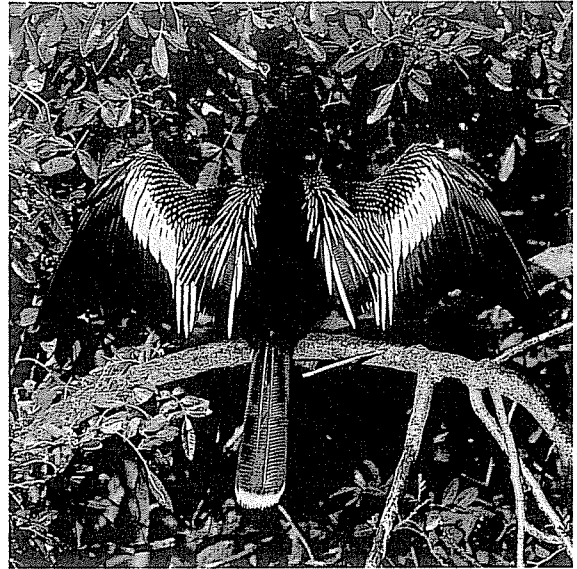


FRENCH:
Anhinga d'Amérique
SPANISH:
Anhinga americana, *Pato aguja*,
Cotua agujita, *Cotua real*,
Bigua vibora
OTHER NAMES:
Snake-bird, *Water Turkey*

Anhinga

Anhinga anhinga



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The Anhinga is among the most distinctive of North American birds, with long, snakelike neck, straight bill, large fanlike tail resembling that of a turkey (*Meleagris gallopavo*; from which the former name Water Turkey was derived), corrugations on its central rectrices, and unique swimming, flight, and behavior patterns. This truly aquatic species spends its life in water or on branches overhanging protected, usually freshwater streams and ponds. Unlike most aquatic birds, Anhingas have fully wettable plumage and dense bones, adaptations that allow them to achieve neutral buoyancy in water, facilitating a slow, stalking hunting habit while submerged in shallow aquatic vegetation, where they spear fish. The neck vertebrae are arranged to allow a strong and rapid stab. While the bird is swimming on the surface, its body is usually submerged, with only the head

The Birds of North America

Life Histories for the 21st Century

and snakelike neck visible, making it obvious why the term "snake bird" is often applied. The word "Anhinga" is derived from a Tupi (Brazilian) Indian name, *anhingá* or *anhangá*, for the devil bird, an evil spirit of the woods (Jobling 1991). The wettable plumage of this species results in considerable loss of body heat underwater, with a concomitant need for large amounts of time spent sunning and drying feathers later. One habitat requirement of this bird is the availability of logs and branches near the water onto which

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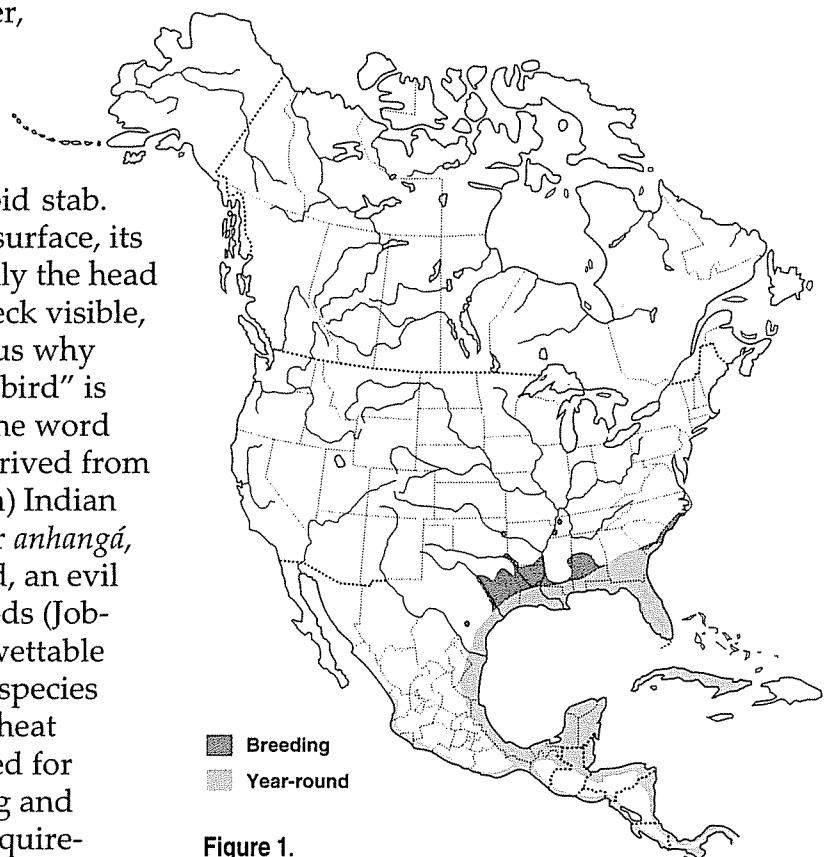


Figure 1. Distribution of the Anhinga in North and Central America and the western Caribbean. This species also breeds in South America. See text for details.

individuals can climb in order to sun. The strong dependence of this bird on sun warmth for thermoregulation limits its northern distribution. Anhingas are strong fliers, often soaring at great altitude above their wetland habitats with wings held flat and neck out, presenting a distinct cross. This species is social and nests colonially, often with long-legged wading birds. It builds its nests in trees overhanging water, and the young birds, which can swim long before they can fly, often escape by jumping into the water.

Some aspects of this species have been well studied. Musculature, molt, and adaptations for flight and swimming have been described in detail by Owre (1967) and Casler (1973); comparative behavior by van Tets (1964); thermoregulation by Henneman (1982, 1983, 1985); systematics by Siegel-Causey (1988, 1996, in press); and breeding behavior and ecology by Meanley (1954), Owre (1967), Allen (1961), and Burger et al. (1977, 1978). Relatively little is known about social organization, demography, migration, or movements. Nearly all studies of this bird have been done in the United States; little is known about it in Central and South America.

DISTINGUISHING CHARACTERISTICS

Largely black waterbird the size of a small to medium-sized heron; length 75–95 cm. Distinctively shaped, with small head; very long, often curved neck; long daggerlike bill; and long, fan-shaped tail (tail up to 30% of total length). Often observed swimming (frequently with body submerged and only head and neck extending above surface of water), perched with wings and tail spread to dry, or soaring during flight with neck extended, tail spread, and wings held flat. Body plumage entirely black, with distinctive pattern of silvery to white streaks and spots on upper back, scapulars, and wing-coverts. Tail stiff and fanlike, resembling that of the Wild Turkey; outer webs of central rectrices (R1) and of longest scapular have transverse corrugations. Sexes similar in appearance, except female duller, with head, neck, and breast buffy instead of black, and tail tipped buffy instead of white. Both sexes develop sparse white feathering on sides of head and neck in breeding (Definitive Alternate) plumage.

Young naked at hatching; later have thick, buffy-tan to white down. Juveniles of both sexes resemble adult female, except blackish areas replaced by brownish, and whitish markings on upperparts reduced or less distinct; subsequent subadult plumages are progressively more adult-like. Definitive plumage not attained until third

calendar year. Sexes similar in size in *A. a. leucogaster*, but males larger than females in *A. a. anhinga* (Siegel-Causey in press).

Anhinga is the only member of its family (Anhingidae) in the Americas. Whether it is perched, flying, or swimming, the unique structure and plumage pattern of the Anhinga make it unlikely to be confused with any other species in the Americas. Cormorants (*Phalacrocorax* spp.) are somewhat similar in structure, plumage, and behavior, but Anhingas are readily distinguished by much longer neck; longer, more pointed bill (lacking the distinct terminal hook found in cormorants); and longer tail. Cormorants also do not typically swim with body submerged and only head and neck exposed above surface of water.

DISTRIBUTION

THE AMERICAS

Breeding range. Figure 1. Breeds in appropriate habitats in eastern half of Texas, where found principally in coastal plain and farther inland throughout most of eastern third of the state (Oberholser 1974, Telfair 1980, Texas Breeding Bird Atlas [BBA] 1987–1992 unpubl.). Also from easternmost Oklahoma (locally and irregularly from McCurtain Co. (at least formerly) north to Sequoyah Co. (Baumgartner and Baumgartner 1992), s. Arkansas (very locally; James and Neal 1986), extreme w. Tennessee (very locally; Nicholson 1997), central (local) and s. Mississippi (Turcotte and Watts 1999), central Alabama, southern half of Georgia, lower coastal plains of S. Carolina (north to Aiken Co. and possibly Marlboro Co.; McNair and Post 1993), and N. Carolina (Am. Ornithol. Union 1998), south to Gulf Coast and s. Florida (Lowery 1955, Stevenson and Anderson 1994, Am. Ornithol. Union 1998).

South of U.S., breeds in Cuba (lowlands), including Isle of Youth (Raffaele et al. 1998), and in Mexico from Tamaulipas and e. Nuevo León on Atlantic slope, and from s. Sinaloa on Pacific slope south along both slopes of Mexico and Central America to e. Panama (Ridgely and Gwynne 1989, Stiles and Skutch 1989, Howell and Webb 1995), and in South America in humid lowlands of Colombia and Ecuador, Trinidad, Tobago, and Netherlands Antilles, and Amazonia (including Venezuela, the Guianas, and Brazil southeast of the Andes) south to Río de la Plata, Buenos Aires Province, in central Argentina (Blake 1977, Hilty and Brown 1986, Canevari et al. 1991, de Graaf and Rappole 1995, Am. Ornithol. Union 1998).

Winter range. Figure 1. Resident throughout much of breeding range except in U.S., where breeders usually withdraw in winter south to south

coastal S. Carolina, southern half of Georgia, s. Alabama, s. Mississippi, southern half of Louisiana, and coastal plain of Texas (Christmas Bird Count [CBC] data). Winter distribution probably varies with extreme low temperatures (Henneman 1985); this species occasionally winters farther north in U.S. (e.g., s. Arkansas; James and Neal 1986). Resident status and philopatry not studied in Florida or other states in southern end of U.S. winter range. CBC survey maps suggest that densest concentrations in U.S. in winter are in peninsular Florida, with highest numbers in central and nw. Florida, including Polk, Alachua, Marion, and Levy Cos.

Other records. Wanders widely, during both spring and fall, to n. U.S. and e. Canada. Casually recorded north to n. California, Arizona, Colorado, Nebraska, Illinois, Wisconsin, s. Ontario, Ohio, Pennsylvania, New Jersey, and New York (Am. Ornithol. Union 1998, McWilliams and Brauning 2000), with sight reports from Connecticut (Westport; Forster 1988, Zeranski and Baptist 1990) and Massachusetts (Veit and Petersen 1993). Observations along coast of ne. U.S. have increased during 1990s, with as many as 30 observed in 1 flock during 1996 in Maryland (Walsh et al. 1999, McWilliams and Brauning 2000). May also be increasing in central states, including Wisconsin (Robbins 1991, Granlund 1997), Illinois (Bohlen and Zimmerman 1989), Indiana (Keller et al. 1979), Missouri (Robbins and Easterla 1992), and Kansas (Thompson and Ely 1989), as well as in Florida Keys (Stevenson and Anderson 1994). Casually recorded in West Indies in Bahamas (Andros, Cayman Is. (Little Cayman), Hispaniola, St. Lucia, and Grenada (Bond 1993, Raffaele et al. 1998). Although limit of southern distribution is believed to be n. Argentina, 1 *A. a. anhinga* specimen was collected in Tierra del Fuego in 1984 near Puerto Santa Cruz, Argentina (DSC).

OUTSIDE THE AMERICAS

Not recorded.

HISTORICAL CHANGES

Formerly bred in s. Illinois and se. Missouri (Am. Ornithol. Union 1998), but only rare visitor there by 1990s. Formerly bred in Oklahoma (McCurtain Co., 1937), but has disappeared there, probably because of habitat destruction (Sutton 1967, Baumgartner and Baumgartner 1992). Former breeding in Kentucky (Reelfoot Lake, until early 1950s), but since that time considered extirpated as a breeding species (Palmer-Ball 1996). In Texas, considerable reduction of breeding range between 1930s and 1960s (Oberholser 1974). In Arkansas, retraction of breeding range since 1950s (formerly

Phillips, Ashley, Mississippi, Arkansas, Hempstead, and Lafayette Cos.; as of mid-1980s, breeding only in Hempstead, Lafayette, and Little River Cos.; James and Neal 1986). In S. Carolina, breeding range has extended inland to Aiken and Marlboro Cos., and nesting distribution was more inland from 1987 to 1993 than before 1987 (McNair and Post 1993). Population increased and winter range expanded northward in Florida during latter part of twentieth century; winter distribution statewide after 1970s (Stevenson and Anderson 1994). See also Demography and populations: population status, below. Extralimital records also increased during 1990s in areas of U.S. north of breeding range (see The Americas, above).

FOSSIL HISTORY

Evidence of fossil remains from New and Old World from Miocene onward (Martin and Mengel 1975); fossil remains of darters known from Florida from 18 million years ago; remains of this species from the Pleistocene of Florida (Becker 1986). The Anhingidae probably diverged from other Pelecaniformes (cormorants) at least 30 million years ago.

SYSTEMATICS

GEOGRAPHIC VARIATION

Unclear and undocumented, although the individuals of some populations seem distinctive in size. North American *A. a. leucogaster* seems consistently larger than individuals from Mesoamerica, and measurements suggest that *A. a. anhinga* is somewhat larger than *leucogaster* from any areas. Several authors (van Rossem 1939, Griscom and Greenway 1941, Wetmore 1943) discussed morphological variants throughout the range, but few of the patterns have been borne out by subsequent studies. Gyldenstope (1951) suggested that birds from Florida and Brazil were not much different in measurements, and that width of tail-tip varies individually rather than geographically. The latter observation was supported by Owre's (1967) work showing considerable variation in timing of molt of rectrices among individuals, and that differences in width of the white band were due largely to wear. Little is known about the biology, distribution, or geographic variation of *A. a. anhinga*.

SUBSPECIES

Subspecies designations remain speculative and confused; need study. At present, 2 forms recognized (Dorst and Mougouin 1979), on basis of size (*leucogaster* smaller), extent of buffy neck plumage in female (less in *leucogaster*), and degree of terminal

light coloration on tail-feathers (smaller band in *leucogaster*; Palmer 1962, Siegel-Causey in press).

A. a. anHINGA Linnaeus, 1766: Breeds in South America from Colombia and Ecuador, Trinidad, Tobago, and Netherlands Antilles, and Amazonia (including Venezuela, the Guianas southeast of the Andes, Brazil) south to Argentina (Ri  de la Plata, Buenos Aires Province). A few sightings in Tierra del Fuego (DSC).

A. a. leucogaster Vieillot, 1816: Breeds in southern tier of U.S. east of Rocky Mtns. south to Mexico, Central America, and Cuba. Straggler west to Arizona, north to Nebraska and Ontario, and east to Long Island, New York. The precise boundaries between *leucogaster* and *anHINGA* subspecies are unclear; segregation may occur in n. Colombia or south of Panama Canal.

A. a. minima described by van Rossem (1939) for small birds found along Pacific Coast of Mexico, but its status is controversial.

RELATED SPECIES

Because of their totipalmate feet, the Anhingidae and 5 other families (Phalacrocoracidae, Sulidae, Pelecanidae, Phaethontidae, Fregatidae) have traditionally been placed in the same order, Pelecaniformes. Although there is continuing debate on the higher-order status of particular families and even of the order itself (Siegel-Causey 1996), most authorities agree that cormorants and anHINGAs are distinct families and sister groups, probably diverging in the early Miocene. AnHINGAs share with cormorants many unique features found in no other birds, including the occipital xiphoid bone that articulates with the rear of the skull, and feather structures that allow absorption of water into the plumage (Casler 1973, Siegel-Causey 1988). Darters and AnHINGAs have a single carotid artery, nostrils obsolete with no outer openings in adults, and vestigial tongue, as well as unique adaptations of the gut (see Food habits: feeding, below), bones, and air sacs (see Behavior: locomotion, below).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Short-distance partial migrant. Moves regularly between summer nesting habitat in se. and s.-central U.S. to Florida, Louisiana, and Mexico in winter. Much of the Florida population appears to be resident. No information about migration available from Central or South America.

TIMING AND ROUTES OF MIGRATION

Incomplete information. Banding returns show little movement between Central Flyway (Missis-

sippi Valley) and Florida; 100% of 49 returns of birds banded in Mississippi Valley were from Mississippi Valley, Texas, or Mexico (Coffey 1943, 1948, PCF unpubl. analysis of band return records through 1996). Birds banded in Tennessee and Mississippi have been recovered in Louisiana, Texas, and Gulf Coast of Mexico, suggesting circum-Gulf movements during migration. Throughout sites in Florida, fall migration observed Sep and Oct (Stevenson and Anderson 1994), spring movements early Mar and Apr. Extreme dates of occurrence in breeding-only portions of Arkansas 21 Mar–17 Oct (Meanley 1954); in Alabama, 9 Mar–19 Oct (Lowery 1955), in Mississippi, Mar–late Oct (Turcotte and Watts 1999); and in Louisiana, late Mar–late Oct. Vagrants in northern end of range have been seen in spring and summer, though some records are from fall (see Distribution: the Americas, above).

MIGRATORY BEHAVIOR

Few observations published. During migrations in s. Texas, soars in conspecific flocks or with other birds, including Turkey Vultures (*Cathartes aura*), Swainson's Hawks (*Buteo swainsoni*), and Chihuahuan Ravens (*Corvus cryptoleucus*; Oberholser 1974).

CONTROL AND PHYSIOLOGY

No information or data. Migratory movements may be cued by changes in temperature, since AnHINGAs are highly dependent on ambient temperatures and solar radiation to offset thermal losses caused by swimming (Henneman 1982, 1985).

HABITAT

BREEDING RANGE

Shallow, slow-moving sheltered waters with nearby perches and banks available for drying and sunning. Rarely found out of fresh water, though this may have to do more with availability of drying perches than other considerations (Owre 1967); may occur in saltwater habitats in large numbers during severe droughts (Palmer 1962). Usually forages in shallow water, frequently <0.5 m deep (Owre 1967). In s. Florida, inhabits ponds in cypress swamps, freshwater sloughs of saw grass with clumps of willow (*Salix* spp.), and mangrove-bordered salt and brackish bays, lagoons, and tidal streams in coastal sections. Generally not found in extensive areas of open water, though may nest on edges of open bays and lakes. Breeding colonies generally found in fresh water, often in association with other waterbirds, such as herons, egrets, ibises, storks, and cormorants; may breed in saltwater colonies and feed in fresh water (e.g., Tampa Bay,

FL; Cuthbert Lake, FL; Stevenson and Anderson 1994). Although it forages often from and near habitually used nonbreeding perches, does not forage under or near nesting colonies (Meanley 1954). Breeding habitat usually has trees or shrubs (many species and sizes used) growing close to edge of water, with small, slow-moving water bodies nearby that provide shallow, vegetated areas for hunting.

WINTER RANGE

Limited in winter distribution by ability to gather enough insolation through sunbathing to offset thermal losses during swimming (Henneman 1982, 1985). Distribution in se. U.S. is limited to sites with mean monthly Dec temperatures of $>10^{\circ}\text{C}$ and >160 h sunshine / mo; if <160 h, then usually found between 10 and 12°C mean monthly temperature isoclines. This implies that winter range could be extended northward through effects of global warming.

FOOD HABITS

ANATOMICAL ADAPTATIONS

Distal portions of both mandibles have fine, backward-pointing serrations for holding fish. Modifications to eighth and ninth cervical vertebrae allow right-angle kink in neck (Dönitz 1873, Garrod 1878). This, and unique muscle action of the neck, allows a fulcrum for the straight-line stabbing motion with which this species spears its prey. Darters and Cormorants have a proventriculus with separate diverticula or evaginations, and a uniquely bipartite stomach, for which the pyloric valve is a hairlike plug (Garrod 1878, Forbes 1882, Siegel-Causey 1988, in press). The functions of these unique adaptations of the gut are unknown.

FEEDING

Main foods taken. Mainly fish, but also crayfish, amphibians, snakes, lizards, mollusks, leeches, and aquatic insects (J. J. Audubon in Bent 1922, Owre 1975, del Hoyo et al. 1992). Concentrates on slow-moving laterally flattened fish that live in shallow, freshwater habitats.

Microhabitat for foraging. Shallow wetlands, often with both submergent and emergent vegetation, almost always with perches and banks for sunning and perching nearby.

Food capture and consumption. Usually forages alone, swimming slowly and stalking underwater in and around aquatic vegetation. Wings are often cocked open underwater, either to attract fish to the shadow or to counteract sinking. In Florida, may fish by hanging motionless near surface of water

(Nicholson 1961). Captures prey by spearing with rapid thrust of partially opened bill. Usually stabs fish in their sides with both mandibles; uses upper mandible only sometimes on small fish. Side-spearing habit suggests that the usual hunting method is by stalking rather than pursuit; spearing may limit Anhingas to capture of relatively small, laterally compressed fish (Owre 1967). Backward-pointing serrations on tips of both mandibles probably enhance holding of prey after capture (Beltzer 1982). Sometimes eats small items underwater, but more often brings them to surface. Shakes prey vigorously off the bill, tosses it in the air, and catches and swallows it headfirst. Sometimes catches insects out of water.

Fish that are too heavy to lift out of water it drags to shore and gets off its bill by repeatedly swiping it against vegetation; it then subdues the fish with vigorous stabbing (Wellestein and Wiegmann 1986). May capture food too large to eat, such as some catfish (Owre 1967: 129); makes no attempt to swallow such items. Mean of 0.19 capture/min in n. Florida (Lee and Lee 1977); 6–8 small fish captured in 15 min in Florida (Nicholson 1961).

DIET

Major food items. Wide variety of predominantly small to medium-sized wetland fishes, with very small contributions of crustaceans and invertebrates. In Florida, nearly all sunfishes and bass (Centrarchidae) are important food items, as well as killifishes (Cyprinodontidae) and live-bearing fishes (Poeciliidae; Owre 1967). In Alabama, mullet (*Mugil cephalus*), sunfish, catfish, suckers, pickerel, crayfishes, crabs, shrimp, aquatic insects, tadpoles, water snakes, and small terrapins (Imhof 1962). J. J. Audubon (in Bent 1922) fed a tame Anhinga a fish 24 cm long and later 9 fish, each of which was >18 cm long. Largest fish found by Owre in stomachs collected from s. Florida was a warmouth (*Lepomis gulosus*) 132 mm long \times 45 mm deep. The stomach (with contents) of 1 Anhinga weighed $>7\%$ of the bird's total body weight. Occasionally eats crayfish, but Owre (1967) felt that the crayfish hard parts were often material derived from stomachs of ingested fish. Where large crustaceans are abundant, however, the Anhinga may concentrate on these (Owre 1975). Vegetation sometimes found in stomachs, but probably ingested accidentally, though this species has been noted eating hackberries (*Celtis* spp.; Palmer 1962).

Quantitative analysis. Of 14 stomachs collected in s. Florida, 3 were empty; remainder contained 151 identifiable prey items: $>98\%$ were fish; 56.3% of these were live-bearing fishes, 31.7% sunfishes and bass, 8.0% killifishes, and $<1\%$ crustaceans (crayfishes and freshwater shrimps; Owre 1967).

Since the only large fishes (>5 cm) were centrarchids, these items contributed overwhelmingly to dietary biomass. From 16 stomachs collected in Florida, mullet, mojarra (*Eucinostomus* sp.), sunfishes, pickerel (*Esox* sp.), bream, and gizzard shad (*Dorosoma cepedianum*) predominated, with insects in a few, and 1 stomach nearly filled with caddis fly larvae (Trichoptera; Sprunt 1954). Regurgitated food items of Anhinga nestlings in Georgia, in decreasing order of frequency, were bluegill (*Lepomis macrochirus*), flier (*Centrarchus macropterus*), pike (*Esox americanus*), largemouth bass (*Micropterus salmoides*), and eastern chub sucker (*Erimyzon sucetta*; note that invertebrate food items may not have been counted; Hopkins 1970). From 4 stomachs in Argentina, the only prey items were fish, including 2 unidentified Curimatidae, 8 *Eigenmania virescens* (Gymnotiformidae), 1 *Schizodon* sp. (Anastomidae), 1 *Astyanax* sp. (Cichlidae), 1 *Crenicichla lepidota* (Cichlidae), 4 unidentified cichlids, the operculum of 1 unidentified mollusk, and parts of aquatic plants (Beltzer 1982). A single stomach collected from an individual foraging in an agricultural impoundment in Guyana contained 118 prawns (*Macrobrachium jelskii*; Owre 1975).

FOOD SELECTION AND STORAGE

As described above, the Anhinga sometimes impales and then lets go fishes that are too large to eat. Preferentially takes laterally compressed species, and avoids thick-bodied fishes (Owre 1967: 131). Commonly takes fishes as long as 21 cm.

METABOLISM AND TEMPERATURE REGULATION

Low basal metabolism and high thermal conductance for its body size; latter may result from poor feather insulation (Mahoney 1981, Henneman 1982). Because feathers are fully wettable, with no impermeable layer of insulation next to body, immersion in water is energetically costly, and Anhingas spend considerable amounts of time sunning. Spread-wing behavior, usually with back toward sun, is the most common posture while sunning; primary function of this behavior has been shown to be thermal regulation rather than wing-drying (Henneman 1982). Spread-wing sunning is most common at low temperatures and high insolation; black plumage on back, wings, and tail of both sexes may be an adaptation to enhance thermal gain during sunning. At low ambient temperatures (<30°C) and low insolation (<222 W/m²), neck is commonly folded in tight S-shape and pressed against upper body, and occasionally head and neck are laid along back and covered with wings. At temperatures <10°C, Anhingas become inactive and hypothermic (Mahoney 1981). Uses gular-fluttering for cooling when ambient temper-

atures >25°C; rarely uses wing-spreading with gular-fluttering (Henneman 1982). Lack of insulation near body presumably allows cooling by swimming during high temperatures.

At night, Anhingas lower their metabolic rate, body temperature, and thermal conductance. This behavior is calculated to result in a 12 and 8% savings in total energy needed over the course of the night or of a 24-h period (total of 280 kcal), respectively (Henneman 1983).

DRINKING, PELLET-CASTING, AND DEFECATION

Pellets not reported, although cormorants commonly cast pellets (Ainley et al. 1981, Siegel-Causey 1988). Defecates freely at the nest, on perches, in flight, and in water. Guano rarely accumulates at colonies because of arboreal nesting habits, unlike in cormorants, but walking under an Anhinga colony can be treacherous.

SOUNDS

VOCALIZATIONS

Development. Young produce low wheezing call resembling that of young herons. No other information.

Vocal array. Generally silent, and nothing resembling a song is given by this species (see Fig. 2). The most common note from both sexes is a distinctive, rapid, undulating clicking or chattering, similar to a treadle-operated sewing machine, varying to loud, harsh *cruk-cruk-cruk*, given frequently at nest relief during incubation (Burger et al. 1978). Owre (1962: 195–196) described sounds at nest as “squalling-raucus, rapidly-uttered series of *chitter, chitter, chitter, chee, cheur, chitter, chitter*, often rising then falling as they are uttered”; these sounds are not heard outside of breeding season. When both sexes are calling at nest, head usually is drawn up and back, neck arched, mouth open, and head swayed about (Owre 1962). Vocalizations at nest may end with open mandibles thrust into nesting material. Before settling into nest, gives a rolling, repetitive call that is harsher in males. In disputes over perches and territory, clicking becomes prolonged and intensified. When courting on the wing, J. J. Audubon (in Bent 1922) noted whistling note similar to the “eek, eek, eek” of some raptors, the first loudest and the rest diminishing in strength; also gives grunting call notes on the water that resemble calls of cormorants (these have not been mentioned by other sources). At climax of courtship display when tail is cocked and bill is held downward, produces a guttural sound resembling rolling notes of Eastern Screech-Owl (*Otus asio*). Before copulation, produces ≥1 explosive notes, different

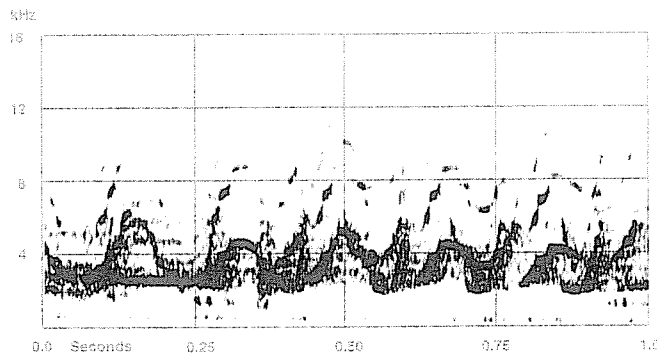


Figure 2. Calls of multiple *Anhinga* nestlings given just prior to adult leaving the nest. From recording no. 17174 in the collection of the Borror Laboratory of Bioacoustics (BLB), The Ohio State University. Prepared by staff of BLB, using a Kay Elemetrics DSP 5500 Sona-Graph (with effective frequency resolution of 300 Hz and a 200-point FFT transform size).

in males and females. Does not have alarm call, but sometimes react to alarm calls of other species (del Hoyo et al. 1992). When sleeping, emits a wheezing sound that may be breathing. No geographic variation in vocalizations reported.

Phenology. No information.

Daily pattern. No information.

Places of vocalization. Away from nest, generally silent, but may make clicking calls and shrill rattling sounds either in flight or from a perch. In the nest, has a much wider repertoire, with harsh croaks, rattles, and grunts.

Social context and presumed functions. No information other than context (e.g., nest relief, courtship, copulation, agonistic encounters, as noted above).

NONVOCAL SOUNDS

None reported.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing etc. Walks with high-stepping gait or waddle, with wings often partially spread for balance. Clumsy on perches and the ground, and when climbing. Legs are set well back on body; legs and feet are adapted for climbing up to perches and for perching. Claws are longer and more curved than in cormorants, and hindtoe is more opposed. Perches generally near and especially over the water in trees and grasses, by hopping or climbing to low spots. Perching is an important function in this species because drying of wings and plumage is critical to thermoregulation (see Food habits: metabolism and temperature regulation, above).

Flight. Direct, strong flapping alternating with gliding. Wings held flat in gliding and soaring flight, neck outstretched, though sometimes held with slight kink. Often uses thermals for soaring, and may achieve altitudes of several thousand feet while so doing (Owre 1967); soaring is enabled by relatively light wing-loading, emarginated vanes of distal primaries, and well-developed alula. May dive suddenly at high speed from great altitude (Bent 1922). Uses its long, prominent tail in accipitrine-like maneuvering among trees and tight quarters. Capable of taking off directly from surface of water or even from submerged position, although these methods are rarely used and inefficient, and wings are more often dried on perch before flight. Before flight from a perch, spreads wings partially and points bill in direction of flight ("Look" and "Crouch" phases of takeoff display; see van Tets 1964). Usually becomes airborne by diving into flight from trees, bushes, rocks, and banks (Owre 1967). Lands from flight to exposed, elevated perches, or makes full-stall landings on water on belly and breast. Makes water landing usually only after short flight from nearby perch. Becomes flightless during complete postbreeding molt of remiges. Mean total wing-loadings of 0.84 and 0.75 g/cm² for males and females, respectively ($n = 8$ adults; Owre 1967). Wing bones are dense and of small caliber, and sternum is nonpneumatic (relatively little air space within the bone; Owre 1967). Flapping rate 4.0 wing-beats/s \pm 0.3 (Palmer 1962).

Swimming and diving. Swims with neutral buoyancy as a result of wetted plumage and dense bones. When at surface, tends to swim low in water, often with only neck and head above water, sometimes with only bill exposed (Bent 1922). Breast-feathers lack hooklets that interlock barbules (Casler 1973), allowing water to penetrate to the skin. May also drink water before diving as a form of ballasting (Owre 1967). Dives most often from water's surface, less often from perches, and rarely from air. Swims using webbed feet for propulsion. Although wings may be slightly open underwater, they are not used for propulsion, and both wings and tail may be used as stabilizers in slow swimming. Skeletal adaptations and musculature of tail allow intricate movements and large range of motion (Owre 1967). Generally swims slowly, more usually stalking prey than pursuing it. Holds bill partially open while swimming, allowing use of upper or both mandibles in spearing. Dives last 30–60 s (W. J. M. Vestjens in Cramp and Simmons 1977). Spends relatively little time at water surface—to handle prey or during short intervals between dives. In Florida, <5–14% of daily time budget is spent foraging in water (Lee and Lee 1977, Henneman 1982). Rarely submerges head to look underneath

water surface as cormorants do; instead submerges entire body. May swim with alternate strokes of feet (J. J. Audubon in Bent 1922), but this is unconfirmed.

Buoyancy may be regulated by inflation of some air sacs, specifically by altering wing position to regulate size of opening to subpectoral diverticula, which may function as buoyancy tanks (Casler 1973). In addition, the large surfaces of wings and tail are used to counteract any tendency to sink. When partially submerged at surface, tends to move in bobs and jerks, perhaps because strokes of feet are the only force counteracting the tendency to sink.

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. Preens often when perched. Commonly scratches head with feet; corrugations on pectinate third toe may function to help clean feathers.

Sleeping, roosting, sunbathing. After swimming, seeks perch immediately, and spreads wings soon after perching, fanning its tail and shaking itself to get rid of excess water. This behavior serves dual purpose of drying and thermoregulation (see Food habits: metabolism and temperature regulation, above). While perched, usually holds neck in S-shape, with bill pointed downward. Uses long, wide tail constantly as a balancing and support appendage when moving among branches. May perch for hours at a time with feet grasping small branches, or may lie on larger branches, with feet either underneath body or stretched out behind. Reduced webbing between third toe and hallux (by comparison with cormorants) may be adaptation for more efficient roosting (Owre 1967). Generally diurnal; no nocturnal behavior recorded. Of 667 waterbirds identified flying over a power line in the Everglades at night using night-vision equipment, none were Anhingas (Deng 1998). J. J. Audubon (in Bent 1922) observed Anhingas returning to roosts habitually, and they changed roost sites only with considerable reluctance and aggression in the new roost. Daily pattern of perching and hunting from same perch is common; moves to communal roosts 0.5–1.3 h before sunset (Lee and Lee 1977). In Mexico, individuals arrived at roost singly between 17:15 and 18:00, sometimes in darkness; arrived earlier in evening and departed later in morning than ciconiiform birds in same roost (05:30; Burger et al. 1977). Within roost site, selects dead branches and snags, though no fidelity to specific perches between nights (Burger et al. 1978). Sleeps with body almost erect, head tucked under scapulars; may emit wheezing sounds (J. J. Audubon in Bent 1922). In rainy weather, may roost for most of the day, and stand motionless and

erect with neck and head stretched upward, as if to allow water to glide off feathers, occasionally rousing and fluffing its feathers.

Daily time budget. During daylight observations at variety of temperatures and seasons, Anhingas in n.-central Florida spent 14.0% of time swimming and hunting, 26.5% sunning, 16.4% preening, and 29.1% perching ($n = 1,386$ observations of 10–15 individuals; Henneman 1982). In n. Florida during fall, <5% of day in water foraging, >90% sunning, preening, and perching (Lee and Lee 1977).

AGONISTIC BEHAVIOR

Physical interactions. One of the most territorial of the Pelecaniformes toward conspecifics, but usually unaggressive toward other species. Agonistic behavior between males is common in colonies, especially on nest; will approach intruders by hopping along branches of tree with spread wings and open bill. Rarely, contestants stab each other on head and neck, sometimes grappling aggressively (W. J. M. Vestjens in Cramp and Simmons 1977, Siegel-Causey in press). Aggressive encounters between females are uncommon and less intense than those between males. In a mixed-species colony in Mexico, the Anhinga demonstrated the highest proportion of conspecific aggression of any species. Tends to be socially dominant to most heterospecifics (usually Ciconiiformes) in mixed-species breeding colonies (Burger et al. 1977).

Communicative interactions. **THREAT DISPLAYS.** Both sexes use bill-waving and gaping to warn intruders away (van Tets 1964). Pointing Display (laterally flattened neck, head, and closed bill stretched forward and waved slowly while tail raised; appearance generally sleek) is thought to be a threat display.

APPEASEMENT DISPLAYS. None reported.

SPACING

Territoriality. Spacing through aggression is evident in roosting and breeding. When foraging, individuals often exclusively use area 10–20 m around a single perch, though the mechanism of spacing in foraging sites has not been reported (Nicholson 1961, Lee and Lee 1977). Both sexes vigorously defend nest sites; nearest nests 1.8–4.6 m apart (Allen 1961, van Tets 1964), though aggressive tendencies decline with breeding cycle such that already paired males on nests may allow close approach of displaying males. Though most breeding males display from established territories, some nonterritorial males have been noted in breeding colonies by both Allen (1961) and Meanley (1954). Males are involved in more aggressive interactions than females while incubating and brooding; in 14 nests, males averaged 7.8 conspecific

Table 1. Summary of agonistic, nest defense, and courtship displays in the Anhinga.

Display / performing sex	Site	Presumed function	References ¹
Bill-waving Both sexes	Nest or roost	Threat	A
Gaping Both sexes	Nest or roost	Threat, "warn intruders"	A
Pointing Display Both sexes	Nest or roost sites	Threat, courtship	A, B
Forward Snap Both sexes	Nest site	Threat, courtship	C
Peering Around Male	Nest site	Courtship, advertisement	B
Wing-Waving Male	Nest site	Courtship, advertisement	B, C
Open-bill, throat vibration Female	Nest site	Courtship	C
Wing-Forward Display Male	Nest site	Courtship	B
Mock feeding Male	Nest site	Courtship, precopulatory	C
Kink-Throat Display Both sexes	Nest site	Nest relief, mate recognition	B

¹References: A = van Tets 1964; B = A. J. Meyerriicks in Palmer 1962; C = Allen 1961.

encounters and females 0.5 during entire incubation period; most conspecific aggression (75%) is performed by nonincubating birds (Burger et al. 1978). No conspecific aggression by adults occurred after hatching. Reluctant to leave roosts when disturbed, and considerable aggression occurs when one bird attempts to join another roost, suggesting individual or group attachment to and defense of roost sites (J. J. Audubon in Bent 1922). When roosting in Mexico, 0.12 aggressive interaction/h/individual overall, the vast majority of these with conspecifics (0.13/h); Anhingas won slightly more than half the aggressive encounters with conspecifics (Burger et al. 1977, 1978). See Table 1 for summary of agonistic displays.

Individual distance. Roosting Anhingas will defend several meters around them (J. J. Audubon in Bent 1922). Internest distances generally are

large by comparison with other Pelecaniformes, varying from 1.8 to 4.6 m (Allen 1961, van Tets 1964). In Mexico, Anhingas nested closer to conspecifics than was predicted by random spacing in the colony (Burger et al. 1978).

SEXUAL BEHAVIOR

Mating system and sex ratio. Repeated and lengthy observations of nesting behavior indicate that this species is socially monogamous (Meanley 1954, Allen 1961, Owre 1967, del Hoyo et al. 1992). No genetic data on relatedness of parents to nestlings, however. No data available on sex ratios.

Pair bond. No information on duration of pair bonds. Some individuals paired before arrival at breeding colonies (Meanley 1954).

COURTSHIP DISPLAYS AND MATE-GUARDING. Primary research on courtship displays has been done by

Allen (1961), Meanley (1954), Owre (1962), and van Tets (1964), and is summarized here (see Table 1 for summary of behavioral displays).

Both sexes engage in soaring early in breeding season, perhaps as part of courtship; males may soar more often than females. Singly or in groups, repeatedly circle and soar over breeding area, high enough to be almost out of sight; then sail down on set wings to perches. May involve close following by individuals of a courting pair (J. J. Audubon in Bent 1922, Owre 1962). These aerial displays are accompanied by pulling at twigs and branches. Some courtship may take place away from nesting sites, involving manipulating and tossing of twigs, and aggressive approaches of females by males, followed by sparring (Owre 1962).

Nest sites later marked by placement of leafy twigs in fork of tree or old nests around which the nest territory is established. Male courtship displays are usually but not always on territories; non-territorial displaying males usually are ignored by females (Allen 1961). From crouched or horizontal position, males may perform Pointing Display (see Agonistic behavior, above) or Peering Around (upright posture, head and neck extended upward halfway, slowly looking right and left; A. J. Meyerrieks in Palmer 1962), usually stimulated by other birds landing nearby. Wing-Waving is a prominent courtship display series: From low crouch or horizontal position, Peering Around followed by head and neck extended to 45°, feathers of head, neck, and median crest erected, wings waved out and back slowly in unison, then alternately, becoming violent enough to shake the perch, 2–3.5 beats/s; primaries remain folded behind secondaries when wing-tips are raised (W. J. M. Vestjens in Cramp and Simmons 1977). After 5–15 s, followed by low horizontal crouch or bow with neck held down in S-shape or deeply inverted U-curve, tail raised over back, head- and neck-feathers erected, wings extended partially, body waved back and forth slowly, feathers vibrated slightly but rapidly. Holds latter stance for several moments; at peak, gives guttural sound resembling low rolling notes of screech-owls (Meanley 1954). May suddenly raise head and neck fully upward, bill pointing to zenith, followed by reverse bow, with back of head brought to back, followed by extreme forward bow. Performs Wing-Waving series at almost any time of day that females are present, and appears to make males more conspicuous by flashing silvery wing-coverts and neck-feathers (Allen 1961).

While seated in nest or from branch near nest, both sexes may show Forward Snap or Snap-Bow (A. J. Meyerrieks in Palmer 1962, van Tets 1964), often in response to approaching birds: Holds body in low crouch with head retracted, head and neck

suddenly darted forward, and bill snapped on twig, fresh leaves, or air, head often vigorously wiggled sideways but twigs not snapped off; accompanied by low-intensity Wing-Waving, tail raised up and sometimes forward, and head-, neck-, and median crest-feathers erected. Male may also perform Wing-Forward Display: From sitting position, quickly extends head fully forward and brings both wings, partly extended, forward and backward in rowing motion. This display intensifies such that wings are brought forward at same time, and head and neck are raised upward and back, and held for several moments. Maximum display rates of Forward Snap, 2–3/min; of Wing-Forward Display, 4–5/min. During courtship, females wander through areas of breeding males, Peering Around and often moving on. After approaching a male that is performing Forward Snaps, female may open bill and rapidly vibrate throat while sweeping head and neck back and forth and performing Pointing Display. Often courting birds cross necks in stiff pointing position. This progression may cause male to display very rapid Wing-Waving, mutual preening, and bill-rubbing, and male may insert his bill into female's throat in mock feeding.

Courtship displays tend to highlight the spread tail with corrugations, and silver on wings. Transverse corrugations of rectrices and scapular feathers are most prominent in nuptial plumage, and may play important function in courtship activities, both by reflecting light and calling attention to the bearer, and possibly through the creation of nonvocal sound during flight displays (Owre 1967).

Kink-Throat Display is given by both males and females before landing, during handling of nest material, and as mutual recognition display at nest; very typical during nest relief. Holds mouth wide open and wags head from side to side; female displays pink mouth-lining, and male displays black mouth-lining; utters repetitive call note, hyoid apparatus pushed forward and downward, with neck in S-shaped position, mouth pointed downward.

Mates often remain at nest site when not incubating, though no significant differences by sex (Burger et al. 1978), and no obvious signs of mate-guarding.

COPULATION; PRE- AND POSTCOPULATORY DISPLAYS. Takes place on nest, lasting about 5 s (Allen 1961). May be preceded by female's stepping onto nest, male's performing bows, waving wings, and ruffling feathers on branch 1–2 m from nest, followed by female's performing similar displays, and by mutual twig-offering (Allen 1961, Palmer 1962). During copulation, necks are extended, and male takes a stick or female's bill in his; female's

head may be pulled upward and backward by male. Pair bond formed with first copulation (Allen 1961). Copulation and associated behavior diminish in intensity and frequency after first day; rare by fourth day, although within-pair copulations may continue up to 15 d from female's initiation of incubation (Burger et al. 1978).

Extra-pair copulations. Extra-pair copulation attempts have been observed in colonies in both Arkansas (Meanley 1954) and Mexico (Burger et al. 1978) up to 15 d after onset of incubation by female participant. No genetic studies of parentage to date.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Occurs in flocks of up to several hundred birds (del Hoyo et al. 1992, Stevenson and Anderson 1994), particularly in winter, though less social and less inclined to flock than are cormorants. During migration, may soar with conspecifics or with several other species. Within colonies, tends to nest closer to other Anhingas than would be predicted by relative species occurrence (Burger et al. 1978). Up to 400 Anhinga nests reported from multispecific colonies of wading birds (Corkscrew Swamp, Collier Co., FL; Phelps 1914 in Howell 1932). Nests in much smaller numbers in many locations (mean of 43 nests/colony in 69 colonies in Florida; Runde 1991), often without other species. No evidence of helpers at nests, social groupings, or extended parental care reported. Frequently roosts both with conspecifics and in mixed-species roosts.

Play. Young several weeks old practice throwing sticks into air and catching them (Stevenson and Anderson 1994).

Nonpredatory interspecific interactions. Occurs often in mixed-species flocks at roosts and in the air, especially with other waterbirds. May nest in and near colonies of other waterbirds, but generally interacts little with other species when doing so, and may allow close nesting by heterospecifics. Most ciconiiform birds are socially subordinate to Anhingas; Anhingas may appropriate freshly built nests of Little Blue Heron (*Egretta caerulea*), Great Egrets (*Ardea alba*), White Ibises (*Eudocimus albus*), or Snowy Egrets (*Egretta thula*; Allen 1961, Terres 1980). During breeding, 25% of agonistic encounters were with other species, and Anhingas won 92% of bouts (Burger et al. 1977). In a roost in coastal Mexico, however, 90% of Anhinga agonistic encounters involved conspecifics, and Anhingas generally were less often involved in aggression than were other species in the same colony (0.12 encounter/bird-h for Anhingas, 0.44 for other species present in roost; Burger et al. 1978). Does not usually feed with other species or in groups, although Nicholson (1961) suggested that Pied-

billed Grebes (*Podilymbus podiceps*) may help scare fish toward Anhingas. Usually flies solitarily or with conspecifics; more rarely, soars with other species (Oberholser 1974).

PREDATION

Kinds of predators; manner of predation. Apparently few predators; no references to death of adults by predation found (Bent 1922). May be susceptible to crocodilians, though rarely found in their stomachs (<1%; Delany and Abercrombie 1986). Anhingas are flightless during complete and nearly simultaneous molt of remiges and rectrices (Owre 1967); probably most vulnerable to predation at that time. Molting birds are said to be much more wary and retiring than nonmolting birds (Owre 1967).

Response to predators. When in water, may submerge quietly or swim partially submerged with only head and neck out of water. When threatened on perch, often escapes by diving into the water. Retiring, low-perching, and rarely found far from water during molt.

BREEDING

PHENOLOGY

Pair formation; nest-building. Pairs may form away from site of breeding (Owre 1962, Meanley 1954). Pair formation may take as little as 3 d. Breeding within a colony or area may be synchronous (Burger et al. 1978) or spread out over months (Palmer 1962, Leber 1980). Time of initiation of nesting activities varies considerably with latitude in U.S., with first activity noted 4 Feb at Merritt I., FL (Girard and Taylor 1979), and third week of Apr in Arkansas (Meanley 1954). In s. Florida, nesting activity found in nearly all months (Sprunt 1954, Stevenson and Anderson 1994). Breeding probably is cued by temperature and availability of food; in Everglades of s. Florida, majority of chicks hatch during mid-dry season, when fish are most concentrated by receding water levels. In Pacific coastal Mexico, breeding is initiated when mangrove flats reflooded during wet season (Burger et al. 1978). Breeding is earlier in Mexico on Caribbean than Pacific Coast, during late dry season. Little is known about timing of breeding elsewhere in Tropics.

First/only brood per season. EGG-LAYING. See Figure 3. Extreme egg dates in Florida Dec–Aug, but nests with downy young have been found as late as Dec; bulk of egg-laying Feb–Jul in peninsular Florida (Sprunt 1954, Stevenson and Anderson 1994). In Louisiana, eggs laid Apr through Jun (Lowery 1955); in Alabama, 27 Apr–16 Jun (Imhof

1962); in S. Carolina, 18 Apr–10 Jun (Post and Gathreaux 1989); in Texas, 14 Apr–27 Jul (Oberholser 1974); in Arkansas, 24 Apr–6 Jun (Meanley 1954). On Pacific Coast of Costa Rica, eggs Aug–Feb (middle of local wet season to late dry season); bulk of laying Sep–Nov (Leber 1980). In Pacific coastal Mexico (Nayarit, San Blas), laying 8–28 Jul (rainy season; Burger et al. 1978).

LAYING OF FIRST TO LAST EGGS IN CLUTCHES. Meanley (1954) found 1- to 4-d intervals between eggs, so clutches could take 3–7 d to complete.

DEPARTURE OF YOUNG FROM NEST OR CESSATION OF CLOSE PARENTAL CARE. Dependent young in Alabama 16 Jun–27 Jul (Imhof 1962). In Arkansas, young depart rookery by mid-Jul (Meanley 1954). In s. Florida, young in nests nearly year-round; bulk of fledging by Jul.

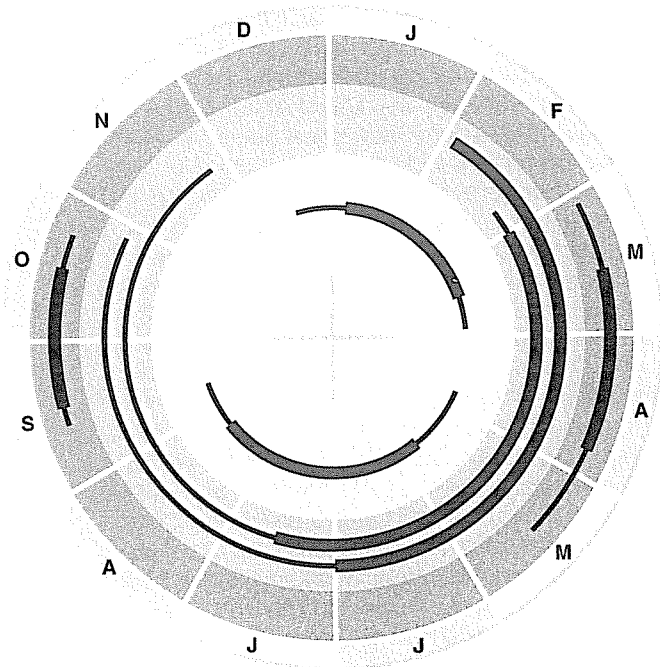
Second/late broods per season. None noted, but secondary attempts are quite possible in the extremely long breeding season of s. Florida.

NEST SITE

Selection process. Nests solitary (Florida Everglades) or in loose groups of several to hundreds of pairs. Frequently nests with other colonial waterbirds, especially herons and egrets (see Behavior: social and interspecific behavior, above). May appropriate freshly built nests of Little Blue Heron, Great Egret, White Ibis, Wood Stork (*Mycteria americana*), or Snowy Egret (Allen 1961, S. Rallo unpubl.).

Site characteristics. Nests are nearly always over water, often in colonial nesting situations, usually with perches nearby. Nest heights variable; depend somewhat on available vegetation: 1.09–3.23 m ($n = 12$) above water (Arkansas; Meanley 1954), 1–4.6 m (Florida; Bent 1922), 3–13.5 m (Alabama; Imhof 1962), up to 30 m (Florida; Sprunt 1954), average 3.91 m \pm 0.80 SD (range 2.5–5.1, $n = 15$ nests, coastal mangroves in Florida; Girard and Taylor 1979), 1.7–2.3 m ($n = 10$ overall; averages of first and second nesting attempts, respectively, in Texas; Taylor and Michael 1971), 1.8–4.0 m (average 2.7 \pm 0.2 SD, $n = 35$ nests, Costa Rica; Leber 1980); average 2.45 m \pm 0.61 SD ($n = 32$; Nayarit, Mexico; Burger et al. 1978). In U.S., nests frequently in cypress (*Taxodium* spp.), buttonbush (*Cephalanthus occidentalis*), willow, red maple (*Acer rubrum*), red (*Rhizophora mangle*) and black (*Avicennia germinans*) mangroves, live oak (*Quercus virginiana*), and water tupelo (*Nyssa aquatica*).

Builds nest anywhere from close to trunk to near distal ends of branches. In Mexico, Anhingas made up 10% of a colony, but Anhinga nests were nearest neighbors 80% of the time, indicating some social tendencies (Burger et al. 1978). Nesting was random with respect to available tree species in the colony:



Molt —
Breeding — Young
Eggs —
Migration —

Figure 3. Annual cycle of breeding, molt, and migration of the Anhinga in North America. Thick lines indicate peak activity; thin lines, off-peak.

41% of 40 pairs nested solitary in tree, 34% in trees with other nesting species, 25% in trees only with other nesting Anhingas. Most of nests (94% of 40 nests) were fully concealed from sunlight; 80% of 32 nests were built at junction of trunk and branches. All nests had exposed perch site nearby (mean height 1.16 m) that was usually used by nonincubating mates; mean distance to nearest neighbors 2.08 m \pm 1.78 SD ($n = 32$); distance to nearest Anhinga nest 1.48 m \pm 1.00 SD ($n = 8$). In Arkansas, 1.8–2.4 m ($n = 20$) between closest conspecific nests (Meanley 1954).

NEST

Construction process. May build new nests, use old nests, or appropriate nests of waders by waiting until adults leave nests. During appropriations, spirited and lengthy fights may occur; Anhingas often eject eggs of other species.

When building own nest, male begins construction before pairing by placing large sticks and green material in forks of trees and collects nearly all nesting material; female finishes building nest. Female may bring new nest material after pair bond is established, as part of nest-relief ceremonies; in Mexico, female accounted for 19% of all nest material presentations throughout nesting period, and male returned significantly more often (75% of time) with green leafy material than did female

(20% of time; Burger et al. 1978). Pair may begin building or adding to nest platform within 20 min of first copulation; nest completed in 1–3 d. Inserts sticks, plant stalks, and feathers with sideways shaking of head into nest rim at 45° angle to the horizontal.

Structure and composition matter. Bulky platform of sticks, somewhat more compact than heron nests, usually over water, often but not always lined with fresh leaves and green twigs (Spanish moss [*Tillandsia usneoides*], willow leaves and catkins, cypress and mangrove leaves commonly are used; aquatic plant material occasionally is included). Presence of green or leafy material generally distinguishes active Anhinga nests from those of wading birds. In a Costa Rican heronry, foundation sticks were 10 mm in diameter, other mangrove sticks were 3–5 mm in diameter, and nests were lined with green mangrove leaves (Leber 1980). In Pacific coastal Mexico, nests in mangroves were composed of 18% mangrove twigs with live leaves attached ($n = 28$ nests; Burger et al. 1978), but no live material lining nest. Excreta tend to accumulate on rim of nest.

Dimensions. In Costa Rica, external diameter 26 cm (range 20–47; Leber 1980). In Mexico, nests shrank during incubation from mean 38.6 cm \pm 9.5 SD wide and 16.2 cm \pm 3.3 SD deep ($n = 24$) at beginning of incubation to 29.0 cm \pm 3.8 SD wide and 15.8 cm \pm 2.4 SD deep ($n = 30$; Burger et al. 1978). Nests appropriated from Great Egrets and Wood Storks are considerably larger than those built by Anhingas.

Microclimate. No information.

Maintenance or reuse of nests, alternate nests. Constantly adds new material to nest until young leave (van Tets 1964, Burger et al. 1978). Increase in addition of nest material just after hatching; half of female nest material trips, but only 5% of male trips, occur after hatching (Burger et al. 1978). Renestings following failure were documented in the same nests in Florida (Girard and Taylor 1979). Nests often persist from year to year, and although some are reused, many are not (Allen 1961).

Nonbreeding nests. None noted.

EGGS

Shape. Obviously pointed at one end. Considerable variation in shape, from elongate (Imhof 1962), to ovate, elliptical ovate, or elongate ovate (Bent 1922), to between subelliptical and long subelliptical (Palmer 1962).

Size. In U.S. National Museum collection, 42 eggs averaged 52.5 \times 35 mm (range 47–57.5 \times 33–37.5; Bent 1922). Twenty eggs—each from different clutches in Florida (15), Texas (1), and unknown location (4)—averaged 52.53 mm \pm 2.24 SD in length,

34.89 mm \pm 1.26 SD in breadth (Palmer 1962). In Costa Rica, average dimensions 52.7 \times 34.1 mm (range 49.6–55.8 \times 32.5–35.1, $n = 24$ eggs; Leber 1980). In Texas, average size 52.6 \times 35.1 mm (Oberholser 1974). Mean of 9 eggs from Charleston, SC, was 55.1 mm \pm 0.9 SD \times 34.9 mm \pm 0.4 SD (Colacino et al. 1985).

Mass and lipid content. Mean mass of 9 fresh eggs collected in Charleston, SC, was 36.3 g \pm 1.25 SD (Colacino et al. 1985). Mean lipid content of 46 eggs from different clutches was 5.6% (Ohlendorf et al. 1978).

Color. Pale bluish green, overlaid with chalky coating that appears to be spottily distributed on surface of egg. Eggs often have brownish or tan splotches; some are wholly covered with brownish tan, perhaps due to material smeared on them in the nest (Bent 1922). Surface of egg may become smooth after it has been incubated.

Surface texture. Covered with chalky layer, about 0.03 mm thick, of pure calcium carbonate in the form of vaterite. This layer probably serves to reduce clogging of pores by water, preening oil, and nest debris. The vaterite covering reduces the conductance and gas exchange of the egg by about 6% (Colacino et al. 1985).

Eggshell thickness. No decrease in thickness found between eggs collected before 1947 and before 1960 (Ohlendorf 1978). Rumbold (1995) found an increase in thickness in eggshells collected near a landfill in the 1980s and 1990s, compared to pre-1946 eggs. Thickness of 5 eggshells collected in 1984 in Charleston, SC, averaged 0.302 mm \pm 0.023 SD (Colacino et al. 1985).

Clutch size. Generally 3–5 eggs. In Arkansas, 29 clutches averaged 3.83 eggs \pm 0.79 SD (range 2–5; Meanley 1954); At Merritt I., FL, mean 4.1 \pm 0.54 SD ($n = 11$; Girard and Taylor 1979); in e. Texas, mean 2.80 ($n = 11$ nests; Taylor and Michael 1971). On Pacific Coast of Costa Rica, mean 3.2 eggs/clutch \pm 0.92 SD (range 2–5, $n = 12$; Leber 1980); on Pacific Coast of Mexico, mean 3.89 \pm 0.58 SD (range 2–5, $n = 16$; Burger et al. 1978).

Egg-laying. Through repeated nest visits, Meanley (1954) found eggs laid at up to 4-d intervals, though predation between visits could have been a confounding factor. Young hatch at 2- to 3-d intervals; 1 instance documented of 2 eggs hatching the same day (Meanley 1954).

INCUBATION

Onset of broodiness and incubation in relation to laying. No data, but given the asynchronous hatching, probably begins with laying of first egg (del Hoyo et al. 1992).

Incubation patch. None mentioned. Incubates at least partly with feet (del Hoyo et al. 1992).

Incubation period. Burger et al. (1978) checked nests daily during egg-laying and incubation and found hatching at 26–30 d from laying; in 9 nests with complete data, first egg laid hatched in average 27.8 d \pm 0.91 SD (range 26–29) after laying.

Parental behavior. Females appear to stay on nest continuously during nest-building and egg-laying, probably to guard nest against loss of nesting material. Female is fed by male during this period (Allen 1961). Both sexes incubate by turns; in Mexico, no significant differences found in total time spent incubating by male (mean 55% of time, range 35–63, $n = 14$ nests) and female (mean 45%, range 37–65, $n = 14$ nests); male incubated significantly more from days 1 to 5 and 26 to 30 than did female; incubation bouts averaged 3.53 h \pm 1.58 SD ($n = 187$ bouts) for males, and 3.25 h \pm 1.56 SD ($n = 196$ bouts) for females, although some birds incubated continuously for up to 8 h (Burger et al. 1978).

Some abandonment of mate and nesting may occur during incubation. Meanley (1954) found 2 nests in which female abandoned nesting after laying and male did all incubating and rearing; the final success of these nests was not documented. Burger et al. (1978) noted that all 3 nests that failed during their study did so after 6, 8, and 9 d of incubation; in all cases, one member of pair abandoned nest, and the remaining member had incubated >75% of time after the mate had left.

Transfer of incubation duty is accompanied by intertwining of necks, undulating chatter calls and Wing-Waving, and Forward Snap (see Behavior: sexual behavior, above), performed mostly by the bird leaving nest. Approaching bird often brings green nesting material (Owre 1962). While incubating, bird may shift slightly, resulting in slow rotation of body around nest (Allen 1961). Mate often remains at nest site when not incubating; no significant differences by sex (Burger et al. 1978): Time spent attending by nonincubating bird decreased as incubation progressed; after day 25, mate returned to nest only to exchange incubation duties. Female tended to come earlier than male before an exchange and to leave more quickly than male afterward. Nest exchanges occurred most often from 07:00 to 09:00 and 14:00 to 15:00 than at other times of day.

Hardiness of eggs against temperature stress; effect of egg neglect. No information, but nests tend to be well hidden from direct sunlight (see Nest site, above).

HATCHING

Preliminary events and vocalizations. No information.

Shell-breaking and emergence. Young hatch at variable intervals of 0–3 d; 2–3 d most common (Meanley 1954). No other information.

Parental assistance and disposal of eggshells. No information.

YOUNG BIRDS

Condition at hatching. Few data. At hatching, young completely naked and reptilelike in appearance; eyes are open. Within 2 d, white down appears on underparts, followed by darker buff-colored down on upperparts. Nearly altricial; very little coordinated movement at hatching; unable to move about or find food within nest. No data on size at hatching.

Growth and development. MASS INCREASE. No information.

GROWTH OF BODY PARTS. Unknown.

MOLT INTO JUVENAL PLUMAGE. Starts at about 5 wk of age.

AGES WHEN CONTOUR FEATHERS APPEAR ON DIFFERENT TRACTS, OR SEQUENCE OF MOLTING AMONG TRACTS. Contour feathers generally start to appear at about 7 wk. No information about specific tracts.

CONTROL OF BODY TEMPERATURE. Until second week, unable to thermoregulate well, and must be protected by adult. Afterward, cooling by gular flutter is evident.

BEHAVIOR. Considerable size difference among siblings because of asynchronous hatching. Fights are frequent at feeding, usually involving pecking, and loss of youngest chicks to starvation is presumed in some cases (Leber 1980). Will regurgitate or leave nest if disturbed by humans.

LOCOMOTION. While still downy (about 2 wk of age), will jump out of nest and land in water; usually able to swim away, and able to climb back into nest (Meanley 1954).

PARENTAL CARE

Brooding. Brooding is nearly continuous through 10 d of age. In Mexico, brooding decreased from 12 to 16 d of age, from mean bout time of 3 h to 50 min. Parents no longer are present continuously after 12 d. After day 16, brooding ceased, and parents returned to nest only to feed; males and females brood roughly equal amounts of time (Burger et al. 1978). One adult brooded chicks to 12 d without mate.

Feeding. Both sexes collect food and feed by regurgitation. In Mexico, females performed average of 43% of feedings (range 38–62), males 57% (range 42–58, $n = 14$ nests; Burger et al. 1978). At first, liquefied and digested food is dribbled into chick's mouth, passing along parent's upper mandible and caught by open bill of young. Older chicks obtain solid food by regurgitation; young inserts head and bill into parent's throat. No comparative information on diet of young versus adults. Chicks beg for food by calling with bill closed and hyoids pushed forward, giving the gular

pouch an angular appearance. Reaching out toward parent as far as possible, young uses its wings to balance and turns its tail upward, sometimes prodding gular pouch of parent with its bill, and wagging its head. At first, chicks fed at least 6 times/d, slowing to 1 time/d at 6 wk of age (del Hoyo et al. 1992).

Nest sanitation. Minimal; fecal material accumulates on rim of nest.

Carrying of young. Not recorded.

COOPERATIVE BREEDING

No helping behavior recorded at nest.

BROOD PARASITISM

Not recorded, despite considerable observations during egg-laying (Meanley 1954, Allen 1961, Owre 1962) and studies of egg-laying patterns (Meanley 1954, Burger et al. 1978).

FLEDGLING STAGE

Departure from nest. By about 2 wk of age, will leap from nest to water if disturbed (Meanley 1954); can climb back to nests (3 m above water) at this age. At 3 wk, chicks begin to leave nest and perch on nearby branches. First flights at 6 wk of age.

Growth. No information.

Association with parents or other young. No information.

IMMATURE STAGE

No information.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Age at sexual maturity not known. Adult plumage is acquired in third calendar year of life. Age at first reproduction probably at least 2 yr (Palmer 1962).

Clutch. See Breeding; eggs, above.

Annual and lifetime reproductive success. In Arkansas, 40% of 20 nests and 70% of 10 nests fledged at least 1 young (2 different years of study) in a colony undergoing intensive human disturbance. In coastal Florida, 71% of 21 nest attempts fledged ≥ 1 young, and 44% of 69 eggs were lost (Girard and Taylor 1979); most failures were due to predation by Fish Crows (*Corvus ossifragus*) and Boat-tailed Grackles (*Quiscalus major*). In Costa Rica, 58% of 11 nests fledged ≥ 1 chick, and 42% of 38 eggs laid were known to have hatched (Leber 1980). In coastal Mexico, Burger et al. (1978) recorded 19% egg loss from laying to hatching, due primarily to abandonment of nests and to eggs being knocked out of nests. Of 36 eggs present at estimated time of

hatching, 97% did hatch, and 86% of 21 nests hatched ≥ 1 chick. Of 42 chicks, 95% lived to 16 d of age (Burger et al. 1978). In Florida, 23.7% of young from 11 broods lived to 8 wk of age (Girard and Taylor 1979).

Number of broods normally reared per season. In northern part of range, timing of breeding suggests that only 1 brood is possible per season. In s. Florida, nesting is possible year-round, and multiple brooding therefore seems likely, but no information. Late broods may be killed directly by freezing temperatures in fall and winter (J. B. Funderburg, Jr. in Stevenson and Anderson 1994).

LIFE SPAN AND SURVIVORSHIP

One Anhinga that was banded in Mississippi and found dead in Veracruz, Mexico, was 9 yr 8 mo old (Kennard 1975). One lived to 16.5 yr in U.S. National Zoo, Washington, DC (Terres 1980). No information on annual survivorship.

DISEASE AND BODY PARASITES

Diseases. "Except for studies on exposure to dioxins and furans, the health of Anhingas has been almost entirely neglected" (D. J. Forrester and M. G. Spalding in press). Newcastle disease reported from a single Anhinga in captivity in Florida. One of 4 Anhingas from central Florida examined in spring and summer 1958 was found to be seropositive for eastern equine encephalitis, and all of 3 nestlings examined from Lee Co., FL, were seropositive for St. Louis encephalitis virus. Botulism not reported for this species. Surveys for blood parasites so far have been negative. A 6-cm filarial worm (*Seratoaspiculum helicinum*) infects the meninges of the Anhinga cerebellum, and although this parasite has been well described (Wyman 1869), the life cycle and effects of this large brain worm on Anhingas are completely unknown. Wyman noted that ≥ 8 worms were often found in Anhinga brains, and that the mass of worms produced a deep indentation in the cerebellum. Unidentified coccidian oocysts were found in a sick Anhinga in Brevard Co., FL. Ascarids probably are the most prevalent and numerous of the helminths in Anhingas, with some 22 species documented (D. J. Forrester and M. G. Spalding in press). Though Owre (1962) suggested that ascarids in Anhingas and cormorants may simply aid in digestion, both Wyman (1869) and Huizinga (1971) reported common perforation of the mucosa of the proventriculus by ascarids, causing hemorrhage and ulcerations. Because of its diet, Anhinga almost certainly comes in contact with the large parasitic nematode *Eustrongylides ignotus*, which can perforate the stomach and penetrate the internal organs of other fish-eating birds (Spalding and Forrester 1993).

Body parasites. Two species of chewing lice (*Ciconiphilus decimfaciatus* and *Pectinopygus anhingidae*) documented in specimens from Florida (Forrester et al. 1995).

CAUSES OF MORTALITY

Exposure. J. B. Funderburg, Jr. (in Stevenson and Anderson 1994) reported all individuals in a second brood near Lakeland, FL, killed by a freeze during Dec 1962. No studies of effects of cold weather on this species, though Henneman (1985) has calculated the geographic limitations of this species that are imposed by its peculiar thermoregulatory needs.

Predation. Delaney and Abercrombie (1986) found remains of Anhingas in <1% of stomachs of 350 American alligators (*Alligator mississippiensis*) in n.-central Florida. Predators of eggs and nestlings include Fish Crows, Boat-tailed Grackles, yellow rat snakes (*Elaphe obsoleta*), and raccoons (*Procyon lotor*; Taylor and Michael 1971, Girard and Taylor 1979, Stevenson and Anderson 1994). Grant (1970) suggested that nest predation by Fish Crows contributed significantly to the decline of Anhingas in N. Carolina. Although red imported fire ants (*Solenopsis invicta*) are common throughout breeding range, no reports of lesions or attacks on Anhinga nests.

Competition with other species. Late-hatching chicks may starve in competition with older brood-mates, and last-hatching chicks are those most likely to die (Burger et al. 1978).

RANGE

Little information; territorial in winter at roosts and feeding sites, suggesting at least temporary site fidelity in winter. No information on site fidelity during breeding, though consistent reuse of colonies suggests that nesting is highly nonrandom. No data on distances dispersed between fledging and first breeding. No information on home range.

POPULATION STATUS

Numbers. Generally difficult to survey because of plumage color and habit of breeding in small colonies; probably grossly underestimated in most aerial surveys. In Florida, aerial and ground surveys statewide in 1976–1978 detected 6,050 breeding pairs in 69 colonies (Nesbitt et al. 1982). A similar survey in Florida in 1986–1989 estimated 9,095 pairs in 189 colonies (Runde 1991). In Texas, surveys of inland and coastal areas showed a maximum of 648 pairs annually during 1973–1980 (Texas Colonial Waterbird Society 1982). In Louisiana, surveys of coastal areas showed 1,426 breeding pairs in 17 colonies in 1976 (Portnoy 1977). In S. Carolina, surveys of entire coastal plain in 1988, 1989, 1994, and 1996 resulted in estimates of 909, 1,470, 6,477,

and 2,272 nesting pairs, respectively (Dodd and Murphy 1997). Taken together, these reports suggest that in mid- to late 1970s, combined U.S. population (estimated) was 10,000–17,000 breeding pairs. Within U.S., Breeding Bird Survey (BBS) maps suggest that the Everglades (Dade, Monroe, Collier, and Broward Cos., FL), upper St. Johns River, FL, s.-central Louisiana, and Okefenokee Swamp, GA, are locations of highest breeding densities.

Trends. BBS results indicate no overall change in population during 1966–1996, though significant declines were noted in Central BBS region (Anhinga range west of w. Mississippi and w. Tennessee; –5.4% decline/yr), and significant increases in Florida region (+4.3%/yr). In Florida, approximately 33% increase in numbers breeding was estimated in statewide aerial surveys from 1976–1978 to 1986–1989 (Runde 1991). Though this increase was not considered significant, a significant decrease in numbers of breeding birds per colony was detected.

Before 1980, nearly all BBS trends in all regions were positive; after 1980, most trends negative, with only the Central region showing a significant decline. In Texas, significant decreases in breeding numbers and distribution, especially inland, between 1930s and 1960s (Oberholser 1974). In Louisiana, apparent decreases between populations in coastal areas surveyed in 1976 (1,426 pairs in 17 colonies; Portnoy 1977) and 1990 (245 pairs in 17 colonies; Martin and Lester 1991), although there were important differences in the methodology of these surveys, and both probably were inefficient at detecting this species. In Arkansas, James and Neal (1986) provided evidence of widespread disappearance of long-occupied historical colonies (see Distribution: historical changes, above), and suggested that a population decline had occurred.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. Although Darters (*Anhinga melanogaster*) have been used for food, the Anhinga in the U.S. has been considered “useless for food,” and there is “no market for feathers” (Bent 1922); some may be nonetheless shot on occasion for sport. Of 53 band returns for this species, 39% were shot, the majority in the U.S. Since this bird takes large quantities of fish in its diet and forages in sites frequented by fishers, entanglement with monofilament line and ingestion of hooks and fishing gear is probably a threat, though quantitative data are lacking. James and Neal (1986) listed “former hunting pressure” as a

Table 2. Geometric mean or range of means of contaminant levels found in Anhingas. TCDD* values are reported in ppb, wet weight; all other contaminants are reported in ppm, wet weight.

Sampling location	Sampling period	Tissue sampled	DDE	PCBs	Mirex	Total TCDD*	Mercury	Source ¹
Florida	1972	Brain			0.03			C
		Fat			0.06			C
		Liver			0.06			C
	1972-1973	Eggs	0.14-0.76	0.21-1.1				A
	1989-1991	Eggs Eggs Nestlings	0.29-0.71	0.006-0.20		0.3-3.6 0.1-0.3		B D D
1989-1994	Eggs Nestlings					0.05-22 0.17-21	D D	
Louisiana	1972-1973	Eggs	0.79-2.1	0.23				A
Mississippi	1972-1973	Eggs	3.50	0.11				A
Georgia	1972-1973	Eggs	0.42	0.25				A

¹Sources: A = Ohlendorf et al. 1978; B = Rumbold et al. 1996; C = Wheeler 1977; D = Rumbold 1995.

*2, 3, 7, 8-tetrachlorodibenzo-p-dioxin

cause of population decline in the twentieth century in Arkansas. Probably little interaction with humans at aquaculture facilities because the nearby (fringing) roosting vegetation necessary for Anhingas is nearly always absent.

Pesticides and other contaminants/toxics. Because of their position in the freshwater aquatic food web, this species has often been considered an excellent bioaccumulator for contaminants, and a number of studies have reported contaminant values for various tissues and locations (Table 2). However, no multisite surveys have been conducted since mid-1970s.

It is unclear what these levels of pesticides and contaminants mean for the health of Anhingas, since there has been no work on specific effects. No reported values have been associated with direct mortality, and levels of pesticides reported by Ohlendorf et al. (1978) and Rumbold (1995) were not associated with eggshell-thinning. Rumbold et al. (1996) found that concentrations of dioxins and furans in Anhinga eggs and nestlings at a Florida landfill (up to 9.5 ppb) were higher than the experimental concentrations at which 50% of pheasant (*Phasianus colchicus*) embryos died, but did not find embryonic mortality or deformities in Anhingas. In the Everglades, Anhinga eggs were found to

have mercury concentrations approaching the 2 mg/kg wet weight that has been found to be toxic to duck embryos (D. Day, Patuxent Wildlife Research Center, pers. comm.). In related species, D. J. Forrester and M. G. Spalding (in press) showed that levels of PCBs, DDT, DDE, and DDD were higher in Double-crested Cormorants (*Phalacrocorax auritus*) from rehabilitation centers in Florida than in birds collected by shooting. Thus, sublethal levels of several pesticides may predispose pelecaniforms to disease and traumatic accidents.

Collisions with stationary/moving structures or objects. Roadkills are uncommon for this species. Of 1,562 birds found dead in and around state parks in Florida, only 1 was an Anhinga (Snyder 1994 in D. J. Forrester and M. G. Spalding in press). Similarly, in a sample of 42,384 birds of 189 species found dead beneath a TV tower in Leon Co., FL, no Anhingas found (Crawford 1981). Even in wetlands, collisions with power lines do not seem to be an important source of mortality, probably because of the diurnal habit and excellent low-speed maneuvering abilities of this species. Of 41,717 birds observed passing through a 550-kV transmission power line in the Everglades during daylight hours, 1,562 (3.7%) were Anhingas; none collided with the power line (Deng 1998).

Degradation of habitat. In Arkansas, continuing drainage of forested lowlands and swamps for agricultural development has been a major contributor to the decline of the Anhinga population (James and Neal 1986).

Disturbance at nest and roost sites. In Arkansas, 40% of 20 nests produced at least 1 young in a colony heavily disturbed by human activity; disturbance apparently was a main factor contributing to this low success (Meanley 1954). Oberholser (1974) listed human disturbance as a major contributor to population declines in Texas during mid-twentieth century. Investigators entering colonies may cause nest abandonment and egg-scavenging, though this has not been documented directly for this species. Rodgers and Smith (1997) found that nonnesting Anhingas had the greatest flushing distance of any waterbird approached by boat (mean 37.4 m \pm 17.4, $n = 12$); flushing distance was less when nesting (mean 23.6 m). Unlike many waterbirds studied by Klein et al. (1995) at a heavily visited wildlife refuge in Florida, Anhingas did not respond to increasing frequency of visitation by changing roosting or feeding distribution. However, Anhingas did respond to a graded increase in experimental disturbance (drive by < stop < get out < taped noises < approach) with increased frequency of alarm behaviors and calls, and moving away from the disturbance. In wildlife refuges, Anhingas are often exposed to high levels of human disturbance, simply as a result of their preference for deeper water in borrow ditches close to roads.

MANAGEMENT

Conservation status. Not considered a migratory species; no federal or state protection listed, though considered "in need of management" in Kentucky. Not considered to be declining within U.S., though few comparative surveys are available (see Demography and populations: population status, above). This wetland species probably declined to some degree as result of the 50% loss of habitat thought to have occurred in the U.S. during the twentieth century. Anhingas sometimes are considered a pest on aquaculture ponds in s. U.S. (Siegel-Causey in press), but they have much less impact than cormorants, herons, or egrets.

Measures proposed and taken. Rodgers and Smith (1997) recommended a buffer distance of 120 m for roosting or nesting Anhingas—one of the largest for waterbirds. No other conservation measures proposed for this species to date, although Anhingas may benefit from wetland conservation actions taken as a result of endangerment of other waterbirds (e.g., Wood Storks).

Effectiveness of measures. No information.

APPEARANCE

MOLTS AND PLUMAGES

Little is known about the molts of Anhingas, and most descriptions of plumages are based on scanty museum specimens, or observations from the nineteenth century. Almost no information exists on this subject for *A. a. anhinga*. The following descriptions apply to *A. a. leucogaster*, and are based on Palmer 1962 and on examination of specimens, unless otherwise stated.

Hatchlings. Naked at hatching; skin buffy yellow, bill and iris black, legs and feet buffy yellow. Soon acquires coat of short, thick gray to buffy-tan down, with very light-buff to white down on extremities. Natal down becomes whiter with age (Stevenson and Anderson 1994).

Juvenal plumage. Molts from nestling down at about 3 wk of age; remiges and rectrices begin to grow rapidly, presumably until fledging. Body-feathers are apparently last to molt in this progression (J. J. Audubon in Bent 1922); silver-gray markings on wings and upperparts may be apparent while down is still present on breast.

"Head down to upper breast cinnamon buff, becoming darker brownish on rest of underparts; back feathers dusky, bordered lighter brownish; wings and tail mostly dusky, some rather diffuse silvery-gray markings on wing coverts, scapulars, possibly upper back"; sexes alike (Palmer 1962: 359).

Basic I plumage. Prebasic I molt described as "a gradual molt" beginning "within a few weeks after flight is attained," but no information on the length of this molt, or on which feathers are replaced. No information on how incoming Basic I feathering differs from Juvenal plumage, but Palmer (1962: 359) suggests that in Basic I plumage the back-feathers probably lack the "brownish edges" found in Juvenal plumage. Sexes alike.

Alternate I plumage. Prealternate I molt incomplete; at least some head-, neck-, body-, and tail-feathers replaced (perhaps only the central pair of rectrices [R1] are replaced; Owre 1967). Molt occurs before age 1 yr; plumage worn about age 10–14 mo.

Head down through upper breast dull grayish buff; rest of body a mixture of dusky and black. Wings and tail mostly dusky, with more whitish on wings and scapulars than in Juvenal plumage. Sexes alike.

Basic II plumage. Prebasic II molt occurs during summer and fall of second calendar year (Bent 1922); presumably complete molt. Basic II is first plumage in which sexes become differentiated.

MALE. "Head, neck, and upper breast black but brownish intermixed. About same amount of white as in Alt.[ernate] I"; at least some individuals of

both sexes have slight corrugations on the central rectrices (Palmer 1962: 359).

FEMALE. "Probably differs in degree from Def. [initive] Basic but details not available" (Palmer 1962: 359).

Alternate II plumage. Prealternate II molt occurs during spring of second calendar year; no additional information on timing or extent of this molt.

Very similar to Definitive Alternate plumage in both sexes, except Alternate I male has duller dark feathering, smaller mane, fewer plumes, and shorter scapulars, and Alternate I female lacks clear-cut chestnut band on breast (Palmer 1962).

Definitive Basic plumage. Figure 4. Little information on timing or extent of Definitive Prebasic molt. Definitive Prebasic molt presumably complete; in adults, Definitive Basic plumage "acquired after breeding and worn several months" (Palmer 1962: 358). Primaries molt simultaneously. Simultaneous replacement of remiges may occur in all species of Anhingidae, the only family of Pelecaniformes in which this has been described (Palmer 1962, Owre 1967). Birds approaching Prebasic molt have ragged, frayed, dull brownish remiges and rectrices. Bent (1922) reported that rectrices are molted in Apr in some individuals, and some birds may have fresh remiges in early summer.

MALE. Entire plumage black (glossed green on head, neck, and part of body), with the following exceptions: Tail deep brownish subterminally, paling to white at tip (white tip may disappear with wear). Upper back-feathers have small central pale-silver gray spot. Lesser wing-coverts centrally spotted, and median and greater wing-coverts have pale silvery gray outer web and innermost portion of inner web (more extensive on median-coverts), forming broad silver-gray patch on wing; innermost greater-coverts and innermost secondaries, however, are black with silver-gray streak along shaft (mainly on inner portion of outer web). Scapulars lanceolate and elongated, and rearmost scapulars broader and greatly enlarged, completely overlying tertials. All scapulars have median silver-gray streak along shaft, except largest (rearmost) feather has broad silver-gray streak mainly on inner web, and large scapulars underlying this feather are black with silver-gray spot at tip. Outer webs of central pair of rectrices (R1) and longest scapular feather (not inner secondaries, contra Palmer 1962) have transverse corrugations, although corrugations are more pronounced in Definitive Alternate plumage (Owre 1967). Other long scapulars overlying inner greater-coverts also have less noticeable and more widely spaced indentations.

FEMALE. Head, neck, and upper portion of breast and back tawny buff (becoming darker and more

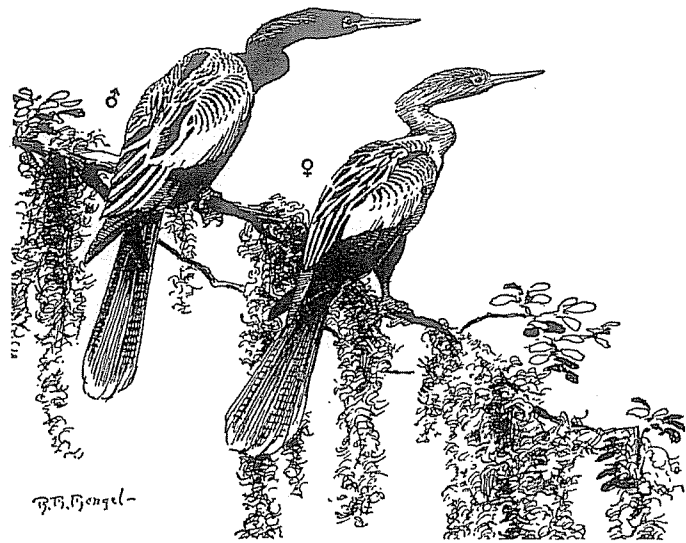


Figure 4. Male and female Anhingas in Definitive Basic plumage. Drawing by R. Mengel. From Palmer 1962.

brownish on crown and whitish on lower portion of face and chin), with rich chestnut band across breast, separating buff on throat from blackish belly (chestnut band less pronounced in North American birds than in Central and South American birds). Feathers of upper back have brown edges and white centers; remainder of feathering similar to that of Definitive Basic male, except dark portions more dusky brownish than black.

Definitive Alternate plumage. Definitive Prealternate molt incomplete; includes all feathering except remiges; molt occurs "well before breeding" (Palmer 1962: 359). Molt of rectrices appears to be almost continuous throughout year, although outer and inner rectrices may be molted at different times. Transverse corrugations in central pair of rectrices (R1) and longest scapulars; most prominent in specimens obtained during or just after Prealternate molt. Corrugations flatten with age of feather, until they become indistinct (Owre 1967).

MALE. Similar to Definitive Basic male, except black surfaces become more glossy and olivaceous (DSC); feathers of hindneck somewhat elongated, forming a mane; series of filamentous plumes (white with violet or brownish cast, fading to white) present on sides of crown, nape, and upper neck; silvery-white areas in feathering somewhat larger and scapulars more elongated. No information on whether plumes on head and neck persist until Prebasic molt or are shed early.

FEMALE. Similar to Definitive Basic female, except some whitish, loose-webbed feathers are present on side of head and upper neck.

Table 3. Linear measurements (mm) of 3 populations of adult Anhingas. Data given as mean \pm SD (range). From Siegel-Causey in press.

Subspecies Region <i>n</i> (male/female)	<i>leucogaster</i> Se. U.S. (27/44)	<i>leucogaster</i> Mesoamerica (15/7)	<i>leucogaster</i> Caribbean (1/4)	<i>anhinga</i> South America (30/31)	All (89/85)
Culmen					
Male	81.2 \pm 3.4 (71–81)	75.4 \pm 5.8 (67–81)	81	88.9 \pm 5.3 (77–99)	83.4 \pm 6.4 (64–99)
Female	77.4 \pm 3.8 (68–83)	72.4 \pm 5.7 (61–83)	75.0 \pm 1.2 (74–76)	85.3 \pm 4.5 (76–96)	78.8 \pm 7.0 (61–96)
Wing					
Male	329.6 \pm 9.9 (307–347)	312.3 \pm 11.8 (299–330)	315	333.3 \pm 16.0 (307–365)	328.9 \pm 13.6 (299–365)
Female	326.3 \pm 10.4 (304–348)	312.2 \pm 10.4 (293–328)	320.3 \pm 3.8 (316–325)	333.1 \pm 11.9 (312–361)	325.2 \pm 13.0 (293–361)
Tarsus					
Male	40.3 \pm 1.1 (38–43)	39.1 \pm 0.9 (38–40)	40	42.8 \pm 1.7 (39–46)	41.1 \pm 1.8 (38–46)
Female	40.0 \pm 1.4 (38–43)	38.3 \pm 1.7 (36–43)	40.3 \pm 1.2 (39–42)	42.2 \pm 2.4 (35–46)	40.4 \pm 2.3 (35–46)
Tail					
Male	243.9 \pm 9.4 (220–262)	234.5 \pm 11.3 (218–245)	250	250.4 \pm 16.0 (210–280)	245.3 \pm 14.1 (195–281)
Female	246.3 \pm 11.1 (230–282)	234.5 \pm 8.9 (218–250)	239.2 \pm 18.1 (218–260)	250.8 \pm 16.9 (205–295)	245.6 \pm 14.4 (205–296)

BARE PARTS

Bill and gape. Bill long and slender, with cutting edges serrated on terminal half. In Definitive Basic plumage, bill yellow with dusky-greenish tip and ridge in both sexes. In Definitive Alternate plumage, upper mandible dull olivaceous and lower mandible yellow, with edges and tip tinged greenish, in male; upper mandible brown and lower mandible dull orange in female. As courtship advances, bill of male becomes vivid yellow, almost orange-yellow; more muted in female. Bare-part coloration of breeding birds persists into rearing period.

Iris. Scarlet to ruby red (Palmer 1962). Also described as bright carmine in breeding male and dark brown, yellowish, or pink in female (Oberholser 1974).

Bare skin on head. In Definitive Basic plumage, bare facial skin dusky brown and gular pouch yellowish or dusky. In Definitive Alternate plumage, lores and bare skin immediately below eye become iridescent emerald or even turquoise in males, and dull greenish slaty in females, and gular pouch becomes bright orange in males and muted orange in females as courtship advances. Female also has black mark beginning on rictus and continuing down into gular sac. Bare-part coloration of breeding birds persists into rearing period.

Legs and feet. Foot totipalmate, with webbing between all toes. Legs and feet mostly dusky olive, with somewhat paler yellowish or brownish webs (Palmer 1962).

MEASUREMENTS**LINEAR**

Data shown in Table 3 reveal geographic, subspecific, and gender-related differences in linear measurements, although few patterns are statistically robust. In all populations of *A. a. leucogaster*, male has significantly longer culmen than female ($p < 0.05$); in all other measures, sexes are similar. For *A. a. anhinga*, male is larger than female in length of wing, culmen, and tarsus. Multivariate analysis of Anhinga variation in these measures indicated that southeastern and Mesoamerican populations were distinct from each other and distinct from all other Anhingas. In addition, birds identified through plumage as members of either *anhinga* or *leucogaster* subspecies were morphologically distinct. No differences were found in specimens originally identified as members of *minima* subspecies (see Owre 1967, Oberholser 1974), which were considered to be *leucogaster* (Siegel-Causey in press).

MASS

Range 1,325–1,350 g (Norris and Johnston 1958, Palmer 1962, del Hoyo et al. 1992).

PRIORITIES FOR FUTURE RESEARCH

Although reproduction, nesting and courtship behavior, and ecology have been relatively well studied in this species, there are still major gaps in our knowledge. Other than generalities of distribution, very little is known about this species

in Central and South America, especially its comparative reproduction, the southern limit of breeding and distribution, diet, and levels of contamination. The distinction between subspecies of *Anhinga* is vague and confused, and the influences of diseases and contaminants on this species remain poorly documented. Despite the apparently social nature of this species, there is no information on the degree or nature of extended parental care, dynamics of roost membership, or mate or breeding-site fidelity. Finally, almost nothing is known about the survivorship of the Anhinga, which is evidently a long-lived bird with few predators. Although the Anhinga is declining in parts of its range and vulnerable through its clear preferences for wetland habitat, the conservation of this species appears to be almost nonexistent, with no actions recommended or taken in areas of decline.

ACKNOWLEDGMENTS

We gratefully acknowledge the help of the Borror Laboratory of Bioacoustics and the Florida Museum of Natural History for help with vocalizations, and the Birds of North America staff for help with gathering information on this species and organizing the material. We thank Don Forrester and Marilyn Spalding for help on diseases, contaminants, and parasites of this species. Cover photo © T. Vezo/VIREO; photographed in January 1998 in Florida.

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The Birds of North America is supported by charitable and governmental organizations including: The Office of Migratory Bird Management (USFWS), National Fish and Wildlife Foundation, The McLean Contributionship, The Geraldine R. Dodge Foundation, The Richardson Foundation, and the American Birding Association. Benefactors of this program include Wallace C. Dayton and Joseph and Helen Taylor.

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RECOMMENDED CITATION

Frederick, P. C., and D. Siegel-Causey. 2000. Anhinga (*Anhinga anhinga*). In *The Birds of North America*, No. 522 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

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