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FRESHWATER WETLANDS, RAINFALL, AND THE BREEDING ECOLOGY OF WHITE IBISES IN COASTAL SOUTH CAROLINA

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ABSTRACT.—The numbers of White Ibises (*Eudocimus albus*) nesting on Drum Island in the Cooper River and on Pumpkinseed Island in Winyah Bay, the two largest wading bird colonies along the South Carolina coast, declined from over 12,000 pairs at each site in a very wet year (1984) to less than 2000 pairs at each site in 1985, one of the driest springs on record. The following year, when the area around Pumpkinseed Island received slightly above average rainfall, but the area around Drum Island received slightly below average rainfall, the number of pairs breeding at Pumpkinseed increased to 5132, while the number of pairs at Drum decreased to 388. On Drum Island, the percent of ibis eggs that resulted in fledgings declined from 39% in 1984 to 3% in 1985. Other more piscivorous wading birds breeding on Drum Island did not exhibit similar declines in numbers or in reproductive success in 1985. On Pumpkinseed Island a substantially lower proportion of ibises flew inland to feed on crayfishes in freshwater wetlands in 1985 and 1986 than in 1984. At both sites, nestling diets contained a lower proportion of crayfish in 1985 than in 1984, and many more nestlings starved or were abandoned by their parents in 1985, and to a lesser extent in 1986, than in 1984.

We suggest that declines in both the numbers of nesting ibises and in reproductive success at the two sites resulted from the relative unavailability of crayfishes during dry periods. At Drum Island, mortality associated with food stress was exacerbated by Fish Crow (*Corvus ossifragus*) predation on eggs and young. Although alternative prey such as fiddler crabs are consumed by adult ibises, the osmotic concentration of these prey results in unacceptable salt loading in developing nestlings. White Ibises breeding in salt marshes along the South Carolina coast appear to depend heavily upon freshwater wetlands as a source of food for their nestlings. *Received 8 Nov. 1988, accepted 10 March 1989.*

White Ibises (*Eudocimus albus*) are long-legged, tactilely foraging wading birds (Kushlan 1978) that feed mainly on crustaceans, aquatic insects, and fishes (Nesbitt et al. 1974, Kushlan and Kushlan 1975). Although White Ibises were first reported breeding in South Carolina only in 1922 (Wayne 1922), the number of ibises along the South Carolina coast has long been linked with rainfall (Catesby 1731–43). More recently, researchers have suggested that reproductive effort in White Ibises, as well as in at least 10 other species of ibises (Threskiornithidae) (Table 1), is affected

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TABLE 1

SPECIES OF IBISES IN WHICH REPRODUCTIVE EFFORT IS REPORTED TO BE AFFECTED BY SEASONAL VARIATION IN RAINFALL AND SUBSEQUENT CHANGES IN FOOD AVAILABILITY

Species	Source
Sacred Ibis (*Threskiornis aethiopica*)	(Urban 1974)
Australian White Ibis (*T. molucca*)	(Carrick 1962)
Straw-necked Ibis (*T. spinicollis*)	(Carrick 1962, Waterman et al. 1971)
Waldrapp (*Geronticus eremita*)	(Robin 1973)
Bald Ibis (*G. calvus*)	(Manry 1985a)
Green Ibis (*Mesembinibis cayennensis*)	(Thomas 1979, Luthin 1983)
Whispering Ibis (*Phimosus infuscatus*)	(Thomas 1979, Luthin 1983)
White Ibis (*Eudocimus albus*)	(Dusi and Dusi 1968; Kushlan 1976, 1979; Ogden et al. 1980)
Scarlet Ibis (*E. ruber*)	(ffrench and Haverschmidt 1970, Thomas 1979, Luthin 1983)
Glossy Ibis (*Plegadis falcinellus*)	(Carrick 1962)
White-faced Ibis (*P. chihi*)	(Ryder 1967)

by variation in seasonal rainfall because of subsequent changes in the availability of prey. Here we: (1) compare the feeding ecology and reproductive success of White Ibises at the two largest coastal colonies in South Carolina during wet and dry years, (2) describe a causal link between rainfall and ibis reproductive success, and (3) discuss the importance of freshwater wetlands and crayfishes in the breeding ecology of this species.

METHODS

Study areas.—Coastal South Carolina, which experiences a mild maritime climate, receives an average of 110–130 cm of rain annually. The driest season, which typically occurs in October–November, is followed by increasing rainfall that peaks in March, and by a second wet period from June through early September (Barry 1980).

We studied White Ibises in coastal South Carolina during the breeding seasons of 1978–1986 on Pumpkinseed Island in Winyah Bay near Georgetown, South Carolina (K.L.B., J.J., P.F.); and during the breeding seasons of 1984–1986 on Drum Island, in the Cooper River, Charleston, South Carolina (W.P.) (Fig. 1). The two sites, which are 85 km apart, together with a single, recently established, large colony in coastal North Carolina 140 km to the northeast of Pumpkinseed Island (Shields and Parnell 1986), represent the three northernmost large colonies (>1000 pairs) of the Atlantic Coast population of White Ibises (Osborn and Custer 1978).

Pumpkinseed Island is a 9-ha marsh island in Winyah Bay. The island, which is regularly inundated by high tides, is vegetated with a dense stand of mostly black needle rush (*Juncus roemerianus*), along with some big cord grass (*Spartina cynosuroides*) and smooth cord grass (*S. alterniflora*) in low-lying areas. A narrow strip of marsh elder (*Iva frutescens*) occurs along the northeastern edge of the island. Although a few ibises may nest in marsh elder along with Great Egrets (*Casmerodius albus*) and Black-crowned Night-Herons (*Nycticorax nycticorax*), most nest on matted-down clumps of black needle rush (Frederick 1985) along

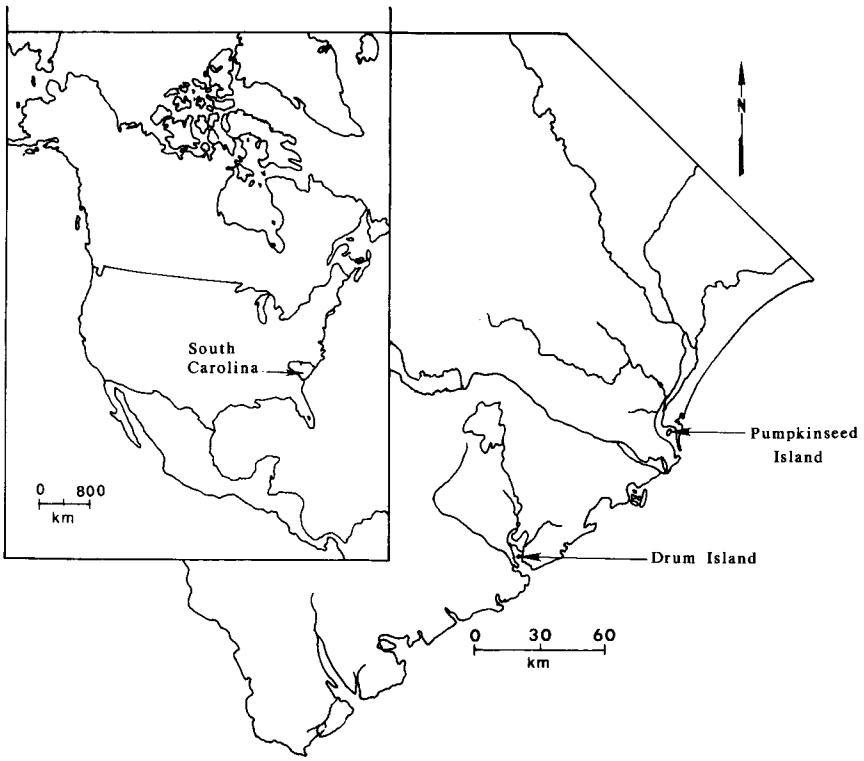

FIG. 1. Location of Pumpkinseed and Drum islands in coastal South Carolina.

with Glossy Ibises (*Plegadis falcinellus*), Little Blue Herons (*Egretta caerula*), and Tricolored Herons (*E. tricolor*). White Ibises have nested on Pumpkinseed Island at least since 1967 (Frederick, unpubl. data).

Drum Island is a 75-ha dredge-spoil island in the lower Cooper River within 3 km of downtown Charleston, South Carolina. The island is vegetated with white mulberry (*Morus alba*), hackberry (*Celtis* sp.), and groundsel (*Baccharis* spp.). Most ibis nests are in a 10-ha stand of mulberry at the southern end of the island among lesser numbers of nesting Great Egrets, Snowy Egrets (*E. thula*), Little Blue Herons, Tricolored Herons, Cattle Egrets (*Bubulcus ibis*), Green-backed Herons (*Butorides striatus*), Black-crowned Night-Herons, Yellow-crowned Night-Herons (*N. violaceus*), and Glossy Ibises. Ibises have nested on Drum Island since 1957 (The Charleston Museum, unpubl. data). Although White Ibises are usually the most numerous species of wading birds at both sites, at least seven other Ciconiiforms nest on Pumpkinseed Island (Bildstein et al. 1982), and at least nine other Ciconiiforms nest on Drum Island (Post, unpubl. data).

Population estimates and reproductive success.—We censused ibis nests on Pumpkinseed Island from fixed-wing aircraft flying at approximately 150 m during a series of counts timed to document peak numbers of nests and to assess the effects of extreme high tides on the survivorship of eggs and young nestlings (Frederick 1987). Flights were made on 5 June

1979, 12 May 1980, 28 April 1981, 5 May and 15 June 1982, 13 April 1983, 14 May 1984, 4 May 1985, and 8 May 1986. Comparisons of aerial counts with ground counts of marked quadrats indicate >95% accuracy of the aerial counts (De Coursey, pers. comm.)

We censused wading bird nests on Drum Island from the ground. In addition to counting nesting White Ibises, we also counted nesting Great Egrets, Snowy Egrets, Little Blue Herons, Tricolored Herons, Cattle Egrets, Green-backed Herons, Black-crowned Night-Herons, Yellow-crowned Night-Herons, and Glossy Ibises. In 1984 the census involved extrapolation from a 6-m × 395-m (0.237-ha) transect. In 1985 the census was based on 115 100-m^2 (1.2 ha total) randomly chosen plots. In 1986 the estimate was based on 110 100-m^2 plots (1.1 ha). To estimate nesting success of birds on Drum Island, we visited the site weekly and marked each active nest with a numbered flag. Flagged nests were considered successful when young reached the age at which they were able to climb into the canopy.

Nestling diet.—At Pumpkinseed Island we collected disgorged regurgitant, by throat massage when necessary, from 8- to 24-day-old nestlings in late June–early July 1984, late May and late June–early July 1985, and late May and mid–July 1986. We immediately estimated the percent by volume of fiddler crabs (*Uca* spp.), crayfish (*Procambarus* spp.), fish, insects, and other invertebrate prey in each sample. On Drum Island regurgitant was fixed in 10% formalin in the field and then transferred to 70% ethanol for later analysis.

Foraging ecology.—Numbers of ibises feeding on fiddler crabs on the Bly Creek Drainage (cf. Bildstein 1983), a portion of the North Inlet salt marsh approximately 6 km from Pumpkinseed Island, were recorded during dawn-to-dusk observations collected over 7- to 10-day intervals during May–August 1984 (N = 15), March–July 1985 (N = 11), and March–August 1986 (N = 15). Concurrently, the numbers of ibises flying over the same salt marsh enroute to more distant freshwater swamps 10–40 km from the colony site (determined by following several flocks in a fixed-wing aircraft) were counted from dawn-to-dusk during "composite days" over the same 7- to 10-day intervals. (Each composite day consisted of a series of 2–4-h nonoverlapping watches conducted during all times between dawn and dusk over the course of a 7- to 10-day period.)

Rainfall.—Monthly rainfall data from North Charleston (15 km from Drum Island) for July 1983 through June 1986, and from Georgetown (13 km from Pumpkinseed Island) for July 1978 through June 1986 were compared with monthly, 30-year means collected at the two sites (U.S.D.C. 1974–1986). Variation in the amount of winter–spring rainfall at Georgetown, where it has been studied in some detail, is positively correlated with the degree of flooding in bottomland forest swamps used by foraging ibises nesting at nearby Pumpkinseed Island (E. Blood pers. comm.). This same relationship between rainfall and flooding appears to hold for the area around the Drum Island colony site.

RESULTS

Nesting populations.—The numbers of White Ibises nesting on Pumpkinseed Island were relatively constant during the first four years of the study, when between 6000 and 8000 pairs bred on the island. The number of nesting pairs increased in 1983 and again in 1984, when almost 13,000 pairs bred on the island, before decreasing in 1985 by 85% to less than 2000 pairs. The decline in the number of nesting birds occurred despite the fact that the numbers of ibises returning to the area in late March and early April were similar in 1984 and 1985. In 1986 more than 5000 pairs again bred on the island (Table 2). Similarly, although over 13,000 pairs of ibises bred on Drum Island in 1984, the number of birds nesting on

TABLE 2

NUMBERS OF WHITE IBISES NESTING ON PUMPKINSEED ISLAND NEAR GEORGETOWN, SOUTH CAROLINA, 1979–1986, AND ON DRUM ISLAND NEAR CHARLESTON, SOUTH CAROLINA, 1984–1986

	Numbers of breeding pairs							
	1979	1980	1981	1982	1983	1984	1985	1986
Pumpkinseed Island	7933	6669[a]	7887	7814	10,035	12,973	1976	5132
Drum Island	NC[b]	NC	NC	NC	NC	13,763	949	388

[a] Pumpkinseed Island colony sizes for 1980–1984 are from Frederick 1987.
[b] No count.

the island decreased in 1985 by 95% to fewer than 1000 pairs. A further decline to 388 pairs occurred in 1986 (Table 2). The numbers of herons and egrets that were recorded nesting on Drum Island in 1984 and 1985 failed to show a similar catastrophic decline (Table 3).

Reproductive success.—On Pumpkinseed Island, where White Ibises nested near the ground in black needle rush, mortality during the egg stage usually resulted from tidal inundations (Frederick 1987). In 1984, for example, an estimated 42% of the nests were flooded by high tides during the egg and early nestling stages on 16–17 May (Frederick 1987). In 1985 50% of the nests were lost during the egg stage to high tides on 5 May. Similarly, exceptionally high tides between 18 and 24 May 1986 caused the death of 16 of 30 3–15-day-old young whose growth we were monitoring. In 1984 avian predation, probably by Fish Crows, accounted for the loss of 8% (N = 468) of ibis eggs (Frederick 1987). Although nestling losses to avian predators were not studied in detail on Pumpkinseed Island, Black-crowned Night-Herons were seen taking small nestlings in

TABLE 3

NUMBERS OF OTHER SPECIES OF HERONS AND EGRETS NESTING ON DRUM ISLAND 1984–1985

Species	Numbers of breeding pairs		% deviation from 1984
	1984	1985	
Small white herons[a]	2209	1628	−26%
Great Egret	797	779	−2%
Tricolored Heron	720	934	+30%
Black-crowned Night-Heron	683	524	−30%
All species combined	4409	3865	−12%

[a] Small white herons include Little Blue Herons, Cattle Egrets, and Snowy Egrets.

TABLE 4
REPRODUCTIVE SUCCESS OF HERONS AND EGRETS BREEDING ON DRUM ISLAND 1984–1985

	Percent of eggs producing fledglings[a]				
	1984		1985		% change from 1984
	N	%	N	%	
Great Egret	20 (7)[b]	80%	99 (42)	57%	−29%
Tricolored Heron	54 (18)	44%	149 (50)	60%	+36%
Black-crowned Night-Heron	35 (12)	40%	100 (34)	40%	0%
White Ibis	390 (158)	39%	347 (166)	3%	−92%

[a] Young that were capable of climbing out of nests. (Great Egret nestlings were able to do this at 26 days-of-age, Tricolored Herons at 24 days-of-age, and White Ibises and Black-crowned Night-Herons at 21 days-of-age.)
[b] Number of eggs (number of nests).

1984, 1985, and 1986. The extent of this predation is unknown, but observations indicated that it was limited to very small young (Frederick 1985, see also Rudegeair 1975), and that it was not substantial (i.e., <10%). Starved, desiccated, and seemingly abandoned nestlings up to 30 days old were quite common in 1985, especially in June and July among late nesters. Although a few starved young were seen in 1986, again mainly among late nesters, none were seen in 1984.

On Drum Island, where ibises nested in white mulberry and thus were not subject to tidal inundation, egg predation by Fish Crows was the only significant source of egg mortality. In 1985 and 1986 68% and 96%, respectively, of egg losses were attributed to predators. As was the case on Pumpkinseed Island, dozens of starved, desiccated ibises were seen on Drum Island in 1985, but not in 1984. As a result of the combined effects of avian predation and apparent adult abandonment, 39% of 390 eggs monitored in 1984, but only 3% of 347 eggs monitored in 1985 produced fledged young. There were no similar declines in the reproductive success of herons and egrets breeding on the island (Table 4).

Adult foraging behavior.—At Pumpkinseed Island the peak number of ibises flying inland to feed in freshwater swamps was higher in 1984 than in either 1985 or 1986 (Fig. 2). In 1984 large numbers of adult ibises continued flying to and from freshwater swamps through June and into July. In 1985 the numbers of ibises flying inland to freshwater swamps declined sharply in early May; and in 1986 the decline occurred in late May (Fig. 2). In all three years, declines in the numbers of birds flying inland were accompanied by simultaneous increases in the numbers of birds feeding in a salt marsh 6 km north of the colony site (Fig. 2).

Nestling diets.—On Pumpkinseed Island, although nestlings were still being fed large numbers of freshwater crayfishes in late June–early July

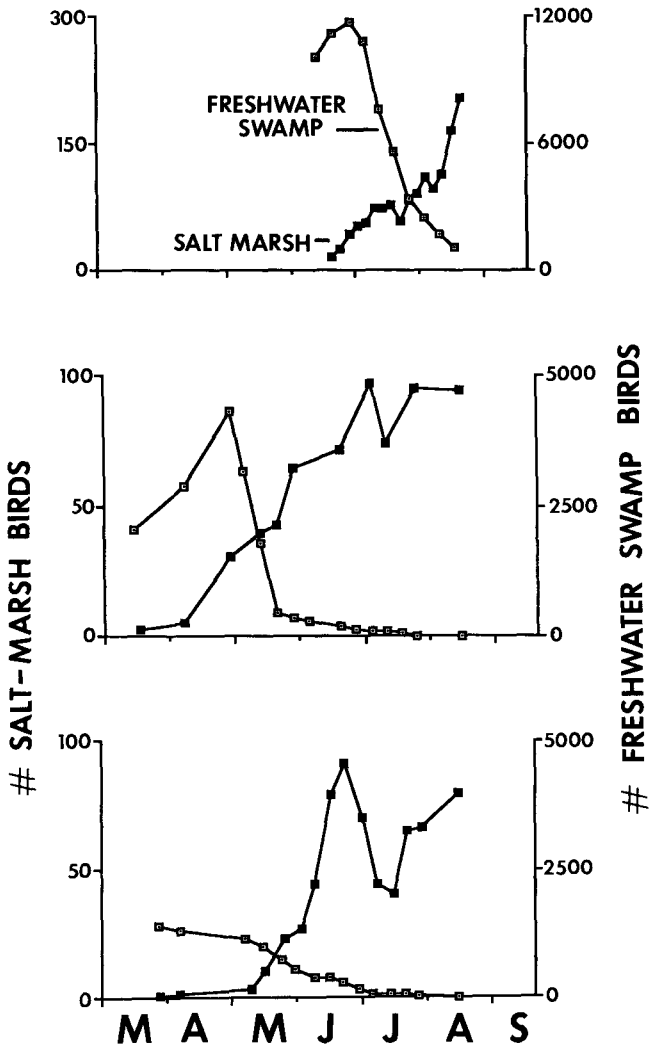

FIG. 2. Three-week running means of the numbers of adult ibises seen: (1) flying inland to feed in distant freshwater swamps, and (2) feeding on a nearby saltwater marsh. Freshwater swamp counts represent the total number of adult ibises seen on composite days of observations collected weekly between March and August. (See Methods section for definition of composite day.) Salt-marsh counts are based on the mean number of adult ibises seen feeding on the 65-ha salt-marsh site during single days of dawn-to-dusk hourly counts.

TABLE 5

PERCENT BY VOLUME OF PREY IN REGURGITANT TAKEN FROM 8- TO 24-DAY-OLD WHITE IBIS NESTLINGS ON PUMPKINSEED ISLAND IN 1984, 1985, AND 1986

		1985		1986	
	1984 (N = 28)	Early (N = 23)	Late (N = 32)	Early (N = 35)	Late (N = 36)
Collection dates	28 June–3 July	23–29 May	12 June–6 July	11–26 May	13–20 July
Prey					
Crayfish	85	39	1	81	0
Fiddler crabs	2	44	82	8	20
Fishes	5	7	11	5	45
Insects	5	6	3	1	17
Other invertebrates	3	6	2	6	18

1984, crayfishes were not a significant portion of the diet late in the breeding season in either 1985 or 1986 (Table 5). In 1985 ibises switched from feeding crayfishes to their nestlings to feeding mainly fiddler crabs. In 1986 ibises switched from crayfishes to fishes, and, to a lesser extent, to fiddler crabs and insects (Table 5). On Drum Island, in 1985 crayfishes made up only 20%, by number, of the diet (N = 22). The majority of the diet was grass shrimp (*Palaemonetes* sp.) and mud crabs (*Sesarma* sp.), both of which are found in brackish water.

Rainfall.—Total rainfall during the six months preceding the start of hatching (approximated as 1 May) at both sites was substantially above the 30-year mean in 1984, and substantially below the mean in 1985. In 1986 rainfall during the same period near Pumpkinseed Island was slightly above the 30-year mean, whereas near Drum Island it was slightly below the mean (Table 6). Regression analysis of rainfall and colony size at Pumpkinseed Island during the 8-year period from 1978 to 1986 revealed: (1) that more ibises nested in wet years than in dry years, and (2) that variation in rainfall during the 6-month period preceding hatching explained 71% of the annual variation in the maximum number of ibises nesting at the site ($P < 0.05$) (Fig. 3).

DISCUSSION

Although the proximate reasons differ among species, rainfall ultimately affects the breeding biology of a number of species of ibis (Table 1). Manry (1982, 1985a, b) has linked declines in the numbers of breeding Bald Ibises (scientific names are in Table 1) in southern Africa to reduced

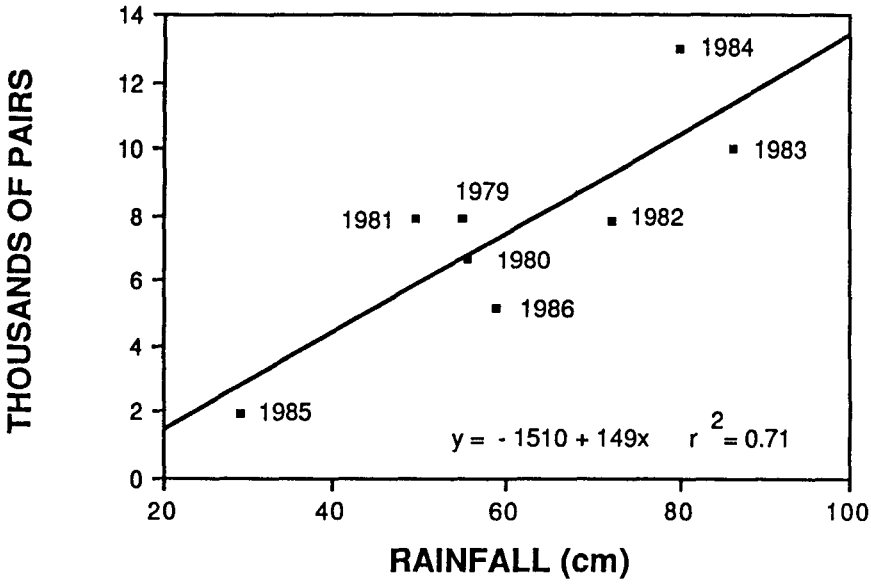

FIG. 3. Linear regression analysis depicting the relationship between the numbers of pairs of ibises breeding on Pumpkinseed Island and the amount of rainfall at Georgetown, South Carolina, during the six-month period (November–April) preceding the initiation of hatching at the colony site. (The relationship is significant at $P < 0.05$.)

grazing and grassland burning during drought years which, in turn, reduced the availability of essential insect prey. Individuals that did breed during dry years laid smaller clutches and were more likely to desert their nests and allow their chicks to starve (Manry 1985a). Similar reductions in the numbers of Waldrapps breeding in Morocco have been reported by Robin (1973). In Ethiopia and South Africa, Sacred Ibises breed only after the onset of the rainy season. However, it is not clear whether they do so in response to increased food availability, or because of reduced predation pressure (Urban 1974, Clark and Clark 1979). In Australia, Straw-necked, Australian White, and Glossy ibises are nomadic breeders that restrict their reproductive attempts to sites experiencing heavy flooding rains (Carrick 1962, Waterman et al. 1971, Woodall 1985), presumably because of their dependence on aquatic food sources (Carrick 1959). In western North America, White-faced Ibises shift breeding locations in response to rainfall patterns and often fail to nest in drought years (Ryder 1967). Luthin (1983) reports a similar response in Whispering, Green, and Scarlet ibises to flooding rains in the llanos of Venezuela. Scarlet

TABLE 6

PERCENT DEVIATION FROM 30-YEAR MEAN IN RAINFALL AT GEORGETOWN AND CHARLESTON, SOUTH CAROLINA, DURING THE 6- AND 12-MONTH PERIODS PRECEDING THE 1984–1986 HATCHING PERIODS FOR WHITE IBISES

Breeding season	Number of months preceding the initiation of hatching[a]	Percent deviation in rainfall from 30-year mean[b]	
		Georgetown	Charleston
1984	6	+62	+48
	12	+4	−5
1985	6	−41	−56
	12	−10	−38
1986	6	+20	−13
	12	+14	+4

[a] The initiation of hatching is approximated as 1 May in each of the three years.
[b] Data are from the U.S. Department of Commerce weather stations at Georgetown and Charleston, South Carolina.

Ibises also restrict their breeding to rainy periods in Surinam and Trinidad (Snow and Snow 1964, ffrench and Haverschmidt 1970).

For White Ibises, Kushlan (1976) reports a similar response to rainfall for populations in South Florida, where the number of breeding birds was 35 times greater in a wet year than it had been in the previous drought year. Because most White Ibises breeding in Florida feed near water, usually along the edges of flooded areas to a depth of about 25 cm, Kushlan (1979) attributed the dramatic shift in the numbers of breeding birds to the lack of a sufficient receding line of shallow aquatic habitat during the drought. That the only successful breeders during the drought were in the smaller coastal colonies in tidally inundated areas supports this notion. Similar reports of White Ibises feeding along the receding or advancing edges of flooded pastures (Bateman 1970), clearcuts (Stinner 1983), and rice fields used as breeding sites for crayfishes (Martin and Hamilton 1985) strengthen the argument that water depth is extremely important to White Ibises feeding in aquatic habitats. Our data indicate that the same situation holds for White Ibises breeding in coastal South Carolina. During each breeding season we saw large numbers of ibises flying long distances (in some instances 40 km one-way) inland to secure crayfishes from flooded bottomland hardwood forests (Fig. 2), where crayfishes tend to concentrate along the rising and falling water's edge in spring during periods of inundation of this habitat (cf. Pollard et al. 1982). In drought years, such as 1985 and 1986, when there is little or no inundation of these bottomland flood-plains, the little shallow aquatic habitat available dries out earlier

in the season, and crayfishes burrow into the substrate (cf. Pollard et al. 1982) and are no longer readily available to ibises (cf. Audubon 1840–1844). In response to this loss of a prey base, those ibises that do breed during the drought must turn to alternative sources of food, including fishes, fiddler crabs, insects, and other invertebrates (Table 5).

White Ibises are primarily tactile foragers in aquatic habitats (Kushlan 1977), and their probing behavior in such situations is apparently "effective for catching crayfishes but not fish," except in unusual circumstances (Kushlan 1979). With the exception of fiddler crabs, other invertebrates apparently are not available in densities sufficient to support large numbers of breeding ibises. Although fiddler crabs are readily abundant near both of the coastal colonies we studied, and although they are taken by some ibises throughout the breeding season (Bildstein 1983, 1984), they do not appear to be used heavily by parental ibises as food for their nestlings as long as crayfish are available (Table 5, Fig. 2). Indeed, our data together with those collected by researchers in Florida (Ogden et al. 1980, Kushlan 1979) indicate that unless crayfish comprise the bulk of the nestling's diet, large numbers of ibises will not breed successfully, even in areas with an abundance of fiddler crabs. Although in coastal South Carolina crayfishes have a substantially higher caloric content than do fiddler crabs (4.1 kcal/g versus 2.3 kcal/g; see also Kushlan 1979, Shanholtzer 1973), the latter are more readily available closer to both colony sites, and they are caught by the few ibises that do feed upon them during the nestling period at rates that should permit parental ibises to meet the caloric requirements of their developing young (cf. Bildstein 1987). Yet in spite of the availability of fiddler crabs within 5–10 km of both sites, most individuals breeding at Pumpkinseed Island—where flight paths to feeding areas were followed closely in 1984, 1985, and 1986 (Fig. 2)—flew up to 40 km inland to feed on crayfishes, as long as this prey was available each season. (See Pennycuick and De Santo [1989] for estimates of flight speeds and energetic costs incurred during such flights.)

Fiddler crabs are osmotic conformers, and because they inhabit salt marshes, are saltier than are freshwater crayfishes (800–1100 mOSM versus 500–600 mOSM). Salt glands are prominent features above the orbits of 10–12-day-old white ibis embryos, and nestling ibises possess functional salt glands at least by the time they are 20 days old. However, captive-reared 20- to 25-day-old nestlings fed a diet of either fiddler crabs or crayfishes spiked to the osmotic concentration of fiddler crabs survived and developed only if fresh water was available as a supplement to these salty diets (Johnston and Bildstein 1990). As fresh water is not normally available to nestlings at either colony site, and as there is no indication that adults bring fresh water to the young, fiddler crabs do not appear to

be physiologically available as a food source for nestling ibises. Recently fledged, free-flying juveniles, as well as adult ibises, readily consume fiddler crabs in coastal South Carolina (Wayne 1922, Bildstein 1983), apparently because they are able to secure the necessary fresh water needed to dilute the osmotic concentration of their prey.

During the especially dry breeding season of 1985 (Table 6), the relative amount of crayfish prey in the diet of nestling ibises declined early in the season (Table 5), presumably as a result of the earlier drying-out of inland bottomland hardwood forest flood-plains. In that year, many of the adult ibises that returned to both Drum Island and Pumpkinseed Island in March did not breed (Table 2) and, at least at Pumpkinseed Island, those that did breed fed their nestlings fiddler crabs (Table 5). Nestlings from which we recovered predominantly fiddler crab prey were usually lethargic, and several were moribund. Parental care at both colonies seemed to wane, perhaps as a result of this type of nestling behavior, and at both colonies parent ibises abandoned large numbers of young in 1985. At Pumpkinseed Island these young, many of which were ambulatory, wandered from the vicinity of their nests before they were capable of feeding on their own and then starved. At Drum Island, many recently abandoned young were preyed upon by Fish Crows (Table 4) whose populations were quite high, apparently as a result of the recent establishment of a nearby garbage dump. Dusi and Dusi (1968), reporting a similar drought-related increase in Fish Crow predation at a wading bird colony in Alabama, also attributed the increased predation to the abandonment of nestlings by adults unable to secure sufficient prey for their young. In 1986 when spring rainfall was near normal at Pumpkinseed Island, but still somewhat below normal at Drum Island (Table 6), the numbers of breeding ibises rebounded at Pumpkinseed Island but continued to decline at Drum Island (Table 2). Nestlings at Pumpkinseed Island fared better in 1986 than in 1985. In both years, parent ibises switched from crayfishes to alternative prey during the nestling season (Table 5), but in 1986 alternative prey included a greater amount of osmotically benign items such as fishes (Table 5). Similarly, we suggest that a relatively greater dependence upon fish prey (Post unpubl. data) enabled most other species of wading birds nesting at Drum Island to breed successfully in 1985 (Table 4).

Even in coastal areas, where White Ibis populations typically are more stable than they are inland (Kushlan 1976), rainfall—by inducing shifts in prey availability—has a dramatic effect on the breeding success of the species. During droughts in coastal South Carolina, ibises nesting in tidal areas respond to low rainfall not because of drought-induced fluctuations in prey availability in the immediate vicinity of the nest but because low

rainfall reduces the availability of essential freshwater prey in more distant inland bottomland swamps.

In Trinidad, where Scarlet Ibises roost and sometimes nest in coastal mangrove swamps, nonbreeding individuals typically feed on brackish-water prey such as crabs and polychaete worms (ffrench and Haverschmidt 1970, Bildstein unpubl. data). During the breeding season, however, parent ibises fly inland from their coastal colony sites to collect freshwater prey for their young (ffrench and Haverschmidt 1970). These observations, together with the possibility that Scarlet and White ibises may be color morphs of the same species (Ramo and Busto 1987), suggest that Scarlet Ibises too are physiologically constrained in their choice of prey for developing young. Wildlife managers and conservationists interested in maintaining populations, as well as in reversing recent declines in the numbers of Scarlet Ibises should consider acquiring sufficient acreage of inland wetlands, as well as coastal habitat, to support this species.

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