inland colonies took different prey than did those from coastal colonies (Table 2).

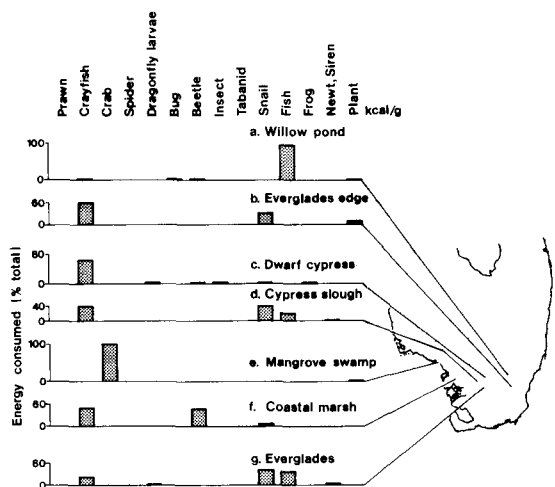


FIGURE 4. Prey consumption by White Ibis in various habitats outside the nesting season. Prey eaten are expressed as percentage of total energy consumption. Sample sizes: a = 2, b = 1, c = 7, d = 1, e = 1, f = 2, g = 3.

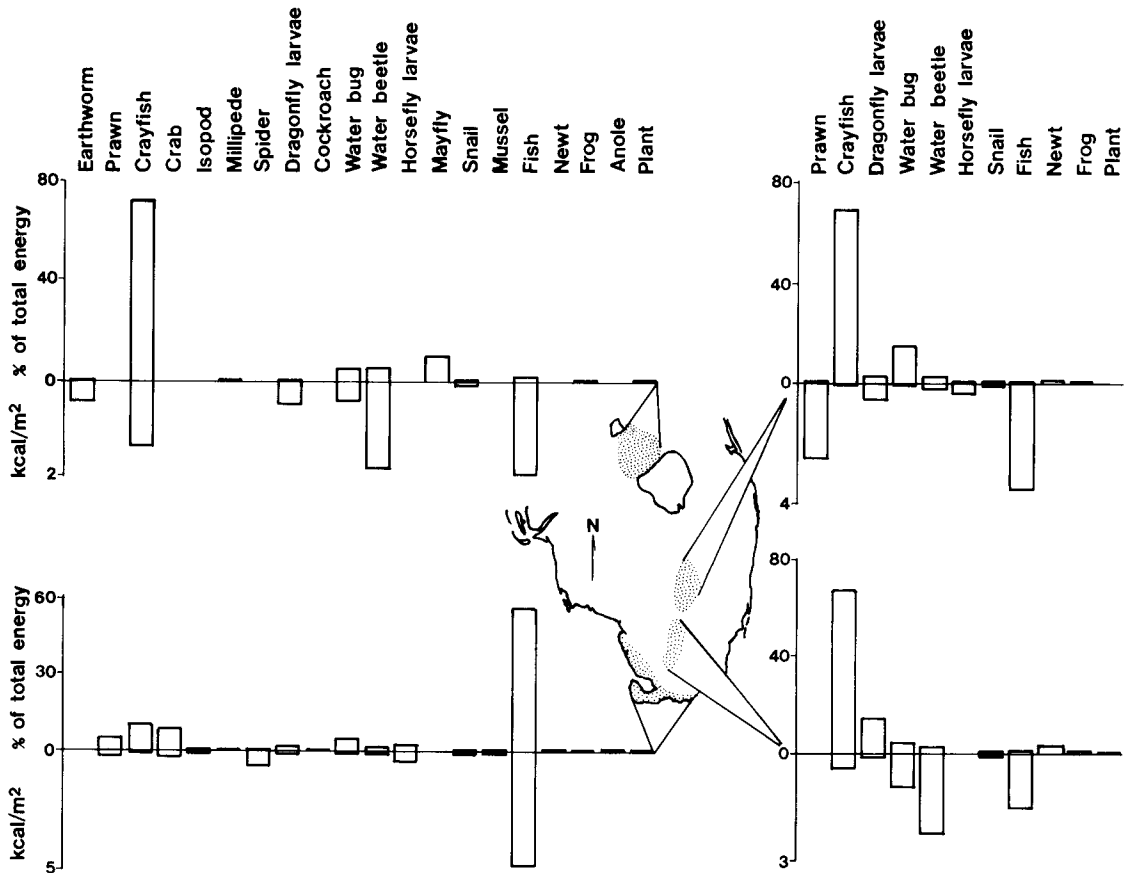


FIGURE 5. Typical prey consumed by and prey available to White Ibis using four foraging areas during nesting. Stippled portions of map are feeding areas used. From north to south these areas are Lakes region (n = 14), northern Everglades (n = 26), southern Everglades (n = 34), and coastal (n = 60).

When water levels rose in the Everglades late in the nesting period, ibis from the southern Everglades colony changed their foraging from the remaining drying pools and ponds of the Everglades to coastal swamps. This change was reflected in types of prey taken (Fig. 6). In the northern Everglades, ibis changed their foraging area when water management procedures almost completely drained a Water Conservation Area. They switched prey from the usual Everglades diet of crayfish to fish, which in this case made up 96% of the diet contrasted with 0.1% under more typical conditions for

the northern Everglades colonies (Fig. 5). This change was associated with the extremely high availability of fish in ponds and pools concentrated by the lowering of the water level (Fig. 6).

ENERGY CONTENT OF FOOD DURING NESTING

The energy content of foods taken by ibis in primary feeding sites, those used most extensively during nesting, fell within the relatively narrow range of 3.9 to 4.5 Kcal/g (Table 3), even though the type of prey taken differed in some cases. Energy content of food available to ibis in most primary sites was also similar, 6.0 to 7.2 Kcal/m². The energy content of diets in the secondary sites used by different colonies differed notably. Food consumed by the northern Everglades colony during the drainage of a Water Conservation Area had 5.1 Kcal/g at locations having a food availability of over 120 Kcal/m² (Table 3). The energy content of this diet was the same as that taken under very similar conditions in ponds just prior

TABLE 2. Matrix of overlap values¹ for food consumed by White Ibis from four colony types.

	Lakes	Northern Everglades	Southern Everglades
Northern Everglades	.97		
Southern Everglades	.95	.97	
Coastal	.37	.21	.10

¹ $c = (2 \sum x_i y_i) / (\sum x_i^2 + \sum y_i^2)$ where x_i and y_i are the proportion of total energy consumed at colonies x and y .

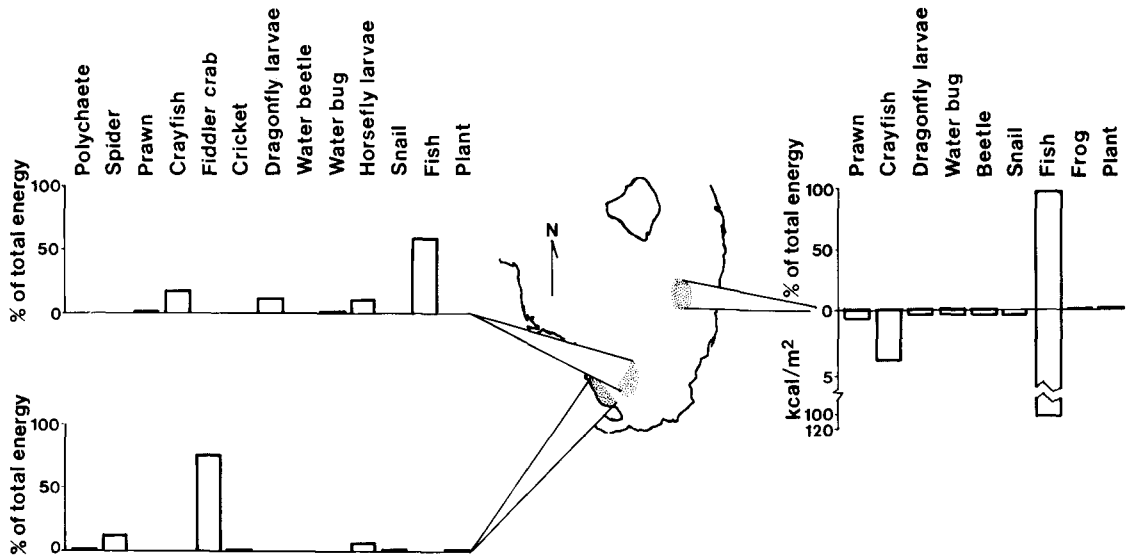


FIGURE 6. Prey consumption by nesting White Ibis in response to particular conditions in the Everglades. Left graphs: Food before and after shift of foraging ibis from southern Everglades to the coast in response to rising water levels midway through nesting (n = 11 before shift, n = 15 after shift). Right graph: Food of northern Everglades ibis feeding during management draw-down of a water conservation area (n = 6). Prey differed from that typically taken in northern Everglades habitats (see Fig. 5).

to the nesting season (Fig. 4b). This shows that ibis take advantage of unusual abundance of prey. After the rainy season began, however, northern Everglades ibis were forced to use flooded pastures. There the energy content of the diet fell to 2.9 Kcal/g, with an availability of 0.2 Kcal/m². When this occurred, ibis concluded their nesting. Southern Everglades ibis moved into coastal habitats after the beginning of the rainy season. Here available energy was approximately 3.5 Kcal/m², and ibis were able to continue nesting.

PREY SELECTIVITY

There was no overall relationship between the availability of a prey type and its con-

sumption by White Ibis in the four major colonies. Slightly more water beetles were eaten with increased relative availability ($r = .88, P < .05, F(\text{slope}) = 6.79, P < .1$), whereas crayfish taken at the three inland colonies comprised a large part of the diet irrespective of their availability and their consumption did not change with increased availability ($r = .78, P < .05, F(\text{slope}) = 1.56, P > .1$).

Considering diet at the four major colonies (Fig. 7), only crayfish, crabs, frogs, and newts were selectively eaten wherever they were taken. Fish and prawns were taken below their relative availability at each colony. Selectivity for dragonfly larvae, water beetles, and snails was inconsistent among

TABLE 3. Energy content of prey consumed and prey available at various colonies.

Colonies	Feeding sites ¹	Energy content	
		Prey consumed (Kcal/g)	Prey available (Kcal/m ²)
Lakes	Marsh and pasture (P)	4.3	6.0
Northern Everglades	Everglades marsh (P)	3.9	6.8
	Ponds in marsh (A)	5.1	120.4
	Flooded pasture (A)	2.9	0.2
Southern Everglades	Everglades marsh (P)	4.5	7.2
	Coastal mangrove swamp (A)	3.5	—
Coastal	Coastal shore (P)	4.2	—
	Coastal mangrove swamp (P)	4.3	7.0

¹“(P)” indicates primary feeding habitat for the colony; “(A)” indicates alternate feeding sites.

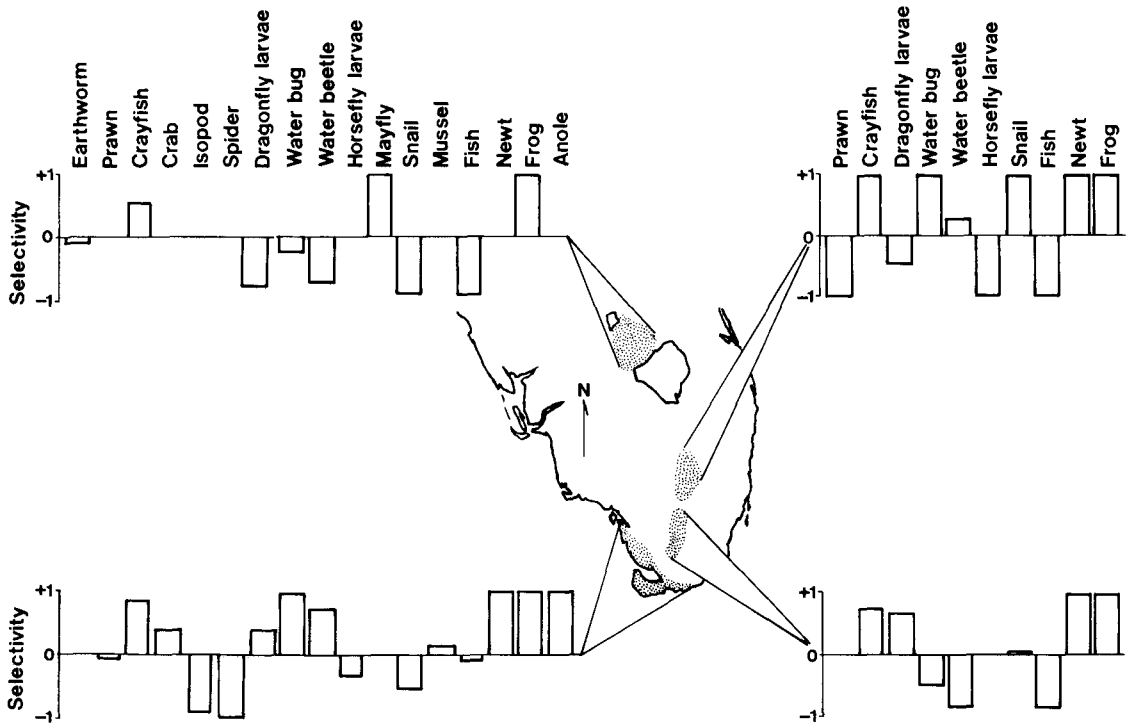


FIGURE 7. Selectivity of White Ibis for different prey at the four colony types. Selectivity was measured by an index which relates prey taken to prey availability in the environment. (See text and Fig. 5 for details.)

the colonies. There was also no relation between selectivity and caloric content of prey (Fig. 8).

Density can have a major influence on prey selection. However, fish and important invertebrates in Everglades marshes reached maximum densities when water levels were as high or higher than the ibis' usual foraging range (5 to 10 cm), and in

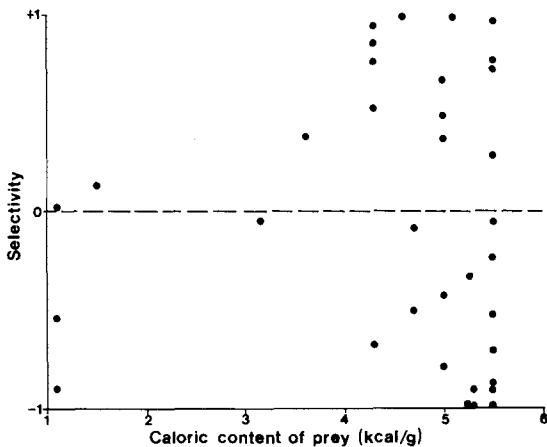


FIGURE 8. Scatter diagram showing lack of correlation between selectivity of White Ibis for various prey and the energy content of the prey.

some cases too high (25 cm) for White Ibis to wade (Fig. 9). Ibis, therefore, fed on these organisms in marshes when they were below the maximum density at which they can occur. The density of fish became greatest in marshes within the ibis' usual range of foraging depth, but this density apparently was not high enough to permit ibis to selectively take them. Fish were taken by ibis in ponds and other depressions where densities were greater than in marshes (Fig. 4a, 6). Prawns also reached high densities in ponds but were seldom taken.

The pattern of prey selection in the White Ibis was demonstrated best by crayfish and fish, which together made up 70% of the ibis' diet and represented the two extremes of prey selectivity. For fish, selectivity was very low at low availability, increasing only to -0.1 at a density of 5 Kcal/m², with no further increase even at extremely high densities (Fig. 10). In contrast, crayfish were highly selected at low and intermediate densities. Only during the draw-down (open symbols, Fig. 10) were crayfish eaten proportionately below their relative abundance. When fish were extremely dense, ibis switched from crayfish to fish. This change in prey selection was energetically valuable, as the caloric content of crayfish

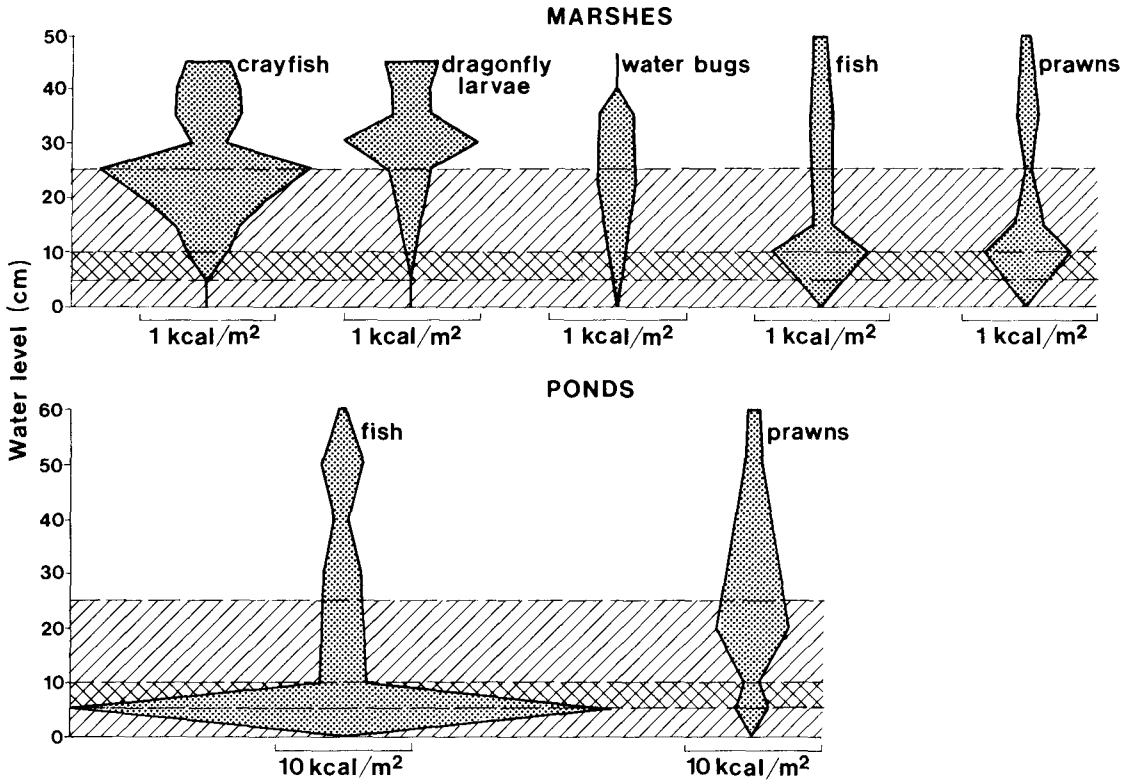


FIGURE 9. Density of White Ibis prey in marshes and ponds related to water level. Width of the figure at a particular water level represents the density of that prey when the level of the water was of the depth indicated. Single cross hatching shows the water levels at which ibis can feed. Double cross hatching shows the water levels at which ibis usually feed.

was 3.6 Kcal/g and that of fish 4.6 to 5.6 Kcal/g.

This pattern of prey selectivity helps to explain ibis feeding ecology. The probing method of feeding by the ibis apparently was effective for catching crayfish but not fish, except where they were very numerous. The suggestion of increased consumption of beetles with increasing availability implied a relation between density and catchability, but consumption of this prey

even at higher densities was still below its relative abundance. This indicates that increased density of some prey to the maximum encountered under typical natural conditions was not sufficient to offset the ineptitude of ibis in capturing them.

Fish was a food category composed of several species. Because of the importance of fish in the ibis' diet, I analyze individual prey species in Figure 11. Sheepshead minnow, marsh killifish and least killifish at coastal colonies and flagfish, golden topminnows and bluespotted sunfish at inland sites made up a greater proportion of the diet than they did of the available fish. Although no fish species was taken selectively when all available prey are taken into account, some fish species apparently were more likely to be caught than others, probably because either their behavior or morphology rendered each of these species differentially susceptible to White Ibis predation.

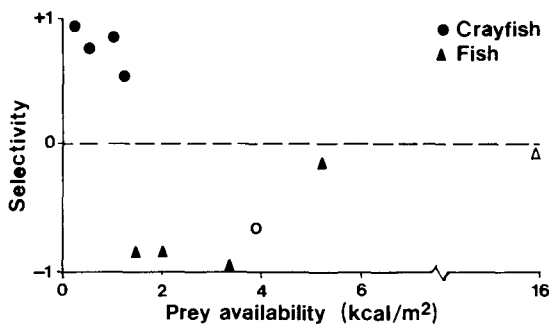


FIGURE 10. Relation between prey density and selectivity of White Ibis for crayfish (circles) and fish (triangles) at four colony sites (closed symbols) and during the draw-down in the Everglades (open symbols).

DISCUSSION

MOVEMENT IN SOUTHERN FLORIDA

In summer, White Ibis move to coastal habitats and later, by a series of shifts, throughout the interior of the Florida peninsula.

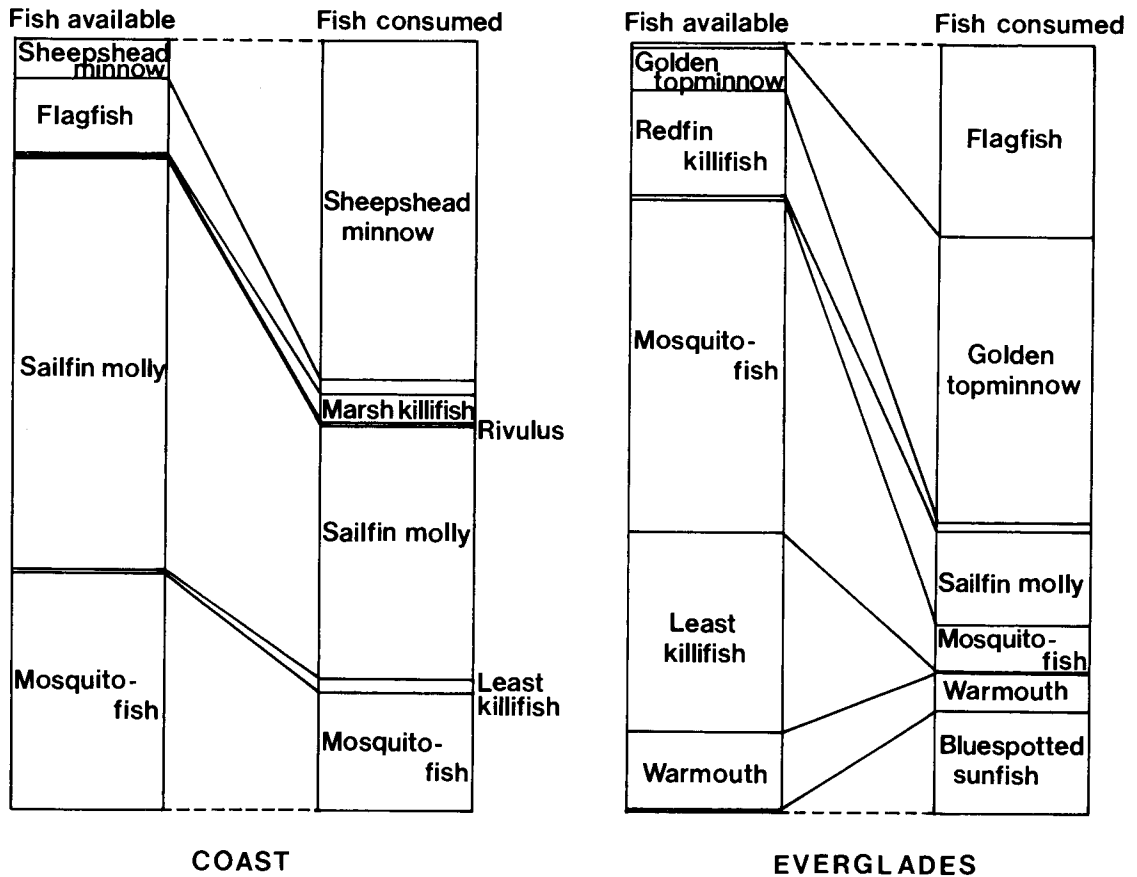


FIGURE 11. Availability and consumption of fish species on the coast and in the Everglades: sheepshead minnow (*Cyprinodon variegatus*), flagfish (*Jordanella floridae*), marsh killifish (*Fundulus confluentus*), rivulus (*Rivulus marmoratus*), sailfin molly (*Poecilia latipinna*), least killifish (*Heterandria formosa*), mosquitofish (*Gambusia affinis*), golden topminnow (*Fundulus chrysotus*), redfin killifish (*Lucania goodei*), warmouth (*Lepomis gulosus*), bluespotted sunfish (*Enneacanthus gloriosus*).

Segments of their population thereby successively occupy newly suitable foraging areas and use most of the available habitat of southern Florida during the course of a year. This pattern of habitat use is an adaptation to the wet-dry seasonal cycle of the southern Florida environment (Kushlan 1976b). The sequential availability of such productive habitats over the year allows the marshes and swamps of the southern Florida wetlands to support relatively large populations of both wintering and resident wading birds.

Several other species of birds undertake analogous movements in fluctuating environments within the region. The shifts of the Wood Stork in southern Florida correspond to changing availability of prey but differ in timing and sequence from those of the White Ibis (Kushlan et al. 1975, Ogden et al. 1976, 1978). Unlike the Wood Stork, the ibis is not completely dependent on falling water levels to concentrate prey, but rather on having water sufficiently shallow

to make foraging possible. Herons and other marsh birds apparently also move seasonally throughout southern Florida. These movements are poorly known but may coincide generally with those of ibis.

Nomadism permits ibis to avoid habitats with unsuitable foraging conditions, such as those with high water levels or those suffering from previous prey depression during a seasonal cycle (Charnov et al. 1976). It also permits the identification and use of suitable foraging habitat and the establishment of nesting colonies at locations that provide access to such foraging habitat (Kushlan 1976a). Relocation of colonies from one year to the next, and variation in the proportion of the population nesting in any one year, are further adaptations of White Ibis to variations of the annual wet-dry cycle. Such an annually dynamic reproductive effort, noted for other species by Nichols et al. (1976), is geared to the availability of habitat for foraging; it is advantageous to ibis by avoiding ineffective repro-

ductive effort in years when food is scarce. Ibis also nest at different times in different years. Although the large inland colonies usually form in spring, as they did during this study (Kushlan 1977a), they can, when conditions are poor, delay nesting until later in the year (Kushlan 1976a, Kushlan and White 1977).

PREY CONSUMPTION

Southern Florida White Ibis concentrated upon different prey in various south Florida habitats. The most significant difference was the greater role played by crayfish in inland than in coastal diets. The diet was particularly variable outside of the nesting season (Fig. 4). During nesting, there were important differences in prey taken at coastal vs. inland colonies (Table 2).

The pattern of diet within the region resulted from the way ibis selected feeding habitats and prey during the course of the year. Variations in prey taken during non-nesting periods (Fig. 4) reflected the divergent foraging opportunities used during this period of low energy demand. Except for use of willow ponds immediately before nesting, the energy value of prey taken outside of nesting was less than that taken at primary sites during nesting: 2.85 ± 1.0 Kcal/g ($n = 15$) vs. $4.24 \pm .16$ Kcal/g ($n = 5$; Mann Whitney U -test, $P < .01$). The relatively high caloric content of food obtained in primary feeding areas during nesting demonstrates the ability of ibis to choose good foraging habitat during this period of high energy demand (Kushlan 1977a), and it is reflected in the ibis' methods of colony site selection (Kushlan 1976a). However, ibis can also switch foraging, either to unusually good areas when these become available or to poorer, but often acceptable, secondary feeding areas when primary sites become unavailable because of drought or flood.

PREDATION TACTICS

Nonvisual foraging restricts the manner and type of predatory tactics available to the White Ibis. The foraging bout of any predator can be divided into pursuit time, handling time, and search time. Pursuit time was zero for the ibis, a searching predator. Handling time rose exponentially with prey size (Fig. 2) which resulted in a high robbing rate for large items; ibis were the primary victims of prey-robbing behavior common in mixed-species aggregations of wading birds (Kushlan 1978c). Ibis apparently responded to this pressure by selec-

tively releasing large prey. As a result, actual prey were small, and handling time per item swallowed was effectively zero in most circumstances. Whereas handling time ultimately limited prey size, it was tactically inconsequential in most situations as only small prey were taken.

Given this constraint of handling time, ibis forage so as to make the most of their search time. Such tactics involve selection of both prey and habitat, factors that may be approached quite differently. Because of its nonvisual foraging, an ibis might be expected to search its within-patch environment in "fine-grained" manner; that is, it should encounter potential prey in the proportion in which they occur within the patch (MacArthur and Pianka 1966). Because ibis depend on patch-foraging, however, a bird may also be expected to search potential habitat in a "coarse-grained" manner; that is, certain habitats will be used regardless of relative abundance. These predictions on prey selection and habitat selection are testable with available data.

Prey selection. A searching, nonvisual predator may be expected to be a generalist (MacArthur 1972:61-62), and ibis do take a wide variety of prey (Kushlan and Kushlan 1975). Food habits vary outside the nesting season (Fig. 4), but specialization is apparent in the birds' selection of certain prey such as crayfish during the nesting period when energy demand was high. Selectivity indicates that the White Ibis tends to specialize despite its mode of foraging. This is a deviation from the expectation of nonvisual, searching predators and suggests that within-patch foraging may not be fine-grained.

Many models of predator-prey relations (Poole 1974), presuppose a direct relation between prey capture and prey density, that is, a fine-grained response to prey density. Tinbergen (1960) and succeeding investigators found that this was generally untrue in visually foraging predators. It is nonetheless a particularly appealing hypothesis that the feeding success of a nonvisually foraging animal should be directly proportional to prey density. However, the functional response of ibis is more complex than such a hypothesis would suggest, and ibis are in fact highly selective in their choice of certain prey (Fig. 7). Patterns of prey consumption also differ among types of prey. A curve suggesting the response of ibis to increasing prey density is shown in Figure 12A. When there is no apparent interaction among prey types, ibis effectively show no functional

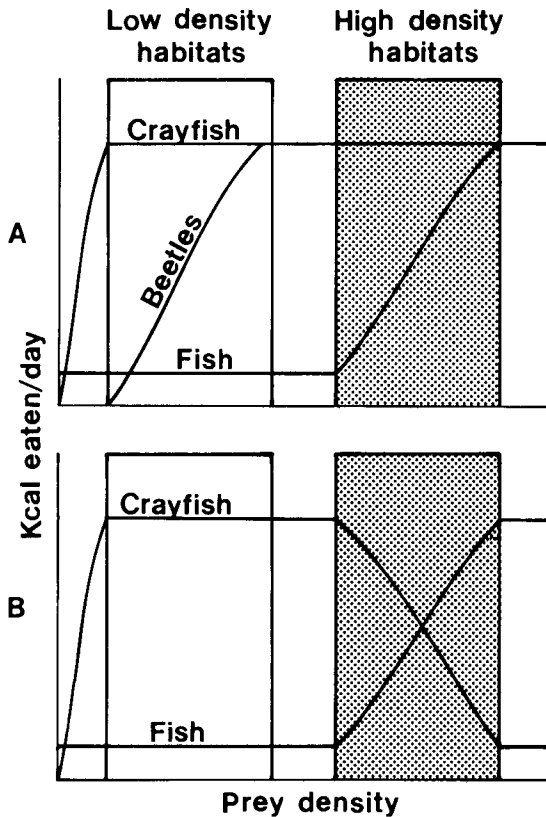


FIGURE 12. Diagram of functional relation between prey density and prey consumption for different categories of prey. (A) As prey density increases from habitat to habitat, consumption of some prey (e.g., crayfish) does not change, consumption of some prey (e.g., water beetles) increases with increasing density, consumption of other prey (e.g., fish) increases only in high density habitats, reflecting the differing ability of the predator to capture each type of prey. (B) In habitats of high prey density switching from one prey type to another can occur because of changes in relative catchability.

response to some prey (e.g., crayfish) at the densities encountered in the wild. Their response to some prey (e.g., water beetles) increases as prey density increases, but they respond to other prey (e.g., fish) only above a high threshold density. Thus absolute density does not determine predation levels, and ibis prey selection appears coarse-grained.

Formulations of predator-prey relations that recognize the existence of selectivity generally postulate that a predator should select prey having the greatest energy value (Emlen 1966, Schoener 1969, 1971, Emlen and Emlen 1975). If handling times for the small items that comprise the ibis' diet are equally small, the profitability of a prey type can be measured by its energy content. Except for switching from crayfish to fish at extremely high fish concentrations, energy content is unrelated to prey selection (Fig.

8). Thus prey profitability is not important in ibis consumption of prey.

Switching prey when fish are plentiful (Fig. 10) reveals much about the nature of ibis prey selection. Murdoch (1969) suggested that switching prey may not be common in nature. Nonetheless, temporary changes in diet often occur and can be considered to be prey switching if the change leads to inclusion of the potential prey having highest density. Prey changes have been ascribed to such factors as palatability (Beukema 1968), learning (Holling 1965), and hunting behavior (Kruuk 1972). Attempts to explain such changes in prey capture in other predators have resulted in theories such as that of a specific search image (Tinbergen 1960, Dawkins 1971, Murton 1971), which in its widest generalization might be considered a selective searching for prey having specific characteristics. However, even a tactile "image" does not exist in an ibis, which must search for all types of prey at the same time and consume whatever it can find, capture, and keep. It is unlikely that behavioral, psychological, or palatability factors compelled ibis to switch to fish because of their low selectivity for fish in situations where fish were abundant. A simpler explanation is that at extremely high fish densities, foraging ibis found and captured fish so frequently that the less concentrated crayfish were not encountered. Although the higher caloric content per gram of fish prey was fortuitous, the overall energy value of the food obtained in that place was greater than that found in the usual primary foraging habitats (5.1 vs. 3.9 Kcal/g). Thus the particular habitat containing an extraordinarily dense fish concentration was energetically valuable, one to which a foraging ibis should return.

The availabilities of various prey may interact to produce a compensatory effect under particular conditions (Fig. 12B). Considered this way, switching prey can be caused by the interaction of catchability and abundance, one prey becoming catchable at high density and therefore being more frequently captured. In predators whose selectivity depends on their preferences, feeding on preferred food alone theoretically influences the selection of less preferred food (Goss-Custard 1977). In the one case where preference corresponded to expectations, the consumption of the preferred (i.e., energetically more valuable) prey was probably the passive result of interference between prey rather than active choice by the predator.

Switching, as well as other patterns of prey selection, resulted from the ibis' differential ability to capture different types of available prey. As a result some items were represented in the diet more than others. Thus, the catchability of specific prey types, rather than their density or energy content, determined to a great extent what ibis ate. This pattern is best shown by their predation on fish. The low representation of fish in the diet (negative selectivity) suggests that they are not easily caught. Fish became important prey only where they were abundant, such as in streams and dried-up pools along the coast and at ponds and pools inland. In no case, despite high densities, were fish proportionately more plentiful in the diet than as available prey. White Ibis consumed nearly the same species of fish as those selected by Wood Storks (cf. Ogden et al. 1976), specialized fish feeders and tactile foragers that occupy much the same habitats as the ibis. Certain characteristics of these particular fish apparently render them more susceptible to capture by tactile foraging wading birds. If true of fish, a prey that was not easily caught by ibises, the same must also be true of more susceptible types of prey, suggesting that certain prey characteristics largely determine the diet of nonvisual predators. In the ibis, nonrandom selection was undoubtedly caused by differences in the morphology and behavior of various types of prey.

For visually foraging predators the catchability of potential prey can be decided prior to attempting capture by weighing those specific characteristics of the prey that influence its susceptibility to capture (Snyder 1975, Kaufman 1974a, b). Such characteristics are not evident to a nonvisually foraging predator. An ibis' selectivity is somewhat passive, at least prior to capture. Its tactics are similar to what Curio (1976) called hunting by speculation. This pattern of selectivity raises questions of how the ibis increases predation when this is necessary. Since the pattern of selectivity depends on the absolute and relative abundances of various potential prey and these abundances differ locally, prey selection depends less on choice of items than on choice of foraging patches.

Habitat selection. The movements of the White Ibis population in southern Florida over the course of a year suggest that these birds should be generalists in their choice of habitat. This idea is supported by the diversity of habitats used both before (Fig. 4) and during (Table 1) nesting. Actually, at

some time in the year ibises may be found foraging in almost any damp habitat shallow enough for wading or walking (Kushlan and Kushlan 1975).

The southern Florida ibises inhabit a seasonally fluctuating, and continually changing, patchy environment where they forage in a relatively coarse-grained manner, searching in certain areas, the locations of which change with time. Success and resultant total energy return relative to foraging effort provide a means by which habitats might appear to differ to ibis. Differences among habitats must be determined by individuals or flocks, testing patches by sampling, learning, and weighing effort against gain per habitat. Such behavior is like the concept of choice of foraging niches based on their relative foraging profitability (Royama 1970, Simons and Alcock 1971). For ibis, total energy value of food taken correlates with habitat selection. Patches are selected according to experience (returning to previously used patches), directional foraging (following birds to feeding grounds) and local enhancement (settling at patches where birds were already feeding) (Kushlan 1976c, 1977c). Local enhancement also brings about aggregations of mixed species at profitable patches. Flocking and group feeding increase the probability of spending hunting time in relatively beneficial habitats while decreasing search time between patches (Ward and Zehavi 1973, Krebs 1974, Kushlan 1977c). The importance of habitat choice explains the adaptive value of several features of the White Ibis such as white plumage, colonial nesting and flocking.

Choice of habitat is therefore probably the critical factor in foraging behavior of the White Ibis. Efficient foraging requires the ability to analyze net gain from a habitat. The ibis must choose habitats with catchable prey, their suitability being related to prey type and synergistic interactions of the availability of various prey types. Given the expense involved in sampling a habitat, especially the time and energy penalty of foraging in potentially unfavorable habitat and of searching between habitats, the ibis has evolved a strategy of feeding on types of prey that do not achieve high densities in localized patches but that can be effectively selected over a range of relatively low densities. Yet it has retained the flexibility to switch to more abundant, although less easily caught, prey when available and to undertake regional movements to use seasonally available habitat patches. This permits

use of a wide variety of foods and habitats, with more selective use of high value patches during periods of high energy demand. The result is a significant variation, both temporally and geographically, in the pattern of energy use.

SUMMARY

The American White Ibis is a tactile-foraging, flocking predator that occupies a seasonally fluctuating environment in southern Florida. The population makes extensive seasonal movements correlated with fluctuating water levels and changes in the availability of foraging habitat. Outside the nesting season, the ibis' diet and habitat selection are highly variable. During nesting, food selection differs between inland and coastal colonies, especially in the relative importance of crustaceans. Nesting ibis consume neither the most abundant nor the most energetically valuable prey. They forage in locations where relatively high energy is available but, unlike Wood Storks, not when or where most prey species reach their maximum seasonal concentrations. Some prey species are taken selectively in most habitats whereas other prey are under-represented in the diet, as demonstrated by the ibis' two most important prey, highly selected crayfish and under-selected fish. Ibis select prey passively before capture. Selectivity depends primarily on the ability of ibis to catch specific types of prey.

The relation between abundance and consumption differed among various prey. Consumption and abundance of crayfish were unrelated except when prey switching occurred in the presence of an extraordinarily high abundance of alternate prey, which may have competitively inhibited capture of crayfish. Thus, prey taken in any situation depended on the types available and on a synergistic relation among them.

Ibis increased efficiency of predation primarily by selection of foraging habitat. Colonial nesting, flocking, aggregative foraging, regional movement, variable colony site selection, dynamic nest timing, and variation in the size of the nesting population help adapt this species to its fluctuating environment.

ACKNOWLEDGMENTS

This study was conducted while I was at the University of Miami, Coral Gables, Florida and was sponsored by the Maytag Chair of Ornithology. I thank Oscar T. Owre for his support throughout the study. I also thank Carl E. Bock, M. Philip Kahl, Herbert W. Kale, II, Marilyn S. Kushlan, Oscar T. Owre, and William B. Robertson, Jr., for reviewing the manuscript.

LITERATURE CITED

- BEUKEMA, J. J. 1968. Predation by the three-spined stickleback (*Gasterosteus aculeatus* L.): The influence of hunger and experience. *Behaviour* 31:1-26.
- CHARNOV, E. L., G. H. ORIAN, AND K. HYATT. 1976. Ecological implications of resource depression. *Am. Nat.* 110:247-259.
- CURIO, E. 1976. The ethology of predation. Springer-Verlag, New York.
- DAWKINS, M. 1971. Perceptual changes in chicks: Another look at the 'search image' concept. *Anim. Behav.* 19:566-574.
- EMLEN, J. M. 1966. The role of time and energy in food preference. *Am. Nat.* 100:611-617.
- EMLEN, J. M., AND M. G. R. EMLEN. 1975. Optimal choice in diet: test of a hypothesis. *Am. Nat.* 109:427-435.
- GIBB, J. A. 1962. L. Tinbergen's hypothesis of the role of specific search images. *Ibis* 104:106-111.
- GOSS-CUSTARD, J. D. 1977. The energetics of prey selection by Redshank, *Tringa totanus* (L.), in relation to prey density. *J. Anim. Ecol.* 46:1-19.
- HOLLING, C. S. 1965. The functional responses of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45:1-60.
- HORN, H. S. 1966. Measurement of "overlap" in comparative ecological studies. *Am. Nat.* 100:419-424.
- IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven.
- KAUFMAN, D. W. 1974a. Differential predation of white and agouti *Mus musculus*. *Auk* 91:145-150.
- KAUFMAN, D. W. 1974b. Differential predation on active and inactive prey by owls. *Auk* 91:172-173.
- KREBS, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). *Behaviour* 51:99-134.
- KRUUK, H. 1972. The spotted hyena. Univ. Chicago Press, Chicago.
- KUSHLAN, J. A. 1974. Quantitative sampling of fish populations in shallow, freshwater environments. *Trans. Am. Fish. Soc.* 103:348-352.
- KUSHLAN, J. A. 1976a. Site selection for nesting colonies by the American White Ibis *Eudocimus albus* in Florida. *Ibis* 118:590-593.
- KUSHLAN, J. A. 1976b. Environmental stability and fish community diversity. *Ecology* 57:821-825.
- KUSHLAN, J. A. 1976c. Wading bird predation in a seasonally-fluctuating pond. *Auk* 93:464-476.
- KUSHLAN, J. A. 1977a. Population energetics of the White Ibis. *Auk* 94:114-122.
- KUSHLAN, J. A. 1977b. Foraging behavior of the White Ibis. *Wilson Bull.* 89:342-345.
- KUSHLAN, J. A. 1977c. The significance of plumage colour in the formation of feeding aggregations of ciconiiforms. *Ibis* 119:361-364.
- KUSHLAN, J. A. 1978a. Feeding ecology of wading birds, p. 249-296. In A. Sprunt, Jr., J. C. Ogden, and S. A. Winkler [eds.], *Wading birds*. National Audubon Society, New York.
- KUSHLAN, J. A. 1978b. Commensal foraging in the Little Blue Heron. *Auk* 95:677-681.
- KUSHLAN, J. A. 1978c. Nonrigorous foraging by robbing egrets. *Ecology* 59:649-653.
- KUSHLAN, J. A., AND M. S. KUSHLAN. 1975. Food of White Ibis in southern Florida. *Fla. Field Nat.* 3:31-38.
- KUSHLAN, J. A., AND D. A. WHITE. 1977. Nesting wading bird populations in southern Florida. *Fla. Sci.* 40:65-72.
- KUSHLAN, J. A., J. C. OGDEN, AND A. L. HIGER.

1975. Relation of water level and fish availability to Wood Stork reproduction in the southern Everglades, Florida. Open-File Rept., U.S. Geological Survey, Tallahassee, Florida.
- MACARTHUR, R. H. 1972. Geographical ecology. Harper and Row, New York.
- MACARTHUR, R. H., AND E. R. PIANKA. 1966. On optimal use of a patchy environment. *Am. Nat.* 100:603-609.
- MURDOCH, W. W. 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39:335-354.
- MURTON, R. K. 1971. The significance of specific search image in the feeding behavior of the Wood Pigeon. *Behaviour* 40:10-42.
- NICHOLS, J. D., W. CONLEY, B. BATT, AND A. R. TIPPON. 1976. Temporally dynamic reproductive strategies and the concept of *r*- and *k*-selection. *Am. Nat.* 110:995-1005.
- OGDEN, J. C., J. A. KUSHLAN, AND J. T. TILMANT. 1976. Prey selectivity by the Wood Stork. *Condor* 78:324-330.
- OGDEN, J. C., J. A. KUSHLAN, AND J. T. TILMANT. 1978. The food habits and nesting success of Wood Storks in Everglades National Park in 1974. U.S. Natl. Park Serv., Natl. Res. Rep. 16, Washington, D.C.
- POOLE, R. W. 1974. *Quantitative ecology*. McGraw-Hill, New York.
- ROBERTSON, W. B., JR., AND J. A. KUSHLAN. 1974. The southern Florida avifauna, p. 414-452. In P. J. Gleason [ed.], *Environments of south Florida: present and past*. Miami Geol. Soc., Miami, Fla.
- ROYAMA, T. 1970. Factors governing the hunting behavior and selection of food by the Great Tit (*Parus major* L.). *J. Anim. Ecol.* 39:619-667.
- SCHOENER, T. W. 1969. Models of optimal size for a solitary predator. *Am. Nat.* 103:272-313.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2:369-404.
- SIMONS, S., AND J. ALCOCK. 1971. Learning and the foraging persistence of White-crowned Sparrows *Zonotrichia leucophrys*. *Ibis* 113:477-482.
- SNYDER, R. L. 1975. Some prey preference factors for a Red-tailed Hawk. *Auk* 92:547-552.
- TINBERGEN, L. 1960. The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. *Arch. Neerl. Zool.* 13:265-343.
- WARD, P., AND A. ZAHAVI. 1973. The importance of certain assemblages of birds as "information-centers" for food-finding. *Ibis* 115:517-534.

South Florida Research Center, Everglades National Park, Homestead, FL 33030. Accepted for publication 23 January 1979.

Condor, 81:389
© The Cooper Ornithological Society 1979

RECENT PUBLICATIONS

The Birds of Paradise and Bower Birds.—William T. Cooper and Joseph M. Forshaw. 1979. David R. Godine, Boston. 304 p. Slipcase. \$150.00. The most gorgeous birds inspire books to match them. Here is a folio-size volume in the tradition of monographs by Elliot (1873) and Sharpe (1891-8). Planned as a companion to Gilliard's (1969) book, it offers color plates of every species, which that work lacked. Cooper's paintings are superb in every respect and they have been reproduced perfectly. Many of his field sketches accompany the text, illustrating details of posture or plumage. The text repeats some basic data from Gilliard but mostly presents information—published and unpublished—that has been gained since his time. Species accounts are organized as to description, distribution (with maps), subspecies, and general notes (status, habitat, food, calls, displays, nesting, and eggs). Although few ornithologists will be able to afford this volume, those who admire fine bird art as well as those who are studying these particular birds should endeavor to see it.

The Peregrine Falcon in Greenland/Observing an Endangered Species.—James T. Harris. 1979. University of Missouri Press, Columbia. 255 p. \$15.95. In this narrative of a summer's research in western Greenland, the author examines an endangered species from both scientific and humanistic perspectives. He interweaves three themes—the search for falcon eyries, the

history of one falcon family that was observed closely, and the development of his feelings toward the species and the individual birds. This personal account is backed by a thorough résumé of the wider status of the peregrine, including its peril from pesticides. The writing is accurate in dealing with science, vivid in telling the story, and eloquent in conveying the author's feelings. This book is not just for falcon enthusiasts but for anyone concerned about the interactions between mankind and wildlife. Photographs, list of references, index.

Voices of some Galápagos Birds.—Recorded, narrated, and produced by John William Hardy. Tape cassette, ARA-4. Available: Holbrook Travel Agency, 3520 NW 13th St., Gainesville, FL 32601 and ARA Records, 1615 NW 14th Ave., Gainesville, FL 32605. "This recording is designed to acquaint the visitor [to the Galápagos Islands] with the most commonly heard songs and calls encountered in one of the formally-conducted tour sessions of a week or so. Birds of the shores and lowlands are thus emphasized." Fourteen species, including eight Darwin Finches, are presented in cuts of generous length and very good quality. Several of the finches have been recorded at more than one place in order to show inter-island variation. Hardy's narration is informative. The cassette should be helpful in learning identification of birds before a trip and in evoking memories afterward.