

*Eudocimus albus*SPANISH:
Corocoro blanco, Coco blanco,
*Ibis blanco, Coclito blanco*FRENCH:
Bec croche, L'Ibis blanc,
Petit flaman (Louisiana)

White Ibis

The White Ibis is a striking, white bird with a long, thin, distinctively decurved bill. It usually nests, feeds, and flies in large conspecific flocks, and in many ways epitomizes the freshwater and coastal wetlands of the southeastern United States. Historically one of the most abundant of North American wading birds, it still maintains large regional populations with a few nesting colonies of 20,000–30,000 pairs.

This is a bird of freshwater and estuarine wetlands—typically cypress swamps, bottomland hardwood and mangrove swamps, as well as freshwater marshes and salt marshes. It is also a nomadic species, which changes roost and colony sites frequently and often migrates or disperses substantial distances. Its feeding and nesting appear to be limited by the changing availability of shallow water feeding sites and of its main prey, crustaceans. Because of salt

The Birds of North America

Life Histories for the 21st Century

ruber) of South America is closely related and is considered by some to be a conspecific color phase.

stress, nestlings do not develop normally on brackish water prey, so nearby freshwater feeding sites are essential for successful breeding at coastal colonies.

No subspecies are recognized, but the Scarlet Ibis (*Eudocimus*



Figure 1.
Normal breeding and nonbreeding
range of the White Ibis.

DISTINGUISHING CHARACTERISTICS

Medium-size wading bird with dark wingtips. Total length: 56–68 cm; weight 750–1,050 g. Relatively long bill, neck, and legs. Bill pink and strongly decurved, longer in males than females. Feet moderately sized with slightly webbed toes, the longest with a cupped nail. Face and legs bare and pink, or flesh colored to red, depending on season. Eyes light blue in adults. Tail relatively short. Juveniles mostly brown; distinguished from dark *Plegadis* ibises by white rump and underparts. Youngest stages of White Ibis and Scarlet Ibis virtually identical until the latter begins to develop pink tinges on rump and elsewhere.

DISTRIBUTION

AOU CHECK-LIST REGION

Breeding range. Primarily coastal from Virginia through Louisiana, and inland from S. Carolina through Florida (Fig. 1). Along both coasts of Mexico, including Baja California, Central America from Belize to Nicaragua, along the Pacific but not Caribbean coast of Costa Rica, and Panama. Extension of breeding range north of Georgia occurred mainly in this century (Wayne 1922, Sprunt 1944, Stephens 1950, Frohring and Beck 1978).

Winterrange. Normally coastal Carolinas south over rest of breeding range and intervening areas. Normal nonbreeding range is wider because of postbreeding dispersals (Fig. 1).

RANGE OUTSIDE AOU CHECK-LIST REGION

Resident and apparently nests in Cuba, Hispaniola, and Jamaica (Hancock, Kushlan, and Kahl 1992). Nests in small numbers in coastal Bolívar and Magdalena, Colombia, in inland Colombia, and in coastal and inland Venezuela. Occurs rarely as far east as the Guianas.

Through n. and e. South America, Scarlet Ibis predominates. However, scarlet birds often documented in the range of the white birds and almost certainly were natural visitors to Florida historically (Simpson 1988). Some scarlets introduced into Florida in the 1950s, others have escaped from captivity more recently. Today, individual scarlet birds nest in the wild in Florida, including Florida Bay (1 May 1980, Kushlan and Frohring unpubl. data). Pink hybrid individuals also nest in the wild in Florida and occur occasionally as far north as coastal S. Carolina (Belser 1989).

SYSTEMATICS

GEOGRAPHIC VARIATION AND SUBSPECIES

Variation poorly understood in this species; species limits in doubt. More information needed on quantitative geographic variation in such characteristics as size and plumage/soft part color to resolve these issues.

White Ibis, *sensu strictu*, appears similar throughout its northern (North American) range. Inherent nomadism of individuals and periodic shifts of populations suggest genetically based geographic variation unlikely in this range. Possible cline of decreasing size from North through Central America and into South America (C. Luthin pers. comm., Wieringen and Brouwer 1990), but data needed from intermediate populations. White birds in South America noticeably smaller than those from North America.

SUBSPECIES; RELATED SPECIES

Relationship of White Ibis of North America and Scarlet Ibis of South America controversial. Ridgway (1884) considered them one species, but more often treated as two. Hancock, Kushlan, and Kahl (1992), who reviewed the controversy and evidence, considered the two forms a single species. Decision based in part on the lack of reproductive isolation between white and scarlet birds in captivity, among feral animals introduced to the range of the other form, and in the wild in South America. Size and color differences do exist between North and South American birds of either color, so the taxonomic allocation of populations of *Eudocimus* ibises in North, Central, and South America remains a matter for intensive study.

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

A highly nomadic species undertaking postbreeding dispersals, migrations, prebreeding intraregional population shifts, and regular rainfall-initiated shifts between interior wetlands and coastal habitats (Kushlan 1976a, 1979a, 1981; Kushlan et al. 1985).

Normal nonbreeding range is from Virginia through the coastal plain of the se. U.S. and along the coast through the rest of the breeding range including the Greater Antilles (Fig. 1). Postbreeding dispersals often take individuals outside this nonbreeding range. Birds, especially juveniles, occur north as far as New York and Vermont, through Midwest North America into Quebec, Illinois, Missouri, N. and S. Dakota, Wyoming, Colorado, s. California, also in some instances in

the Bahamas, Caymans, Puerto Rico, Curaçao, and Trinidad.

Dispersing northern birds begin migration by drifting southward into Georgia, Florida, along Gulf of Mexico to Mexico, also to Cuba. Wintering birds from North America thought not to move as far as Central America, but one bird banded as a nestling in coastal S. Carolina was recovered in Colombia (Post et al. 1985).

TIMING AND ROUTES OF MIGRATION

Migration and dispersal during the North American spring and fall (Fig. 2); quite protracted in fall. No trans-Gulf migration recorded (Stevenson 1957). Although spring migration also protracted, S. Carolina birds return to breeding sites in large numbers over a period of a few days. Much more information needed on migration and wintering sites of specific population segments.

CONTROL AND PHYSIOLOGY OF MIGRATION

No information.

FOSSIL HISTORY

Two indeterminate species of *Eudocimus* reported from Pliocene of N. Carolina and Florida (Wetmore 1956, Olson 1985). *E. peruvians* described from the Pleistocene of Peru (Campbell 1979), but differentiation from modern form is questioned (Olson 1981).

HABITAT

BREEDING RANGE

Nests on barrier, marsh, and spoil islands on the coast, and on islands in lakes inland. Also in gallery forest and in stands of trees within marshes and mangrove swamps. Nest sites are in interior and coastal wetlands, including those within the southeastern mixed forest, outer coastal plain forest, savanna, prairie parkland, and prairie bushland ecoregions of the United States (Bailey 1978). Historically, the largest populations foraged in interior freshwater marshes and swamps of the Everglades.

Most nesting birds forage in inland wetlands, even when breeding on coastal islands, owing to nestlings' need to maintain salt balance (Bildstein et al. 1990, Johnston and Bildstein 1990). Inland feeding habitat mainly shallow seasonal sedge marshes and shallow cypress swamps, as well as lawns, pastures, and shallow ponds. Coastal feeding habitat salt marsh in the north and lagoonal salines and mangrove swamp in the south (Custer and Osborn 1978, Kushlan 1979a, Henderson 1981, Bildstein 1983).

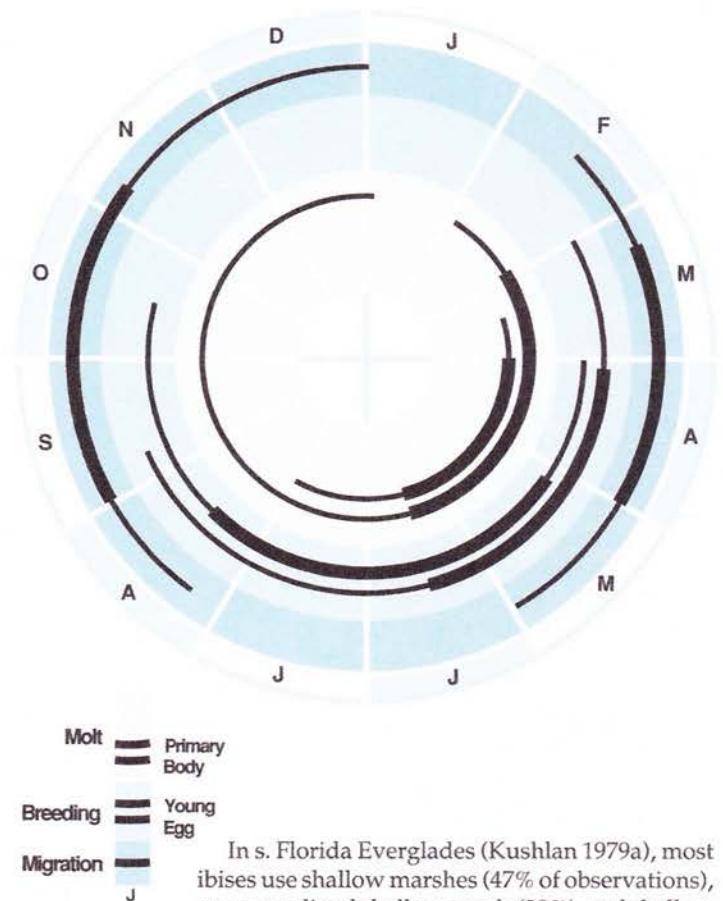


Figure 2. Annual cycle of the White Ibis in se. U.S. The extended molt period refers primarily to prolonged molt of the head feathers. Thick lines equal peak activity, thin lines off peak activity.

In s. Florida Everglades (Kushlan 1979a), most ibises use shallow marshes (47% of observations), sawgrass-lined shallow ponds (29%), and shallow ponds surrounded by willow trees (15%). In coastal areas, ibises use mangrove-lined streams and ponds (61%), sparsely vegetated marshes called marl prairies (19%), and tidal mangrove swamp (14%). In central Florida, they use flooded pastures (56%), isolated marshes (22%), and marshes at the edges of lakes (19%). In N. Carolina, ibises use coastal habitats, 85% in *Spartina* marsh, 11% in tidal creeks (Custer and Osborn 1978). In the Okefenokee Swamp, GA, ibises use wet prairies, blackgum forest, and clear-cuts (Stinner 1983); in Louisiana, commercial crayfish ponds, especially those being drained (Martin and Hamilton 1985).

Generalized microhabitat requirements are broad, as the birds feed in nearly any shallow water or on land in soft substrate or ground vegetation such as lawns and exposed salt marsh. Take prey from the surface of the ground, buried in soil, or within rooted and floating aquatic plants. Also probe in damp mud, especially for crayfish or crab burrows, from which they extract prey. Typically feed in water less than 20 cm deep, generally in 5–10 cm. Use wide range of feeding opportunities, provided prey are available, water levels sufficiently shallow, and substrate soft enough for probing.

In coastal S. Carolina, feeding ibises shift from bottomland cypress swamp and old ricefields managed for waterfowl to salt marshes as their nestlings begin to fledge in early summer (Wayne 1910, Bildstein et al. 1990). In salt marshes, they use high marsh areas dominated by the short form of salt-marsh cord grass; less so areas along creekbanks dominated by the tall form of cord grass (Henderson 1981).

SPRING AND FALL MIGRATION

Shift toward coastal areas outside of the breeding season, depending primarily on local water conditions and hence prey availability inland.

WINTER RANGE

Predominantly coastal, especially in and near mangrove swamps.

FOOD HABITS

FEEDING

Main foods taken. Aquatic crustaceans and insects.

Food capture and consumption. Long, decurved bill, long legs, and neck facilitate foraging while wading in shallow water and probing for prey items beneath the surface (Kushlan 1977b). Eyes situated to focus below head on bill tip. Most foraging, especially when in standing water or soft mud, is tactile, without use of eyes. Bill tips appear to be well innervated, and contact with prey probably elicits a reflex closing action. (More information is desirable on this mechanism.) Even so, captive individuals whose bills have been broken off and reattached or replaced with a prosthesis are capable of feeding on live crustacean prey. Potential prey items seldom pursued, unless on land or in very shallow water.

Feed primarily by tactile probing, but can pick prey items from the surface of the ground or a plant; sweeps bill like spoonbill (Kushlan 1977b, 1978c, 1979b). In *Spartina* marshes, ibises alternate between tactile and visual foraging, both probing for fiddler crabs in burrows and chasing crabs encountered on the surface (Petit and Bildstein 1987). Usually probe while walking slowly, stopping periodically to concentrate probing under a plant or down a crayfish or crab burrow. Bill is inserted into water or substrate closed or with tips held 1–2 cm agape. Bill has slight gap in center, which permits tips to function tweezer-like in grabbing and holding a prey item. Details of the foraging techniques, such as probing, capture, walking, and turning rates, vary according to prey and food availability (Henderson 1981).

Piracy common in some areas, both among ibises and with foraging associates. Ibises are primary victims for other larger birds in aggregations (Kushlan 1978a). Intraspecific piracy occurs at colony sites with adults (mostly males) taking prey from adults (mostly females) regurgitating food to nestlings, as well as directly from nestlings. Ibises used by other species commensally, with visually foraging species following closely behind walking ibis, using it as a beater (Kushlan 1978b). In turn, ibises follow ungulates in flooded pastures in Venezuelan llanos.

Prey items swallowed with a quick forward thrust of head (Kushlan 1978c). Prey also worked toward gullet by closing bill tips, propelling prey backward into slight gap in bill. Hard prey items bitten in mandibles, thereby crushing snails and crustaceans, removing claws of crustaceans and heads of some insects prior to swallowing (Fig. 3). Mud often washed from prey, even if bird must walk to a water source several meters from the capture site. Large prey items often stabbed and bitten into smaller pieces, but handling time increases exponentially with prey size, and such prey are susceptible to piracy (Kushlan 1979a). Proficiency in handling prey improves with age (Henderson 1981).

Feeds in large aggregations and flies in cohesive flocks among feeding and roosting sites (Bildstein 1983, Petit and Bildstein 1986). Aggregations can exceed 5,000 birds in suitable habitat (Kushlan 1979a). White ibises recorded in 70% of wading-bird aggregations counted in s. Florida. Juveniles often flock separately or feed on the periphery of adult flocks, being less successful in foraging than adults even when they are one-year-old (Bildstein 1983, 1984), and taking 2 months to develop flock flying (Petit and Bildstein 1986). Adults on the peripheries of large flocks in salt marshes forage visually more than do birds on the interiors of flocks (Petit and Bildstein 1987). Feeding aggregations form by local enhancement, the attraction of birds to already feeding white-plumaged birds (Kushlan 1976b, 1977e). Individually marked birds return to same feeding site for at least several days. Feed primarily in morning and evening, except while nesting, spending other time resting near feeding site.

Being larger (see Table 1), males have higher overall energy costs (Bildstein 1987). Although free-ranging males and females feeding side-by-side on fiddler crabs had similar capture rates, suggesting that males need to forage longer than do females (Bildstein 1987), captive males were more successful than females at extracting fiddler crabs from artificial burrows that approached the length of females' bills (S. McDowell and K. Bildstein unpubl. data).

DIET

Major food items. Small aquatic and semi-aquatic organisms, especially crustaceans and aquatic insects. Also fish, especially when these occur in high densities. Specialize on crustaceans, especially freshwater crayfish (Cambaridae) and estuarine crabs (Ocypodidae; Nesbitt et al. 1975, Kushlan and Kushlan 1975, Kushlan 1979a, Bildstein 1983). Total diet is nevertheless exceptionally broad because of ability to pick up whatever items they touch with their bill.

Diet includes aquatic and terrestrial arthropods, polychaetes, snails, frogs, lizards, young snakes, and small fish. Outside the nesting season ibises are primarily coastal, most using mangrove swamps, *Spartina* marshes, and coastal lagoons, where they often specialize on fiddler crabs (*Uca*).

Prey is relatively small. In s. Florida fish and crustaceans average about 2 cm long (fish 2.0 cm [SE = 0.4, n = 341]; crustaceans 2.2 cm [0.6, 62]). In Louisiana crayfish (*Procambarus*) averaged 4.2 cm (2.2, 94) (Martin 1985). Capable of taking considerably larger prey. In Trinidad, for example, Scarlet Ibises take polychaetes (*Nereis*) up to 17 cm long; and in Venezuela white and red forms take 4 cm aquatic insects, 5 cm blue crabs (*Callinectes sapidus*), and 4–6 cm fish. Captive individuals take crayfish in excess of 10 cm.

Quantitative analysis. Diet in s. Florida (Kushlan and Kushlan 1975): inland, crayfish (*Procambarus alleni*) 52% of biomass and 82% frequency, fish 19% biomass, insects 15%; in coastal habitats, crayfish 11% of biomass, fiddler crabs 20%, fish 31%, insects 10%. In n. Florida (Nesbitt et al. 1975): freshwater, crayfish 45% by volume and 70% frequency, insects 37% of volume; salt water, crayfish 46% of volume, 70% frequency, insects 24% of volume, crabs (*Uca*) 5%. In Orange Lake, FL (Baynard 1912): 352 cutworms, 308 grasshoppers, 602 crayfish, and 42 small snakes in 50 regurgitations from young. In coastal Louisiana (Hammatt 1981): mud crabs (*Panopeus herbstii*) 89% by volume and fish 11%, in 16 regurgitations from young. In coastal S. Carolina near Charleston (Post et al. 1985): fish 4% by number, estuarine crabs 63%, crayfish 20%, insects 10% in 22 regurgitations from young. In coastal S. Carolina near Georgetown (Bildstein et al. 1990): mainly crayfish early in the breeding season (39–85%), but less so later, depending upon rainfall. In a S. Carolina *Spartina* marsh, *Uca pugnax* and *U. pugilator* comprised over 95% of the prey taken (Henderson 1981, Bildstein 1983).

NUTRITION

Basal metabolic rate of adult, 81 to 88 kcal/d (Benedict and Fox 1927). Existence metabolism, 113.8 kcal/d and 0.12 kcal/g/d; aviary existence

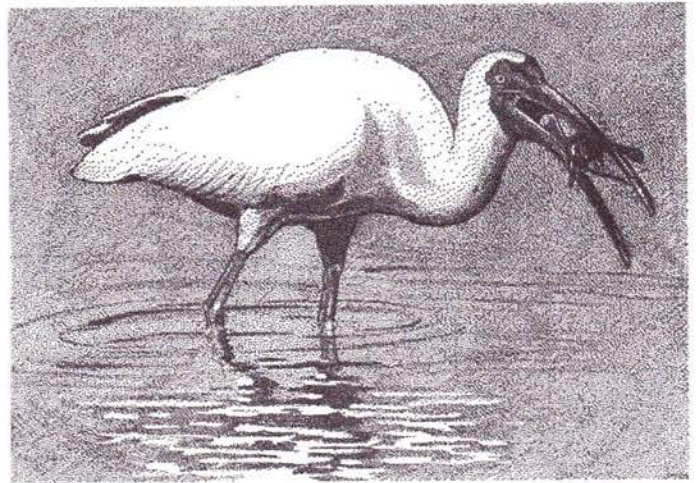


Figure 3.
White Ibis with
prey (crayfish).
By Dan Otte.

metabolism 138.7 kcal/d (Kushlan 1977c). Daily energy expenditure, 164.6 kcal/d, or 21% of body mass. Young require 8,620 cal of food during nestling period and the s. Florida population of 62,000 birds in the mid-1970s required 9.3×10^8 kcal/yr (Kushlan 1977c, 1977d). Assimilation efficiency (AE) of nestlings is 68% to 92% on a diet of shrimp and fish, AE of adult is 80% (55%–92%). Caloric content of feces averages 2.48 kcal/g dry weight (0.22, 66; 1.89–2.95). Daily energy use of young peaks at mass of 600 g, decreases to fledging. Energy content of diet, 2.7 to 4.5 kcal/g. During nesting inland, crayfish made up 60% of energy consumed in s. Florida and 72% in central Florida (Kushlan 1979a). In coastal S. Carolina, adults feeding on fiddler crabs need to do so for 2.5 (females) to 3.5 (males) hr/d (Bildstein 1987).

Because of salt stress, nestlings do not develop normally on brackish-water prey such as fiddler crabs. Even at estuarine colony sites, the bulk of the nestling diet consists of freshwater prey, especially crayfish (Bildstein et al. 1990, Johnston and Bildstein 1990).

DRINKING, PELLET-CASTING, AND DEFECTION

Drink by inserting lower bill horizontally into water and lifting head to allow water to flow into gullet. Nondigestible hard parts, such as fish bones, arthropod exoskeletons, and crayfish gastroliths are cast in pellets. Pellets also may be cast in flight (Below 1979).

FOOD SELECTION AND STORAGE

Food selection exhibited through tactile and visual foraging (Kushlan 1978c, 1979a, Bildstein et al. 1989). During nesting, selectively consume crayfish, crabs, insects, and frogs in higher proportion than available at feeding sites. When feeding on large fiddler crabs, select females over males, apparently avoiding major claw of latter (Bildstein et al. 1989). Poorly able to catch fish,

although some kinds are selected among those available, such as *Cyprinodont variegatus*, *Fundulus confluentus*, *Jordanella floridae*. Do not select relatively high energy prey, but when raising nestlings select low-salt prey (Bildstein et al. 1990). Will reject prey requiring prolonged handling time.

SOUNDS

VOCALIZATIONS

Not very vocal. Begging call of hatchlings, which varies among individuals, is high trill (De Santo et al. 1990). Flight call for both sexes and advertising call of male is a coarse *hunk-hunk-hunk*. Females give squeal during courtship, but vocalizations do not persist. Soft, high-pitched notes uttered at roost.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Walk slowly while foraging. In *Spartina* marshes while searching for fiddler crabs, individuals walk at rates averaging 25 to 40 steps/min, with birds on the peripheries of large flocks stepping more frequently than other birds (Bildstein 1983, 1984; Petit and Bildstein 1987). Birds feeding in aquatic habitats often walk much more rapidly, especially when groping in standing water for fish. Individuals leap over one another as flocks move across feeding grounds. Adults rarely climb except when perched in day roosts. Young are capable of climbing small shrubs and bushes by the end of their second week (De Santo et al. 1990).

Flight. Fly with rapid wingbeats (3.3 flaps/s [0.3, 9; Urban 1974]) alternating with gliding at between 60 to 100 m, sometimes in excess of 45 km/h (Pennycuick and De Santo 1989). Infrequently soar to between 500 and 1,000 m (Bateman 1970), especially when traveling long distances (>20 km) between colony and foraging sites. Cost of powered flight estimated at approximately 0.1 g fat/km (Pennycuick and De Santo 1989). Fly in cohesive flocks, typically in a variable "V" formation or in long skeins. Entire flock may perform intricate maneuvers, especially during prebreeding flights in early spring. Individual birds engage in spectacular aerobatics, including free-fall into roost. Young and adults tend to flock separately during first few months, with young in looser flocks (Petit and Bildstein 1986).

Swimming. Can swim when pressed.

SELF-MAINTENANCE

Preening, headscratching, stretching, bathing, anting, etc. Spend much of the day preening (Rudegear 1975b), usually at day roosts. Often interrupt feeding bouts to preen. Ventrums preened by extending neck out, bill down, and biting feathers with bill tip. Run bill along surface of the wing and bite feathers, working along it or bringing the bill over shoulder to preen underwing. Back preened directly by turning head, lower ventrum by placing head between legs. Pay particular attention to head and neck. Use cupped nail of middle toe to scratch overwing. Oil gland is frequently used by rubbing side of head and bill, then rubbing these on back, rolling head side to side. Frequently shakes head or body with loosely held wings.

Bathe in water 5–20 cm deep. Crouch into water, submerging and shaking first one wing and then the other, or both simultaneously. Usually followed by prolonged preening.

Sunbathing, thermoregulation, temperature metabolism. Interrupt feeding to stand or lie in vegetation in sun with wings drooped. Also shade nest by facing away from sun and spreading wings over contents. As a result, in extreme circumstances entire colonies of incubating and brooding birds may face the same direction. Nestlings have poor thermoregulatory ability and are quickly killed by exposure to sun. When heat stressed, adults and young pant and gular flutter. Bill is gaped and throat oscillated four times/s (Rudegear 1975b). Rate increases with increasing temperature.

Sleeping and roosting. Typically sleep with head tucked under wing over back. Roost close together at traditional sites, usually in the tops of live or dead trees, often with other wading birds. When not on the nest, parents often roost at colony site, especially early in the season.

Daily time budget. In s. Florida, 13 hr roosting and nest attentiveness, 0.75 hr flying, 10.25 hr foraging (Kushlan 1977c). In coastal S. Carolina nonbreeding adults need spend only 2.5 (females) to 3.5 (males) hr feeding on fiddler crabs to meet daily energy needs (Bildstein 1987).

AGONISTIC BEHAVIOR

Physical interactions. Defend territories, position, and mates with forward bill thrusts, by jabbing and biting, and by supplanting flights. Fight with rivals by biting and holding the opponent's head or wing. Mated males, encountering attempted cuckoldry upon returning to nest sites, sometimes pull feathers from intruding males and inflict facial lesions; facial scars, eye injuries, and crippled legs are more common among males than among females. Females are

sometimes pecked around the head and back by males before and after extra-pair copulations. Some of these attacks result in bleeding. Propensity to fight and fighting ability vary considerably among males. Unattended eggs at colony sites are sometimes destroyed by adults prospecting for nest sites.

Communicative interactions. Threat displays include the "forward threat" in which the bird assumes horizontal posture, moves toward or lunges at opponent, may or may not make contact. "Ritualized sparring" at nest site involves two birds standing erect and bill gaping; exchange snaps. In "supplanting flights," a bird flies at its opponent with neck extended and bill gaping, attempts to alight on other bird.

Appeasement displays occur mostly among females. At nesting, head-rubbing display with top of head and nape rubbed on back, bill turned from horizontal to vertical and back to horizontal. Female appeasement display at nest involves a slow approach with head and body low, feathers slicked back, head turned to show side of face to male.

Spacing. Highly aggressive in maintaining individual distances, using bill thrusts, jabs, and biting attacks at both colony and feeding sites. Will defend against other species in aggregations. Individual distance varies with likelihood of piracy, distances increasing when individuals are foraging for large or difficult-to-handle prey.

Territoriality. At colony site, display territory established, advertised, and defended by male. Display sites tightly defended by males with forward threats and short jabs. Supplanting used to attract female. Nest built in display territory and defended by both sexes. No territories on feeding sites except individual distances.

Nature and extent of territory. Nest territory usually extends only as far as incubating or brooding parent is able to stretch its neck. In Louisiana, distance between nests averaged 0.65 m (SE = 0.03, $n = 170$, range = 0–2.0; Hammatt 1981); in S. Carolina in needle rush (*Juncus roemerianus*), 0.69 m ($n = 54$; Frederick 1987a), in mulberry (*Morus* sp.), 1.04 m ($n = 104$; Post et al. 1985); in N. Carolina 0.57 m ($n = 468$; Shields and Parnell 1986); in Florida 0.54 m (Girard and Taylor 1979).

Also defend display and nest areas against other species. Not usually successful against larger or more aggressive egrets. Nest distances generally less within than among species.

Dominance hierarchy. Stable and somewhat linear hierarchies in captive groups are apparently based on relative size, both within and between sexes. Not recorded in the wild.



Figure 4.

Courtship greeting display.

By D. Otte.

SEXUAL BEHAVIOR

Mating system. Monogamous, with frequent extra-pair copulation. Care by both parents is apparently necessary for successful rearing of young.

Pair bond. Courtship behavior well documented (Palmer 1962, Rudegeair 1975b, Hancock, Kushlan and Kahl 1992). Display sleeping, display shaking, display preening, and supplanting flights, are common in "bachelor parties," groups of displaying males. Display flights, in which portions of a flock of sometimes more than several thousand individuals spiral up and down, occur at and around colony sites, especially following rains. Display preening, head rubbing, and bill popping are the primary displays of males. Head rubbing is quickly initiated, and may include a complete roll of the bill from left to right or only a quick touch of the top of the head in a pumping motion, reminiscent of the scratch display of herons. Full bill popping includes twig grasping and nibbling, or may not be accompanied by complete extension of the neck.

Females approach displaying males very cautiously in the appeasement posture, especially showing the side of their face to the male. Male gives forward threats and will attack, grabbing and shaking the female's head. Before pair bonding is complete, female often becomes bloodied. During courtship, the pair uses greeting displays and mutual stick shaking, typically with necks crossed (Fig. 4); display preening, auto- and allopreening, and standing touching each other. Greeting displays may include twig grasping and honking vocalizations by males, and squealing vocalizations by females, the latter disappearing later in courtship.

Copulation takes place at nest site, or on the nest platform. To begin, male places his neck over that of female as they engage in mutual twig grasping. Male mounts, achieving and maintaining his position by treading feet and flapping wings. Both birds remain at nest for several days, before female begins to spend time foraging. Pair remains together for one nesting episode.

Extra-pair copulations. Common in the latter stages of pair formation and even into incubation. Males initiate such copulations; females, although capable of resisting, seldom do so. Over 6% of the fertilized eggs laid may result from copulations outside the mated pair (Frederick 1987a).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Highly gregarious at all times; highly colonial nester, in large and densely populated colonies, crèches when leaving the nest, feed in flocks almost exclusively, roost communally, and fly to and from foraging, roosting, and breeding sites in flocks.

Play. Young at colony sites manipulate twigs and grassy vegetation in their mandibles. Well-fed captive individuals mandibulate prey without eating it.

Interactions other than predation with members of other species. Commensal feeding widely reported, generally other birds following the ibis as it walks slowly through the water (Kushlan 1978b). Also subject to piracy from other species feeding within its aggregation (Kushlan 1978a). Usually, relatively large prey are stolen.

Predation. Predation on adults probably not important. Alligators (*Alligator mississippiensis*) and perhaps large birds of prey take adults. Unguarded eggs and hatchlings are at great risk to crows, grackles, both adult and ambulatory young Black-crowned Night-Herons (*Nycticorax nycticorax*), gulls, and perhaps vultures, as well as to northern opossums (*Didelphis marsupialis*) and raccoons (*Procyon lotor*). At some locations as many as 44% of the eggs are lost to Fish Crow (*Corvus ossifragus*) predation (Shields and Parnell 1986). Nestlings are vulnerable to night-herons until they are at least two weeks old. The impact of predation on eggs and nestlings is exacerbated when food for ibises is scarce and parents must spend more time away from their nests (Dusi and Dusi 1968, Bildstein et al. 1990). Eggs and young are also at risk when other birds steal nest material.

Crows usually take all the eggs in a clutch, such predation being highest nearest crow nests. Predation by crows is reduced with greater nest attentiveness by parental ibises (Shields and Parnell 1986) and increased where elevated perch sites for crows are available within a colony. Percent nest

exposure affects vulnerability to avian predation (Rudegeair 1975b, Allen-Grimes 1982). Percent of eggs lost to avian predators varies from 7% to 75% among colony sites (Post et al. 1985, Shields and Parnell 1986, Frederick 1987c).

Males tend to remain at the nest, as any departures put nest and its contents at risk (Kushlan 1973a). Defense is by use of standard threat repertoire, including attacks, most directed at conspecifics. Ibises are extremely wary, both when nesting and foraging, more so than other wading birds nesting or foraging with them. In coastal S. Carolina, feeding individuals flush during flyovers of large birds, including Great Blue Herons (*Ardea herodias*), Ospreys (*Pandion haliaetus*), and Red-tailed Hawks (*Buteo jamaicensis*), as well as helicopters and fixed-wing aircraft. When feeding in areas with tall and short vegetation, ibises avoid tall vegetation, possibly to aid detection of predators. In S. Carolina *Spartina* marshes, flocking behavior is not linked to increased hunting success, suggesting that flocking during feeding is a response to predation risk (Petit and Bildstein 1987).

BREEDING

PHENOLOGY

Pair formation. In North America, onset of breeding readiness depends on photoperiod, as captive birds in Florida and S. Carolina begin to experience soft-part changes in early spring. In coastal S. Carolina, massive courtship flights occur near colony sites following spring rains. In Florida, nesting can be delayed for many months until feeding conditions become suitable (Kushlan 1976a). In coastal S. Carolina, late nesting is often the result of late arrival of spring migrants from farther south. Owing to considerable variation in nesting synchrony, an entire nesting episode can last eight weeks to four months.

Nesting starts when conditions are suitable for highly effective foraging, primarily the availability of sufficiently shallow freshwater wetlands (Kushlan 1976a, Bildstein et al. 1990). Actual timing differs substantially across range, even during seasonal drying period in Everglades. In coastal colonies, nesting occurs during or immediately following the "big rains" season. In s. Florida, nesting in the interior ends by early summer, whereas coastal colonies nest well into summer. Such rains probably provide foraging sites in freshwater wetlands near coastal colony sites (Bildstein et al. 1990).

In Florida (Rudegeair 1975b) and in coastal S. Carolina, pairs form within two weeks of their

arrival in spring. Nest building usually begins in late spring to late summer, earlier (late Mar to May) in interior s. Florida than farther north or along the Florida coast (May-Jun; Kushlan 1973b, 1977c). In S. Carolina, nest building usually begins between early Mar and early Jun (Beckett 1965), usually within ten days after the birds arrive from the south. In N. Carolina, in late Mar to early Apr (Allen-Grimes 1982, Shields and Parnell 1986). See Fig. 2.

Second brood per season. Will re-nest following nest failures early in the breeding season. Evidence suggests that ibises sometimes initiate second attempts in different colony sites, as well as visit several colony sites before initiating their first attempt. Hence it is difficult to separate late first nesting attempts from early second attempts. Extremes for eggs in s. Florida, Mar-Sep; for S. Carolina, Apr-Jul (Bildstein et al. 1990). For coastal Georgia, as late as Jul (Teal 1965). In coastal S. Carolina, most eggs hatch in May and Jun. Recently fledged individuals are first seen on nearby salt-marsh feeding sites in mid- to late Jun, flying to more distant freshwater wetlands one week later.

NEST SITE

Selection process. Colony sites usually develop from roost sites through the formation of daytime bachelor parties that form at the roost and on the ground nearby. Nests are near, but not necessarily on, the display site. Female sites the nest platform and builds the nest, which may be some distance from display site. Nest building is usually synchronous (onset within 4 d) within "neighborhoods" of 25 to 50 pairs in large colonies (Frederick 1987a). Although individuals maintain nest territories (see Territoriality), neighborhoods form as tight aggregations of nests with few nests added after the initial establishment of a neighborhood. In coastal S. Carolina, where White Ibises nest in colonies with other ciconiiforms, the presence of nesting individuals of earlier-nesting species may prompt ibises to nest at a colony site.

Site characteristics. Nest in live and dead woody vegetation. Nests are typically in branch crotches, but also on multiple close branches and in herbaceous vegetation. In the latter, often supported on grass culms. As many as 47 nests in a single tree (Audubon 1844). In n. Florida in one colony (Rudegear 1975b), 67% in *Tamala littoralis*, 12% in *Quercus* spp., 4% each in *Sabina silicicola*, *Sabal palmetto*, and *Ilex vomitoria*, 9% in vines; in another colony, 86% in *Sambucus canadensis*, 14% in *Acer rubrum*. In coastal Louisiana in one colony, 99% in live and 1% in dead *Avicennia nitida* (Hammatt 1981). In a colony in coastal N. Carolina 38% in scattered red cedar (*Juniperus silicicola*),

remainder in maritime thickets (Allen-Grimes 1982).

In a survey of 232 colonies, 30% were in mangrove (*Avicennia*, *Laguncularia*, *Rhizophora* spp.; Hingtgen et al. 1985). Also in Australian pine (*Casuarina equisetifolia*), Brazilian pepper (*Schinus terebinthifolius*), lantana (*Lantana camara*), buttonwood (*Conocarpus erectus*), live oak (*Quercus virginiana*), laurel oak (*Q. laurifolia*), bay (*Persea borbonia*), red mulberry (*Morus rubra*), elder (*Iva frutescens*), willow (*Salix* spp.), wax myrtle (*Myrica cerifera*), swamp tupelo (*Nyssa aquatica*), common baldcypress (*Taxodium distichum*), cactus, grasses or sedges (*Cladium jamaicense*, *Scirpus* spp., *Juncus roemerianus*, *Spartina cynosuroides*), or on the ground (Audubon 1844, Bent 1926, Dusi and Dusi 1968, Kushlan 1973b, Rudegear 1975b, Schreiber and Schreiber 1978, Girard and Taylor 1979, Frederick 1987c, Bildstein et al. 1990).

Grasses and sedges appear to be used when higher nest sites are not present or are being used by earlier-nesting species. Nest platforms often contain fresh leaves, replenished by the male during incubation. In n. Florida, averaged 12.0 ft (5.3, $n = 999$) aboveground; in coastal S. Carolina 2.95 m (0.09, $n = 104$) in mulberry (Post et al. 1985); 0.32 m (0.10, $n = 64$) in needle rush (Frederick 1987c). In coastal Louisiana, averaged 0.14 m (0.014, $n = 170$) aboveground in black mangrove (*Avicennia* sp.; Hammatt 1981); and in Florida 1.78 m in white mangrove (*Laguncularia recemosa*; Girard and Taylor 1979). At colonies where ibises nest later than other ciconiiforms, nests tend to be lower than those of other species, possibly because higher sites are less available.

NEST

Construction process. Actual nest site selection falls to the female, who also has primary responsibility for building the nest. Sticks are brought by the male. In n. Florida, 38% of the sticks placed by female, 35% by female predominantly, 27% by male and female equally (Rudegear 1975b). Males steal nesting material from existing nests, often in conjunction with attempted extra-pair copulations (Frederick 1987a). No evidence that ibises use the abandoned nests of earlier-nesting species in mixed-species colonies, but Glossy Ibises (*Plegadis falcinellus*) sometimes use abandoned White Ibis nests (Allen-Grimes 1982).

Female grabs nesting material crossways, shoves it into the nest platform, and moves it up and down, in a tremble shoving motion. Once twig is caught in nest material, can be further adjusted, removed, or replaced. Nest construction takes place throughout the day; usually takes less than seven days to build a nest.

Structure and composition. Nest usually constructed of twigs, even in herbaceous colony sites; but low herbaceous nests often consist of matted and woven herbaceous vegetation from the immediate vicinity, and some completed ground nests with eggs consist of fewer than 20, 10–20 cm pieces of cord grass (*Spartina* spp.). At a black mangrove colony site in coastal Louisiana, 65% of nesting material black mangrove, 35% *Spartina alterniflora* (Hammatt 1981). Twigs may be broken from nearby branches, found on ground under colony, pilfered from old or nearby nests, or gathered at some distance from the colony site. Sometimes lined with nearby grasses, moss, and cypress leaves (Wayne 1922, Stephens 1950). Discarded rope, paper, and plastic occur infrequently.

Dimensions. Nest measurements variable (Rudegeair 1975b, Frederick 1987c). Outside diameter: n. Florida, 10 in (1.89, $n = 1051$); coastal S. Carolina, in shrubs (*Iva frutescens*) 287 mm (16.9, $n = 10$), in grass (*Spartina cynosuroides* and *Juncus roemerianus*) 253 mm (28.7, $n = 20$). Height: coastal S. Carolina, in shrubs 91.2 mm (11.6), in grass 57.2 mm (10.8, $n = 20$). Inside diameter and depth not recorded.

Microclimate. Some nests, especially those placed low in live woody vegetation, have 100% canopy cover; others in herbaceous vegetation have little, if any, canopy cover. Insulative value of nest not recorded.

Maintenance or reuse of nests; alternate nests. Nest maintained through hatching, and sometimes for several days thereafter, with additional sticks and lining added. In coastal N. Carolina, 12% of the nests were reused once, and 1% were reused twice. Young had fledged from 29% of these reused nests (Allen-Grimes 1982). In coastal S. Carolina, nests are rarely reused. Material may be pilfered for next nest. No alternate nests recorded.

EGGS

Shape. Varies from subelliptical to long subelliptical, sometimes quite elongated.

Size. Florida: length, 57.53 mm (3.16, $n = 20$); diameter 38.65 mm (1.51, $n = 20$), Drum Island, SC (1957–1963): length, 58.23 mm (2.59, $n = 79$); diameter 38.68 mm (1.43, $n = 79$); W. Post unpubl. data, Charleston Museum of Natural History). Dwarf eggs occur. MASS: coastal N. Carolina (fresh): 50.8 g (5.7, $n = 30$); Vleck et al. 1983). Each egg approximately 6% to 7% of female mass.

Eggshell thickness. S. Carolina: pre-1947, 0.334 mm ($n = 27$); 1972–1973, 0.335 ($n = 20$); Blus and Lamont 1979).

Color: Spotted with brown over a base color ranging from cream to blue-green at hatching and

fading to white thereafter. Surface texture: smooth and nonglossy.

Egg laying. Eggs normally laid every other day (Rudegeair 1975b, Shields 1985), with most clutches completed within a week. The first egg is laid five to six days after the beginning of copulations, and additional eggs are laid at one- to two-day intervals. Eggs are laid early in the morning.

Male is extremely aggressive and spends more time at the nest than does female during nest building and egg laying. Male guards nest and female from other ibises, especially from nearby males collecting nest materials or seeking extra-pair copulations. Number of extra-pair copulations correlated with time female spends alone at nest (Frederick 1987a). Males guard nest during day, females guard at night. Unattended eggs destroyed by other ibises at the colony.

Nest is abandoned following predation, tidal inundation, and aggressive interactions with neighboring ibises. No evidence for replacement of lost eggs or clutches. If clutch is lost, pair abandons nest and nest site. Intraspecific egg dumping suggested by some indirect evidence but not demonstrated.

INCUBATION

Onset of broodiness and incubation in relation to laying. Eggs covered after laying, but incubation begins with last egg.

Incubation patch. Not seen on adults that were trapped two to seven days after eggs hatched (Frederick 1986).

Incubation period. On average 21 days. Details of variation unknown.

Parental behavior. Males incubated 55% ($n = 11$ pairs, 38%–68%) of the time during daylight observations (Frederick 1987b). Eggs and mate defended by male, who remains in residence throughout early nesting. Later, pair alternates nest attendance with the male feeding in early morning and evening, and attending the nest during most of the day (Kushlan 1976c). Larger size of male is primarily an adaptation for nesting, the presence of the larger bird of the pair ensuring against nest predation or nest material robbing; lone females are susceptible to being driven from the nest (Frederick 1987a).

Time at nest low early in incubation (15.8 min/pair), increasing to high point at three weeks. Overall, inattentiveness about 31 to 33 min/d (Rudegeair 1975b). Time off eggs averaged 1.9 times and 1.9 min/hour on rainy days, and 4.3 times and 13.9 minutes per hour on sunny days. Incubating birds tend to flush more readily early in incubation than later, as well as during windy conditions (Shields and Parnell 1985). Some ibises

attempt to incubate eggs while floating above them during tidal inundations of the nest (Frederick 1987c). When temperature is over 34°C, eggs are shaded rather than incubated. Other activities during incubation (times/h): preen, 2.6; twig pull, 1.9; feather ruffle, 0.20; head shake, 0.12; tail flick, 0.26; stretch, 0.24; scratch, 0.56 (Rudegear 1975b).

Early in incubation changeovers include appeasement behavior and mutual head rubbing and bill popping. Later, no obvious displays.

Hardiness of eggs. No detailed information. Appear to be susceptible to heat and cold, as incubating birds sit tight in rain and shade during heat. Eggs left unguarded are generally destroyed or lost to nest-material piracy. Eggs covered with brackish water for more than one hour during tidal inundations early in incubation have hatched (Frederick 1987c).

HATCHING

Preliminary events and vocalizations. Young vocalize during pipping. Sequential eggs in clutch hatch one to two d apart.

Shell breaking and emergence. Young break hole in shell with egg tooth, eventually cutting a circle approximately one third of way from blunt end of shell. Hatchlings usually emerge one to two d after initial pipping.

Parental assistance and disposal of eggshells. No parental assistance recorded. Eggshells disposed of by adult, who picks up shell and tosses it away from nest with lateral shake of head.

YOUNG BIRDS

Condition at hatching. Bill straight and flesh-colored (#5, Smithe 1975-81) with a dark neutral gray (Color 83) tip. Bare skin of face, legs and feet flesh color. Head and neck covered with dense, shiny jet black (#89) down, projecting caudally. Several white feathers form a spot on the crown of approximately 30% of nestlings. Remainder of body with sparse pale neutral gray (#86) down, except for shoulders and wings, which are covered with dark neutral gray (#83) down (De Santo et al. 1990).

Weak and uncoordinated; spend most of the time sleeping in a prone position. Eyes closed. Cannot stand or raise head at hatching; legs small and underdeveloped. On day 1 begging consists of jerky lateral head movements.

In coastal S. Carolina, hatchling mass: 36.3 g (4.10, $n = 72$); bill (measured from tip to feather line), 17.6 mm (0.90, $n = 72$); tarsus, 16.1 mm (1.28, $n = 72$); middle toe, 18.0 (1.18, $n = 72$); wing chord, 22.5 (1.57, $n = 72$; De Santo et al. unpubl. data.).

Growth and development. Biomass grows rapidly in first and third week, slower in second week during the period of feather maturation (Kushlan 1977d). Growth of captive birds may be retarded. Growth rate may vary at a single colony site within and among years depending on the availability of appropriate prey. Mass increase modeled by logistic growth equation, $K = 0.185$, asymptote = 700 g, $t(10-90) = 23$ days.

Body parts grow at different rates, with legs, feet, and toes developing quickly, and bill much retarded (Kushlan 1977f).

Eyes begin to open at 1 to 3 d, and are completely open by day 9. Irises raw umber (color #223) through first month. By month 5 outer ring medium plumbeous (#87), inner portion Pratt's Payne's gray (#88; details in De Santo et al. 1990).

Feather tracts visible at hatching. No visible feather growth until day 4 or 5, when primaries begin to emerge; followed by feathers in humeral and alular tracts, as well as secondaries and tertiaries on days 6 to 10. Spinal and ventral tract feathers and rectrices emerge on days 8 to 12; crural and femoral feathers on days 24 to 32. Much of the down on crown replaced on days 32 to 46, but some remains for days after birds leave the colony site during weeks 7 and 8. Primaries completely unsheathed by days 45 to 60.

White egg tooth sloughed at 5 to 9 d. After 3 d, facial skin and orbital area darken to light neutral gray (#85). This color change proceeds distally until the proximal third of both mandibles is dark neutral gray. Remainder of bill becomes salmon color (#6). A band that darkens to dark neutral gray appears distal to the nares between 7 and 10 d. Bill begins to curve downward at day 14. Dark neutral gray areas of bill expand until most of the bill is dark by the beginning of week 5. During this time the pattern of the pied bill varies considerably among same-age nestlings (De Santo et al. 1990). At 6 wk bill light neutral gray, changing to pale pinkish buff (#121D) at the base and salmon color distally by week 9. Bare skin of face turns light neutral gray around day 2, and bluish gray by day 3. It is deep vinaceous (#4) by 5 weeks, turning flesh color beginning in third month (De Santo et al. 1990). By 6 mo, bare skin is fleshcolor but paler than in adults. Juvenile legs and feet gray, turning to flesh color by third year.

Nestlings easily overheated during the first week. Shaded from sun by parents during first ten days. Seek shade in vegetation thereafter. Chilling as a result of tidal inundation of nests containing younger than ten-day-old nestlings is the principal cause of nestling mortality at a coastal colony site in S. Carolina (Frederick 1987c).

Incapable of holding head up for first day or so. Hatchlings lie on side with head back or down, brooded by parent. By day 3 chicks beg with loud trills while holding their head up and extending their wings; shuffle to edge of nest to defecate. Legs, feet, and toes become large and strong quickly. By day 6 chicks crawl on their tarsometatarsi. Free-living chicks beg continually unless being incubated. During week 2 chicks flap one or both wings while begging, and by the end of week 2 are capable of leaving the nest to flee approaching humans. Trilling vocalizations, which vary among individuals, become longer and louder throughout the first four weeks (De Santo et al. 1990). By week 3 can climb out of nest onto limbs or ground, but cannot climb back into nest in tree if they fall out; can swim if they fall in water. Also by week 3 they pirate food from each other, and in colonies with nests near the ground, crèche in groups of at least 30 similar-aged juveniles, ranging at least 20 m from their nest. By week 4 chicks spend most of their time perched on vegetation away from their nests or wading and probing in shallow water.

Siblicide not reported. Chicks are pirated of their food by other chicks as well as by marauding adults.

Flight develops gradually. At two weeks chicks begin to spend much time flapping wings. Can fly short distances in colony by fourth or fifth week. Sustained flights of more than 50 m occur by week 6. Juveniles begin to leave island colony sites, crossing water boundaries of 750 m or more to feed with adults and other juveniles at end of week 7 (De Santo et al. 1990).

PARENTAL CARE

Brooding. Adults continue brooding and shading young immediately from hatching to day 10. Young can move from their nest by week 2, at which time both adults forage at the same time, and young are brooded usually only at night. By week 3 brooding has ceased. Male broods early in the day, female later in the day and at night. In Florida most feedings early and late in day. Young have corresponding endogenous rhythm (Kushlan 1976c). Feeding rhythms can differ elsewhere, at different stages of the nesting cycle, and with different food supplies.

Feeding. Fed beginning second day. Both parents feed young. In coastal S. Carolina, males responsible for 57% of regurgitations ($n = 11$ nests, 38%–72%) to small nestlings (Frederick 1987b). Adults feed young directly. Adult grasps chick's bill, stimulating it to raise its head, and then regurgitates into its mouth. After a week, young initiate feeding with a begging display by poking at and touching parent's bill, while flapping one or

both wings. Nestling head placed in bill of adult. Series of head jerks and bobs results in regurgitation by adult directly into the bill of the young. Infrequently, food regurgitated onto the nest floor, where it may be picked up by young. Transfer takes three to ten seconds. After two weeks young often drape one wing over the back of the feeding adult. Adult may delay feeding or delay return to the nest, or may place bill out of reach of nestlings. When young are capable of short flights, parents sometimes induce flying by alighting close to young and then taking off with the young in pursuit. Other young and even adults pirate food directly from feeding adult, as well as from recently fed young (Rudegeair 1975b).

Food of young usually same as adults'. Much macerated throughout raising of young. Only slightly, if at all, diluted with water; no indication that water alone is brought to young. Adults in coastal colonies feed freshwater prey, especially crayfish, when available, rather than locally abundant fiddler crabs, which are also taken by adults (Bildstein et al. 1990). Young fed as frequently as nine times per day. Younger chicks fed more frequently than older chicks. Amount of food brought per trip not recorded, but load sometimes fills entire gullet from gizzard to mouth.

Largest bird fed first after commencement of active begging. Adult may attempt to feed all young, but considerable competition. Larger young often climb atop smaller young in gaining access to food (Rudegeair 1975b). Adults sometimes terminate feeding by standing erect, or later by flying away.

Nest sanitation. Young move to edge of nest to defecate over the side by day 3, usually upon being fed. No fecal sacs. No invertebrate associates in the nest are recorded. Parental carrying of young not recorded.

COOPERATIVE BREEDING

Nonbreeding second-year birds, which typically comprise less than 1% of all individuals at a colony, often interact with nestlings. These second-year helpers often move among nests, interacting with several broods per hour, preening and shading nestlings. Nestlings beg from helpers but food transfers not reported. Helpers tend nestlings only when adults are absent, withdrawing from nest when adults return, sometimes chased from the site by returning adults. Results of helping with respect to the parents or young unknown; may provide useful experience for nonbreeding second-year birds. Helping occurs regularly at a coastal colony in S. Carolina, but because second-year birds are so few at this colony, few nestlings interact with helpers.

BROOD PARASITISM

Interspecific brood parasitism not reported. In coastal S. Carolina, intraspecific parasitism, or egg dumping, estimated responsible for 2.7% of eggs laid. Dumping occurs at least during host's egg-laying sequence, and possibly before and after. Effect on host and host's response to egg dumping unknown.

FLEDGLING STAGE

Behavior. Young spend considerable time perched in vegetation at this time, and they engage in short flights, especially when parents return with food. Crèches of up to several hundred similar-aged young form at this time.

Departure from nest. Young leave mainland colonies as early as 40 d after hatching, one to two weeks later at island sites requiring flights over water. Radiotelemetered young left an island colony in coastal S. Carolina at 47 to 56 d of age ($n = 8$; De Santo et al. 1990). Some chicks follow after adults, begging as they leave the colony; others depart alone or with several young. Departures occur throughout the day. Aborted attempts at departure occur frequently, with chicks flying from <20–100 m over water at island colonies before returning to the site. Some young return to roost at colony after initial departure. No indication that adults feed young away from the site.

Growth. Leave colony at 79% of adult mass, which is not achieved until two years. Middle toe at 100% of adult size at 29 d; tarsus at 98% adult size upon departure from colony, adult size at 52 d; central rectrices at 92%, adult size at 55 d; 8th primary at 93%, adult size at 74 d; bill at 68%, adult size at 112 d (Kushlan 1977f).

Association with parents and other young. Do not associate with parents outside of colony site. Form juvenile flocks for at least several months, possibly longer (Bildstein 1983, Petit and Bildstein 1986). Long-term stability of these flocks unknown.

Ability to get around, feed, and care for self. Young typically probe for food at the colony site and make sustained flights of 50 m or more for at least one week prior to departure. Feeding on the ground, they sometimes consume large quantities of mud. Feeding behavior similar to that of adults, but handling times longer and intake rates approximately 40% adult rate for at least several weeks after leaving colony site (Henderson 1981, Bildstein 1983). Often choose inappropriate habitat. Require several weeks to fly in flight lines typical of the species (Petit and Bildstein 1986).

IMMATURE STAGE

At least a portion of the immature population accompanies adult breeders at colony sites, where

they roost together and often interact with nestlings (see Cooperative breeding). Second-year immature birds, which often flock together, feed at approximately 70% the rate of adult breeders (Bildstein 1984).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. First nesting in third summer, at age of two years. Nest yearly thereafter if conditions appropriate. No records of two successful nesting attempts by individuals in a single year.

Clutch size. 2–5, averaging 2–3 depending on location; 6–7 eggs in single nests at a coastal S. Carolina site probably represent egg dumping. In s. Florida Everglades 2.45 (SD = 0.67, $n = 51$); coast 2.20 (0.64, $n = 290$); central Florida 2.49 (0.56, $n = 202$; Kushlan 1977c). n. Florida inland 2.16; coast 2.07 (Rudegeair 1975b). At a coastal N. Carolina colony site, 2.23 ($n = 287$) in 1981 (Allen-Grimes 1982), 2.65 ($n = 262$) in 1983, and 2.46 ($n = 493$) in 1984 (Shields 1985). Clutch size decreased over the course of the season in 1981 (2.32, Apr; 2.10, May; 1.95, Jun; Allen-Grimes 1982). In coastal Louisiana 1.97 (0.70, $n = 100$; Hammatt 1981). In coastal S. Carolina 2.55 ($n = 380$; Frederick 1987c). Clutch sizes smaller on the coast than inland, at least at some locations in some years, suggesting a physiological or ecological constraint.

Annual reproductive success. In Florida, number of young per nest at 40 days: Everglades 1.05 (SE = 0.22, $n = 42$), coast 1.03 (0.18, $n = 93$), central 1.03 (0.16, $n = 21$). In coastal N. Carolina 1.05–1.30 over two years ($n = 755$). In coastal Louisiana 10% of laid eggs produced 35-day-old young ($n = 102$ nests); in coastal S. Carolina over two years at a single colony site 39% ($n = 390$ eggs) and 3% ($n = 347$). Considerable annual variation in per-pair productivity is typical at colony sites, depending upon local conditions. At many sites fewer than 50% of nesting attempts are successful. In coastal N. Carolina, 1.70 young per successful pair ($n = 129$).

Nesting success is determined ultimately by the availability and quality of the prey base during nesting. Sites must be available that are shallow enough for feeding. Pairs appear to choose nesting sites based on hydrologic conditions (Kushlan 1976a). Nesting success determined in large part by how water levels fluctuate during nesting (Frederick and Collopy 1989). Because water levels fluctuate in most nesting areas, White Ibises require a succession of suitable feeding sites through the nesting season (Kushlan 1989b). Food quality is

also critical to nesting success, as White Ibises specialize on crustaceans. Furthermore, chick survivorship is closely tied to a diet of low salt content (Johnston and Bildstein 1990).

Number of broods per season. Normally one, except when renesting occurs following failure of early nesting attempts.

Proportion of total females that rear at least one brood to nest-leaving stage. Generally unknown: in coastal Georgia 5 of 14 nests (36%) fledged young (Teal 1965). Less than 10% at some sites in some years.

LIFE SPAN AND SURVIVORSHIP

Free-ranging: at least 16 years 4 months (Clapp et al. 1982); captive: at least 20 years (Spil et al. 1985).

MORTALITY AND DISEASE

Nestling mortality, which can be high, is greater during first 20 d than thereafter. Young per nest in Florida (20 d after hatch): Everglades 1.38 (0.49, $n = 53$), coast 1.14 (0.45, $n = 64$), central Florida 1.25 (0.43, $n = 133$) (Kushlan 1977c). Nestling survivorship to 10 d in coastal N. Carolina: 89% ($n = 410$ hatched eggs), 86% ($n = 596$ eggs), and 68% ($n = 284$ nests) during three years at the same colony site (Allen-Grimes 1982). Nestling survivorship to 35 days in coastal Louisiana: 55% ($n = 102$ nests; Hammatt 1981).

Nineteen species of trematodes, 2 species of cestodes, 16 species of nematodes, and 1 acanthocephalan reported from 40 nestling ibises collected in salt- and freshwater habitats in Florida (Bush and Forrester 1976). Approximately half of the species were found in at least 5% of the examined birds and are considered typical fauna. Birds from freshwater habitats harbored more nematode species, those from saltwater habitats more cestodes. Nestlings lacked four of the species found in adults in the same habitats, including the nematode (*Skrjabinoclavia thapari*), which uses fiddler crabs as an intermediate host. Both juvenile and adult ibises were, however, infested with the single acanthocephalan species, *Southwellina dimorpha*, which uses crayfish as an intermediate host. Also harbor two species of mallophagans (*Plegadiphilus eudocimus* and *Ardeicola robusta*; Forrester 1980), and two species of subcutaneous mites (Acarina: Hypoderidae; Pence 1971).

RANGE

Initial dispersal from natal site. Natal philopatry not demonstrated. Two nestlings individually marked at a coastal colony site in S. Carolina bred at a coastal colony site 100 km NE in N. Carolina.

Fidelity to breeding site and winter home range.

Propensity to change colony sites, so nesting numbers fluctuate annually. Individually marked breeding birds have returned in later years to a colony site in coastal S. Carolina (Frederick 1987c). But elsewhere within S. Carolina, reciprocal shifts annually in numbers of pairs breeding at traditional colony sites suggests considerable movement, probably due to changing environmental conditions.

Dispersal from colony. Occurs soon after leaving colony site. Numerous late-summer and fall sightings of young-of-the-year inland in N. and S. Carolina. Isolated fall reports of individuals inland as far north as Pennsylvania, N. Dakota, and Wyoming (Findholt 1984, Post et al. 1985).

Home range. Long term: migrant, at least in northern portion of range, with some degree of breeding colony site fidelity. But also nomadic, at least over several hundred kilometers, when environmental circumstances preclude local breeding. Short term: will travel at least 40 km one way to secure food during breeding season.

POPULATION STATUS

Estimates or counts of density. The most numerous ciconiiform wading bird in many areas where it regularly occurs. In s. Florida, historical populations numbered near 100,000 individuals; within last two decades >50,000, including over 35,000 in one colony (Kushlan 1973b, Kushlan and White 1977). In S. Carolina, recent populations range from 10,000 to 30,000 pairs, with over 20,000 pairs in one colony (Post et al. 1985, Bildstein et al. 1990). Colonies of over 5,000 pairs frequently reported (Osborn and Custer 1978, Frederick 1987c). In winter, in the continental U.S., small populations found in coastal S. Carolina, Louisiana, and Texas, but the greatest concentrations in peninsular Florida, especially along the Gulf Coast near Tampa Bay (Root 1988).

Trends. Range has increased and consolidated over past decades. Because of propensity to change colony sites, nesting numbers fluctuate annually and among decades in any one area (Kushlan 1977c, 1979c). As a result, some local populations, such as that nesting in the Florida Everglades, have decreased markedly in the past few years. Even so, numbers as a whole continue to be relatively high for a large wading bird. The decrease in the Everglades is because water management has altered the natural hydrologic regime of the marsh (Kushlan 1987, 1989b). Similarly, in Trinidad, the cessation of breeding by Scarlet Ibises also appears to be due to an altered hydrologic regime (Bildstein 1990). Whether such populations have decreased primarily through mortality or

population shifts remains unknown. In Trinidad, at least, the latter seems to have played a major role.

POPULATION REGULATION

Although annual reproductive success is low, populations continue to be maintained. Apparently, nomadic tendencies and an ability to postpone nesting mean that some reproduction occurs each year. Nesting failures and high mortality among inexperienced young are probably important components of population regulation. On a local scale, predation of eggs and nestlings, especially when exacerbated by reduced prey availability and competition for nest sites, have the potential of exerting a strong effect.

At a well-studied S. Carolina colony (cf. Bildstein et al. 1990), the number of breeding ibises plummeted from over 10,000 pairs in 1989 to zero in 1990, following the passage of a category 4 hurricane. Although the site itself suffered little habitat modification as a result of the storm, nearby freshwater feeding sites, which have been shown to be essential for successful breeding at the site (Johnston and Bildstein 1990), underwent substantial saltwater inundation as the result of the storm surge that accompanied the hurricane (Shepherd et al. 1991). See Food Habits: nutrition, for a discussion of the importance of freshwater prey to nestling ibises.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Although their impact on shellfish aquaculture is negligible, White Ibises are considered a threat by commercial crayfish farmers in Louisiana, where they are shot as vermin (Martin and Hamilton 1985). The birds (adults, young, and eggs) have been eaten by local residents, (Bent 1926), and this tradition continues throughout the species' range. Their appealing taste may derive from their crustacean diet. Restrictions on hunting have been effective in some areas.

Disturbance continues to be one of the primary causes of reduction in the numbers of breeding birds in various areas. This disturbance is generally due to intrusion by local residents into the colony, but researchers censusing colonies also can cause damage. Unattended eggs and young are highly susceptible to predation, nest destruction by neighbors, and exposure to heat, rain, or cold. Nest desertion due to disturbance is highly likely before egg laying and very likely during incubation. Eggs are more susceptible to predation and nestlings more susceptible to heat and cold

stress. Researchers and resource managers should avoid colony entrance unless absolutely necessary, and then only for less than 30 minutes per colony area every two days, only in morning or early evening.

Although the species continues to suffer direct assault by humans, its major threat is the destruction of appropriate colony sites and wetland foraging areas.

MANAGEMENT

In both the temperate and neotropical portions of the range, the best hope is for the preservation of large tracts of coastal and inland wetland habitat and of specific nesting sites (Kushlan 1983, 1986; Parnell et al. 1988).

Protection of colony sites is difficult because of the birds' tendency to shift sites frequently. As the number of potential colony sites decreases, especially along the coast, protection of remaining sites becomes even more important.

Foraging sites must also be protected and managed, as in many cases specific water conditions are required for foraging to succeed (Kushlan 1981, 1983, 1986, 1989a, b; Bildstein et al. 1990, Bildstein 1990). The species is able to shift easily and quickly among foraging areas to avoid unfavorable conditions, or take advantage of newly created foraging opportunities. Even so, because nestling ibises require a diet of freshwater prey to grow and develop normally, conservation plans should include the preservation of freshwater wetlands within foraging range of both inland and coastal colony sites.

APPEARANCE

MOLTS AND PLUMAGES

Juveniles have a brownish gray to sandy brown head, neck, and uppersides; white undersides and rump. Head and neck streaked Vandyke brown (Smithe 1975-81: color #121) and creamy white, giving an overall impression of glaucous (#80), darkest on head and upper neck (De Santo et al. 1990). Feather streaking becomes narrower on throat and lower neck and is represented by shaft streaks on breast (Beebe 1914). Concealed portion of feathers mostly white. Mantle and uppersides of wings blackish neutral gray (#82). Lower back, rump, undersides, including under wing coverts, creamy white to white. Tail coverts and proximal part of tail white; distal part blackish neutral gray. Concealed portion of feathers mostly white. Variable amount of white on tail and other feathers. Some individuals have isolated white contour feathers on mantle and upper wings. By three

Table 1. Mean and SE of measurements of adults from Florida (University of Miami Reference Collection) and in the collection of the American Museum of Natural History (AMNH).

	FLORIDA		AMNH	
	FEMALE	MALE	FEMALE	MALE
Bill, mm	142 ± 1 (12)	111 ± 1 (16)	136 ± 1 (26)	108 ± 1 (22)
Wing, mm	302 ± 2 (12)	277 ± 3 (12)	295 ± 1 (26)	266 ± 1 (21)
Tail, mm	108 ± 1 (11)	98 ± 1 (17)		
Tarsus, mm	102 ± 3 (12)	87 ± 1 (16)		
Longest toe, mm	70 ± 1 (12)	61 ± 1 (16)		
Mass, g	1,036 ± 30.3 (12)	764 ± 17.1 (16)		

months, feathers of mantle, wings, and tail fade to Vandyke brown; then to dilutions of sepia (#119) by eight to ten months, when bird appears dark drab (#119B) or drab-gray (#119D).

In the second year, from late winter through early fall, birds have a white or mottled body feathering while retaining sandy brown streaking on head and neck. The prebasic I molt leading to this plumage begins in Feb with the replacement of juvenal feathers with white feathers. This begins with greater upper wing coverts and feathers on the back, followed by scapulars, and spreads posteriorly to the tail (Beebe 1914), although considerable overlap occurs. Thus, white feathers replace dark in a seemingly disorganized manner. By mid-summer, the body is mostly white, except for upper back and median upper wing coverts. The body molt is usually completed by fall.

Timing of molt varies considerably (Fig. 2). Individuals usually complete 90% of body molt within 60 days; however, initiation of molt can be delayed by several months. Consequently, birds with mottled body feathering can be seen from Feb through Aug, and even in fall. If juvenal remiges and rectrices are pulled out before two months old, they are replaced by dark feathers, by lighter feathers from two to four months, and by white feathers after six months. The darker feathers remain on the head and neck through the first year, allowing identification of this age class. White feathers begin to replace juvenal feathers of head and neck beginning in Oct–Dec of second year. The existence of a prealternate I molt has not been determined. If present, it is an incomplete replacement of body feathers, limited mainly to feathers of the head and neck. Feather coat maintains at least flight feathers of basic I plumage, including dark-tipped four outer primaries (Beebe 1914).

Definitive prebasic molt includes feathers of head, neck, and back, which become soiled during

nesting. These are replaced beginning in late summer. Molt begins on the back, spreading to wing scapulars, coverts, remiges, and rectrices. Primaries are replaced in late summer to early fall.

Timing of molt is seasonal (Fig. 2). Prebasic I molt begins in Feb, continuing through fall; primaries not shed until following spring. Definitive basic molt begins after nesting in late summer, continuing through winter.

Description. Sexes alike. In the basic I and definitive adult plumage, all feathers are white, except for the tips of four longest primaries. These are iridescent dark green. The existence of an alternate I plumage is not documented. A pale buffy wash on head, neck, and back of some individuals is the result of soiling.

BARE PARTS

Bill is salmon or flesh color (color #5) in basic plumage. During courtship, proximal portion of the bill turns geranium (#12); distal part turns black in North America. The amount is variable, usually about two thirds but in some cases the entire bill. Bill returns to salmon color slowly, often leaving distal portion gray for several months. Irides sky blue (#66) in all seasons by two years old. In definitive basic plumage, legs are flesh color, except during courtship, when they turn geranium.

During courtship, bare skin turns geranium, fading to flesh color during nesting. Both sexes (not male alone as often reported) develop a bright red, naked throat pouch, typically larger in females than in males, which expands to 2–3 cm in diameter during pair formation (Kushlan 1973a, Rudegair 1975a or b). Courtship coloration is enhanced in captive birds maintained on diets including canthaxanthin (S. McDowell and K. Bildstein unpubl. data). Increased vascularization may also play some role (see Frederick 1986).

MEASUREMENTS

Males significantly larger than females in all measurements with little overlap (Table 1). Adults larger than juveniles in most measurements for first six to nine months. Measurements from s. Florida breeding population (Kushlan 1977a) and American Museum of Natural History collection (Bildstein 1987) show general sizes. Geographic trends in body size cannot be evaluated; more information is needed on this topic.

ACKNOWLEDGMENTS

We thank T. De Santo, A. Dinep, P. Frederick, P. Frohring, W. Post, and J. W. Johnston for their comments or for use of unpublished data. Financial, logistical, and other support for our studies was provided by the National Park Service, the U.S. Fish and Wildlife Service, the University of Miami Maytag Chair of Ornithology, East Texas State University, the University of Mississippi, the Belle W. Baruch Institute of the University of South Carolina, Winthrop College, the Savannah River Ecology Lab, the National Science Foundation, the American Philosophical Society, the Southern Regional Education Board, and the Whitehall Foundation. Cover photo by Crawford H. Greenwalt / © VIREO.

REFERENCES

- Allen-Grimes, A. W. 1982. Breeding biology of the White Ibis at Battery Island, North Carolina. M.S. thesis, Univ. North Carolina-Wilmington.
- Audubon, J. J. 1844. The birds of America. Vol. VI. Audubon and Chevalier, London, England.
- Bailey, R. G. 1978. Description of the ecoregions of the United States. Forest Service, U.S. Dept. Agric., Ogden, UT.
- Bateman, D. L. 1970. Movement-behavior in three species of colonial-nesting wading birds: a radio-telemetric study. Ph.D. diss., Auburn Univ., Auburn, AL.
- Baynard, O. E. 1912. Food of herons and ibises. *Wilson Bull.* 24: 167-169.
- Beckett, T. A. 1965. Drum Island 1964. *Chat* 29: 43-46.
- Beebe, C. W. 1914. Notes on the ontogeny of the White Ibis, *Guara alba*. *Zoologica* 1: 241-248.
- Below, T. H. 1979. First reports of pellet ejection in 11 species. *Wilson Bull.* 91: 626-628.
- Belser, C. G. 1989. A Scarlet Ibis or a hybrid White Ibis x Scarlet Ibis in South Carolina. *Chat* 53: 90-91.
- Benedict, F. G. and E. L. Fox. 1927. The gaseous metabolism of large birds under aviary life. *Proc. Amer. Philos. Soc.* 66: 551-534.
- Bent, A. C. 1926. Life histories of North American marsh birds. U.S. Natl. Mus. Bull. 135.
- Bildstein, K. L. 1983. Age-related differences in the flocking and foraging behavior of White Ibises in a South Carolina salt marsh. *Colonial Waterbirds* 6: 45-53.
- Bildstein, K. L. 1984. Age-related differences in the foraging behavior of White Ibises and the question of deferred maturity. *Colonial Waterbirds* 7: 146-148.
- Bildstein, K. L. 1987. Energetic consequences of sexual size dimorphism in White Ibises (*Eudocimus albus*). *Auk* 104: 771-775.
- Bildstein, K. L. 1990. Status, conservation and management of the Scarlet Ibis, *Eudocimus ruber* in the Caroni Swamp, Trinidad, West Indies. *Biol. Conserv.* 54: 61-78.
- Bildstein, K. L., S. G. McDowell, and I. L. Brisbin. 1989. Consequences of sexual dimorphism in sand fiddler crabs, *Uca pugilator*: Differential vulnerability to avian predation. *Anim. Behav.* 37: 133-139.
- Bildstein, K. L., W. Post, P. Frederick, and J. W. Johnston. 1990. Freshwater wetlands, rainfall, and the breeding ecology of White Ibises in coastal South Carolina. *Wilson Bull.* 102: 84-98.
- Blus, L. J. and T. G. Lamont. 1979. Organochlorine residues in six species of estuarine birds, South Carolina, 1971-1975. *Pestic. Monit. J.* 13: 56-60.
- Bush, A. O. and D. J. Forrester. 1976. Helminths of the White Ibis in Florida. *Proc. Helminthol. Soc. Wash.* 43: 17-23.
- Campbell, K. E. Jr. 1979. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. *R. On. Mus. Life Sci. Contrib.* 118: 1-203.
- Clapp, R. B., M. K. Klimkiewicz, and J. H. Kennard. 1982. Longevity records of North American birds: Gaviidae through Alcidae. *J. Field Ornithol.* 53: 81-124.
- Custer, T. W. and R. G. Osborn. 1978. Feeding habitat use by colonially breeding herons, egrets, and ibises in North Carolina. *Auk* 95: 733-743.
- De Santo, T. L., S. G. McDowell, and K. L. Bildstein. 1990. Plumage and behavioral development of nestling White Ibises. *Wilson Bull.* 102: 226-238.
- Dusi, J. L. and R. T. Dusi. 1968. Ecological factors contributing to nesting failure in a heron colony. *Wilson Bull.* 80: 458-466.
- Findholt, S. L. 1984. Status and distribution of herons, egrets, and ibises and related species in Wyoming. *Colonial Waterbirds* 7: 55-62.
- Forrester, D. J. 1980. Hematozoa and Mallophaga from the White Ibis, *Eudocimus albus* L., in Florida. *J. Parasitol.* 66: 5-8.
- Frederick, P. C. 1986. Parental desertion of nestling White Ibis (*Eudocimus albus*) in response to muscle biopsy. *J. Field Ornithol.* 57: 168-170.
- Frederick, P. C. 1987a. Extra-pair copulations in the mating system of White Ibis (*Eudocimus albus*). *Behaviour* 100: 170-201.
- Frederick, P. C. 1987b. Responses of male White Ibises to their mate's extra-pair copulations. *Behav. Ecol. Sociobiol.* 21: 223-228.
- Frederick, P. C. 1987c. Chronic tidally induced nest failure in a colony of White Ibises. *Condor* 89: 413-419.

- Frederick, P. C. and M. W. Collopy. 1989. Nesting success of five ciconiiform species in relation to water conditions in the Florida Everglades. *Auk* 106: 625-634.
- Frohning, P. C. and R. A. Beck. 1978. First breeding record of the White Ibis, *Eudocimus albus*, in Virginia. *Am. Birds* 31: 73-74.
- Girard, G. T. and W. K. Taylor. 1979. Reproductive parameters for nine avian species at Moore Creek, Merritt Island National Wildlife Refuge, Florida. *Fla. Sci.* 42: 94-102.
- Hammatt, R. B. 1981. Reproductive biology in a Louisiana estuarine heronry. M.S. thesis, Louisiana State Univ., Baton Rouge.
- Hancock, J. A., J. A. Kushlan, and M. P. Kahl. 1992. Storks, ibises, and spoonbills of the world. Academic Press, London.
- Henderson, E. G. 1981. Behavioral ecology of the searching behavior of the White Ibis (*Eudocimus albus*). M.S. thesis, Univ. South Carolina, Columbia.
- Hingtgen, T. M., R. Mulholland, and R. W. Repenning. 1985. Habitat suitability index models: White Ibis. U. S. Fish Wildl. Serv. Biol. Rept. 82 (10.93).
- Johnston, J. W. and K. L. Bildstein. 1990. Dietary salt as a physiological constraint in White Ibises breeding in an estuary. *Physiol. Zool.* 63: 190-207.
- Kushlan, J. A. 1973a. Promiscuous mating behavior in the White Ibis. *Wilson Bull.* 85: 331-332.
- Kushlan, J. A. 1973b. White Ibis nesting in the Florida Everglades. *Wilson Bull.* 85: 230-231.
- 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. Wading bird predation in a seasonally fluctuating pond. *Auk* 93: 464-476.
- Kushlan, J. A. 1976c. Feeding rhythm in nestling White Ibis. *Wilson Bull.* 88: 656-658.
- Kushlan, J. A. 1977a. Sexual dimorphism in the White Ibis. *Wilson Bull.* 89: 92-98.
- Kushlan, J. A. 1977b. Foraging behavior of the White Ibis. *Wilson Bull.* 89: 342-345.
- Kushlan, J. A. 1977c. Population energetics of the White Ibis. *Auk* 94: 114-122.
- Kushlan, J. A. 1977d. Growth energetics of the White Ibis. *Condor* 79: 31-36.
- Kushlan, J. A. 1977e. Significance of plumage color in the formation of feeding aggregations of ciconiiforms. *Ibis* 119: 361-364.
- Kushlan, J. A. 1977f. Differential growth of body parts in the White Ibis. *Auk* 94: 164-167.
- Kushlan, J. A. 1978a. Nonrigorous foraging by robbing egrets. *Ecology* 59: 649-653.
- Kushlan, J. A. 1978b. Commensalism in the Little Blue Heron. *Auk* 95: 649-653.
- Kushlan, J. A. 1978c. Feeding ecology of wading birds, pp. 249-296 in *Wading birds* (A. Sprunt, IV, J. C. Ogden, and S. Winckler, Eds.). Res. Rept. No. 7, Nat. Audubon Soc., New York.
- Kushlan, J. A. 1979a. Feeding ecology and prey selection in the White Ibis. *Condor* 81: 376-389.
- Kushlan, J. A. 1979b. Prey choice by tactile-foraging wading birds. *Proc. Colonial Waterbird Group* 3: 133-142.
- Kushlan, J. A. 1979c. Design and management of continental wildlife reserves: lessons from the Everglades. *Biol. Conserv.* 15: 281-290.
- Kushlan, J. A. 1981. Resource use strategies in wading birds. *Wilson Bull.* 93: 145-163.
- Kushlan, J. A. 1983. Special species and ecosystem preserves: colonial waterbirds in U.S. National Parks. *Environ. Manage.* 7:201-207.
- Kushlan, J. A. 1986. Responses of wading birds to seasonally fluctuating water levels: strategies and their limits. *Colonial Waterbirds* 9: 155-162.
- Kushlan, J. A. 1987. External threats and internal management: the hydrological regulation of the Everglades. *Environ. Manage.* 11: 109-119.
- Kushlan, J. A. 1989a. Avian use of fluctuating wetlands, pp. 593-604 in *Freshwater wetlands and wildlife* (R. R. Sharitz and J. W. Gibbons, Eds.). U. S. Dept. Energy, Symp. Ser. No. 61, Oak Ridge, TN.
- Kushlan, J. A. 1989b. Wetlands and wildlife, the Everglades perspective, pp. 773-796 in *Freshwater wetlands and wildlife* (R. R. Sharitz and J. W. Gibbons, Eds.). U. S. Dept. Energy Symp. Ser. No. 61, Oak Ridge, TN.
- Kushlan, J. A. and M. S. Kushlan. 1975. Food of the 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., L. G. Morales, and P. C. Frohning. 1985. Foraging niche relations of wading birds in tropical wet savannas, pp. 663-682 in *Neotropical ornithology*, A.O.U. Monograph 36.
- Martin, R. P. 1985. Ecology of foraging wading birds at crayfish ponds and the impact of bird predation on commercial crayfish harvest. M.S. thesis, Louisiana State Univ., Baton Rouge.
- Martin, R. P. and R. B. Hamilton. 1985. Wading bird predation in crawfish ponds. *La. Agric.* 28: 3-5.
- Nesbitt, S. A., W. M. Hetrick, and L. E. Williams, Jr. 1975. Foods of the White Ibis from seven collection sites in Florida. *Proc. Ann. Conf. Southeast. Assoc. Game and Fish Comm.* 28: 517-532.
- Olson, S. L. 1981. The generic allocation of *Ibis pagana* Milne-Edwards, with a review of fossil ibises (Aves: Threskiornithidae). *J. Vert. Paleontol.* 1: 165-170.
- Olson, S. L. 1985. Early Pliocene ibises (Aves, Plataleidae) from south-western Cape Province, South Africa. *Ann. S. African Mus.* 97: 57-69.
- Osborn, R. G. and T. W. Custer. 1978. Herons and their allies: atlas of Atlantic Coast colonies, 1975-1976. U. S. Fish Wildl. Serv. FWS/OBS-77/08.
- Palmer, R. S., Ed. 1962. *Handbook of North American birds*, Vol. 1. Yale Univ. Press, New Haven, CT.
- Parnell, J. A., D. G. Ainley, H. Blokpoel, T. W. Custer, J. L. Dusi, S. Kress, J. A. Kushlan, W. E. Southern, L. E. Stenzel, and B. C. Thompson. 1988. Colonial waterbird management in North America. *Colonial Waterbirds* 11: 129-169.
- Pence, D. B. 1971. The hypopi (Acarina: Hypoderidae) from the subcutaneous tissue of the White Ibis, *Eudocimus albus* L. *J. Parasitol.* 57: 1321-1323.
- Pennyquick, C. J. and T. De Santo. 1989. Flight speeds

- and energy requirements for White Ibises on foraging flights. *Auk* 106: 141-146.
- Petit, D. R. and K. L. Bildstein. 1986. Development of formation flying in juvenile White Ibises (*Eudocimus albus*). *Auk* 103: 244-246.
- Petit, D. R. and K. L. Bildstein. 1987. Effect of group size and location within the group on the foraging behavior of White Ibises. *Condor* 89: 602-609.
- Post, W., P. S. Coleman, and C. G. Belser. 1985. A study of the reproductive biology of wading birds nesting on Drum Island, South Carolina. *Charleston Mus. Ornithol. Contrib.* 6.
- Ramo, C. and B. Busto. 1982. Son *Eudocimus ruber* / *E. albus* distintas especies? *Doñana Acta Vertebrata* 9: 404-408.
- Ramo, C. and B. Busto. 1987. Hybridization between Scarlet Ibis (*Eudocimus ruber*) and the White Ibis (*E. albus*) in Venezuela. *Colonial Waterbirds* 10: 111-114.
- Root, T. 1988. *Atlas of wintering North American birds*. Univ. Chicago, Chicago, IL.
- Rudegeair, T. 1975a. The gular pouch of the female White Ibis. *Auk* 92: 168-169.
- Rudegeair, T. 1975b. The reproductive behavior and ecology of the White Ibis (*Eudocimus albus*). Ph.D. diss., Univ. Florida., Gainesville.
- Schreiber, R. W. and E. A. Schreiber. 1978. Colonial bird use and plant succession on dredged material islands in Florida. Vol. 1: Sea and wading bird colonies. U. S. Army Engineer Waterways Expt. Sta. Vicksburg, MS. Tech. Rep. D-78-14.
- Shepherd, P., T. Crockett, T. L. De Santo, and K. L. Bildstein. 1991. The impact of Hurricane Hugo on the breeding ecology of wading birds at Pumpkinseed Island, Hobcaw Barony, South Carolina. *Colonial Waterbirds* 14: 150-157.
- Shields, M. A. 1985. A study of Fish Crow predation on eggs of the White Ibis at Battery Island, North Carolina. M.S. thesis, Univ. North Carolina-Wilmington.
- Shields, M. A. and J. F. Parnell. 1986. Fish Crow predation on eggs of the White Ibis at Battery Island, North Carolina. *Auk* 103: 531-539.
- Simpson, M. B. Jr. 1988. Status of the Scarlet Ibis in South Carolina: historical records from John Abbot and Alexander Wilson. *Chat* 52: 4-5.
- Smithe, F. B. 1975. *Naturalist's color guide*. American Museum of Natural History, NY.
- Spil, R. E., M. W. Van Walstijn, and H. Albrecht. 1985. Observations on the behaviour of the Scarlet Ibis, *Eudocimus ruber*, in Artis Zoo, Amsterdam. *Bijdr. Dierkd.* 55: 219-232.
- Sprunt, A. Jr. 1944. Northward extension of the breeding range of the White Ibis. *Auk* 61: 144-145.
- Stephens, J. L. 1950. White Ibis found nesting in North Carolina. *Chat* 14: 49-50.
- Stevenson, H. M. 1957. The relative magnitude of the trans-Gulf and circum-Gulf spring migrants. *Wilson Bull.* 69: 39-77.
- Stinner, D. H. 1983. Colonial wading birds and nutrient cycling in the Okefenokee Swamp ecosystem. Ph.D. diss., Univ. Georgia, Athens.
- Teal, J. M. 1965. Nesting success of egrets and herons in Georgia. *Wilson Bull.* 77: 257-263.
- Urban, E. K. 1974. Flight speed and wing flapping rate of Sacred Ibis. *Auk* 91: 423.
- Vleck, C. M., D. Vleck, H. Rahn, and C. V. Paganelli. 1983. Nest microclimate, water-vapor conductance, and water loss in heron and tern eggs. *Auk* 100: 76-83.
- Wayne, A. T. 1910. *Birds of South Carolina*. Contrib. Charleston Mus. 1.
- Wayne, A. T. 1922. Discovery of breeding grounds of the White Ibis in South Carolina. *Bull. Charleston Mus.* 17: 27-30.
- Wetmore, A. 1956. Checklist of the fossil birds of North America and the West Indies. *Smithson. Misc. Coll.* 131, No. 5.

ABOUT THE AUTHORS

James A. Kushlan received his doctorate from the University of Miami, studying the ecology of the Everglades and its wading birds. He is currently Professor of Biology at the University of Mississippi and Chair of the Department of Biology. He has studied wading birds and wetlands for over twenty years, publishing over 150 papers on these topics. He also is coauthor of the *Herons Handbook* (1974, Harper and Row) and *Storks, Ibises, and Spoonbills* (1992, Academic Press). He has served in numerous professional capacities. He is a Fellow of the American Ornithologists' Union and Co-chair of the Herons Specialist Group (ICBP/IWRB/IUCN).

Keith Bildstein received his Ph.D. from Ohio State University, studying the wintering ecology of birds of prey in open-habitats of the north-central U.S. Following graduation (1978), he taught briefly at the College of William and Mary and then went on to Winthrop College, Rock Hill, SC, where he was professor of biology and ecology for 14 years. While at Winthrop, he began research on ibis feeding ecology, based at the Belle Baruch Institute of Marine Biology. His recent studies have focused on flamingos. He is the author of the forthcoming *White Ibis: Wetlands Wanderer* (Smithsonian Press) and currently Director of Research at Hawk Mountain Sanctuary, Kempton, PA 19529.