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Wetland Feeding Site Use by White Ibises (*Eudocimus albus*)[1] Breeding in Coastal South Carolina

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Abstract.—We monitored the activity of radiotagged adult White Ibises (*Eudocimus albus*) breeding at a coastal colony site on Pumpkinseed Island, Georgetown County, SC, during 3 breeding seasons. A total of 11 nesting adults (4 each in 1987 and 1988, and 3 in 1989) wearing backpack radiotelemetry units were monitored from the ground and from fixed-wing aircraft. Ibises caring for prefledged young concentrated their foraging efforts in swamps, abandoned rice fields, impoundments, and ponds (15 such sites were used totaling 76% of all observations of radiotagged ibises), ranging from 4 to 32 km from the colony site. Saltmarshes 2 to 5 km from the colony site were visited less often by parental ibises (4 such sites were used by 4 ibises, totaling 25% of all observations). Adult ibises fed primarily crayfishes and fishes to their prefledged young. After their young fledged, or their nests failed, ibises ceased visits to abandoned rice fields, decreased visits to freshwater swamps, and doubled their relative use of saltmarsh feeding habitat.

The estimated cost of traveling to freshwater feeding sites could be 1.5 to 13.5 times greater than that of traveling to the saltmarsh feeding sites. The use of non-saltmarsh habitats during chick rearing suggests that the prey available at saltmarsh sites, primarily fiddler crabs (*Uca* spp.), are a less preferred prey for prefledgling ibises. *Received 22 July 1996, accepted 22 September 1996, revision received 7 April 1997.*

Key words.—*Eudocimus albus*, feeding ecology, foraging costs, habitat use, prey selection, *Procambarus* spp., radiotelemetry, *Uca* spp., wetlands, White Ibis.

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White Ibises (*Eudocimus albus*) breed in freshwater and brackish-water wetlands in the southeastern United States (Kushlan and Bildstein 1992). The feeding ecology of ibises at a large, traditional colony site on Pumpkinseed Island in Winyah Bay, South Carolina has been studied in detail since the late 1970s (Bildstein 1983, Petit and Bildstein 1986, Bildstein *et al.* 1990, De Santo 1992, Bildstein 1993). In general, ibises at this site feed in nearby saltmarshes more frequently after their young have fledged than they do earlier in the season, when many adults fly inland to freshwater feeding sites (Bildstein *et al.* 1990). These observations are consistent with regurgitation samples collected from nestling ibises, which contain mostly crayfishes (*Procambarus* spp.) (Bildstein *et al.* 1990, De Santo 1992). Fiddler crabs (*Uca* spp.), which adult ibises readily catch in the region's saltmarshes (Bildstein 1987), are rarely fed to the young except during drought

years, or late in the breeding season when crayfishes are less available (Bildstein *et al.* 1990, De Santo 1992). Fiddler crabs have a higher salt content (1,080 mOsm kg^{-1}, 30 ppt NaCl) than do crayfishes (535 mOsm kg^{-1}, 12 ppt NaCl) (Johnston and Bildstein 1990). High osmolarity diets, like those containing fiddler crabs, depress growth rates and increase mortality of both captive and wild prefledged young (Johnston and Bildstein 1990, De Santo 1992).

To date, investigations of the feeding ecology of coastally breeding White Ibises have been conducted at the population level (Kushlan 1979, Bildstein 1983, Petit and Bildstein 1986). Relatively little is known about the habitat use of individual birds. In an attempt to determine if feeding habitat use of individuals is indeed influenced by their stage of breeding (i.e., caring for young) as studies of populations have indicated, we monitored the habitat use of radiotelemetered White Ibises during the breeding season.

Here we (1) present information on habitat use of radiotelemetered adult White Ibises during and after caring for young; (2) determine the distances parental ibises traveled to feeding sites; and (3) use these data to quantify and compare the relative costs associated with foraging in freshwater wetlands and nearby saltmarshes.

Figure 1. Feeding sites used during chick rearing by radiotagged White Ibises captured on Pumpkinseed Island, South Carolina, 1987-1989. (See Table 3 for abbreviations and site information; saltmarshes are stippled.) Map also shows the Pumpkinseed Island breeding colony site in Georgetown County, and the coastal plain area of South Carolina in which radiotelemetry searches of radiotagged White Ibises were conducted in 1987-1989 (designated by the polygon).

METHODS

Study Site

The study was conducted in May-August 1987, June-September 1988, and May-September 1989, in the coastal plain surrounding the North Inlet Estuary Long-term Ecological Research site on Hobcaw Barony, 6 km southeast of the city of Georgetown, SC (33°16'N, 79°12'W; Fig. 1). Ibises in the area breed on Pumpkinseed Island, a 9-ha, low-lying marsh island in Mud Bay, a shallow northeastern extension of Winyah Bay (Frederick 1985). Thousands of White Ibises, together with smaller numbers of at least 8 other species of wading birds (Ciconiiformes) have bred at this traditional colony site since at least the late 1960s (Bildstein *et al.* 1990, Bildstein 1993). For a more detailed description of the colony site see Christy *et al.* (1981) and Bildstein *et al.* (1982).

Two river systems enter the Atlantic Ocean near the colony site. The confluence of the Waccamaw, Pee Dee, Black, and Sampit rivers drains into Winyah Bay and enters the ocean 10 km south of the colony site. The North and South Santee rivers drain into the ocean 20 km southwest of the colony site (Fig. 1). Beginning in the late 1800s, many of the region's coastal plain freshwater marshes were diked and used for tidal rice cultivation (Gresham and Hook 1982). Since the abandonment of rice cultivation in the late 19th century, many relict rice fields reverted to natural marshes, while the dikes of others have been repaired, and the impounded waters are managed for aquaculture (including crayfish farming) and waterfowl (Wharton *et al.* 1982).

Numerous natural freshwater swamps are found in the region's coastal plain (Wharton *et al.* 1982), and within the large watersheds of the major river systems (Barry 1980, Wharton et al. 1982).

Radiotagging

In each year of the study, 3 to 4 breeding White Ibises (i.e., those tending nests containing at least 1 nestling [1-8 days old] were captured using self-tripping traps at nests; see Frederick 1986 for description of trap). The ages of young were estimated from growth measurements and plumage development of known age nestlings measured in nearby nests (see De Santo *et al.* 1990). Nests selected for capture attempts were located throughout the colony such that disturbance was not concentrated in any 1 area. Aside from containing young, the nests were haphazardly chosen. Captured adults were transported to the periphery of the island where their gender was determined based on sexually dimorphic features (cf. Kushlan and Bildstein 1992), and radiotagged.

Each bird was telemetered either with a 15-g solar-powered transmitter (Male 1 and Female 1) (donated by the Savannah River Ecology Laboratory, Aiken, South Carolina; manufacturer unknown; measuring 40 mm long × 15 mm wide × 13 mm thick, and with a 27-cm long antenna); or with a 23-g battery-powered transmitter (Males 2-3 and Females 2-8) (Telonics, Telemetry-Electronics Consultants, Mesa, Arizona; Model 070; measuring 30 mm long × 28 mm wide × 12 mm thick, and with a 42-cm long, multi-stranded, stainless steel, teflon-coated antenna). The signal life of the battery-powered units was estimated at 60-75 days. The signal life of 6 transmitters worn by ibises who remained in the area until the end of the breeding season ranged from 69 to 99 days.

Telemetry units were attached to the birds using a 7-g backpack harness constructed of teflon ribbon. A piece of rubber innertubing (50-mm long × 40-mm wide) was attached to the bottom of the transmitter to reduce irritation to the bird and to prevent the feathers from covering the plate on the solar transmitters. The combined mass of the harness and transmitter ranged from 2 to 4% of the mass of the bird (female body mass ranged from 700 to 840 g; male body mass 950 to 1,100 g). A detailed description of radiotransmitter attachment can be found in De Santo (1992).

Prior to their use in the field, backpack harnesses and transmitters were tested on several captive ibises maintained in aviaries at the Savannah River Ecology Laboratory. Captive radiotagged ibises accepted the harnesses and behaved and flew short distances normally.

Each telemetered bird received a U.S. Fish and Wildlife Service aluminum leg band, and in 1988 and 1989, an orange patagial tag (Safety Flag Manufacturing Company, Pawtucket, Rhode Island). Harnessing and banding typically took under 20 min.

Nesting Activity and Habitat Use

Nine transmittered birds were monitored from the ground between 50 and 162 h each (Table 1). The transmitter attached to Female 5 worked intermittently during the study, and the transmitter attached to Male 3 was removed 2 days after attachment due to harness failure. Birds were monitored with a hand-held Yagi H-antenna and a TR-2 Receiver (Telonics, Telemetry-Electronics Consultants, Mesa, Arizona) at the Pumpkinseed Island colony site 15 min to 15 h a day on 11 to 47 days. In 1987, readings were taken from a 3-m tower near the northern end of Pumpkinseed Island, and in 1988 and 1989, they were taken from an additional portable 2-m tower near the southern end of the island. Readings were also taken from an 18.5-m tower on the saltmarsh 5 km north of the colony site. Upland areas elsewhere within Hobcaw Barony were monitored from a truck, and saltmarshes near the colony site were monitored from a boat. Readings were taken from fixed-wing aircraft fitted with Yagi antennae secured with brackets to the underside of each wing strut. One to 2.5-h surveys, 9 in 1987, and 19 each in 1988 and 1989, were conducted during daylight hours (0800-1900) between mid-June and early September (Table 1). Between 70 and 100% of the flights occurred during morning hours (0800-1200) in each of the 3 years. Coverage included land areas within a 45-km radius of the breeding colony site (Fig. 1).

Searches typically followed a similar route: from Georgetown airport to the breeding colony site, across

Table 1. Sampling effort and number of days in contact with radiotagged adult White Ibises captured on Pumpkinseed Island, South Carolina, 1987-1989.

Bird	Ground monitoring		Aerial monitoring		No. days in contact (% days)[2]
	Sampling period	Hours (days)[1]	Sampling period	Hours (no. flights)[1]	
1987					
Male 1	23 May-27 August	50 (24)	19 June	1 (1)	10 (42)
Female 1	23 May-20 June	50 (24)	19 June	1 (1)	10 (42)
Female 2	26 May-27 August	91 (37)	19 June-27 August	14 (9)	28 (67)
Female 3	9 June-24 June	30 (11)	19 June-27 August	2 (3)	7 (54)
1988					
Male 2	18 June-24 September	158 (47)	22 June-25 August	22 (19)	50 (100)
Female 4	9 June-25 August	162 (44)	22 June-25 August	22 (19)	43 (81)
Female 5	11 June-25 August[3]	109 (31)	22 June-25 August	22 (19)	34 (83)
Female 6	18 June-25 August	154 (40)	22 June-25 August	22 (19)	48 (100)
1989					
Male 3	21 June-23 June[4]	5 (3)	20 June	1 (1)	3 (100)
Female 7	18 June-7 July	54 (19)	20 June-7 July	10 (6)	10 (53)
Female 8	18 June-7 September	88 (32)	20 June-7 September	27 (19)	32 (74)

[1]Represents total sampling effort or hours of search until contact with bird was lost.

[2]Includes contact during ground and aerial monitoring. Flights and ground monitoring overlap.

[3]Transmitter inoperable 12-27 June.

[4]Bird was injured on 23 June and removed from field.

Hobcaw Barony, up the Waccamaw and Pee Dee rivers, down the Black River, across to the Sampit River and Santee River Delta. Signals were detected up to 5 km from the observation towers and up to 10 km from the aircraft. Maps showing feeding sites were drawn from U.S. Geological Survey topographical maps (1:24,000 scale).

The breeding activity of radiotagged adults was monitored whenever possible. Five nests within 75 m of an observation tower were observed visually, and 5 others were checked by walking into the colony every 4 or 5 days. By 15 days of age, ibis young become ambulatory and form creches of juveniles; at this time they spend little time at the nest and are difficult to locate (De Santo *et al.* 1990). Beyond this age, much of our information about breeding status was inferred from activity of radiotagged adults.

We collected feces or regurgitant from the nestlings of 4 radiotagged adults (2 each in 1988 and 1989), which we analyzed for taxonomic composition (see De Santo 1992 for methods).

RESULTS

Reactions to Radioharnesses

Eight ibises (Males 1 and 3, Females 1, 2, 4, 5, 6, and 8) returned to their nests within 30 min after attachment of their transmitters, and remained there for 1.5-5 h. Three ibises (Male 2, Females 3 and 7) left the colony site immediately, but returned to their nests by the next nest check (12-48 h later).

Male 3 returned to its nest following attachment of the harness, but was observed the following day in a swamp entangled in his harness. This individual was removed from the field and transported to the Savannah River Ecology Laboratory for recuperation, where it died 6 days later.

Nest Attendance and Nesting Success

The nests of 2 adults (Females 3 and 7) failed, and these ibises were not located at the colony site thereafter, nor were they found within our search area 7 to 12 days following nest failure (Table 2). Five adults (Females 2, 4, 5, and 6, and Male 2) continued to return to the colony site until their young reached fledging age (43-59 days old), and remained in the area 21-57 days beyond their last known visit to the colony site when their young were 72 to 103 days old (Table 2). Male 1 and Female 1 stopped returning to the colony site prior to the time that their young would have fledged, and were not located within the search area 8 or 9 days after their last known visit to the colony site, a behavior consistent with that of the 2 ibises known to have abandoned their nests (Females 3 and 7). Female 8 also stopped re-

Table 2. Date of last known visit to the breeding colony site, and radio contact within a 45-km radius of the breeding colony site by radiotagged White Ibises captured on Pumpkinseed Island, South Carolina in 1987-1989, and the age of their young at the time of these observations.

	Last located at colony site		Last located in search area	
Bird	Date	Age (days) of young	Date	Age (days) of young
1987				
Male 1	10 June	25	19 June	—[1]
Female 1	11 June	22	19 June	—[1]
Female 2	16 July	55	27 August	98
Female 3	12 June	2	24 June	—[1]
1988				
Male 2	29 July	46	24 September	103
Female 4	5 August	59	25 August	80
Female 5	18 July	44	25 August	83
Female 6	26 July	43	25 August	72
1989				
Female 7	30 June	17	7 July	—[1]
Female 8	11 July	28	7 September	85

[1]Nests of Females 3 and 7 failed. Nests of Male 1 and Female 1 are presumed to have failed based on behavioral observations (i.e., adults did not return to colony prior to fledging age of their young).

turning to the colony site prior to fledging age of her young, but remained in the search area for an additional 25 days.

We were able to observe Male 1, and Females 1, 2, and 8 at their nests. These adults brooded and fed young at their nests with unmarked adults (probably their mates). Both members of the radiotagged breeding pair (Female 7 and Male 3) were observed brooding and feeding their young. We were able to document the duration of nest attendance and absence for 7 radiotagged adults. These adults spent from 15 to 255 consecutive min tending young at the nest ($\bar{X} \pm SE = 61 \pm 11$ min; N = 25), and they were absent from the colony site for 15 to 480 consecutive min ($\bar{X} \pm SE = 136 \pm 29$ min, N = 22).

One female (Female 7) continued to brood her young for at least 9 days after losing her mate (Male 3) (see reactions to radioharnesses), and was last detected within our search area 15 days later.

Feeding Site Use During and After Chick Rearing

A summary of feeding sites used by radiotagged ibises is presented in Table 3. Telemetered ibises were located on an average of 66% (SE = 11) of our aerial searches.

Ibises caring for young visited a variety of wetlands including 3 abandoned rice fields, 6 freshwater swamps, 4 impoundments, 2 ponds, and 4 saltmarshes ranging from 2 to 32 km from the colony site (Table 3, Fig. 1).

Table 3. Type, direction and distance from breeding colony site, and period of use of feeding sites of radiotagged adult White Ibises captured on Pumpkinseed Island, South Carolina, 1987-1989. Feeding sites are shown on Figs. 1 and 2.

	Period of use			
Feeding site	Chick rearing	Postchick rearing	Both	Distance (km), direction from colony
Abandoned rice fields				
ARF-1	X			21, WSW
ARF-2	X			29, NNE
ARF-3	X			4, NW
Freshwater swamps				
FWS-1	X			32, W
FWS-2	X			4, NNW
FWS-3		X		9, WNW
FWS-4	X			5, N
FWS-5	X			10, SSW
FWS-6	X			5, N
FWS-7	X			22, W
Impoundments				
IMP-1		X		14, SW
IMP-2			X	5, SW
IMP-3	X			10, SSW
IMP-4	X			20, SSW
IMP-5	X			13, SW
Ponds				
P-1			X	5, N
P-2	X			29, SW
Saltmarshes				
SM-1			X	2, NE
SM-2			X	2, NNE
SM-3		X		7, NNE
SM-4			X	5, N
SM-5			X	5, NE

Table 4. Composition of fecal and regurgitant samples collected from the young of radiotelemetered White Ibises, Pumpkinseed Island, South Carolina, 1988-1989.

Nest (sample type)	Date collected	Age of young (days)	Known feeding habitats used during chick rearing	Composition of regurgitant
Male 2				
(regurgitant)	22 June 1988	15	Pond, saltmarsh	70% bony fish, 30% aquatic Hemipteran
Female 5				
(regurgitant)	17 June 1988	14	Unknown	98% bony fish, 1% crayfish, 1% aquatic Hemipteran
Female 7				
(fecal)	21 June 1989	8	Freshwater swamp	100% crayfish exoskeleton
Female 8				
(regurgitant)	28 June 1989	15	Impoundment, abandoned rice field	100% crayfish
(regurgitant)	6 July 1989	23		100% crayfish
(fecal)	18 June 1989	5		100% crayfish exoskeleton
(fecal)	21 June 1989	8		100% crayfish exoskeleton

Regurgitant and fecal samples collected from the young of radiotelemetered birds consisted of bony fish, crayfish, and insects, but not fiddler crabs (Table 4). Although 5 parental ibises fed on saltmarshes, these birds were known to return to the colony site from saltmarsh visits on only 10% of their 40 visits.

Foraging habitat use differed between the chick rearing and post chick rearing stages (χ^2_1 = 121.5, P = 0.001). Following chick rearing, ibises continued to visit several non-saltmarsh wetlands (2 impoundments, 1 freshwater swamp, and 1 pond) up to 14 km from the breeding colony site (Table 3, Fig. 2) but with less frequency than during chick rearing. At this time, saltmarshes (5 sites) were used by all but 1 of the 7 ibises. One ibis visited saltmarshes only after chick rearing. Overall, after their young had fledged, use of saltmarshes doubled, while the use of freshwater swamps and abandoned rice fields decreased to nearly 0% (Fig. 3). By comparison, during chick rearing, 76% of the observations of foraging ibises were in wetlands other than saltmarshes (abandoned rice fields, freshwater swamps, impoundments, and ponds; Fig. 3).

Ibises fed closer to the colony site following the chick-rearing period than during chick rearing (6 vs. 12 km, respectively; t_{26}=2.276, P=0.03; Fig. 4). The farthest feeding site visited after chick rearing was less than half the distance to the colony site as the farthest site used during chick rearing (14 vs. 32 km, respectively; Fig. 4).

Feeding-site Fidelity

While caring for young, 10 of the 11 ibises we monitored visited ≤3 feeding sites. One female (Female 4), however, used at least 12

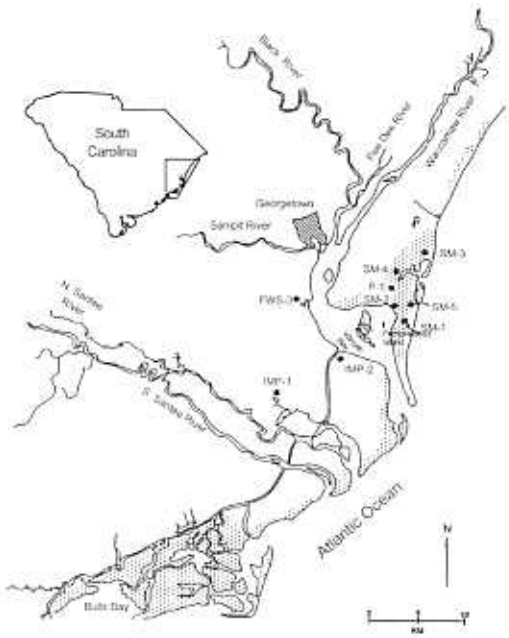

Figure 2. Feeding sites used following chick rearing by radiotagged White Ibises captured on Pumpkinseed Island, South Carolina, 1987-1989. (See Table 3 for abbreviations and site information; saltmarshes are stippled.)

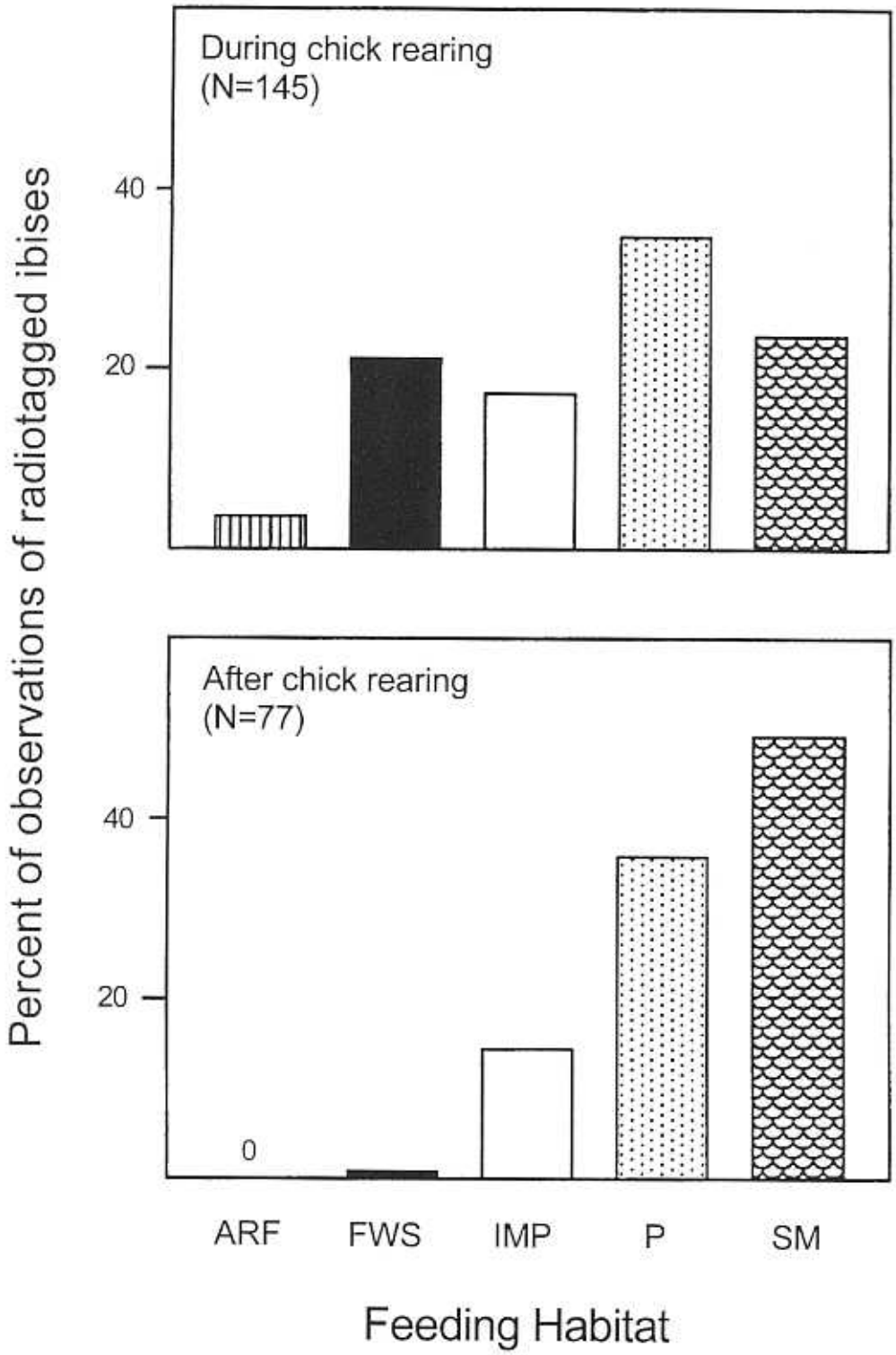

Figure 3. Type of feeding habitat (ARF = abandoned rice field, FWS = freshwater swamp, IMP = impoundment, P = pond, and SM = saltmarsh) used (given as a percent of total observations) during chick rearing and following chick rearing by radiotagged White Ibises captured on Pumpkinseed Island, South Carolina, 1987-1989.

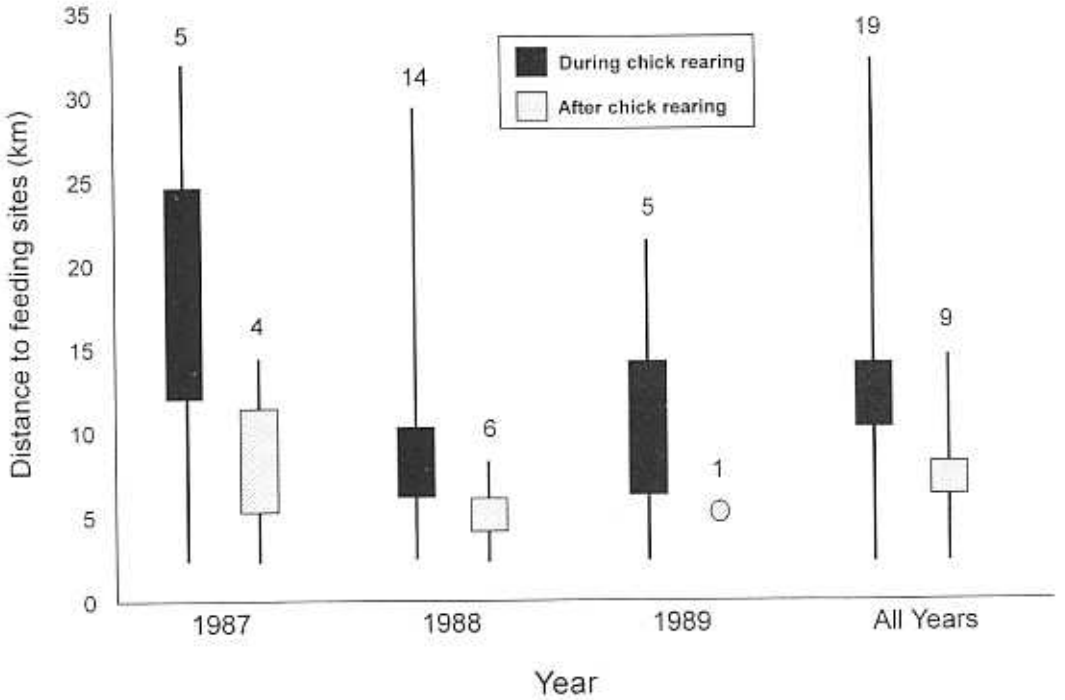

Figure 4. Distance to feeding sites during and after chick rearing used by parental White Ibises radiotagged on Pumpkinseed Island, South Carolina, 1987-1989. Histograms represent ± 1 SE of the mean; bars above and below represent ranges; number of feeding sites is shown above histograms. Only one site was located in 1988 after chick rearing and its distance is shown as a circle.

feeding sites. Following chick rearing, the 7 ibises we continued to monitor used up to at least 4 sites. In some cases (Females 4, 6 and 8), ibises were found to use the same sites following chick rearing that they had used during chick rearing, others (Female 5 and Male 2) visited both new and old sites, and others (Females 2 and 3) visited only new sites.

DISCUSSION

The distance to feeding sites used by ibises in the current study (2-32 km; Fig. 4) are comparable to those reported by Bateman (1970: 2-19 km), Frederick and Collopy (1989: 2-33 km), and Kushlan (1976: < 1-44 km), but are longer than those reported by Custer and Osborn (1978: 1-6.7 km).

Most birds showed site fidelity and used at least 2 to 4 sites throughout the period of observation (see also Bateman 1970). In 1988, however, 1 individual visited 12 sites. Ibises may have had difficulty finding suitable foraging sites and prey in 1988. A brackish-water (approximately 250 mOsm kg^{-1}) pond (P-1) near the colony site that contained fishes (including *Fundulus heteroclitus* and *Gambusia affinis*) but not crayfishes (De Santo, unpubl. data) was heavily used by foraging ibises in 1988 but not in 1987 or 1989. We found that the nestling diet in 1988 contained significantly more fish and fewer crayfish than in 1987 or 1989, and we also noted lower survival and depressed growth of nestlings raised in 1988 as compared to those raised in 1987 and 1989 (De Santo 1992). These observations indicate that feeding conditions were poorer (i.e., lack of crayfishes) during 1988.

While caring for prefledged young, radiotagged ibises used both saltmarshes and non-saltmarsh wetlands (Table 3, Fig. 3), but they concentrated feeding efforts in non-saltmarsh wetlands perhaps to obtain prey other than fiddler crabs to feed to their young. Regurgitant and fecal samples collected from the young of radiotagged adults contained fishes, crayfishes, and insects, but

not fiddler crabs (Table 4). These results are consistent with our population level food-habit studies conducted concurrently with this study which indicated that nestlings are most often fed crayfishes, and occasionally fishes and insects (De Santo 1992). Fiddler crabs, which have a high salt content (Johnston and Bildstein 1990, De Santo 1992) are rarely fed to nestling ibises (Bildstein *et al.* 1990, De Santo 1992). When the nestling diet does contain fiddler crabs, nestlings experience depressed growth and increased mortality (De Santo 1992) presumably because of the high salt content of these prey (Johnston and Bildstein 1990).

Following nest failure or the fledging of their young, adult ibises doubled their use of saltmarshes and decreased their use of non-saltmarsh wetlands such as abandoned rice fields and freshwater swamps (Fig. 3). The frequency of use of impoundments and ponds was relatively unchanged. Once their young fledged or following nest failure, when adults are no longer constrained by the dietary needs and physiological capabilities of their young, they may switch to feeding at nearby saltmarshes where fiddler crabs are readily abundant.

The greater use of habitats other than saltmarshes during chick rearing, and the more frequent use of saltmarsh feeding sites following chick rearing (Fig. 3) are consistent with previous studies conducted at the site (Bildstein *et al.* 1990). When birds were rearing young, large numbers of adults flew toward freshwater feeding sites along the Waccamaw, Pee Dee, and Black rivers. Coincidental with fledging of young at the colony site, there was an increase in the numbers of adult ibises feeding on a saltmarsh directly north of Pumpkinseed Island (SM-4 on Fig. 2) and a decline in the numbers flying to inland sites.

This study demonstrates that individual parental White Ibises concentrate their foraging effort in freshwater swamps and impoundments at considerable distance from the breeding colony site. Considering the greater travel time required to reach feeding sites, it is more costly energetically to feed in freshwater swamps than in nearby saltmarshes. For example, it could take a 900-g ibis flying 47 kph approximately 60% longer (4.5 vs. 2.8 min) and could require 60% more energy (3,470 vs. 2,178 J) to travel to the nearest crayfish feeding site (3.5 km) than it would to travel to the nearest saltmarsh (2.2 km) (cf. Pennycuick and De Santo 1989). Many of the freshwater feeding sites used by the birds in this study were located much further away (up to 32 km from the colony site). The cost of foraging and the time required to travel to these sites could be as much as 13 times greater than that expended to reach the nearest saltmarsh (31,680 J; 40.5 min). Adult ibises are more efficient at assimilating energy from crayfishes than from fiddler crabs (79 vs. 66% assimilation, respectively; De Santo 1992). It is possible that by foraging on crayfishes, adults are able to meet the nutritional demands of their young as well as offset some of the energetic costs they incur during the long flights to crayfish feeding sites.

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