

White Ibis

Eudocimus albus

Order:

PELECANIFORMES

Family:

THRESKIORNITHIDAE

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The White Ibis is a striking, white wading bird with a long, 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. Ibises are known for frequent shifts in roost and colony sites ([Bildstein 1990](#), [Gehlbach 1981](#)), substantial dispersal and migration distances ([Frederick et al. 1996](#), [Melvin et al. 1999](#)) and variable breeding seasons ([Heath 2002](#), [Piazza and Wright 2004](#), [Frederick et al. 2006](#)). Nomadic movements and flexible reproductive schedules allow ibises to exploit the changing availability of shallow water feeding sites and concentration of its main prey, crustaceans and small fishes ([Kushlan 1979d](#), [Gawlik 2002](#)). Because of salt stress, nestlings do not develop normally on brackish water crustaceans, so nearby freshwater feeding sites are essential for successful breeding at coastal colonies ([Johnston and Bildstein 1990](#)).

The dependence of White Ibis on favorable feeding conditions in wetlands, the conspicuous nature of their large flocks and colonies, and their eye-catching appearance has made the species a symbol for wetland conservation and restoration, especially in Florida where ibis habitat is threatened by development, pollution, and water management. Numerous studies have investigated trends in White Ibis distribution, abundance and reproductive success ([Crozier and Gawlik 2002](#), [Crozier and Gawlik 2003b](#), [Frederick and Ogden 2001](#), [Frederick et al. 2001](#), [Frederick and Ogden](#)

[2003](#), [Stolen et al. 2005](#), [Herring 2008](#)), and/or ibis contaminant levels ([Frederick et al. 2002](#), [Frederick et al. 2004a](#), [Heath and Frederick 2005](#), [Rodgers 1997](#)), and used this information to infer ecosystem health.

No subspecies are recognized, but the Scarlet Ibis (*Eudocimus ruber*) of South America is closely related and is considered by some to be a conspecific color morph.



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

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Appearance

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.

Similar Species

Juveniles mostly brown; distinguished from dark *Plegadis* ibises by white rump and underparts. Youngest stages of White Ibis and Scarlet Ibis are virtually identical until the latter begin to develop pink tinges on rump and elsewhere.

Detailed Description

White Ibis have 10 functional primaries, 9 secondaries (including 3-4 tertials), and 12 rectrices. No substantial geographic variation in plumage aspect or molt strategies has been reported.

Plumages

See Bent ([Bent 1926](#)), Palmer ([Palmer 1962a](#)), Oberholser ([Oberholser 1974](#)), Hancock et al. ([Hancock et al. 1992](#)), and Bildstein ([Bildstein 1993](#)) for detailed plumage-aspect descriptions. Sexes show similar aspects in all plumages, with exception of variation to p7 in definitive aspect of some females (see below).

Natal Down primarily black, dark brown and gray, blackest on head and brownest on throat ([Bent 1926](#), [Oberholser 1974](#)).

Juvenile Plumage

(Jun-Dec). Aspect with head, neck, and upper breast brownish gray to sandy brown; mantle and uppersides of wings blackish neutral gray (#82); and rump, uppertail coverts, undersides, and underwing coverts white to creamy white. Head and neck streaked Vandyke brown ([Smithe 1975](#): color #121) and creamy white, giving an overall impression of glaucous (#80), darkest on head and upper neck ([De Santo et al. 1990](#)); streaking becomes narrower on throat and lower neck and is represented by shaft streaks on breast ([Beebe 1914](#)). Body feathers with concealed white bases. Primaries, secondaries, and rectrices blackish neutral gray with white bases. By three months, juvenile 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).

Formative/First Alternate Plumage

(Oct-Aug). Early replaced formative feathers of head and neck dark, similar to juvenile feathers; later replaced feathers of back increasingly white. Thus, individuals in second spring and summer retain sandy brown streaking on head and neck but mostly white to white back. Tertials and central 1-4 rectrices sometimes white; otherwise, dark juvenile upperwing coverts and flight feathers retained. If juvenile 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 ([Beebe 1914](#)), indicating how hormonal change affects pigment deposition.

Second Basic Plumage

(Sep-May). Aspect similar to definitive basic plumage (below) but head and neck feathers fringed brownish. Most to all of these replaced by white feathers during 2nd prealternate molt in Feb-Jun; some individuals become indistinguishable from older birds in definitive aspect by Jun.

Definitive Basic Plumage

(Oct-Apr). All feathers white, except for tips of three or four longest primaries, iridescent dark green. Occasional females can have tip of p7 partially or entirely white ([Pyle 2008](#)) thus having only three outer primaries (p8-p10) with dark tips. Most to all males appear to have dark tip to p7 and four dark-tipped primaries overall. Extent of black to p7 may correlate with age in females; study needed.

Definitive Alternate Plumages

(Apr-Sep): Aspect similar to that of definitive basic plumage (above) but some to most head and neck feathers apparently replaced, contrastingly glossy when fresh. Head, neck, and back can become soiled buff to brownish in some individuals by summer.

Molts

Molt and plumage terminology follows Humphrey and Parkes ([Humphrey and Parkes 1959](#)) as modified by Howell et al. ([Howell et al. 2003](#), [Howell et al. 2004](#)). White Ibis appears to exhibit a Simple Alternate Strategy ([Howell et al. 2003](#)), including complete prebasic molts, a single partial first-cycle molt, and limited prealternate molts in definitive cycles ([Figure 2](#)). The single inserted first-cycle molt may represent a merging of preformative and first prealternate molts formerly present in ancestral species ([Pyle 2008](#)); study needed. Individuals can be aged through first part of 2nd cycle, after which definitive aspect assumed.

Prejuvenile (First Prebasic) Molt

complete, May-Jul, in or near nest.

Preformative/First Prealternate Molt

Limited-partial, Oct-Apr, commencing on or near breeding grounds and completing on non-breeding grounds. Includes most to all body feathers, and sometimes 1-2 tertials and 1-4 central rectrices, but no wing coverts or other flight feathers. Begins with greater upperwing coverts and feathers on the back, followed by scapulars, and spreads posteriorly to the tail ([Beebe 1914](#)), although considerable overlap occurs. Some head feathers possibly replaced twice, in which case both preformative and first prealternate molts could be defined ([Pyle 2008](#)); study needed.

Second Prebasic Molt

Complete, Apr-Oct, variably on or near breeding and/or non-breeding grounds. May start earlier in tropical populations.

Second And Definitive Prealternate Molt

Limited-partial, Feb-Apr, on or near non-breeding grounds. Includes feathers of the head and neck; possibly other body feathers, but no wing coverts or flight feathers.

Definitive Prebasic Molt

Complete, Jul-Sep, on or near breeding grounds, often in dense mangroves. Individuals usually complete 90% of body molt within 60 days; however, initiation of molt can be delayed in breeding individuals. Molt begins on back, spreading to wing scapulars, coverts, remiges, and rectrices. Flight feathers replaced in late summer to early fall: primaries replaced distally (p1-p10), secondaries replaced proximally from s1 and s5 and distally from the tertials, and rectrices likely replaced distally (r1-r6) on each side of tail. Molt appears to complete fairly rapidly and may include brief periods of flightlessness, not affecting feeding or predation risk within dense molting habitats.

Field studies from [Heath 2002](#) showed the following molt details: No significant differences between male and female molt patterns or brood patch development. Of birds captured during courtship display (n = 15), 50% had begun to develop brood patches; by egg production and incubation, 90% showed bare, vascularized brood patches (n = 26). During chick rearing, brood patches were less vascularized and birds tended to groom feathers over the bare area. Some birds captured in the chick-brooding stages showed down growth in the brood patch region (12%, n = 17).

Most White Ibises (85%; n = 27) molted 5 – 85% of their body feathers during the pre-breeding stage. During the breeding season, ibises molted a lower proportion of their body feathers (5 – 20%) than pre-breeding birds, but reproductive birds did show signs of molt in all stages. Of display birds, 33% (n = 18) had at least 5% of feathers in sheaths. In other stages: 16% of birds in egg production (n = 19), 14% of incubating birds (n = 14), and 15% of chick rearing birds (n = 20) were also molting ([Heath 2002](#)).

Bare Parts

Bill, Gape, and Facial Skin

Bill pinkish with dusky bands in juvenile, becoming salmon or flesh color (color #5) later in first cycle and in Oct-Mar during definitive cycles. Loral skin blackish in juvenile, becoming pinkish during first cycle. During courtship in Mar-Apr, loral skin and proximal portion of the bill turns geranium (12) distal part turns black in North America: amount variable, usually about two thirds but in some cases the entire bill. Bill returns to salmon color slowly in Jun-Oct; distal portion often remaining gray for several months. Both sexes (not male alone as often reported) also 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 1973d](#), [Rudegeair 1975a](#) or [Rudegeair 1975b](#)). 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 1986b](#)).

Iris

Dark in juvenile, becoming sky blue (#66) in all seasons by end of second cycle.

Legs And Feet

Dark in juvenile becoming flesh color by end of second cycle. During adult courtship they turn geranium, along with bill and facial skin.

Measurements

Male significantly larger than female in all measurements; little overlap ([Table 1](#), [Babbitt and Frederick 2007](#), [Herring 2008](#)). Adults larger than juveniles in most measurements for first 6-9

months.

Potential cline of decreasing size from North America through Central America to South America ([Van Wieringen and Brouwer 1990](#)), but data needed from intermediate populations. White birds in South America noticeably smaller than those from North America ([Hancock et al. 1992](#)).

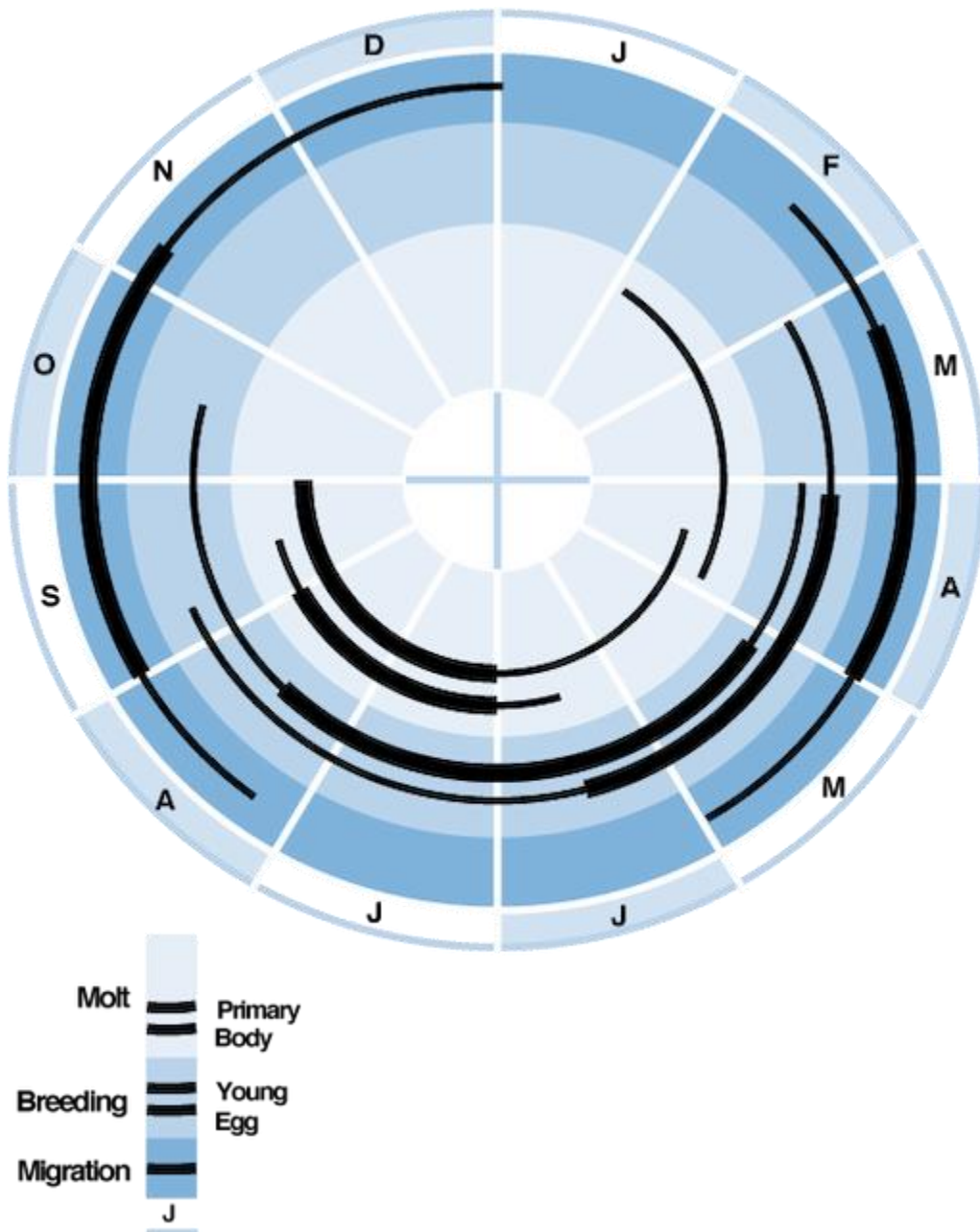


Figure 2. Annual cycle of the White Ibis

Systematics

Geographic Variation

Populations of the White Ibis *sensu stricto* are similar throughout the species' North American range. Potential cline of decreasing size from North America through Central America to South America ([Van Wieringen and Brouwer 1990](#)), but data needed from intermediate populations. White birds in South America noticeably smaller than those from North America, and South American birds in full breeding condition have the bill more fully black, with breeding males there more likely to have the throat sac fully developed ([Hancock et al. 1992](#)).

Subspecies

Hancock et al. ([Hancock et al. 1992](#):155) summarized extensive morphological data and concluded that the White Ibis was comprised of two subspecies differing in size and in bare part development and coloration when in full breeding condition. "Northern" birds, those that occur from Panama northward (type locality = South California), would be *E. a. albus* (Linnaeus, 1758), which averages larger and in full breeding condition has the bill only partly black and male gular sacs underdeveloped. Because Hancock et al. ([Hancock et al. 1992](#)) followed Ramo and Busto ([Ramo and Busto 1982](#), [Ramo and Busto 1987](#)) in treating the Scarlet Ibis as conspecific with the White Ibis, the name *E. a. ruber* (Linnaeus, 1758) was available for birds in South America, which average smaller and in full breeding condition have the bill largely black and male gular sacs well developed. White birds in South America are most commonly seen pairing with scarlet birds ([Ramo and Busto 1987](#)), suggesting that the white birds in South America are a color morph of that species. However, with the treatment of the Scarlet Ibis as a distinct species ([American Ornithologists' Union 1998a](#)), the South American subspecies of the White Ibis is unnamed (Patten in prep.).

Related Species

The traditional order Ciconiiformes may be an artificial assemblage of long-legged waterbirds ([Olson 1978b](#)), with ibises (Threskiornithidae) a transitional group with similarities to the cranes (Gruiformes) and shorebirds (Charadriiformes). DNA evidence supports a paraphyletic grouping but nevertheless suggests that storks, ibises, herons, and flamingos are closely related ([Sibley and Ahlquist 1990](#), [Sheldon and Slikas 1997](#)). Within the Threskiornithidae, the genus *Plegadis* is posited to be sister to the genus *Eudocimus* ([Mayr and Short 1970](#)).

Relationship of the White Ibis of North America and Scarlet Ibis of South America remains controversial. Ridgway (1884) considered them one species, but more often they have been treated as two. Hancock, Kushlan, and Kahl ([Hancock et al. 1992](#)) reviewed the controversy and evidence and concluded that the two form a single species. Their decision was 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 further study.

Distribution, Migration, and Habitat

Distribution in the Americas

Breeding Range

Nomadic tendencies and shifting populations year to year make accurate depiction of breeding range a moving target. In general, however, primarily coastal from Virginia through Louisiana and Texas, with centers of abundance in the Carolinas, Florida, Louisiana and Texas; also inland from the coast in S. Carolina through Florida; local in the Caribbean, and along both coasts of Mexico and Central America south to coastal n. South America; rare and local along Pacific coast in Ecuador and Peru ([Figure 1](#)).

For details on distribution of US populations since 2000, see Demography and Populations: population status.

In Mexico and n. Central America, sea level to 150 m from Baja California Sur, Sonora and Tamaulipas south along both coasts to Chiapas (possibly El Salvador) and n. Honduras (Bay Islands) ([Howell and Webb 1995](#)). In Costa Rica, locally common resident in lowlands of both slopes, with centers of abundance in Golfo de Nicoya, Tempisque basin, and Rio Tempisque; occasionally common in Rio Frio region and locally farther south ([Stiles and Skutch 1989](#)). In Panama, primarily Pacific slope with nesting recorded on islands in Panama Bay and on Azuero Peninsula in Herrera and Los Santos ([Ridgely and Gwynne 1989](#)). Common breeder on Cuba, especially coastal regions (Isle of Pines; northern cays; [Garrido and Kirkconnell 2000](#)), and on Hispaniola, but rare and local on Jamaica and not known to breed elsewhere on Caribbean islands (e.g., Bahamas, Puerto Rico, Windward Isles) ([Raffaele et al. 1998](#)), nor on Trinidad or Tobago ([French 1991a](#)).

In Colombia, possible breeder but no clear records ([Hilty and Brown 1986](#)). Known to breed in Venezuela along north coast, but rare; local inland in south (llanos), where mixed colonies (Scarlet and White, and hybrids) are found, with Scarlets predominating ([Hilty 2003](#)). Along Pacific coast of n. South America, in Ecuador, rare and local breeder: "... Numbers ... highest in the Rio Guayas estuary ... where the species is resident and almost certainly breeds. ... small nesting colony also seen in mangroves near Puerto Pitahaya in El Oro in Apr 1993.... Presumably the species breeds locally in Manabi' and Esmeraldas as well, as there is no evidence of any surge in numbers when migrants would be expected to be arriving from the north" ([Ridgely and Greenfield 2001a](#)). In Peru, may breed in small numbers along the northwest coast, but confirmation lacking (T. Schulenberg).

Through n. and e. South America, Scarlet Ibis predominates. However, scarlet birds often documented in the range of white birds and almost certainly were natural visitors to Florida historically ([Simpson 1988a](#)). Some Scarlet Ibis 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](#)).

Winter Range

In winter, coastal Carolinas south over rest of breeding range. Normal non-breeding range is wider because of post-breeding dispersal, often northward in late summer and fall – e.g., regular as far north as Delaware ([Hess et al. 2000b](#)) and se. NY State (Long I., Levine 1998; [Figure 1](#)).

Nature of Migration

A highly nomadic species undertaking postbreeding dispersals, migrations, prebreeding intraregional population shifts, and regular rainfall-initiated shifts between interior wetlands and coastal habitats (Kushlan [Kushlan 1976c](#), [Kushlan 1979d](#), [Kushlan 1981](#); [Kushlan et al. 1985](#), [Frederick et al. 1996](#), [Melvin et al. 1999](#)). In general, breeds along Gulf and south Atlantic coasts, inland and coastal sites in Florida, Cuba and coastal Central and South America. Winter range varies; usually southern portion of North American range, Gulf coast, Greater Antilles, coastal Central and South America (see Distribution). Links between specific breeding and non-breeding ranges are unknown. Postbreeding dispersals often take individuals outside normal nonbreeding range ([Figure 1](#)). 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 (www.ebird.org).

Dispersing northern birds begin migration by drifting southward into Georgia, Florida, along Gulf of Mexico to Mexico, also to Cuba. In 1950s and 1960s numerous birds banded in S. Carolina as nestlings were recovered in Cuba. Wintering birds from North America may move as far as Central America, and one bird banded as a nestling in coastal S. Carolina was recovered in Colombia ([Post et al. 1985](#), [Melvin et al. 1999](#)).

Timing and Routes of Migration

Timing and routes remain unclear. Band returns suggest a general north – south migration corridor ([Melvin et al. 1999](#)). Large flocks of ibises move south through s. Florida in fall (Oct-Nov); species also winters along the Florida coast and inland wetlands (JH). Birds wintering in s. Florida tend to depart roosts for northern breeding areas mid-Mar through Apr ([Frederick et al. 2001](#)). Although departure for spring migration is protracted, S. Carolina birds return to breeding sites in large numbers over just a few days, suggesting birds linger along migration route until conditions permit more rapid dispersal into breeding areas.

Likely trans-Gulf/Caribbean migration: ibises banded in North America have been recovered in Cuba and Central and South America. Also large flocks of ibises regularly fly south from the Florida Keys (across the straits of Florida) in September and October (JH). More information needed on migration and wintering sites of specific population segments.

Control and Physiology of Migration

No information.

Habitat in 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 1978c](#)). Historically, the largest populations foraged in interior freshwater marshes and swamps of the Everglades ([Bancroft 1989](#), [Ogden 1994](#)).

Most nesting birds forage in freshwater 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 1978a](#), [Kushlan 1979d](#), [Henderson 1981](#), [Bildstein 1983](#)).

In s. Florida Everglades ([Kushlan 1979d](#)), 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%); density of foraging birds positively correlated with % open prairies ([Surdick 1998](#)). Ciconiiform birds in general prefer open, sparse emergent vegetation ([Lantz 2008](#)). 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 1978a](#)). In the Okefenokee Swamp, GA, 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. Although their sample size was low, Gawlik and Crozier ([Gawlik and](#)

[Crozier 2007](#)) showed that water depth was a more important ibis foraging habitat cue than change in water depth (drying rate).

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](#), [De Santo et al. 1997](#)). 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](#)).

Habitat in Migration

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

Habitat in the Overwintering Range

Few data. Predominantly coastal, especially in and near mangrove swamps, *Spartina* marshes, and coastal lagoons, where they often specialize on fiddler crabs (*Uca*). In Florida Bay, forage on mud-flats and swallow tidal wetlands (JH). In S. Florida, wintering birds regularly found in freshwater marshes in large numbers, moving across the landscape following drying pools of water.

Historical Changes to the Distribution

Extension of breeding range north of Georgia occurred mainly in 20th century ([Wayne 1922](#), [Sprunt 1944a](#), [Stephens 1950](#), [Frohring and Beck 1978](#)). Large increases in population 1980-2005 in Texas, Louisiana, South Carolina, and N. Carolina, decreases in s. Florida ([Frederick et al. 1996](#); see Demography and Populations: status and trends). Northward dispersal post-breeding accelerated in 1970's and 80's, perhaps with expansion of breeding range into Virginia during that period (e.g., Delaware: [Hess et al. 2000b](#); NY State: [Levine 1998](#)).

Fossil History

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

Diet and Foraging

Feeding

Main Foods Taken

Aquatic crustaceans and insects.

Foraging Conditions

Prey availability depends on multiple environmental variables. In a controlled study that manipulated prey availability, more ibises foraged in ponds with high prey density and low to medium water depths than in ponds with lower fish density and deeper water (Gawlik 2002). In the Florida Everglades, foraging ibises were most likely to be found in low water ($14.0 \text{ cm} \pm 5.0 \text{ SD}$, max depth 24 cm), high crayfish density, and wet prairie areas (Surdick 1998, Lantz 2008). Decoys placed in shallow water ($10.5 \pm 0.67 \text{ cm}$) with low vegetation ($25.6 \pm 5.14 \text{ cm}$) were more successful at attracting ibises to foraging areas than decoys placed in deeper water ($17.1 \pm 1.85 \text{ cm}$) with taller vegetation ($49.0 \pm 9.18 \text{ cm}$) (Heath and Frederick 2003).

In *Spartina* marsh, ibises forage most often in areas with $< 30 \text{ cm}$ vegetation (Petit and Bildstein 1987). In a study on the effect of periphyton density, water depth, water temperature, wind speed, vegetation density, Julian date, time after sunrise, fish density, prawn density and crayfish density on foraging success, only periphyton density negatively affected ibis foraging success; fish density was positively correlated with success (Surdick 1998). Emergent vegetation density and structural complexity were important factors determining foraging success (Adams and Frederick 2008a).

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. 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. Can pick prey items from the surface of the ground or a plant; sweeps bill like spoonbill (Kushlan Kushlan 1977b, Kushlan 1978b, Kushlan 1979e). 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 apart. Bill has slight gap in center, which permits tips to function tweezer-like in grabbing and holding a prey item. Potential prey items seldom pursued, unless on land or in very shallow water.

Review by Kelly et al. (2003) refers to foraging behavior in Kushlan (Kushlan 1976a) to describe the following techniques used by ibis: stand and wait, walk slowly ($\leq 1 \text{ step/s}$), walk quickly ($\geq 1 < 2 \text{ steps/s}$), running ($> 2 \text{ steps/s}$), foot raking, head swinging, groping, probing, pecking, stealing, and prey dropping. Prey dropping describes a focal bird repeatedly dropping a prey item

rather than eating it. Foraging techniques vary according to prey type and availability (Henderson 1981).

Prey items swallowed with a quick forward thrust of head (Kushlan 1978b). 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. 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 1979d). Proficiency in handling prey improves with age (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 1978c, Frederick and Bildstein 1992). 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 (Frederick 1985). Ibises used by other species commensally, with visually foraging species following closely behind walking ibis, using it as a beater (Kushlan 1978a). In turn, ibises follow ungulates in flooded pastures in Venezuelan llanos.

Intra-specific predation rare, but reported from one colony in s. Florida where a fledgling attacked and probably ate a nestling (Herring et al. 2005).

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 1979d). 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, Bildstein 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 1976d, Kushlan 1977f). Most (97%, n = 286) ibises leaving colony landed near or with conspecifics in foraging flocks (Smith 1995d). Three-dimensional decoys placed in flock-like arrangement can successfully lure individuals to specific areas (Crozier and Gawlik 2003a, Heath and Frederick 2003). Individually marked birds may 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.

Males larger than females (see Table 1), thus have higher overall energy costs (Bildstein 1987b). 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 1987b), captive males were more successful than females at extracting fiddler crabs from artificial burrows that approached the length of females' bills (Bildstein et al. 1989).

Diet

Major Food Items

Small aquatic and semiaquatic 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 1979d](#), [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, newts ([Kushlan 1980](#)), 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*). However, in winter many forage in freshwater areas, particularly in s. Florida. In non-breeding season in Florida, earthworms, cockroaches and other insects in lawns are common prey, especially during the wet season when flooded wetlands are typically too deep for foraging.

Most information on prey from boluses collected from young birds. In s. Florida fish and crustaceans averaged about 2 cm long (fish 2.0 cm [SE = 0.4, n = 341]; crustaceans 2.2 cm [0.6, 62]). In another study crayfish averaged 18.7 mm (se = 0.4 mm) carapace length (equivalent to approximately 3.3 cm total length, [Dorn et al. 2008](#)). Compared with available crayfish, ibises selected larger size classes (> 20mm). In s. Florida fish commonly consumed when available include mosquitofish (*Gambusia holbrooki*), flagfish (*Jordanella floridae*) and occasionally sunfish (*Lepomis spp.*, [Dorn et al. 2008](#)). In Louisiana crayfish (*Procambarus*) averaged 4.2 cm (2.2, 94) ([Martin and Hamilton 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 ibis 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 long.

Quantitative Analysis

Diet in inland 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 same region [Dorn et al. \(2008\)](#) report high variability (11-fold difference) in proportions of fish and crayfish consumed among colonies. 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 1976](#)): 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](#)).

In llanos of Venezuela ([Aguilera et al. 1993](#)): coleoptera 48%, other insects 34%, crustaceans 3%, fish 7% of prey items from 9 ibis stomachs.

Food Selection and Storage

Food selection exhibited through tactile and visual foraging (Kushlan [Kushlan 1978b](#), [Kushlan 1979d](#), [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](#)). Able to catch small fish in situations when they are trapped in shallow water, although some kinds are selected among those available, such as *Cyprinodon variegatus*, *Fundulus confluentus*, *Jordanella floridae*. Do not select relatively high energy prey, but when raising nestlings select low-salt prey (crustaceans and fish) captured at freshwater sites ([Bildstein et al. 1990](#), [De Santo et al. 1997](#)). Will reject prey requiring prolonged handling time.

Nutrition and Energetics

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 metabolism 138.7 kcal/d ([Kushlan 1977d](#)). 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 [Kushlan 1977d](#), [Kushlan 1977c](#)). 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.

For inland Florida nesters, crayfish made up 60% of energy consumed in s. Florida and 72% in central Florida ([Kushlan 1979d](#)). In coastal S. Carolina, adults feeding on fiddler crabs need to do so for 2.5 (females) to 3.5 (males) hr/d ([Bildstein 1987b](#)). 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 Defecation

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

Sounds and Vocal Behavior

Vocalizations

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. Birds in foraging flocks give soft *honk* noises.

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](#), [Bildstein 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 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 Santo 1989](#)). Ibises arriving to foraging areas or colonies may 'stoop' from high altitudes – folding wings and losing altitude rapidly. 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

Chicks reported to swim if they fall in water ([Audubon 1844](#)).

Self-Maintenance

Preening, Headscratching, Stretching, Bathing, Anting, Etc

Spend much of the day preening ([Rudegeair 1975b](#)), usually at day roosts. Often interrupt feeding bouts to preen. Ventral surface (belly) 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 under-wing. Back preened directly by turning head, lower belly 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. Allo-preening noted only during courtship and nest-building.

Bathe in water 5–20 cm deep. Crouch into water, submerging and shaking first one wing and then the other, or both simultaneously, as though in flapping flight. Usually followed by prolonged preening. Group bathing common during courtship at edges of colonies.

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 ([Rudegeair 1975b](#)). Rate increases with increasing temperature.

Sleeping And Roosting

Typically sleep with head tucked underwing 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 1977d](#)). 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 1987b](#)).

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 (Frederick 1986a, Babbitt and Frederick 2007). Propensity to fight and fighting ability vary considerably among males. Males fight with males of similar bill length, and longer bills are important in determining outcome of fights over mates and nests, and in captivity, determining whether males breed (Babbitt and Frederick 2007). 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 (Frederick 1987b). Some of these attacks result in bleeding. Unattended eggs at colony sites are sometimes destroyed by adults prospecting for nest sites (Frederick 1987c).

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

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 in immediate area of nest (see Sexual Behavior) 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 1976); in S. Carolina in needle rush (*Juncus roemerianus*), 0.69 m ($n = 54$; Frederick 1987b), in mulberry (*Morus* sp.), 1.04 m ($n = 104$; Post et al. 1985); in mangroves in Florida 0.54 m (Girard and Taylor 1979).

Dominance Hierarchy

Stable and somewhat linear hierarchies in captive groups are apparently based on relative size, both within and between sexes ([Bildstein 1993](#)). In a captive flock, male Scarlet Ibises with longer bills were more likely to win male-male interaction than males with shorter bills ([Babbitt and Frederick 2007](#)). No information on dominance hierarchies in the wild.

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 1962a](#), [Rudegeair 1975b](#), [Hancock et al. 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. Group bathing by hundreds of birds at a time may also be a form of display, usually performed on the edges of breeding colonies during courtship. Display preening, head rubbing, and bill popping are the primary mating 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 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 sometimes becomes bloodied. During courtship, the pair uses greeting displays and mutual stick shaking, typically with necks crossed ([Figure 3](#)); 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 the 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. Female cradles male by partially lifting wings while standing, raises tail during final moments. 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 ([Frederick 1987b](#)). 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.

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 ([Smith 1995d](#)).

Play

Young at colony sites manipulate twigs and grassy vegetation in their mandibles. Well-fed captive individuals pick up and work over prey in their bills without eating them.

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 1978a](#)). Also subject to piracy from other species feeding within its aggregation ([Kushlan 1978c](#)). 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 Fish Crows (*Corvus ossifragus*) ([Shields and Parnell 1986](#)). Boat-tailed Grackles (*Quiscalus major*), both adult and ambulatory young Black-crowned Night-Herons (*Nycticorax nycticorax*), gulls, and perhaps vultures, as well as to Northern Opossums (*Didelphis marsupialis*), Raccoons (*Procyon lotor*), and rat snakes (genus *Elaphe*). At some locations as many as 44% of the eggs are lost to Fish Crow predation ([Shields and Parnell 1986](#)) and at others little or no nest predation ([Frederick and Collopy 1989c](#)). 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 1968a](#), [Bildstein et al. 1990](#)). Eggs and young are also at risk when other ibis steal nest material and knock out nest contents.

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 1987a](#)). Disturbance increases rates of predation significantly (see Conservation and Management).

Males tend to remain at the nest, as any departures put nest and its contents at risk and females at risk of extra-pair copulations ([Kushlan 1973d](#), [Frederick 1987b](#)). 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 fly-overs 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

In North America, onset of breeding readiness depends on photoperiod, as captive birds in Florida and S. Carolina begin to experience bare-part color changes in early spring (March). In coastal S. Carolina, massive courtship flights occur near colony sites following spring rains in March and April.

In Florida, nesting can be delayed for many months until feeding conditions become suitable, even until late summer or fall ([Kushlan 1976c](#)). 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 8 wk to 6 mo ([Williams 2007b](#)).

Nesting starts when conditions are suitable for highly effective foraging, primarily the availability of sufficiently shallow freshwater wetlands ([Kushlan 1976c](#), [Bildstein et al. 1990](#)) to produce high prey availability ([Gawlik 2002](#), [Herring 2008](#)). Actual timing differs substantially across range, even during seasonal drying period in Everglades. In coastal colonies in temperate zone, nesting occurs during or immediately following the “big rains” of the late winter and spring. In s. Florida, nesting in the interior ends with the onset of rainy season (Jun – Jul), whereas coastal colonies in the same area historically nested well into summer ([Ogden 1994](#)). Due to differing topography, such rains probably provide foraging sites in freshwater wetlands near coastal colony sites in S. Carolina ([Bildstein et al. 1990](#)) but interrupt drying patterns and prey availability in flat, continuous wetlands of s. Florida.

Nest building usually begins in spring to late summer, earlier (late Feb to Jun) in interior s. Florida than farther north, or along the Florida coast (Mar-Jun; [Kushlan 1973e](#), [Kushlan 1977d](#), [Frederick et al. 2001](#)). In S. Carolina, nest building usually begins between early Mar and early Jun ([Beckett III 1965](#)), usually within 10 d after the birds arrive from the south. In N. Carolina, in late Mar to early Apr ([Allen-Grimes 1982](#), [Shields and Parnell 1986](#)). See [Figure 2](#).

Will renest following nest failures early in the breeding season, though the proportion doing this is unknown and may be small. Some ibises may 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 ([Williams 2007b](#)). Extremes for eggs in s. Florida, Feb–Sep; for S. Carolina, Apr–Jul ([Bildstein 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. In captivity with unlimited food, 3 – 4 nesting attempts and 3 broods possible over nearly 6-month breeding season in n. Florida (PCF unpubl.).

Physiology

White Ibises have cyclic gonad development that corresponds to reproductive activity; endocrine patterns are similar to other seasonal breeders with bi-parental care. Males and females have high testosterone concentrations during the display stage that decrease later during incubation and chick rearing ([Heath et al. 2003](#)). Testosterone concentrations are correlated with female bare part color change ([Heath and Frederick 2006](#)). Female estradiol is highest during display and chick rearing stages, male estradiol lowest during copulation. Female progesterone remains high during reproduction, male progesterone does not change.

Ibis body condition changes during reproductive activity, and between years ([Herring 2008](#)). Males may store energy before the egg-laying stage when they spend most of the time at the nest. Female condition improved from non-breeding to display stages, then decreased throughout the rest of the season ([Heath and Frederick 2003](#)).

Adult body condition appears to be critical for nesting. In captivity, mean gain of 107 g for males and females in the month prior to courtship; individuals capable of gaining this amount in < 14 d. During incubation, males lost an average of 43.2 g (4.6%; n = 14;) while females lost an average of 21.7 g (2.9%); n = 3). Females varied significantly in body condition throughout the nesting stages while male condition followed a similar trend but did not vary significantly. Highest body condition indices in both sexes were observed during courtship ([Babbitt and Frederick 2008](#)).

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 1987b](#)). Although individuals maintain nest territories (see Behavior: territoriality), neighborhoods form as tight aggregations of nests with few nests added after the initial establishment of a neighborhood. 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. In coastal NC, 94% of colonies were on islands created by dredge-spoil operations.

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 ([Rudegeair 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 1976](#)). In a colony in coastal N. Carolina, 38% in scattered red cedar (*Juniperus silicicola*), remainder in maritime thickets ([Allen-Grimes 1982](#)). In S. Carolina, nearly 100% of nests in one large colony on clumps of black needlerush (*Juncus roemerianus*, [Bildstein 1993](#)). In Everglades of Florida, nesting primarily in willow (*Salix* spp), cypress (*Taxodium distichum*), mangroves (*Avicennia*, *Lanuncularia* and *Rhizophora*) cattail (*Typha* spp.) sawgrass (*Cladium jamaicense*) and pond apple (*Anona glabra*).

In a survey of 232 colonies throughout the North American breeding range of this species (east coast US, Carolinas to Florida), 30% were in mangrove (*Avicennia*, *Laguncularia*, *Rhizophora* spp.; [Hingten et al. 1985](#)); also in Australian pine (*Casuarina equisetifolia*), Brazilian pepper (*Schinus terebinthifolius*), lantana (*Lantana camara*), button-wood (*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 1968a](#), [Kushlan 1973e](#), [Rudegeair 1975b](#), [Schreiber and Schreiber 1978a](#), [Girard and Taylor 1979](#), [Frederick 1987a](#), [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 3.65m ft (1.6, $n = 999$) 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 1987a](#)). In coastal Louisiana, averaged 0.14 m (0.014, $n = 170$) above ground in black mangrove (*Avicennia* sp.; [Hammatt 1976](#)); 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

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 ([Rudegeair 1975b](#)). Males steal nesting material from existing nests, often in conjunction with attempted extra-pair copulations ([Frederick 1987b](#)), though females will also steal material from unoccupied nests. 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 dead twigs, even in herbaceous colony sites; but low herbaceous nests often consist of matted and woven herbaceous vegetation from the immediate vicinity or from living clump of grass supporting nest, 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 1976](#)). 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 vary ([Rudegeair 1975b](#), [Frederick 1987a](#)). Outside diameter: n. Florida, 254 mm (4.8, 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, 57.5 mm (± 3.2 SE; $n = 20$); diameter 38.7 mm (1.51; $n = 20$), Drum Island, SC (1957–1963): length, 58.2 mm (2.6, $n = 79$); diameter 38.7 mm (1.4, $n = 79$; W. Post unpubl. data). 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 1979b](#)).

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 ([Baicich and Harrison 1997](#)).

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 ([Heath 2002](#)). 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 1987b](#)). 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, aggressive interactions with neighboring ibises, human disturbance, or poor foraging conditions especially during rain-caused “reversals” of drying wetlands ([Frederick and Collopy 1989a](#)). No evidence for replacement of lost eggs or clutches. Intra-specific 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 continuous incubation begins with last egg.

Incubation Patch

Vascularized brood patches present on 90% of incubating males and females ([Heath et al. 2003](#)).

Incubation Period

On average 21 d, 22 d from first egg laid to hatching of first egg (Frederick unpublished). Details of variation unknown.

Parental Behavior

In S. Carolina, males incubated 55% ($n = 11$ pairs, 38%–68%) of the time during daylight observations ([Frederick 1987c](#)). 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 1976b](#), though considerable variation among pairs. Larger size of male may be an adaptation for nesting -- larger bird of the pair may help to defend nest, contents and paternity; lone females are susceptible to being driven from the nest [Frederick 1987b](#), [Frederick 1987b](#)). Bill length is important in intraspecific dominance, and in an analysis of 16 members of ibis subfamily Threskionithinae, male bill length was highly correlated with colonial breeding behavior ([Babbitt and Frederick 2007](#)).

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 1985](#)). Some ibises attempt to incubate eggs while floating above them during tidal inundations of the nest ([Frederick 1987a](#)). When temperature is $> 34^{\circ}\text{C}$, 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 ([Rudegeair 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 1987a](#)). % Eggs hatched (as a proportion of eggs in nest at hatch date) in Everglades over 6 yr averaged 90.3% (range 85.4% - 97.2%, [Semones 2003](#)).

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 1-2 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 (age 1 d), 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

Rapid gain in biomass in first and third week after hatch, slower in second week during period of feather maturation ([Kushlan 1977c](#)). 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, $t(10-90) = 23$ d.

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

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 (4-5 d after hatching), 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 wk, turning flesh color beginning in third month ([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 ten days. Seek shade in vegetation thereafter. Chilling as a result of tidal inundation of nests containing young < 10 d old was the principal cause of nestling mortality at a coastal colony site in S. Carolina ([Frederick 1987a](#)).

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 tarso-metatarsi. Free-living chicks beg continually unless being brooded. 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. During times of food shortage, larger male nestlings may survive better than females ([Adams and Frederick 2008b](#)).

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 > 50 m occur by week

6. Juveniles begin to leave island colony sites, crossing water boundaries of ≥ 750 m 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 1976b](#)). 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 1987c](#)). 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 base of parent's bill, while flapping one or both wings. Nestling head placed within 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 3–10 s.

After two weeks young often drape one wing over the back or neck of the feeding adult and pull adults head downwards. 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](#), [Frederick 1985](#)).

No indication food of adults and young differs, but no studies. Food much macerated during early chick phase, apparently by muscular stomach, less so as young grow. 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](#)). Food type varies with local availability of prey, and may switch from crustaceans to fish ([Dorn et al. 2008](#)). 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 chick 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. Young may follow adults by flying in latest stages of feeding.

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 $< 1\%$ 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 occurred 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 by Other Species

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. Young marked with radio transmitters left an island colony in coastal S. Carolina at 47 to 56 d of age ($n = 8$; [De Santo et al. 1990](#)), and radio tagged chicks in Florida Everglades left at 51 – 70 d of age (mean = 61d, $n = 122$ radio-tagged young, [Semones 2003](#)). 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; 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 1977a](#)).

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 spring or summer, at age of 2 yr. Ibises in captivity may breed as early as second spring (9 – 10 mo of age). Nest yearly thereafter if conditions appropriate. No records of two successful nesting attempts by individuals in the wild 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, mean clutch size ranges 2.20 (coastal habitat, SD = 0.64, n = 290, [Kushlan 1977d](#)) to 2.72 (interior marshes, SD = 0.534, n = 94, [Frederick and Collopy 1989a](#)); central Florida 2.49 (0.56, n = 202; [Kushlan 1977d](#)); 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 1976](#)). In coastal S. Carolina 2.55 (n = 380; [Frederick 1987a](#)).

Clutch sizes smaller on the coast than inland, at least at some locations in some years, suggesting a physiological or ecological constraint. In captivity with unlimited food, mean clutch size varied between years 2.66 (mostly first time breeders, n = 38, SE = 0.197), 3.28 (mostly second time breeders, n = 53, SE = 0.45, [Frederick unpublished](#)). A similar study of approximately 400 mixed-age Scarlet Ibises in captivity reported 2.4 ± 0.7 SD ([Babbitt and Frederick 2008](#)).

Annual Reproductive Success

In Florida, mean number of young/nest at 40 d of age: Everglades 1.05 (SE = 0.22, n = 42 nests), coast 1.03 (0.18, n = 93), central Florida 1.03 (0.16, n = 21 ([Kushlan 1977d](#)); at 20 d of age, 2.11 (SD = 0.65, n = 245) – 1.1 (SD = 1.11, n = 267) ([Frederick and Collopy 1989a](#)). In coastal N. Carolina 1.05 – 1.30 young fledged/nest over 2 yr (n = 755 nests). In coastal Louisiana only 10% of laid eggs produced 35 d-old young (n = 102 nests); in coastal S. Carolina over 2 yr at a single colony site, 39% (n = 390 eggs) and 3% (n = 347) produced 35 d-old young.

Considerable annual variation in per-pair productivity is typical at colony sites, depending upon local conditions. In coastal N. Carolina, 1.70 young per successful pair (n = 129, [Allen-Grimes 1982](#)). Nest success from all reports in all locations (% nests with eggs producing ≥ 1 young to 20 d of age, prorated for daily survival throughout the period) varied from <5% to 70%. No obvious geographic pattern in this variation, and this complete range of production was exhibited even within the Everglades. In N. Carolina, nest success 59% ([Allen-Grimes 1982](#)); Lake Okeechobee FL, 34 – 47.8%; Everglades, FL, 5 – 70% ([Herring 2008](#), see also summary in [Semones 2003](#)).

Nesting success and productivity are determined both by predation on nest contents, and by availability and quality of available prey before and during nesting. Nest failure in s. Florida is often triggered by rising water resulting in dispersed prey and poor foraging ([Frederick and Collopy 1989a](#), [Herring 2008](#)), and abandonment of entire colonies or sections thereof is common during these conditions. In four years in Everglades (1986, 1987, 2001 and 2002), abandonment accounted for 47% (n = 168 nests), 68% (n = 90 nests), 96% (n = 422) and 97% (n = 324) of nest failures ([Frederick and Collopy 1989a](#), [Semones 2003](#)). In years with high food availability in the Everglades, both adults and young were in better physiological condition and had lower stress levels than in years with poor food availability ([Herring 2008](#)). In years with high food availability, fledging success was 86.8%, compared with <20% in year with poor food availability. Clutch size and numbers of fledglings decreased by 21% and 26% in years of low food availability ([Herring 2008](#)).

In captivity, breeding and production of Scarlet Ibis young was related to body condition. Mean difference in mass between successful and non-successful breeding groups were 18.92 g (2.0%) for males and 31.42 g (4.2%) for females in 1998, and 16.81 g (1.8%) for males and 16.88 g (2.3%) for females in 1999 ([Babbitt and Frederick 2008](#)).

White Ibises require a succession of suitable feeding sites through the nesting season in order to maintain nesting ([Kushlan 1989b](#), [Herring 2008](#)). Although successful nesting has often been reported on diet of crustaceans ([Bildstein 1993](#), [Frederick and Collopy 1989a](#)), high food availability and productive nesting in Everglades is often associated with a high proportion of fish in the diet ([Herring 2008](#), [Dorn et al. 2008](#)). In coastal/estuarine situations, chick survivorship depends on a diet with low salt content ([Johnston and Bildstein 1990](#)).

Parental care and nest success may also be negatively affected by contaminants such as mercury ([Heath and Frederick 2005](#)). Ibises raised in captivity on diets with mercury levels typical of those found in the Everglades food chain had significantly lower proportions of nest starts producing eggs than controls and high proportions of male-male pairing (P. Frederick unpublished).

Number Of Broods Per Season

Probably one, except when renesting occurs following failure of early nesting attempts. Two radio telemetry studies of breeding adults in Everglades suggest either no renesting following nest failure or successful nesting (Herring pers. comm.), or confirmed renesting in a small % of failures ([Heath 2002](#)). In captivity, up to 3 broods per season.

Proportion Of Total Females That Rear At Least One Brood To Nest-Leaving Stage

Not known. In captivity with unlimited food, 30 – 34% of mixed age females and 34% of males produced eggs or young ([Babbitt and Frederick 2008](#)). Some of these birds were old enough to be reproductively senile. In known-age birds, 100% of second-time breeders (age 3 yr) attempted to breed.

Life Span and Survivorship

Life span, free-ranging: at least 16 years 4 months ([Clapp et al. 1982b](#)); captive: at least 20 years ([Spil et al. 1985](#)).

No data on survivorship in the wild.

Disease and Body Parasites

Diseases and parasites well studied in Florida, and summarized in detail by Forrester and Spalding ([Forrester and Spalding 2003](#)). 23 species of trematodes, 18 species of nematodes, 2 cestodes, 2 acanthocephalans, 3 species of mites and 5 species of chewing lice found in ibises, nearly all in Florida. Of trematodes, some in high proportions of birds examined (eg, 61 – 75%).

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 (*Skryabinoclavia thapari*), which uses fiddler crabs as an intermediate host.

Both juvenile and adult ibises were, however, infested with a single ancanthocephalan species, *Southwellina dimorpha*, which uses crayfish as an intermediate host. *Eustrongylides ignotus* found in 5 of 162 nestling ibises, and was the probable cause of death in four of these individuals. Only two protozoans reported from ibises, and of these *Haemoproteus plataleae* were by far the most common. No bacterial related diseases reported for this species. No antibodies to Eastern equine encephalitis detected (n = 12), and antibodies to St. Louis encephalitis found in 1 of 12 birds examined from s. Florida.

Causes of Mortality

Nestling mortality is greater during the first 20 d after hatching than thereafter. Although ibises typically lay 2-5 eggs, the number of young/nest in Florida 20 d after hatch declined considerably: Everglades 1.38 (0.49, n = 53), coast 1.14 (0.45, n = 64), central Florida 1.25 (0.43, n = 133) ([Kushlan 1977d](#)). Nestling survivorship to 10 d of age in coastal N. Carolina: 89% (n = 410 hatched eggs), 86% (n = 596 eggs), and 68% (n = 284 nests) during 3 yr at the same colony site ([Allen-Grimes 1982](#)). Nestling survivorship to 35 d in coastal Louisiana: 55% (n = 102 nests; [Hammatt 1976](#)). Nestling survivorship to 21 d in Everglades 37 – 83%.

Using radio telemetry, Semones ([Semones 2003](#)) measured survival in Florida: from 22 d to independence, 67 – 97%; to 60 d, 59 – 94%; and to 90 d, 44 – 78%. Young birds can be susceptible to inter-specific (e.g. Black-crowned Night Herons, [Davis 1993a](#)) or rarely, intra-specific predation ([Herring et al. 2005](#)). Complete abandonment of nests happens when food resources become unavailable, and nestlings in entire colonies or large portions thereof can die during these events ([Adams et al. 2008](#)).

Causes of adult mortality poorly known. Many ibis bands recovered in Cuba during the 1950s and 1960s came from hunters ([Frederick et al. 1996](#)). At least 50 adult ibises were killed during a single fire in the Florida Everglades ([Epanchin et al. 2002](#)). Ibises may be susceptible to alligator predation because of feeding habits and habitat, but there are few quantitative studies of this (see [Delany 1986](#)).

Range

Initial Dispersal From Natal Site

For juvenile birds banded at their natal site, 26% of returns found at the banding site at least 5 mo later ([Melvin et al. 1999](#)). Returns from outside the banding location ranged between 18.5 - 2,479 km (mean = 545 km, [Melvin et al. 1999](#)). These distances may represent post-fledging dispersal or migratory movements. Natal philopatry has not been demonstrated and, given enormous fluctuations in colony size and occupancy, is probably weak. Two nestlings

individually marked at a coastal colony site in S. Carolina bred at a coastal colony site 100 km northeast in N. Carolina. Young birds more likely to disperse north or inland of colony than adults ([Frederick et al. 1996](#)).

Fidelity To Breeding Site And Winter Home Range

Strong propensity to change colony sites, so nesting numbers fluctuate annually ([Frederick et al. 1996](#)). Small numbers of individually marked breeding birds have returned in later years to a colony site in coastal S. Carolina ([Frederick 1987a](#)) and s. Florida (JH). One ibis returned to within 8 km of capture site in N. Everglades in next winter (Herring pers. comm.). Within S. Carolina, reciprocal shifts annually in numbers of pairs breeding at traditional colony sites suggest considerable movement, probably due to changing environmental conditions.

Dispersal From Colony

Among 10 marked adult birds breeding in s. Florida, dispersal between successive breeding colonies within the same year ranged from 29-54 km, average = 42 km (n = 5). The other 5 ibises wintered in s. Florida but dispersed > 150 km in the year following successful reproduction because of poor breeding conditions (JH). Following unsuccessful breeding attempts, radio-tagged adults dispersed to a site >30 km from colony (Herring pers. comm.)

Home Range

At a coastal site in South Carolina, ibises traveled 4-32 km to freshwater wetlands to secure food for nestlings ([De Santo et al. 1997](#)). This is comparable to distances flown from freshwater colonies in s. Florida (<1 km – 33 km, [Frederick and Collopy 1989a](#) and JH), and a lake colony (0.1-33.3 km, mean = 2.7, n = 286, [Smith 1995c](#)). Ibises nesting in a North Carolina estuary flew shorter distances (1-6.2 km, [Custer and Osborn 1978a](#)).

Population Status

Estimates Or Counts Of Density

The most numerous ciconiiform wading bird in many areas where it occurs. Extreme inter-annual variation in local nesting numbers due in part to highly nomadic breeding habits. All measurements of population size are counts or estimates of breeding birds on nests. These likely to be underestimates because of visual occlusion by vegetation, asynchronous nesting, and incomplete or nonsystematic survey technique ([Frederick et al. 2006](#), [Williams 2007b](#)). See below:

Numbers/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 1977d](#), [Kushlan 1979b](#)). 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 [Kushlan 1987](#), [Kushlan 1989b](#)). Similarly, in Trinidad, the cessation of breeding by Scarlet Ibises also appears to be due to an altered hydrologic regime ([Bildstein et al. 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.

Total Population. Frequent inter-year movements and low breeding site fidelity mean that opportunities for estimates of entire U.S. population are rare. During 1930s some evidence that vast majority of birds were breeding in south Florida (as below), up to 400,000 birds, more regularly 250,000. By 1970s, range-wide estimates suggested peak of 350,000 breeding birds, and by 1991, 102,000, an apparent declining trend. Since that time, years with simultaneous counts in Texas, S. Carolina, N. Carolina, Florida, and Louisiana indicate a minimum of 166,000 breeding birds in 2001, and 209,000 in 2004. This suggests U.S. population has held steady or increased somewhat since 1991. Note that sources of error in counts of ibis colony sizes are nearly all biased to result in undercounts, sometimes by very large amounts ([Williams 2007b](#)).

South Florida. In 1930s and 1940s, 100,000 – 400,000 individuals breeding in several years, 50,000 – 250,000 more commonly ([Crozier and Gawlik 2003b](#)). The majority of ibises in the U.S. may have been concentrated by drought in s. Florida in the mid-1930s, suggesting a peak population of > 400,000 breeding adults at that time. By 1970s, maximum counts of at least 50,000 breeding individuals in each of 3 yr, including > 35,000 in one colony ([Kushlan 1973e](#), [Kushlan and White 1977b](#)). Breeding population averaged 9,200 pairs (range 500 – 26,000) 1986 – 1999. Approximately 50% decrease in nesting numbers between 1985 and 1994, coincided with large increases in Louisiana. Large increase in breeding numbers 2000 - 2007, average 44,511 birds (range 25,000 – 65,000).

S. Carolina. (W. Post, in litt., editing and consolidation by PCF): First statewide estimates from 1975 suggested about 80,000 breeding birds (40,000 on Drum Island, Charleston Co., 39,000 on Pumpkinseed Is., Georgetown Co.). During normal rain cycles, total state population 28,000 – 40,000 birds usually found in 1-2 coastal and 1 – 2 inland colonies. Large inland colonies in Lake Marion (16,000 birds in 1999) and Boykin, in Kershaw Co. (6,000 birds in 2000, Post and Gauthreaux 1989). In non-drought years, breeding about equally divided between coastal and inland locations.

Population in S. Carolina has declined since 1975, with no birds nesting in large central-coast colonies. Large interior colonies likely abandoned because of persistent drought in late 1990s and early 2000's. Since 2000, main colonies have been near the mouth of the Savannah River, in Jasper Co. (8,000 birds in 2000), and near Yemassee, in Colleton Co. (20,000 birds in 2000). No statewide surveys since 2005.

N. Carolina. Between 1977 and 2007, 3,878 - 34,086 nesting birds in coastal zone, with markedly increasing trend. Since 2000, average of 31,820 nesting birds annually. Important colonies at Battery I. (Brunswick Co., to 26,000 breeding birds 2007), Morgan I. (Carteret Co., to 2,880 birds, 2007), and Roanoke Sound Island “G” (Dare Co., to 2,920 birds, 2006).

Texas (R. Telfair): Between 1973 and 2000, annual breeding population fluctuated between 3,200 and 64,000 birds (Texas Col. Waterbird Soc., unpubl.). Notable colonies at N. Deer Island (Galveston Bay, Galveston Co., to 44,000 birds), Lavaca Bay Spoil (Cameron Co., to 6,600 birds), Dressing Pt. (Matagorda Co., to 12,000 birds), Demijohn Lake (Liberty Co., to 16,000 birds). In general, the wetter the winter-to-spring season, the larger the number of breeding birds (Telfair II 2002). Increase over time, from average of 7,800 birds statewide early 1970s to average of 17,600 birds 1993 – 2006.

Louisiana. Spotty record of monitoring in this state, compared to other states in the species range, despite evidence of a large proportion of nesting in U.S. occurring there. Minimum of 40,000 breeding birds reported as early as 1950, though survey probably not systematic or statewide. More thorough surveys suggested 44,000 - 82,000 breeding birds between 1972 and 1976. A large increase in breeding and wintering numbers in mid – late 1980s was associated with a rapid increase in crayfish aquaculture (Fleury and Sherry 1995). Numbers of breeding birds during late 1980s (26,000 – 76,000) did not suggest an increase, but these surveys were not statewide.

Two systematic surveys in 2001 (48,000) and 2004 (68,000 breeding birds) suggest Louisiana remains an important place for breeding ibises in the southeast. Large colonies in 2001 survey include northwest of Lake Pontchartrain (19,000 birds, Tangipahoa Parish), northwest of Ville Platte (8,200 birds, Evangeline Parish), northwest of Raceland (7,300 birds, LaFourche Parish) and west of Houma (4,000 birds, Terrebonne Parish).

In winter, in the continental U.S., small populations found in coastal S. Carolina, Louisiana, and Texas, but greatest concentrations in peninsular Florida (> 1 individual/CBC party hour), especially along the Gulf Coast near Tampa Bay (Root 1988b; <http://www.mbr-pwrc.usgs.gov/bbs/cbc.html>). From 1999-2003 Christmas Bird Count counts, 41,000 – 48,000 individuals in Florida (<http://www.mbr-pwrc.usgs.gov/bbs/cbc.html>).

Trends

See above. Range increased and consolidated 1930s – 1990s. The Everglades/s. Florida population declined by > 95% from the 1930s to 1970s, and by an additional 80% from the highs of the 70s to the highs of the 80s (Rodgers et al. 1996c). During late 1990s to 2006, population apparently increased sharply.

Decreases in the Everglades are likely the result of water management that has altered the natural hydrologic regime of the marsh (Kushlan 1987, Kushlan 1989b). In addition, exposure to mercury may have hindered reproductive success.

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.

McFarlane (2002) found the Texas breeding population between 1973-2000 had an annual increasing trend of 3.0%. Breeding Bird Survey data for Texas (Sauer et al. 2005) give annual trends of +8.4% (1966-1979), +8.9% (1980-2005), and +18.3% (1966-2005).

Over the entire range, Breeding Bird Survey (BBS) data suggest a slight positive trend in the U.S., 1966-2006 (Sauer et al. 2007). This echoes the analysis (above) of colony counts throughout the range. For 1980-2006: Florida (+2.2%/yr); Georgia (-1.5%); S. Carolina (-7.7%); N. Carolina (+3.9% [few data]); Texas (+8.0%) (Sauer et al. 2007).

Population Regulation

Although local annual reproductive success may be low at a particular colony, the southeastern population appears to be stable or increasing. Apparently, dispersal patterns and an ability to postpone nesting mean that some reproduction occurs each year within the North America range. However, at a local scale populations and reproductive effort can fluctuate dramatically. For example, 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. Similarly, several years with over 200,000 birds breeding in the Everglades in the 1930s were interspersed with years when fewer than 1,000 bred (Ogden 1994).

Nesting failures (Semones 2003) and predation of eggs and nestlings, especially when exacerbated by reduced prey availability (Frederick and Collopy 1989a) and competition for nest sites, have the potential of exerting a strong effect on reproductive rates. High mortality among young, disease or exposure to contaminants, and habitat loss are probably important components of mortality rates. High availability of food throughout the reproductive season seems to be a driver of adult physiological condition and fecundity.

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 have been shot as vermin (Martin and Hamilton 1985). Historically, this species (adults, young, and eggs) has been eaten by local residents (Bent 1926), and this tradition continues throughout its range. The appealing taste may derive from their crustacean diet. Restrictions on hunting have been effective in some areas, but hunting is not considered an important threat.

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 working in 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 entering the colony unless absolutely necessary, and then only for < 30 minutes per colony area every two days, only in morning or early evening.

White Ibis are known to be exposed to contaminants found in wetlands, with the majority of reports and work on mercury. During the 1980s and early 90s in s. Florida, individuals had 0.05-1.46 (mean = 0.89) $\mu\text{g/g}$ total mercury in liver, with higher levels found in nestlings than in fledglings or adults ([Sundlof et al. 1994](#)). Feathers of adult in the Florida Everglades: 0.33 – 20 ppm fw, nestlings 0.33-20 ppm (n = 94; [Heath and Frederick 2005](#)). Mercury levels in adult feathers typically < 5ppm fw during 1900 – 1970, but large increase to 20 ppm in 1990s, decrease after 1998 ([Frederick et al. 2004a](#)).

In experiments with captives, ibises on chronic methylmercury diets (0.05, 0.1, 0.05 ppm ww in diet) -- spanning the range of contamination in diets of wild ibis in s. Florida -- showed no differences from controls in mass, health parameters, learning ability or juvenile hormone expression ([Adams and Frederick 2008a](#), Frederick unpublished). However, all mercury-dosed birds had significantly lower reproductive success as a result of male-male pairings that appeared to be dose-dependent (range 27 – 44% of males). No observations of male-male pairings reported from field, but no studies capable of detecting this to date in s. Florida.

Colony near a municipal solid waste combustor (3 yr study, 1989-1991; Florida): eggs: DDT range: not detectable (ND) - 1200 $\mu\text{g/kg}$ wet wt; DDE: 32 - 1600; Heptachlorepoxyde: ND - 57; Dieldrin: ND - 610. Nestlings DDT: ND-8; DDE: 4-110; Heptachlorepoxyde: ND-20; Dieldrin: ND-35 ([Rumbold et al. 1997](#)). White Ibis livers (mg/kg): mercury range 0.35-3.00, lead 0.05-0.71, PCBs <0.05-0.63, DDE: 1.40-2.30, n = 3 ([Rodgers 1997](#)). Livers of dead White Ibis nestlings (n = 4): lead 0.18-0.28, copper 18-55, cadmium 0.02-0.21 $\mu\text{g/g}$ ([Spalding et al. 1997](#)).

White Ibis feather concentrations: individuals exposed to high concentrations of one contaminant also had high concentrations of other contaminants ([Spalding et al. 1997](#)) suggesting polluted areas, and potential endocrine effects, could disrupt normal behavior ([Heath and Frederick 2005](#)).

Management

Federally designated a Bird of Conservation Concern in Bird Conservation Areas 31 (peninsular Florida) and 37 (Gulf Coastal Prairie–U.S. portion only), but not area 27 (Southeastern Coastal Plain, [U.S. Fish and Wildlife Service 2002c](#)). On the state level White Ibises have been listed as a Species of Special Concern by Florida, a species of Moderate Conservation Concern by Alabama, but are not listed in any other states in their range.

Ibis management may benefit from general recommendations by waterbird conservation and watchdog groups such as the Stork, Ibis & Spoonbill Specialist Group of Wetlands International or the Waterbird Conservation for the Americas who published the North American Waterbird Conservation Plan (NAWCP, [Kushlan et al. 2002](#)). The NAWCP lists White Ibis as a species of moderate concern because of its population trends and restricted breeding and non-breeding ranges.

No specific management plan has been created for this species. However, plans for Everglades restoration could restore natural hydrological cycles that favor White Ibis reproduction. In both the temperate and neotropical portions of the range, preservation of large tracts of unpolluted coastal and inland wetland habitat and of specific nesting sites is critical ([Kushlan 1983](#), [Kushlan 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 increasingly important. Disturbance at colony sites is a key factor in nest failure in this species.

It is known that ibises have nested frequently on dredge-spoil islands made by humans, and the creation of the intracoastal waterway may have been beneficial in providing safe nesting places in productive riverine and estuarine habitat ([Parnell et al. 1988](#)). However, it is also clear that vegetation on dredge spoil islands may become less suitable for ibises if allowed to progress to a situation dominated by tall trees with little understory.

Foraging sites must also be protected and managed, as in many cases specific water conditions are required for foraging to succeed ([Kushlan 1981](#), [Kushlan 1983](#), [Kushlan 1986](#), [Kushlan 1989a](#), [Kushlan 1989b](#); [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. Integrated management strategies including colony site protections and water level foraging sites, particularly during the breeding season, are necessary.

Priorities for Future Research

Although ibises are one of the most conspicuous wetland species in North America, and are frequently used as bio-indicators, we still have a poor understanding of their within-year movements and connectivity between habitats. Better descriptions of links between breeding colony sites and foraging areas, particularly during the onset of breeding and the chick period, would be helpful to inform both the nature and spatial scale of appropriate management actions.

Similarly, we know very little about patterns of White Ibis movements between years, especially in areas outside the southeastern USA. Better descriptions of the spatial scale and periodicity of inter-annual shifts in breeding locations (and the underlying factors that cause these movements)

would be helpful to understand population regulation, to interpret regional population trends, and to develop regional water management strategies. Also interesting and useful to understand would be the connectivity between Caribbean populations and populations in the se. USA, and perhaps even South American.

We understand little about the developmental ontogeny of behavior in this species, although current studies of captive birds may give us new insights (P. Frederick). Only recently have studies begun to address the evolution of behavioral and morphological features in this species. Continuing research on ibis social structure, behavioral ecology, and evolution of interspecies relationships would be interesting.

The difficulty in estimating sizes of large breeding aggregations of ibises continues to be an impediment to understanding population dynamics and regulation in this species. Of the various kinds of bias in estimation, breeding asynchrony probably produces the largest error. While the effects of asynchrony and overlapping starts and failures within a colony can be estimated to help produce counts of total nest starts, it is unclear how often ibises re-nest in the wild following either failure or successful nesting. Propensity to re-nest therefore seems to be a key missing parameter in our ability to accurately estimate population size in this species.

Similarly, our ability to estimate the U.S. population is severely hampered by the lack of coordinated surveys of colonies throughout the region; in the past century there have been fewer than 5 opportunities to do this with any confidence. The extreme lack of philopatry in this species, and its propensity for rapid intra-regional movements between breeding sites, makes simultaneous, region-wide survey effort a necessity for managing the population.

Existing research strongly indicates that very large numbers of ibises are able to quickly recruit to very dense food resources distributed across hundreds of kilometers of range. Yet is it unclear how these birds are able to do this; an understanding of the cues involved is probably critical for conserving productive wetlands, understanding the scale and type of management conducive to this species, and avoiding the creation of ecological traps.

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