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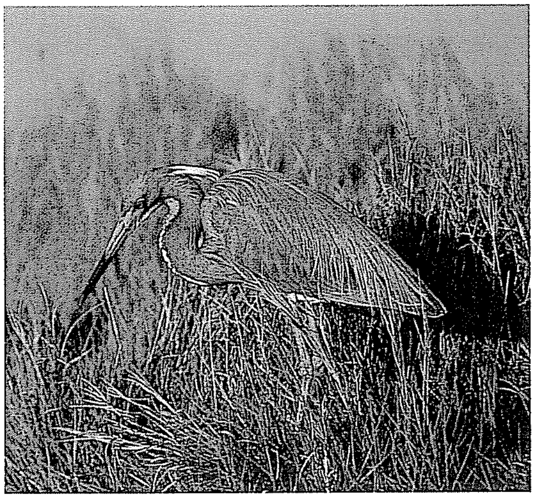
Egretta tricolor

Tricolored Heron

FRENCH:
Aigrette tricolore
SPANISH:
Garceta tricolor, Garza pechiblanca



Formerly known as the Louisiana Heron, this slender day-heron is found only in the New World, and is one of 4 North American herons in the genus *Egretta* (Snowy Egret [*Egretta thula*], Little Blue Heron [*E. caerulea*], and Reddish Egret [*E. rufescens*]). Until the arrival of the Cattle Egret (*Bubulcus ibis*) in the 1950s, this species was probably the most numerous North American heron (see Demography and populations: population status, below). Although probably not commercially important to the plume trade at the turn of the twentieth century, the Tricolored Heron undoubtedly suffered because of its habit of nesting with more valuable species.

The diet of this heron consists almost entirely of small estuarine and marsh fishes, which it acquires through a diverse array of foraging behaviors. This species is less social in foraging habits than are most other North American herons, typically feeding either solitarily or at the edge of mixed-species groups. The Tricolored Heron is also more commonly associated with coastal habitats than are all other herons except the Reddish Egret. In the United States, food availability and, indirectly, the amount and type of habitat appear to control the number of breeding attempts.

The Birds of North America
Life Histories for the 21st Century

Tricolored Herons are probably declining throughout their North American range. This species is among the most studied of the

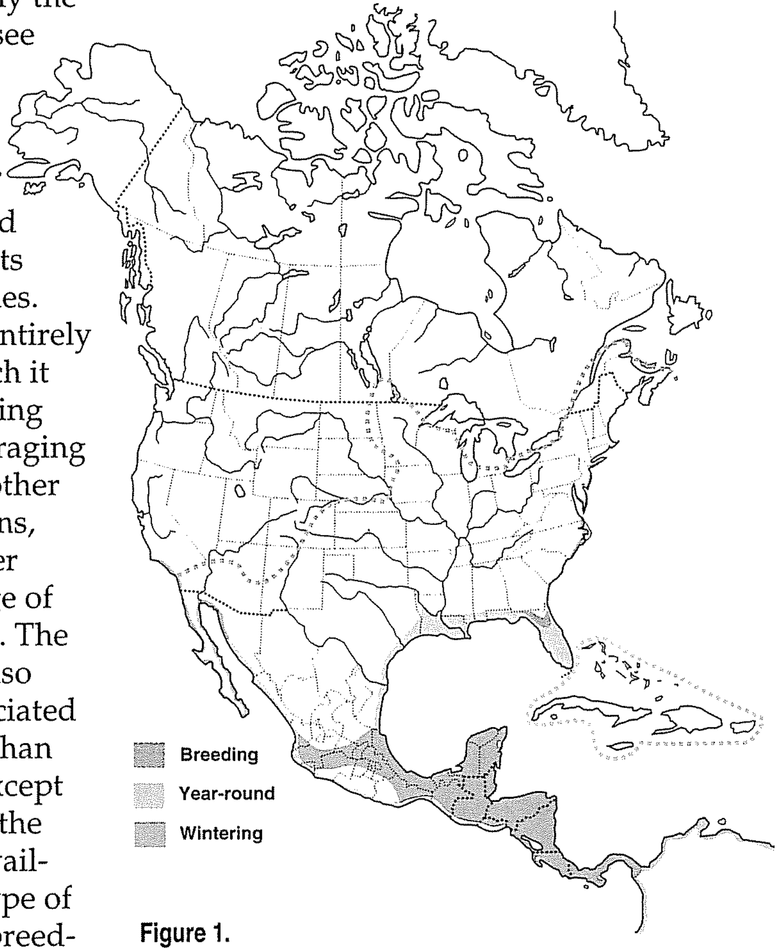


Figure 1.
Distribution of the Tricolored Heron in North and Central America and the western Caribbean. This species also breeds in South America. See text for details. Wandering birds are observed during the spring and summer north to the orange dotted line and occasionally occur north to Oregon. This species is a local resident within the green dotted line and breeds irregularly along the Atlantic coast north to southern Maine.

Order CICONIIFORMES Family ARDEIDAE

North American herons: its breeding behavior and displays are particularly well documented (Rogers 1978a, b), as are many aspects of its foraging ecology and behavior (Kushlan 1978, Rodgers 1983, Kent 1986a, b) and nesting ecology (Jenni 1969, Maxwell and Kale 1977a, Post 1990, Frederick et al. 1992). Although much is known about the Tricolored Heron in the U.S., little information is available from the Caribbean and Central and South America. Basic information is needed on estimates of its survival, descriptions of its winter habitat, and molt patterns.

DISTINGUISHING CHARACTERISTICS

Medium-sized, delicately built heron with dark upperparts contrasting with white breast and belly in all plumages and ages; generally easy to distinguish from other New World herons. The only small North American heron with white underparts and foreneck, slaty dark back and neck. Neck and bill quite slender. Adult length 60–70 cm, wingspan 95 cm, bill 9–11 cm (Palmer 1962). Sexes similar in plumage, but male somewhat larger than female (mean mass of male 415 g, of female 334 g; Dunning 1993, see Appendix 4). For nonbreeding (Basic plumage) individuals, head, neck, wings, and tail slate gray; long feathers on back purplish maroon; breast, belly, rump, and underwing-coverts white; chin white; throat marked with tawny or chestnut. In breeding (Alternate plumage) individuals, both sexes acquire new white head (crest) plumes, mauve to violet neck- and mantle-feathers; rufous tinge more obvious on scapulars, back of neck; filamentous plumes of mantle, lower scapular plumes are buff-colored; legs become pinkish; bill and face become bluish at base; bill black at tip. Breeding males have magenta iris during courtship; inner margin of iris rose to scarlet in females (Rodgers 1978a). In nonbreeding males and females, inner iris margin pink; iris brown. Head and neck of immatures mostly russet; wings marked with same.

DISTRIBUTION

THE AMERICAS

Breeding range. In U.S., breeds primarily along immediate coastline of Atlantic Ocean and Gulf of Mexico; breeding extends into coastal plain in the se. U.S., particularly in Florida and along Gulf Coast. Occasionally breeds in Kansas and other interior locations far from coast.

Along Atlantic Coast, has bred irregularly (most records during 1970s and 1980s) north to s. Maine (Stratton I., York Co.; Osborn and Custer 1977), n. Massachusetts (House I., Essex Co.; Veit and Petersen 1993), and sw. Connecticut (Norwalk Is., Fairfield Co.; Bevier 1994). Breeds more regularly along Atlantic Coast of Long I., NY (western portion of south shore; Andrle and Carroll 1988), New Jersey (Long Beach I. south to Cape May; Osborn and Custer 1977), Maryland and Virginia portions of Delmarva Peninsula (Robbins 1996, Virginia Breeding Bird Atlas [BBA] unpubl.), N. Carolina, S. Carolina, and Georgia (Osborn and Custer 1977). Breeds throughout Florida (including inland sites), where most numerous in south and along coasts; least numerous along coast of panhandle (Stevenson and Anderson 1994); and along coastal plain of Alabama, Mississippi, Louisiana, and Texas (Lowery 1955, Portnoy 1977, Texas Colonial Waterbird Society 1982, Dusi and Dusi 1988, Texas BBA unpubl.). Also breeds in upper Delaware Bay (Pea Patch I.; Hess et al. in press), and in lower Chesapeake Bay (Dorchester and Somerset Cos., MD; Robbins 1996).

Has bred up to several hundred kilometers inland in S. Carolina (Berkeley Co., 1 record in 1986; Belser and Post 1987). However, also summers regularly in several counties of central Kansas, particularly Cheyenne Bottoms National Wildlife Refuge (Barton Co.), where breeding has been attempted with varying success since 1974 (Thompson and Ely 1989). Sites of other interior breeding records include several locations in w. and n.-central Texas (occasional to regular in Austin, Colorado, and Marion Cos.; Oberholser 1974, Runnels 1980), rarely to S. Dakota (Skadsen 1986, Meeks et al. 1996) and N. Dakota (Schmidt 1979).

In Middle America, breeds along Pacific Coast from central Sonora, Mexico, south to El Salvador; along Atlantic Coast of Tamaulipas and n. Veracruz, Mexico; and at a few sites along east coast of Yucatán Peninsula, and west coast of s. Baja Peninsula (Howell and Webb 1995). Also recorded breeding on Pajaros I. in Tempesque Basin of w. Costa Rica (Stiles and Skutch 1989), and in Panama on Taborcilla I., w. Panama Province, and less commonly on coast of Herrera Province (Ridgely and Gwynne 1989).

In the Caribbean, breeds on the Bahamas, Cuba, Cayman Is., Jamaica, Hispanola, Puerto Rico, and Virgin Is. (St. Thomas) (Bond 1993, Raffaele 1989, Evans 1990, Wetmore and Swales 1932).

In South America, primarily a coastal bird. Common below 1,000 m in Colombia and Ecuador in brackish or salt water (Hilty and Brown 1986). Occasionally breeds southward on Pacific Coast to s. Peru. On Atlantic Coast of South America, locally common in Venezuela (Margarita, Los Roques, La Orchila Is.; Meyer de Schauensee and Phelps 1978), commonly breeds in large numbers in Suriname and Guyana (DeJonghe et al. 1992, Haverschmidt and Mees 1994); breeds sporadically on northeastern coast of Brazil, probably to mouth of Amazon River (Maranhao and Paui; Blake 1977). Also breeds on Aruba, Curacao, Bonaire (Voous 1983), and Trinidad (ffrench 1991). Southern range of breeding and abundance throughout South America remain poorly documented.

Winter range. In U.S., winters locally along Atlantic Coast from s. New Jersey and Delaware south (warm winters only; Sibley 1993); more commonly winters from coastal S. Carolina south throughout remainder of breeding range. Numbers decline in northern part of Florida Peninsula during winter (Stevenson and Anderson 1994). Also winters in very small numbers in s. California along coast from city of San Diego south, and very infrequently at Salton Sea, lower Colorado River, and along coast of Orange Co. (Small 1994).

In Middle America, winters coastally throughout Baja California, along both coasts of Mexico and Central America from Sonora and Tamaulipas south to s. Panama, in interior throughout Central Volcanic Belt of Mexico, and from s. Mexico and Yucatán Peninsula south to s. Panama. In Costa Rica, found primarily in lowlands of both slopes, and in Panama primarily on Pacific slope (Ridgely and Gwynne 1989, Stiles and Skutch 1989, Howell and Webb 1995).

OUTSIDE THE AMERICAS

A single record for the Azores (Parrott and Philllips 1987).

HISTORICAL CHANGES

Between 1940s and 1970s, breeding range expanded northward along East Coast of North America (Ogden 1978, Parnell et al. 1986) in coastal areas from N. Carolina to Maine. First nesting records: Virginia—1941, now regular breeder; Maryland—1958, now regular breeder; New Jersey—1951, now regular breeder; New York—1955, now regular breeder (Andrle and Carroll 1988); Connecticut—1976, now occasional breeder (Bevier 1994); Massachusetts—1976, now rare breeder (Veit and Petersen 1993). Vagrancy and extralimital sightings also increased dramatically since 1970s; large numbers of sightings in northern tier of eastern and midwestern states, Canada, and sw. U.S. (see above). Though reported breeding in California (Scammons and San Ignacio Lagoons; Grinnell 1928) in 1920s, no recent reports of breeding in that state.

Wintering range also expanded northward, with breeding range. Now frequently recorded on Christmas Bird Counts (CBCs) from New Jersey southward on Atlantic Coast; a rare vagrant previously. Only 1 individual noted in Maryland before 1895; first state records were 1937 in Delaware, 1920 in New Jersey, 1925 in New York, and 1940 in Massachusetts. Although Bent (1926) listed this heron as rarely wintering in Louisiana, Fleury and Sherry (1994) demonstrated a rapidly growing winter population there between 1967 and 1993.

FOSSIL HISTORY

Identified from Pleistocene sediments of Florida (Wetmore 1931). *Egretta subfluvia*, identified from late Miocene and early Pliocene of Florida (Becker 1985), shares some characters with Tricolored Heron. Closely related Little Blue Heron identified from late Pleistocene of California and Florida, and Snowy Egret from Pleistocene of Florida (Wetmore 1931, Brodkorb 1963, Campbell 1980).

SYSTEMATICS

First described in 1776 by P. L. Statius-Müller as *Ardea tricolor*. Placed in monotypic genus *Hydranassa* by Baird in 1858, a classification maintained by Bock (1956). Merged into genus *Egretta* following study of skeletal and behavioral characteristics (Payne and Risley 1976). The latter classification is generally followed at present (Hancock and Elliot 1978, Am. Ornithol. Union 1983, Sheldon 1987).

GEOGRAPHIC VARIATION

Specimens collected in Baja California are larger than those in e. U.S. (see Appendix 4), and races from ne. South America are smaller than other races (see below). No information on plumage variation within any races.

SUBSPECIES

Three subspecies recognized on basis of size (see Appendix 4) and color of upperparts, chin, and median line of foreneck (Palmer 1962, Blake 1977, Payne 1979).

E. T. RUFICOLLIS *GOSSE, 1847*. From North America south to South America west of Orinoco River delta, and Caribbean north of Trinidad. Larger than the other 2 subspecies, slaty upperparts, white chin and foreneck. Included under *ruficollis* as a synonym is the name *occidentalis* (Huey 1927), ascribed to breeding populations in Baja California and northward wanderers in w. U.S., said to be larger, but this is disputed (see van Rossem in Grinnell 1928); *occidentalis* was recognized by Payne (1979).

E. T. RUFIMENTUM *(HELLMAYR) 1906*. Found only on Trinidad and possibly Tobago. Small; similar in size to nominate race (see below); neck and upperparts more blackish; chin and middle of throat dark chestnut; foreneck more or less strongly tinged rufous. This race synonymized under nominate *tricolor* by Payne (1979).

E. T. TRICOLOR *(STATIUS-MÜLLER) 1776*. Found east and south of Orinoco River delta on northeastern coast of South America. Smaller than *ruficollis* but similar in size to *rufimentum*; neck and upper surface of body lighter, more slaty gray; chin white instead of chestnut; median line of foreneck paler than that of *rufimentum*, closer to medium chestnut. Intergradation among the 3 races is suspected in zones of contact in n. South America (Bull 1985) and Caribbean (Wagenaar Hummelinck and Van der Steen 1977).

RELATED SPECIES

Based on behavior, skeletal, and muscular characteristics, probably closely related to Little Egret (*Egretta garzetta*), Snowy Egret (*E. thula*), Slaty Egret (*E. vinaceigula*), Eastern Reef Heron (*E. sacra*), and Little Blue Heron (*E. caerulea*; Sheldon 1987). Two cases reported of hybridization with Snowy Egrets (A. Sprunt in Dickerman and Parkes 1968, Meeks et al. 1996).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Most individuals breeding on Atlantic Coast north of S. Carolina are migratory. South of this area, observed in breeding range throughout year, although numbers decline in some areas during winter (e.g., S. Carolina, Louisiana, n. Florida). Latitude of wintering site may vary considerably, with many migrants remaining in se. U.S.; others continue to Caribbean or Central and South America, where northern birds are thought to overlap extensively with southern races during winter. On Yucatán Peninsula (Sian Ka'an Biosphere Reserve located on Caribbean coast), only about 20% of the birds present during peak winter counts were present in summer, suggesting that many winter birds are migrants from elsewhere (Lopez-Ornat and Ramo 1992). Greatly increased sightings during Apr and May in n. U.S. and Canada since 1940 suggest that birds sometimes overshoot intended target when migrating northward. After breeding, individuals wander widely both along coasts and inland to upper Midwest, sw. U.S., and s. Canada (see below).

TIMING AND ROUTES OF MIGRATION

Little information on routes of migration. Observations of offshore migrants and banding recoveries indicate that birds move between Florida and Cuba and between Florida and Central America. Regular appearance of migrants in Bermuda indicates this species' capacity to cross large expanses of water. Birds wintering in s. California might originate from breeding areas in Baja California, thus wintering north of their breeding grounds. Timing of migration difficult to determine in many areas because species is present throughout year in all but northernmost portions of breeding range. Some individuals (possibly immatures) remain in Central American winter range throughout year.

In Panama, casual observation suggests departure northward in Feb (Wetmore 1965). Transients have been recorded on Bermuda 25 Mar–21 May (Amos 1991). Spring migrants (as indicated by offshore migrants, tower kills, etc.) observed in n. Florida by early or mid-Mar (Stevenson and Anderson 1994). Arrive in Maryland mid- to late Apr (Robbins 1996); Cape May, NJ, last week of Apr (Sibley 1993); and Massachusetts late Apr–early May (Veit and Petersen 1993). Wandering birds may appear during spring north of regular breeding areas.

In northern midwestern states and Canada, numerous sightings after 1970, during Apr–early Jun (Bull 1985, Janssen 1987, Bolen 1989, Peterjohn 1989, Robbins 1991, Veit and Petersen 1993).

After breeding season, individuals wander in many directions, particularly northward. After breeding, birds disperse both along coast (Willlard 1977, Telfair 1979) and inland, sometimes long distances. Sightings in mountains of N. Carolina, Virginia, inland Massachusetts, Tennessee, Ohio, Arkansas, Missouri, Kansas, Oklahoma, Colorado, inland Texas, New Mexico, and Arizona during Jul and Aug. In Canada, sightings and occasional records in southern reaches of all provinces except British Columbia and Prince Edward I. (Godfrey 1986). In Ohio, rare but regular to w. Lake Erie marshes (Peterjohn 1989). In California, has been recorded north to Sonoma and Lassen Cos. (Small 1994). Strays occur widely along watercourses of interior, sw. U. S., including: Arizona north to Camp Verde (Yavapai Co.); s. New Mexico; e. Colorado; central and w. Texas, along Rio Grande; lower Colorado River; and Salton Sea—all mainly between Apr and Aug (Phillips et al. 1964, Oberholser 1974, Andrews and Righter 1992). In Colorado, sightings peak in May. Occasionally wanders south to Chile on Pacific Coast of South America (Araya and Chester 1993).

In fall, moves south from breeding grounds in U.S. to wintering grounds in Caribbean and Central America; timing less clear than in spring. "Flybys" peak in Cape May, NJ, Aug–Sep (Sibley 1993); most birds leave Maryland by late Sep or early Oct (Robbins 1996). Regularly recorded in Bermuda early Sep–mid-Nov, occasionally as early as 5 Aug

(Amos 1991). Timing of migration outside of ne. Atlantic Coast difficult to determine because of species' variable presence throughout year.

Birds banded in se. U.S. have been recovered in Honduras, Nicaragua, Florida, Greater and Lesser Antilles, Venezuela, Colombia, and Panama; most recoveries from individuals banded in Texas are from Mexico and Central America (PCF). All sightings at northernmost edge of western range, in San Diego Bay, CA, are during winter (Dec–Feb), suggesting northward movement in fall and winter (Grinnell 1928, Cogswell 1977, Garrett and Dunn 1981). Will migrate over water: observations of birds at sea (eastern coast of Florida; Stevenson and Anderson 1994); apparent arrival of trans-Gulf migrants in spring (S. Cardiff unpubl. data); regular occurrence at Bermuda and other isolated islands in Caribbean (see Distribution, above).

MIGRATORY BEHAVIOR

No information.

CONTROL AND PHYSIOLOGY

No information.

HABITAT

BREEDING RANGE

Breeds mostly in coastal habitats, including estuaries, salt marshes, mangrove swamps, river deltas, lagoons, and salinas, but also frequently in freshwater areas (e.g., Florida Everglades and se. U.S. coastal plain; Belser and Post 1987). During 3 yr in Everglades (1987–1989), 75% of nests were in brackish or marine habitats, 25% in fresh water (Frederick et al. 1992). On Yucatán Peninsula, more likely to be found in saltwater habitats than fresh (Lopez-Ornat and Ramo 1992).

Generally breeds on islands or areas of higher ground that support small trees or shrubs, surrounded by open water or inundated wetland vegetation. Colonies usually surrounded by landscapes that include a variety of wetland habitats (see Bancroft et al. 1994; see also Breeding: nest site, and Food habits: feeding, below).

SPRING AND FALL MIGRATION

Little information. Migrants probably move among variety of wetland habitats during continental migration, especially along rivers and through coastal wetlands. Some migration over open water, with sightings 100+ km off Atlantic Coast of Florida (Stevenson and Anderson 1994); stopover habitats on intervening islands in Caribbean thus probably important but undocumented. Apparent trans-Gulf migration during spring suggests that coastal habitat in Louisiana and Mississippi may be important for incoming migrants (S. Cardiff unpubl. data).

WINTER RANGE

In Florida, mangrove swamps (e.g., red mangrove [*Rhizophora mangle*], black mangrove [*Avicennia germinans*]), salt marshes, coastal mudflats, cypress (*Taxodium distichum*) swamps, canals, ditches, freshwater herbaceous marshes, and lake edges (Palmer 1962, Rodgers et al. 1996). In Louisiana, a variety of fresh- and saltwater wetland habitats; increasingly noted in aquaculture and rice culture impoundments (Fleury 1994). In Texas, CBC data suggest no use of habitat farther inland than Austin (Telfair 1979). In California, coastal lagoons and tidal flats in San Diego Co., usually along channels in glasswort (*Salicornia*) marshes (Garrett and Dunn 1981). In Central and South America, coastal mangrove swamps and mudflats; in Central America, to 1,500 m (freshwater; Costa Rica); northern birds thought to overlap extensively with southern races during winter.

FOOD HABITS

FEEDING

Main foods taken. Small fishes make up >90% of diet in nearly all regions; insects, crustaceans, and frogs taken probably only when superabundant (Appendix 1).

Microhabitat for foraging. Able to forage in wide variety of habitats by shifting foraging behaviors and taking advantage of either flock or solitary foraging strategies (Murdich 1978). Forages entirely in wetlands, even more so than other herons, usually in open or semiopen areas with low vegetation (Kushlan 1978). Uses brackish or salt water most frequently; in coastal N. Carolina, Custer and Osborn (1978) recorded no use of available freshwater habitat, but see Bent 1926 and Belser and Post 1987. Observed foraging in slightly deeper water than Snowy Egret or Little Blue Heron, often in water touching belly-feathers. Powell (1987) suggested 18 cm as maximum foraging depth, as determined by leg length.

Foraging may be particularly productive in thick aquatic vegetation of freshwater lakes—e.g., torpedograss (*Panicum repens, Hydrilla*) sp. mats—which supports weight of stalking birds but allows access to fishing sites (Jenni 1969, Smith and Collopy 1995). On Lake Okeechobee, FL, open, wet prairies dominated by spike rushes (*Eleocharis*) selected in much greater proportion than availability would suggest (Smith et al. 1995). In salt marshes of New Jersey, uses edges of potholes and channels as sites from which to strike (Willard 1977). In w.-central Florida, foraged more often along shoreline than other herons (46.7% of observations), 20% of time in pools and open water, and 12% in canals ($n = 98$ observations; Kent 1986a).

Foraging habitat probably constrained to foraging radius (mean 5.6 km ± 6.0 SD, up to 25 km in Florida Everglades; $n = 265$; Bancroft et al. 1988) around breeding colony; postbreeding birds shift foraging habitat significantly farther from colony than during breeding (Bancroft et al. 1990).

Food capture and consumption. Wide variety of foraging behaviors, including Standing-and-Waiting, Walking Slowly, running pursuit followed by low crouch and quick, nearly horizontal slanting stabs into water (see descriptions of these behaviors in Kushlan 1978). Crouch often very deep, with neck touching breast-feathers, and belly nearly touching water (Willard 1977). Active pursuit common in 2 forms: loping chases, with flapping wings and lunging strikes, or tight pirouetting while turning in direction of open wing. May also feed by covering head and forward body with outstretched wings (Canopy-Feeding), or may use feet (Foot-Raking) to flush bottom-dwelling prey, particularly in cold weather (McIlhenney 1936, Meyerriecks 1971). May also strike at prey while hovering over water (Rodgers 1971, Hancock and Elliott 1978).

Foraging behaviors vary according to habitat. Active techniques found more often at coastal than inland sites (Meyerriecks 1962, Jenni 1969). On coastal flats, used Standing, Walking Slowly, Disturb-and-Chase ("Disturbing-and-Chasing" in Kushlan 1978), and Standing-and-Chasing 17.0, 36.7, 35.6, and 10.7% of the time, respectively (Kent 1986b). Rodgers (1983) reported that vast majority of foraging behavior in a coastal area in Florida was Walking Slowly and Walking Quickly.

Striking efficiencies are higher with Walking Slowly than with Disturb-and-Chase and higher along shorelines, canals, and in pools than in open water (Kent 1987). An entirely diurnal feeder; not noted feeding at night, even in mixed-species nocturnal flocks (L. Bryan unpubl. data, G. V. N. Powell unpubl. data). In multispecies foraging aggregations, usually found at edge of group; not reported to benefit greatly from piracy, beating, or other social interactions (Kushlan 1978).

DIET

Major food items. Mostly small fish; topminnows and killifishes (Poeciliidae and Cyprinodontidae) are the most common food items in U.S. (see Appendix 1). No information from outside of U.S.

Quantitative analysis. All recent studies indicate that small fishes constitute >89% of diet consistently over range in se. U.S. (see Appendix 1). Much of the diet (often >50%) is composed primarily of killifishes (genus *Fundulus*), represented by both estuarine species such as mummichog (*F. heteroclitus*), and by freshwater species such as golden topminnow (*F. chrysotus*). Live-bearers (Poeciliidae) are another important group of prey animals, and cichlids (Cichlidae) probably become important in Central and South American range (Haverschmidt and Mees 1994).

Despite this overwhelming dominance of fishes in diet, 2 studies early in twentieth century reported that insects make up large part of diet (O. Baynard in Bent 1926, E. A. Chapin in Sprunt 1954). In freshwater areas of n. Florida, Baynard found >200 grasshoppers (Orthoptera) in a single stomach, and in 50 young birds, 2,876 grasshoppers, 8 frogs, 17 cutworms (Noctuidae), 6 lizards, 67 crayfish (Macrura), but no fishes. In other studies, invertebrate food items represented tiny proportion of diet, including clam worms (Annelida), spiders (Arachnida), weevils (Coleoptera), giant water bugs (Belostomatidae), dragonflies (Odonata), water beetles (Hemiptera), and ground beetles (Carabidae). Marine crabs (*Uca* spp.) are sometimes captured in coastal areas, but never eaten, suggesting aversion (Kent 1986b).

FOOD SELECTION AND STORAGE

In Tampa Bay, FL, percentage of consumption of fish in classes 18–30 mm, 31–52 mm, 53–75 mm, and 76–100 mm was 43, 34, 15, and 8% of diet, respectively (Kent 1986b). Took relatively larger fishes than Snowy Egret, relatively smaller fishes than Little Blue Heron, and had a much higher predominance of fish in diet than the other 2 species. Mean weight of whole fishes recovered from regurgitated boluses of nestlings in a s. Florida colony was 0.4 g ± 0.50 SD and averaged total length of 30 mm ± 10 SD ($n = 83$ prey items; Bancroft and Jewell 1987). Mean volume of prey items in central Florida was 0.46 ml ($n = 15$ boluses; Jenni 1969). In coastal S. Carolina, 88% of fishes captured were 1–5 cm in total length ($n = 90$ regurgitated boluses; Post 1990). In coastal Everglades, fishes ranged from 13 to 44 mm in total length; vast majority were 19–35 mm long ($n = 514$ fish; Ogden 1977).

NUTRITION AND ENERGETICS

Basic energy requirements for nonbreeding adults estimated as 322 kJ/d; nesting attempt (adults and young) estimated to require 116,911 kJ of energy to complete; breeding adults expend 63,037 kJ per nesting attempt; young expend 26,937 kJ from hatch to fledging (Frederick and Powell 1994). In Tampa Bay, FL, feeding adults observed to consume 0.94 g/min (267 J/min); estimated foraging times were 51–91 min/d to satisfy minimum daily energetic requirements (n = 98 foraging observations; Kent 1986a).

METABOLISM AND TEMPERATURE REGULATION

Because of higher reflectance of lighter plumages, costs of thermoregulation are higher for dark-plumaged than for light-plumaged *Egretta* herons (Ellis 1980). Nesting in shaded habitats may be an evolutionary response to heat-loading in tropical and subtropical environments; however, light-colored Snowy Egrets also nest in shaded locations. Dark plumage may have other effects, such as making herons less conspicuous to predators, and less likely to be joined by other wading birds in foraging flocks (Kushlan 1978, Caldwell 1986).

DRINKING, PELLET-CASTING, AND DEFECATION

An estimated 1.77 kg (dry weight) feces total are produced by parents and young during a nesting attempt (Frederick and Powell 1994). Pellet-casting not noted in this species, although other herons frequently cast boluses of shell, bone, and other indigestible ejecta.

SOUNDS

VOCALIZATIONS

Development. By 5 d of age, young give begging calls, including weak peeping, and a "harsh note" in response to parents, but calls of young are poorly described. No information on vocal learning or sensitive periods for learning.

Vocal array. No good recordings available; nearly all descriptions are from observations of courtship and nest behavior only; little is known of vocalizations in nonbreeding season. Vocal repertoire limited, though this species is often described as a "noisy" bird (Oberholser 1974).

CALLS. Both sexes give *Aaah* Call during aggressive encounters (see Rodgers 1977, 1978a). Call during startle reactions. Gives *Scaah* Calls when approaching nest with food and when in Alert Posture (see Behavior: agonistic behaviors, below). During courtship, males give *Unh* Calls and groaning sounds; both sexes may give *Culh-Culh* Calls (Rodgers 1978a).

Phenology. Most vocalizations known only from courtship and nesting period; agonistic and alarm calls (*Aaah* and *Aahrr*) are the only ones noted during nonbreeding season.

Daily pattern. During courtship, vocalizations by both sexes are concentrated during early morning and late afternoon, with midday hiatus (Rodgers 1978a). Begging by young chicks is less frequent during early morning than later in day. No information on nighttime vocalizations.

Places of vocalizing. Nearly all vocalizations are described from breeding territory within nesting colonies. The exception is the aggressive *Aaah* Call, also given during aggressive encounters with conspecifics and heterospecifics at feeding sites. *Scaah* Call may be given as breeding birds approach nest, sometimes from 5–10 m outside of breeding territory or in flight.

Social context and presumed functions. Aggressive Upright Display (see Behavior: agonistic behavior, below) and many aggressive behaviors often accompanied by *Aaah* Call; *Aaah* Call also given when humans approach nest. When parents arrive at nests with well-developed young, *Scaah* Call often given by adults (Rodgers 1978a); also used during Alert Posture (see Behavior: agonistic behavior, below; Rodgers 1977). Often gives short guttural *Aahrr* Call as alarm call when flushed. At end of Snap-Stretch Display (see Behavior: sexual behavior, below), males give 1 or more resonant *Unh* Calls, which vary among males from soft and low to harsh and loud, sometimes audible from 10 m. Male also makes groaning sound toward end of courtship bout (J. S. Huxley in Bent 1926). During Circle Flight Display (see Behavior: sexual behavior, below), male gives long series (5–12/display) of *Culh-Culh* Calls while moving bill up and down, which movement may continue after landing; females may follow males during Circle Flight Display, and may give these calls, though they give fewer than males give. Also gives *Cuhl-Culh* Calls during Greeting Ceremony at nest (see Behavior: agonistic behavior, below), mates answering calls from some distance during nest relief (Rodgers 1978a).

Young give begging calls of several kinds, but none described. Because unrelated young are not fed, adults are able to recognize their own young; this recognition is perhaps facilitated by begging sounds of young (Rodgers 1978a). Reciprocal *Cuhl-Cuhl* Calls between male and female during Greeting Ceremony suggest vocal recognition.

NONVOCAL SOUNDS

Audible snap of mandibles by males during Snap-Stretch Display (see Behavior: sexual behavior, below), and rattling by mandibles during Bill-Nibbling by both males and females, produced by rapid opening and closing of bill (see Behavior: sexual behavior, below; Rodgers 1977). During Circle Flight (see Behavior: sexual behavior, below), audible and characteristic *whomp*, *whomp* made by particularly deep wing thrusts.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Walks with alternating steps, varying from slow, purposeful stalking to rapid running with sharp turns, stops, and pirouetting when hunting actively (see Food habits: feeding, above). Young climb by hooking lower mandible over branches, then pulling with neck until wings or feet can gain purchase.

Flight. Typically draws head in while flying, and extends feet behind. Flight steady, with direct wing-strokes; not often in flocks or formations. When descending to roost or colony, often achieves rapid descent by folding wings partly and rocking rapidly from side to side to spill wind in "falling-leaf" display (Bent 1926). Straight-line speeds over ground that were recorded while following breeding adult birds from colonies to foraging areas in Everglades averaged 15.3 km/h (*n* = 265; Bancroft et al. 1990).

Swimming and diving. Belly-feathers often submerged during wading; may partly float in deeper water.

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, and anting Two captive adults spent 62, 24, and 14% of time in resting, feeding, and maintenance behaviors (54/h), respectively (Maxwell and Kale 1976). Wild birds in Florida showed 46.8 and 7.2 maintenance and anti-insect behaviors/h, respectively (movements of head, feet, and bill for preening and insect deterrence; Maxwell and Kale 1976). In presence of mosquitoes, 3,329 movements/h by captives; when mosquitoes absent, only 76 movements/h (Weber and Edman 1972). No information on stretching.

Sleeping, roosting, sunbathing. No information.

Daily time budget. No data.

AGONISTIC BEHAVIOR

Physical interactions. During breeding, displaying males are aggressive toward all birds of both sexes initially; gradually allow females to enter nesting territory. Aggressive displays (from Rodgers 1978b) often include the following:

Alert Posture. Head extended upward, with wings close to body and feathers sleeked, body axis oriented close to vertical; often accompanied by *Scaah* vocalizations.

Upright Display. Neck is extended to an almost vertical position above body, with bill horizontal, and moderate feather erection; often accompanied by *Aaah* Call.

Forward Display. Erection of crest, feathers on upper and lower neck and scapular aigrettes; head and neck extended fully upwards with bill horizontal and wings slightly drooped or extended out to sides; in extreme examples, bill may be opened and dorsal surface of wings presented to intruders; may be followed by aggressive lunge at opponent.

Aerial Fighting. A highly aggressive interaction in which 2 herons fly up from the ground facing each other, repeatedly lunging with bills and thrashing feet; often accompanied by *Aaah* vocalization.

Twig-Shaking. Extends head out and down while leaning forward, grasps and shakes a twig nearby, with slight to moderate erection of crest and neck feathers. Intensity varies; may become more intense at approach of females.

Upright and Forward displays occur in increasingly hostile sequence; Twig-Shaking performances appear to have some agonistic motivation (Rodgers 1978a). Male-male encounters during courtship may escalate to aerial fights. After pairing, male and female participate in defense of territory. Young in nest threaten intruding adults and nestlings by jabbing with bill, and by performing Upright and Forward display after about 3 wk of age (Rodgers 1977). Young lunge and snap at approaching parents, and sometimes must be placated by Greeting Ceremony (see below) of adult; fledglings sometimes perform Greeting Ceremony to each other, which may function in appeasement. On foraging grounds, may defend feeding plots (Oberholser 1974).

Communicative interactions. *Threat Displays.* Include Upright, Forward, and Snap-Stretch (Fig. 2; for description see Sexual behavior: pair bond, below) displays; often used by males as they patrol territories during courtship period, and by both sexes during territorial disputes.

Appeasement Displays. Both sexes use sleeked head to signal appeasement; females use Withdrawn Crouch—body is withdrawn into horizontal posture, with legs bent, head and neck withdrawn into body, bill horizontal, and feathers sleeked—when attempting to appease displaying males (Rodgers 1978a). Greeting Ceremony—arriving bird passes a twig to mate, with all feathers fully erect, wings held out to sides, bill pointed repeatedly upwards, then down towards nest—used throughout nesting period to aid in recognition and to reduce aggression during nest exchanges.

SPACING

Territoriality. May vigorously defend small, local feeding territories (Wible 1957, Palmer 1962), but size and permanence of this area remains poorly documented. Males establish small breeding or display territories in immediate vicinity of nest site

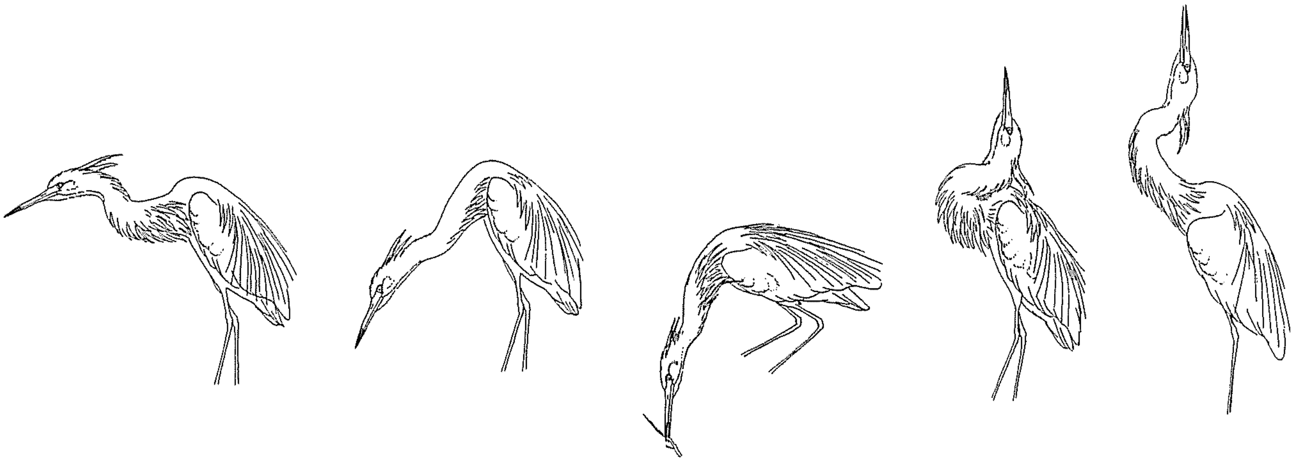


Figure 2. The Snap-stretch Display of the Tricolored Heron. From Rodgers 1977, redrawn by Tony Henneberg.

(Rodgers 1978a); after pairing, both sexes defend these territories. Young birds >3 wk old may also threaten intruding young and adults in absence of parents. Nesting territories are relatively large early in breeding season (4–10 m in diameter) and reach minimum size (2–3 m) just after pair formation (Rodgers 1978a). Mean nearest nest distance averaged 1.14 m (range 0.4–2.4) in Florida (n = 59; Girard and Taylor 1979) and 1.65 m in S. Carolina (n = 34; Post 1990); in Florida, 20% of nearest neighbors were conspecific. In New Jersey, mean nearest conspecific nest distances were between 0.75 and 0.92 m in 2 colonies (Burger 1979).

Males initiate territories by active defense and display, occasionally manipulating twigs or branches and erecting feathers. Construct loose nest foundation in center of territory (Rodgers 1978a).

Individual distance. So far not measured in roosts or colonies other than as internest distances (see above).

SEXUAL BEHAVIOR

Mating system and sex ratio. Monogamous; strong pair bond and dual parental care that last for at least 1 breeding event. Intra- and interspecific brood parasitism may be reproductive strategies employed rarely by females (see below).

Pair bond. *COURTSHIP DISPLAYS AND MATE-GUARDING.* From Rodgers 1977, 1978a. Gives courtship displays at colony, within male display territories. Male displays, often from nest platform but also from other display sites around nest, include preening and erecting feathers on head and neck; Twig-Shaking (see Agonistic behavior, above) and Snap-Stretch Display (Fig. 2; see below); and Circle Flight Display—roughly circular flight by male from nest platform or territory with axis of bill oriented upwards and with very deep wingstrokes creating a *whomp-whomp* sound. A low-intensity Snap-Stretch Display involves occasional bowing below perch. If a female approaches, full Snap-Stretch Display is more common: Erects all plumes, extends wings out and down while lowering head, and then grasps twig; then points bill upward, stretches head, and sways neck while emitting a groaning *unh* sound. The stretch accentuates male's magenta iris, black bill-tip, turquoise cobalt orbital skin, and white throat. Order, duration, progression, and *Unh* Calls are quite variable among males. Courtship-preening may be marked by rapid, erratic movements atypical of normal maintenance behavior. Female often attempts to walk onto nest during Circle Flight Display by male, or may join male in the display. Females are usually chased off the nest platform early in courtship period. After female is allowed to land in core territory, male and female may engage in Bill-Nibbling—male and female open and close mandibles in close proximity to each other's head and body, creating a gentle rattling sound—neck-entwining, mutual preening, and joint twig manipulation. Copulation usually precedes "stable" pair bond. Male may display and defend territory for up to 11 d while forming pair bond with mate. Male remains on nest territory without feeding throughout courtship, and intensively guards female and territory during early egg-laying.

COPULATION; PRE- AND POSTCOPULATORY DISPLAYS. Copulation usually takes place on or very near nest site. Preening and Bill-Nibbling precede copulation. Female solicits by leaning forward and squatting, with neck partly withdrawn. Male mounts by grasping with toes on female's back, flaps for balance, and uses bill to maintain position. Copulation lasts 8–11 s. After copulation, Twig-Shaking (see Agonistic behavior, above) and preening are common, and male and female stand side by side facing opposite directions. Copulation most frequent during egg-laying, but observed throughout early incubation (Rodgers 1978a).

Duration and Maintenance of Pair Bond. There are no banding or marking studies to indicate duration of pair bond. Rodgers (1978a) believed seasonal monogamy to be the rule.

Extra-pair copulations. Not reported to date.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Generally less social in foraging, flocking, and nesting than are other herons. Flocks tend to be smaller than those of other herons (1–7 individuals); often travels solitarily (Burger et al. 1977). During breeding season, forages solitarily in both Florida (Jenni 1969) and Guyana (Llowe-McConnell 1967). Kushlan (1978) typified feeding in mixed-species flocks as "peripheral," and suggested that Tricolored Herons decrease in number as mixed-species flock size increases. In mixed-species foraging flocks, unlikely to have aggressive encounters with conspecifics or heterospecifics (Erwin 1983). Among ciconiiform birds on Lake Okeechobee, FL, least likely to nest in aggregated fashion within mixed-species colonies (Smith and Collopy 1995).

Play. After young leave nest but before gaining independence, often aggregate in small flocks in tops of trees or on the ground, where running chases and short flights can involve apparent mock aggression.

Nonpredatory interspecific interactions. Described as more "quarrelsome" than other species (Bent 1926), but in a mixed-species colony in coastal Mexico, this species was no more aggressive than relative numerical dominance would predict (0.11 interactions per roosting individual/h and 0.07 birds/h for nesting birds; Burger et al. 1977). Lost almost twice as many interactions (70%) as they won; about 25% of aggression with heterospecifics, 75% with conspecifics. Mixed-species foraging groups in Panama show linear dominance hierarchy: Snowy Egret > Tricolored Heron > Little Blue Heron (Caldwell 1981). In Tampa Bay, FL, 0.28 aggressive interactions/h (n = 28 observations) in mixed-species foraging flocks, with no clear interspecific dominance hierarchy (Kent 1986a). Species tends to be on periphery of interspecific foraging flocks, and nests on fringes of colonies, suggesting behavioral avoidance of other species during foraging and breeding.

PREDATION

Kinds of predators; manner of predation. Fish Crows (*Corvus ossifragus*) and American Crows (*C. brachyrynchos*) are known as predators of eggs, especially in coastal colonies (Jenni 1969, Post 1990); may be the most important source of egg loss (McVaugh 1972, Maxwell and Kale 1977a). Boat-tailed Grackles (*Quiscalus major*), Red-winged Blackbirds (*Agelaius phoeniceus*), and Purple Gallinules (*Porphyrula martinicus*) known to take eggs when researchers disturb adult herons from nests (Bent 1926, Jenni 1969, Frederick and Collopy 1989a, Bancroft et. al. 1990). Raccoons (*Procyon lotor*) may prey on young and eggs, but only if water recedes from colony area (Teal 1965, Rodgers 1987, Frederick and Spalding 1994). Black-crowned Night-Herons (*Nycticorax nycticorax*) noted taking young *Egretta* herons and White Ibises (*Eudocimus albus*) in colonies in s. Florida (Frederick and Collopy 1989a) and N. Carolina (Bjork 1986). Predation accounted for 57% of deaths of radio-tagged young in Florida Bay, FL; Bald Eagles (*Haliaeetus leucocephalus*) and Turkey Vultures (*Cathartes aura*) were the most common predators (Frederick et al. 1993). Predation of eggs and young is low in the freshwater Everglades, where crows and eagles rarely occur, and where colonies may be protected from mammals by the presence of alligators (*Alligator mississippiensis*; Frederick and Collopy 1989a). However, alligators may scavenge chicks falling out of nests, may pursue chicks on lower branches, and may jump or climb to 2 m to catch nestlings (Jenni 1969, Smith and Collopy 1995, PCF). In S. Carolina, a colony deserted breeding site after repeated predation of nest contents by Fish Crows and variety of mammals (raccoons, opossums [*Didelphis virginiana*], feral cats [*Felis catus*]; Post 1990).

In Suriname, Greater Black-Hawks (*Buteogallus urubitinga*) preyed on young in nest, and eggs and young often taken by introduced mongooses (*Herpestes auropunctatus*)and Black Vultures (*Coragyps atratus*; Llowe-McConnell 1967). In Panama, Common Black-Hawks (*B. anthracinus*) are the most frequent predators on flocks of feeding herons; Tricolored Heron were attacked more frequently than other species, perhaps because contrasting light and dark coloration make it conspicuous (Caldwell 1986).

Response to predators. In Panama, dark-plumaged Tricolored Herons and Little Blue Herons (also dark) gave more alarm calls in mixed-species flocks than did white-plumaged birds (Caldwell 1986). In colonies, responses to human intruders are limited to alarm calls and approach by adult birds to within 4 m of humans when at nest. Both sexes vigorously defend nest against smaller predators such as grackles and blackbirds (Palmer 1962). For larger predators, no direct attacks or mobbing observed. Alligators may deter raccoons and other mammalian predators from approaching colonies, and adults may favor nesting above alligators (Jenni 1969, Frederick and Collopy 1989a).

At least 2 colonies in Florida occur in vegetation directly above dense concentrations of captive alligators at tourist attractions, despite daily close contact (1–10 m) with large numbers of tourists on boardwalks.

BREEDING

PHENOLOGY

Pair formation; nest-building. Pair formation and nest-building occur almost simultaneously, or at least within several days of each other. Pairs form at the colony; courtship not noted elsewhere. Pairs form during Feb (extreme s. Florida; Stevenson and Anderson 1994) to late May farther north (Bent 1926).

First brood per season. Figure 3. Earliest laying dates are from extreme southern and coastal Florida, including Feb (Girard and Taylor 1979) and Dec (Bent 1926), but more commonly early to mid-Mar (Jenni 1969, Smith and Collopy 1995). Other early dates are 5 Apr in Texas (Oberholser 1974), 10 Apr in S. Carolina (Post and Gauthreaux 1989), 15 Apr in N. Carolina (McCrimmon 1978), 24 Apr in Maryland (Robbins and Blom 1996), and 8 May in Virginia (Kain 1987). Latest laying Jun, rarely Aug, in Florida (Bent 1926, Sprunt 1954), 23 Jun in Texas (Bent 1926), 5 Jun in Maryland (Robbins 1996), 20 Aug in Virginia (Kain 1987).

Mean laying date in coastal Everglades 31 Mar (Bancroft et al. 1994); in Atlantic coastal Florida, 87% of clutches completed between 22 Mar and 6 Apr (Maxwell and Kale 1977a). In Louisiana, laying peaks early Mar–early May (Bent 1926); in N. Carolina, 15 Apr–6 May (McCrimmon 1978).

On s. Yucatán Peninsula (Sian Ka'an Biosphere Reserve), Lopez-Ornat and Ramo (1992) found extreme egg dates of 2 Mar–23 Jun, with timing of breeding generally similar to that in se. U.S. In Colombia, late Jun (La Guajira; Hilty and Brown 1986). In Guyana, eggs laid Feb–Jun; timing of breeding variable and cued directly by onset of rainy season (Llowe-McConnell 1967, Haverschmidt and Mees 1994). In Trinidad, Feb–Aug (ffrench 1991).

Intervals between eggs variable: 2 d between first 2 eggs; 1-d intervals for later eggs (see Eggs, below).

Mean hatching date of first chick in Florida Everglades is 22 d from laying of first egg (Frederick and Collopy 1988).

Young reach independence from parents at 50–59 d of age (see also Fledgling stage, below).

Second/later broods per season. Second broods possible, but evidence can also be interpreted as nest failure followed by renesting (Bancroft and Jewell 1987).

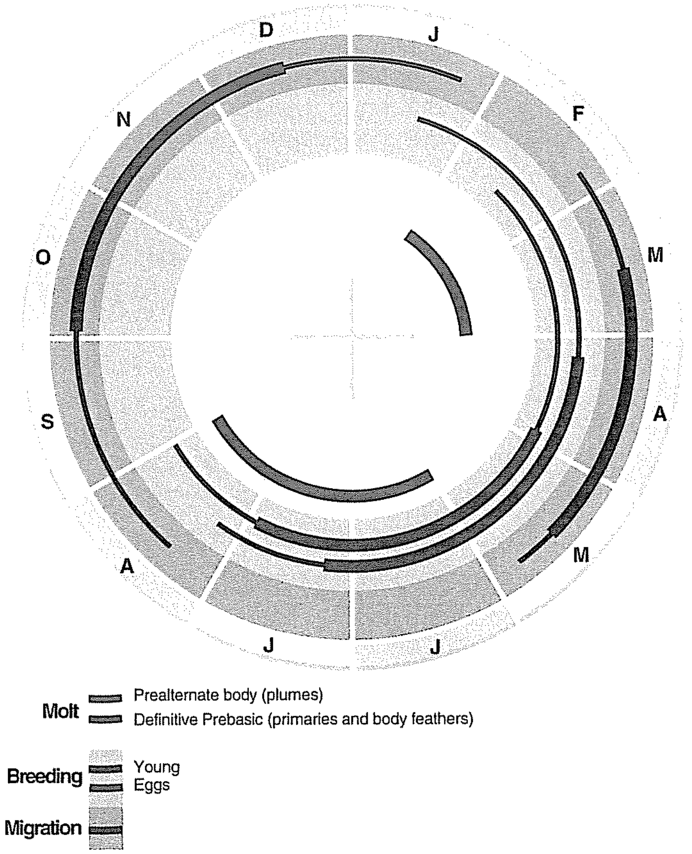


Figure 3. **Annual cycle of breeding, molt, and migration of Tricolored Heron. Thick lines show peak activity; thin lines, off-peak.**

NEST SITE

Although typically nests in mixed-species colonies, may be found in small (2–100 nests) monospecific colonies (Smith 1994, Frederick 1995), and occasionally nests solitarily.

Selection process. Male picks nest territory often before females appear at colony (Rodgers 1978a), and may establish nest site within territory before pair bond is initiated.

Site characteristics. Nests in monospecific or multispecies colonies; in the latter, on edges, usually in denser vegetation than other species; likely to be in conspecific groups. Nests in dense, well-shaded shrubs and small trees between 0.15 and 3.7 m above ground or water. Nests preferentially in densest vegetation (1.5–2 m tall; Rodgers 1978a), and nesting seems to progress during breeding season from densest vegetation on periphery to sparsest in center of colony (Maxwell and Kale 1977a).

Uses wide variety of generally woody vegetation, including small oaks (*Quercus* spp.), red maples (*Acer rubrum*) and other wetland hardwoods, bald cypress (*Taxodium distichum*), *Yucca* sp., groundsel bush (*Baccharis halimifolia*), black mangrove, white mangrove (*Laguncularia racemosa*), buttonwood (*Conocarpus erectus*), red mangrove, willows (*Salix* sp.), wax myrtle (*Myrica cerifera*), buttonbush (*Cephalanthus occidentalis*), mesquite (*Prosopis juliflora*), huisache (*Acacia farnesiana*), prickly pear cactus (*Opuntia*); on salt marsh islands, flattened mats of needle rush (*Juncus roemerianus*). Nest heights vary between 0.14 and 4 m above ground, depending on vegetative structure, competition for nests, and mix of other nesting species (Bent 1926, Jenni 1969, Maxwell and Kale 1977a, Rodgers 1978a, Burger 1979, Girard and Taylor 1979, Post 1990).

In N. Carolina, nests generally below canopy in trees and shrubs; mean height of 2.03 m above ground ($n = 39$ nests; McCrimmon 1978). Mean nest tree diameter 6.2 cm; diameter of branch supporting nest 3.5 cm ($n = 39$ nests). Vegetative density above nest was high by comparison with other species. Mean distance to open space was 6.9 m and distance to colony edge was 15.8 m.

Of 28 nests in an inland n.-central Florida colony, 11% were in red maples, 29% in buttonbush, 39% in box elder (*Acer negundo*), and 4% in willow (Jenni 1969). In coastal Florida, Maxwell and Kale (1977a) reported 64% of nests in black mangrove, 28% in white mangrove, and 7% in red mangrove. In S. Carolina, nested farther out on limbs than do other species of herons, and nests tended to be on smaller, springier branches (Post 1990).

NEST

Construction process. Male begins construction by forming loose platform of large twigs as foundation before pairing with female. Copulation seems to stimulate collection of twigs by males. Males usually collect twigs, females remain at nest site and work twigs into nest; Greeting Ceremony (see Behavior: agonistic behavior, above) frequent during exchanges of nest material. Female works twigs into nest structure using angled, sideways motion. Activity more likely in early morning and late afternoon (Jenni 1969). Between first copulation and laying of first eggs: 4–6 d. Jenni (1969) recorded 4–5 d for construction of 2 nests.

Structure and composition matter. Foundation is made of twigs about 1 cm in diameter and 30–60 cm long. After pair forms, construction is continued with twigs 0.5 cm in diameter and <30 cm long; no green material in nest (Rodgers 1977). In Louisiana, finishing material was fine twigs and cordgrass (*Spartina*) stems. Gathers most twigs from ground in immediate vicinity of nest (Jenni 1969), and often walks down angled branches and stems to ground during nest-building and incubation (Frederick and Collopy 1989a).

Dimensions. Total diameter <30 cm; slight depression in center (Portnoy 1977, Rodgers 1978a). No recognizable differences between nests of Snowy Egret, Tricolored Heron, and Little Blue Heron.

Microclimate. Generally shaded and below canopy, with little exposure to direct sun or aerial predators (McCrimmon 1978, Bjork 1986). No measurements of nest temperature or humidity available.

Maintenance or reuse of nests, alternate nests. Nests generally do not last between seasons, and are rebuilt annually, often appearing in same area of colony and same crotch of tree as in previous season. Abandoned nests may be reused within season. Failed nests and those skewed by accidents often provide foundation for new nests, sometimes producing a large, bulky structure.

Nonbreeding nests. None recorded (Bent 1926, Sprunt 1954, Jenni 1969, Rodgers 1977, 1978a).

EGGS

Shape. Ovate to oval; elliptical ovate or elliptical oval (Bent 1926, Sprunt 1954, Palmer 1962).

Size. Bent (1926) reported that 41 eggs from North America averaged 44.1 x 32.3 mm. In Florida Everglades, Frederick and Collopy (1988) found, in 1986, that 162 eggs from 49 clutches (all eggs in each clutch) averaged 44.44 mm ± 1.64 SD x 32.28 ± 1.12; in 1987, 605 eggs from 194 clutches averaged 44.63 ± 1.75 x 32.22 ± 0.96. In Texas, average size 43.9 x 32.3 mm (no n or SD given; Oberholser 1974). In Trinidad, 8 eggs averaged 40 x 30 mm (ffrench 1991), and in Suriname, 40.9–42.8 x 30.6–30.9 mm (Haverschmidt and Mees 1994).

Mean lipid content of 153 eggs from e. North America was 6.29% ± 0.11 SD (Ohlendorf et al. 1979), and of 5 eggs from Louisiana, 5.9% (Faber and Hickey 1973).

Mass. In Suriname, fresh eggs weighed 20.7–21.5 g (Haverschmidt and Mees 1994). No other egg masses available.

Color. Ground color is pale greenish blue, although descriptions vary. Variation includes pale Niagara green, lichen green, pale greenish blue, and blue with greenish cast (Bent 1926, McVaugh 1972).

Surface texture. Smooth.

Eggshell thickness. Pre-1947 (pre-DDT) mean was 0.240 mm ± 0.013 SD ($n = 8$); post-1947 (post-DDT), 0.236 ± 0.03 SD ($n = 5$); no significant differences between the 2 periods (Faber and Hickey 1973, Ohlendorf et al. 1979). This species does not appear to have been exposed to high enough levels of DDT to have experienced >4% eggshell thinning (Faber and Hickey 1973).

Clutch size. Range 3–5 eggs; 3–4 the most common in North America (see Appendix 2). Bent (1926) cited 6 and 7 in rare cases, and Jenni (1969) found up to 9. In Florida, 3–4, with mean of 3.58 from museum sets (Stevenson and Anderson 1994). In Everglades, clutch size found to be significantly larger in freshwater habitat than in brackish or marine habitats, even when date of laying was controlled for (Frederick et al. 1992). In Maryland, 3–5 (Robbins and Blom 1996); in Delaware, 3.1–3.5 over 3-yr period (Wiese 1979). Early clutches may be larger; at Moore Creek, FL, early clutches averaged 3.1, late clutches 2.6 (Girard and Taylor 1979). Clutch size declines to 2–4 in Central America and Mexico (Howell and Webb 1995); 2–3 cited for Suriname (Haverschmidt and Mees 1994).

Egg-laying. Generally begins after nest mostly completed, but material added to nest throughout egg-laying and incubation. During egg-laying, males guard nest, territory, and female—during courtship and early egg-laying, usually without breaks for feeding (Rodgers 1978a). In n.-central Florida, mean interegg interval of 1.7 d ± 0.10 SD (*n* = 40 intervals; Jenni 1969). First and second eggs laid on consecutive days about half the time, and on alternate days half the time; frequency of consecutive day intervals increases with successive eggs. In coastal Florida, eggs laid on average every 2.1 d ± 0.08 SD (*n* = 47); intervals are slightly less later in clutch (Maxwell and Kale 1977a).

Eggs are replaced continuously, up to 5 in a row, as they are removed by predators (Jenni 1969). Lays replacement clutch when primary clutch destroyed entirely, beginning 2–10 d (mean 5.3) after destruction (*n* = 8 nests; Maxwell and Kale 1977).

Some evidence for low prevalence of intraspecific nest parasitism. Maxwell and Kale (1977a) noted a single egg present in a nest for 7 d, followed by 3 additional eggs; all eggs hatched. Other evidence includes several cases of egg additions during incubation in Everglades (PCF). Exceptionally large clutches reported by Bent (1926; 6 and 7 eggs) and Jenni (1969; up to 9) may be further evidence of egg-dumping. May lay eggs in nests of other species (see Brood parasitism, below).

INCUBATION

Onset of broodiness and incubation in relation to laying. Before uninterrupted incubation, adults may sit on eggs sporadically. Beginning of effective incubation is irregular, typically starting the day after second egg is laid, or the day the third egg is laid (Jenni 1969). In Florida, incubation began with laying of second egg (55% of nests) or first egg (21%; Maxwell and Kale 1977a).

Incubation patch. No information.

Incubation period. Laying of first egg to hatching of first egg computed as mean of 22 d ± 0.74 SD from Everglades data (*n* = 15 nests; Frederick and Collopy 1988). In n.-central Florida, mean of 23.8 d ± 0.19 SD (*n* = 10 nests) from laying of last egg to hatching of last egg (Jenni 1969); in coastal Florida, mean of 23.3 d ± 0.21 SD (*n* = 20 nests) from laying of first egg to hatching of first egg (Maxwell and Kale 1977).

Parental behavior. Both sexes incubate. One parent remains on nest almost continuously during incubation. Early-morning incubation is most intense; during late morning and afternoon, parents frequently stand up. Eggs may be turned regularly (Frederick and Collopy 1989b).

Periods of duty range from 1 to >14 h, most commonly 2–6 h (Rodgers 1978a). Incubation exchanges are frequently in midmorning, mid-afternoon, and early evening; rarely in early morning. No information on relative contributions of incubation times by males and females. Incubation exchanges include Greeting Ceremony (see Behavior: agonistic behavior, above), calling between mates, and presentations of twigs (Rodgers 1977).

Hardiness of eggs against temperature stress; effect of egg neglect. As measured by thermistors inside similarly sized Cattle Egret eggs in direct sun, temperature increases to probable lethal limits in 30 min–1 h during the summer in Florida (PCF). No information on egg neglect, except that high hatching rates (see Hatching, below) are common in context of characteristically delayed incubation.

HATCHING

Preliminary events and vocalizations. Eggs show small pinpoint fractures and pip holes 24–30 h before hatching (PCF). Young emit high-pitched, peeping sound as they hatch, and adults often peer at eggs.

Shell-breaking and emergence. No information on time of day of hatching. Hatching generally takes 24–36 h, but little direct measurement. In Florida, clutches averaged 3.1 d (range 1–5, *n* = 76 nests) to complete hatching, independent of number of eggs in clutch (Maxwell and Kale 1977a). All chicks hatched on same day in some clutches. Time interval between hatching of successive eggs increased with laying order from 0.5 d for first and second eggs to 1.8 d for third and fourth eggs.

Parental assistance and disposal of eggshells. Parents drop eggshells over side of nest; no parental assistance with hatching noted, although parents frequently rise off eggs as they are hatching, and are attentive to calls of hatchlings (PCF).

In coastal Florida, 1.6% of eggs disappeared during incubation, and 1.0% of those that remained failed to hatch (Girard and Taylor 1979). In Florida Everglades, between 1.4 and 18% of eggs present at time of hatching failed to hatch (Frederick 1995; see Appendix 2).

YOUNG BIRDS

Condition at hatching. Semialtricial; wet, with downy feathers over much of body. Chicks can hold head up for brief periods and vocalize (peeping). Legs initially small and not functional for any type of locomotion. Mass at hatching unknown. At hatching, bill averaged 12.7–15.8 mm, wing 15.8 mm, total body length 101.6–107.9 mm (*n* = 65; McVaugh 1972). Top of head covered with long hairlike plumes, army brown to fawn, mixed with shorter gray down on head; back has long, soft, dark gray down; under neck, abdominal region, and femoral tract is coarse, scant, white down (McVaugh 1972).

Eyes partly open at hatching. Bill, feet, and naked skin light green to yellowish. Exposed skin flesh-colored under neck, deep flesh or fleshy gray in auricular region and nape, bright blue to bluish gray around eyes. Deep gray skin covers crown, and remaining body skin varies from fleshy gray to medium gray. Upper mandible fleshy gray to warm gray; black-tipped, with dark gray line only on cutting edge of upper mandible. Pale pink inside nostril; egg tooth present. Lower mandible flesh-colored with small dark tip. Mouth-lining yellow pink to pink. Eye deep-set in protruding dark gray eye-ring. Iris light gray to off-white; pupil black. Tarsus and toes pale bluish pink on top and flesh-colored underneath; varying intensity above. Toenails are pale ivory and hallux toenail darker (McVaugh 1972).

Capable of only short, jerky movements of head and upper body at hatching; within first day can move head toward parent and may be able to receive some well-digested food from parent's bill.

Growth and development. See McVaugh 1972 for detailed body measurements and descriptions of development.

PHYSICAL ABILITY. Just after hatching, nestling can hold head up and move in short, abrupt jerks; little or no reaction to humans at this stage. By 5 d, capable of movement in nest; calls frequently but not when handled by humans. By 11 d, young can climb from nest using bill, wings, and feet; sometimes perch on one side of nest; spend more time in nest than out of it; show fear when handled or approached by humans; call intermittently with harsh note. By 17 d, perch above or to one side of nest and return only to be fed; flee predators and humans by climbing; no call notes heard. At 24 d, young perch away from nest, usually in tops of bushes or trees all day and do not return to nest to be fed. Climb with wings and feet; call at approach by parent; some inter- and intraspecific quarreling and bill-jabbing. By 30 d, tend to perch in intraspecific groups; defend perch area. No call notes heard at this point.

PLUMAGE. At 5 d, head covered with long brownish red down; brownish gray down on back; white down on femoral tract and sparse white down on abdomen. Juvenal feathers emerging; egg tooth still visible; iris gray to off-white; scales developing on tarsi and toes. By 11 d, some Juvenal feathers tipped with long white down, others emerging. Scales well formed on tarsi and toes. Upper mandible dark gray proximally. By 17 d, head covered with long faded white down; some dark gray down remains on back; reddish brown feathers just emerging from sheaths on upper half of neck; lower half well emerged. White underneck-stripe becoming defined. Primary and secondary feathers dark gray; tarsus and toes light gray green. By 24 d, head, neck and body covered with feathers, most of which retain long reddish down. Top of head and neck reddish or brownish red; mantle medium reddish gray; back medium gray; white feather stripe on front of neck well defined; underparts all white. Nails light-tipped and medium horn. By 30 d, some down left on head, otherwise covered by Juvenal feathers; primaries, secondaries, and rectrices medium gray; some pin-feathers on spinal tract. Iris off-white, pupil black, and eye-ring medium gray.

Molt into Juvenal plumage largely complete by 30 d (McVaugh 1972), though molt may continue after fledging (approximately 56 d). Molt into Basic I plumage gradual, through first fall and early winter. No information on ages when contour feathers appear on different tracts, or on sequence of molting among tracts.

MASS INCREASE. See Black et al. 1984; a near-exponential increase in mass to 17 d. After this, growth curve appears to be sigmoidal, with an apparent upper inflection point at 300–350 g, though data are lacking for latter part of pre-independence period (30–60 d).

GROWTH OF BODY PARTS. As with other *Egretta* herons (Werschkul 1979), rapid initial growth of legs, bill, and especially feet, which probably aid in early climbing and movement. At 1 d of age, wing length 101.6–107.9 mm, tarsus 19.5–22.2 mm. The following are mean measurements. At 5 d, wing 31.8 mm, bill 20.6, tarsus 28.6, middle toe 31.8. At 11 d, wing 31.8 mm flattened, bill 30.2, middle toe 55.6, tarsus 39.7. At 17 d, wing 85.7 mm flattened, bill 42.9, middle toe 69.8, tarsus 60.3. At 30 d, wing 184.1 mm flattened, bill 69.8, middle toe 82.5, tarsus 88.9. (*n* = 65 nestlings; McVaugh 1972).

CONTROL OF BODY TEMPERATURE. Thermoregulatory ability develops quickly; by approximately 14 d of age, almost completely able to survive without parental brooding.

BEHAVIOR. Food begging, forward threat, preening, and aggressive vocalizations well developed by 14 d.

LOCOMOTION. Young can swim well for short distances by 14 d of age (Bent 1926); first flights at

25–30 d (Frederick et al. 1992). No information on learning process.

PARENTAL CARE

Brooding. Begins immediately upon hatching, waning to 12 d of age. No information on brooding rhythm.

Feeding. Chicks initially fed at 1–2 d of age; achieve complete independence from parental feedings by 50–56 d of age. Both sexes feed young, though relative contributions are not documented.

Method of Feeding. For first 1–2 d, chicks feed by pecking at pile of food regurgitated by parent near chick's head on floor of nest. By 2–3 d, chicks are strong enough to hold head up and take direct regurgitation from parent's gape. After 1 wk, chicks begin grasping bill of parent, while adult extends mandibles downward with dorsal surface of upper mandible facing offspring. Chick grasps upper mandible and pulls downward; food more or less pours at an angle into chick's open gape. After 2 wk of age, parents can no longer evade the constant begging and grasping of chicks, and they do not spend time on the nest except when actively regurgitating. After 4 wk, young approach adults near nest for feeding; both adult and young must flap wings to maintain balance. Between 4 and 6 wk, young pursue adults on short flights around colony and are usually fed away from nest, an activity that undoubtedly aids in development of flight abilities.

Food of Young. Initially semidigested liquid food regurgitated from parent in small amounts. After 5 d, mostly undigested small fish. Most reports in Appendix 1 are from boluses regurgitated from nestlings and young birds. Small killifishes and live-bearers are the most common prey items.

Rate of Feeding. Frederick and Powell (1994) estimated that 116,911 kJ are necessary for entire brood, over 55-d period. Four to 5 feedings/d up to 7–8 wk, at which point parental care ceases. Feeding trips at irregular times of day (Rodgers 1978a). No information on amount of food brought per trip. Food appears to be apportioned among young by scramble competition, dominated by older chicks; parents do not appear to intervene on behalf of youngest chicks.

Nest sanitation. No obvious form of nest-cleaning; young defecate in nest. Nests are usually quite porous, and feces drip out of nest bottom or dry quickly on nest material. No fecal sacs; young defecate liquid or semiliquid feces directly into nest throughout nestling period.

Carrying of young. No reports, although congeneric Little Blue Heron capable of carrying eggs (Rodgers 1978b).

COOPERATIVE BREEDING

No indication of cooperative breeding in this species (Rodgers 1977, 1978a).

BROOD PARASITISM

Identity of parasitic species. In Florida Everglades, 1 case of Little Blue Heron hatching in Tricolored Heron nest, 1 possible case of Great Egret (*Ardea albus*) egg laid in or transported to a Tricolored Heron nest (PCF). In coastal Florida, 1 case of Snowy Egret chick in Tricolored Heron nest (not known if it hatched there; Maxwell and Kale 1977). The Snowy Egret was 3–5 d younger than the hosts and was outcompeted for food and died by 6 d of age. One well-documented case of Tricolored Heron nestling being hatched and reared by Snowy Egret parents in Florida; the egg appeared following a violent dispute over nest ownership between neighboring Tricolored Heron and Snowy Egret pairs, during which original clutch of Snowy Egret was ejected by Tricolored Heron pair. The Tricolored Heron egg must have been laid during the short period before the Snowy Egret pair regained the nest (Morgan and Morgan 1995).

Response to parasitic mother, eggs, or nestlings. Parents will feed and rear Snowy Egrets and Little Blue Herons; likewise Snowy Egrets will rear Tricolored Heron nestlings (McIlhenny 1934 in Rodgers 1978a, Morgan and Morgan 1995, PCF).

Effects of parasitism on host. Probably small; on 2,113 nest-days (465 nests) observed during egg-laying and 12,289 nest-days (841 nests) during incubation, parasitism was found to occur at <0.1% of nests (PCF).

Success of parasite with this host. Not measured.

FLEDGLING STAGE

Departure from nest. By 17 d of age, young can perch at side of nest; by 21 d, usually perch above nest (McVaugh 1972, ffrench 1991, Frederick et al. 1993). By 24 d of age, young return to nest platform only to be fed. Between 24 and 60 d, young are fed in tops of trees by adults as young develop flight abilities. Age at independence from parental feedings and departure from colony were measured with radio-tagged chicks in Everglades: mean age 59.2 d ± 1.20 SD ($n = 32$; Frederick et al. 1993), and 51–56 d ($n = 6$; Bancroft and Jewell 1987).

With first instances of leaving nest, climbing abilities are well developed; no flight abilities; fully feathered, but many feathers still growing. At independence from adults, have full flight abilities; complete or nearly complete Juvenal plumage; foraging and perch defense behaviors well developed.

Parents often lead young around colony on long flights before feeding in final 2 wk of fledgling stage. This behavior suggests that young eventually follow foraging adults (possibly parents) from colony to foraging grounds on first flights away from colony.

Growth. No information on mass at time of independence, but plateau in mass for nestlings suggests adult body mass or slightly above (Black et al. 1984).

Association with parents or other young. At 3–4 wk of age, young often beg from nonparents but are rarely fed (Rodgers 1978a). No evidence of close association of young and parents or of broodmates following independence.

IMMATURE STAGE

No information.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. No data; first breeding presumed to be during second spring (21–23 mo), on basis of molts.

Clutch. See Breeding: eggs, above. No information on age-specific clutch size. One clutch/yr unless breeding attempt fails; second clutches following successful breeding have been recorded, but are likely to be uncommon (Bancroft and Jewell 1987).

Annual and lifetime reproductive success. See Appendix 2. Typically, 1–2 young survive to fledging. Nest failure associated with interruptions in prey availability because prey become inaccessible during cold winter weather (Frederick and Loftus 1993, Frederick and Spalding 1994). Adults abandoned nests during a drought in Everglades when foraging distances from colony increased to >25 km (Bancroft et al. 1994). Smith and Collopy (1995) found that an average of 12% of entire colonies were aborted or were unsuccessful on Lake Okeechobee, FL.

Generally, 1.7–3 young 14 d of age per successful nest (see Appendix 2.). One and sometimes 2 nestlings/brood (usually smallest individuals) died in nest, of emaciation or starvation (Rodgers 1978a). Broods in n.-central Florida were reduced from an initial 3.7 young/nest at hatching to 2.8 young/successful nest at 2 wk of age; this decrease was also attributed to starvation (Jenni 1969). In Georgia, Teal (1965) found that 32% of chicks were taken by predators, and 9% starved. Smith and Collopy (1995) found 1.6–2.2 young/successful nest by 21 d of age. Frederick et al. (1993) estimated 1.34 young/successful clutch survived to independence in coastal Everglades; 32.3% of chicks died between hatching and independence; major causes of mortality: predation (57%), malnutrition (29%), and disease (9%). Death of young often attributed to starvation (Jenni 1969, Rodgers 1978a), although necropsy results indicated that most of the apparent starvation cases in s. Florida were attributable to disease (Spalding and Forrester 1991). In Guyana, 70% of 10 nests had 2 young, and 30% 3 young, although stage of nestling growth was not given (Llowe-McConnell 1967).

Number of broods normally reared per season. Probably 1. Bancroft and Jewell (1987) found that some radio-tagged individuals switched colonies between breeding attempts in Everglades, but evidence in most cases suggested these were renesting attempts following failed nesting attempts. No evidence of a second cohort of nesting in Everglades colonies (PCF).

Proportion of total females that rear at least one brood to nest-leaving or independence. Of females that attempt to nest, success at rearing at least 1 young to independence varied from 5 to 67% in Florida Everglades (Frederick et al. 1992). Proportion of reproductive-aged females that attempt to breed is unknown, but for Everglades, average of 43% of estimated population of dark herons (Tricolored and Little Blue herons combined) does not breed during peak of incubation and hatching (Bancroft and Sawicki 1995, Frederick 1995).

LIFE SPAN AND SURVIVORSHIP

Rate of survival from hatching to independence is 67.7% (Frederick et al. 1993); from 21 d to independence, 28.6% (Bancroft and Jewell 1987). From recoveries of chicks banded as nestlings in Texas between 1926 and 1976, 79% mortality in first year, and 31.6% annual mortality thereafter; life expectancy at fledging 1.16 yr; 2.69 yr after start of second year (Telfair 1979). Longevity record in the wild 17 yr 8 mo (Clapp et al. 1982).

DISEASE AND BODY PARASITES

Diseases. Verminous peritonitis from the nematode *Eustrongylides ignotus* is known to have effects at population level. A single parasite can cause nestlings to die within a day, usually from hemorrhage and secondary bacterial infection; 10% of wild nestlings examined in s. Florida were infected (Spalding and Forrester 1991, 1993). Two of 2 nestlings and none of 2 adults examined were infected during an epizootic involving several wading bird species in Delaware; 2–11 nematodes/infected bird, resulting in 82% reduction in fledgling success (Wiese et al. 1977).

Another nematode, *Contracaecum microcephalum*, reported from adults (Walton 1927). Among trematodes, both *Ascocotyle* sp. (Hutton 1964) and

Posthodiplostomum sp. (Loftin 1962) reported. These parasites probably do not greatly impair hosts, but little information available.

In Florida, 8.7% of nestlings infected with *Haemoproteus* spp., and 4% with *Trypanosoma avium*, though the effects of these parasites are unknown (Telford et al. 1992). Generally low levels of blood parasites in Florida by comparison with other locations (Spalding and Forrester 1993). Avian cholera (*Pasteurella multocida*) possible in western U.S.

Body parasites. Mallophaga (*Ardeolica nigra*) found in Florida (Spalding and Forrester 1991). Dermestid beetles rarely inhabit nests. Lesions from dermestid beetle larvae (*Dermestes nidum*) found on 1 of approximately 80 nestlings regularly examined in central Florida (Black et al. 1984), and on 2 of 1,483 nestlings examined in Florida Everglades (Frederick and Collopy 1988, Spalding and Forrester 1991).

CAUSES OF MORTALITY

Exposure. In n.-central Florida, young died and nests blew down during windstorms and periods of heavy rain; temporary abandonment of nests by adults usually led to theft of nest material by neighbors and eventual destruction of nest (Jenni 1969).

Predation. Predation of eggs and young (see Behavior: predation, above) can be major source of mortality. In coastal S. Carolina, predation of nest contents by mammals and birds caused decline in nest success across years from 90.4% (incubation) and 80.5% (nestling) to 31.7% (incubation) and 45.9% (nestling; Post 1990). In n.-central Florida, predation resulted in survival of less than half of nest initiations to clutch completion; however, once clutches were completed, nest success was fairly certain (Jenni 1969). Nest predators are rare in freshwater Everglades, because of high water levels, presence of alligators, and few other food sources acting as attractants. Of 144 nests, <2% failed as result of predation (Frederick and Collopy 1989a). In coastal Georgia, estimated 19% of 47 eggs taken by predators (Teal 1965).

Competition with other species. Niche partitioning among Tricolored Herons, Snowy Egrets and Little Blue Herons in marine habitat may result from differences in prey type and size, though these species show significant differences in use of foraging habitat; Tricolored Heron is more common in open water and pools (Kent 1986a, 1986b). In coastal New Jersey, however, almost complete prey size overlap between Tricolored Heron and Great and Snowy egrets, and use of foraging habitat did not differ among Tricolored Heron, Snowy Egret, and Little Blue Heron (Willard 1977). Direct interspecific aggression in foraging flocks is generally rare.

RANGE

Initial dispersal from natal site. In coastal Everglades, Bancroft and Jewell (1987) found 1 radio-tagged fledgling 95 km from natal colony almost immediately after fledging. Another juvenile remained for 3 mo in same cordgrass marsh 4.2 km from natal colony. Young banded in Texas colonies tended to disperse to northeast and southwest along coast rather than inland (Telfair 1979). No information on distances moved between fledging and first breeding.

Fidelity to breeding site and winter home range. May be site-faithful to breeding areas between years as long as there is no history of nesting failure (Bancroft et al. 1994). May switch colonies in local areas within and between nesting seasons (Bancroft and Jewell 1987). At Drum I., S. Carolina, eventually abandoned colony after several years of frequent predation by Fish Crows and mammals (Post 1990). In subtropics and tropics, adults may remain within 100 km of breeding colony during nonbreeding season (Bancroft and Jewell 1987). At temperate breeding sites, seasonal migration to warmer climates is the rule.

Dispersal from breeding site or colony. Postbreeding dispersal much less pronounced in this species than in other ciconiiforms (Palmer 1962, Recher 1972). Postbreeding dispersal seems to be concentrated in coastal habitat, and may result in mid- and late-summer influxes of adults and juveniles (Willard 1977); see Distribution, above.

Home range. Home range not defended; described only from breeding season. In Florida Everglades, mean distance from colony to food source is 5.6 km ± 6.0 SD (n = 265; Bancroft et al. 1990).

POPULATION STATUS

Numbers. During first half of twentieth century, probably the most abundant heron in Florida and se. U.S. (Bent 1926, Howell 1932). During late 1970s, 1 of 3 most common wetland birds in Louisiana and probably the second most abundant heron in North America after Cattle Egrets (Portnoy 1977). In comprehensive breeding surveys of waterbirds in Louisiana, Florida, Yucatán Peninsula, and Atlantic Coast of U.S., Tricolored Herons represented 6–22% of breeding ciconiiform birds (Osborn and Custer 1977, Portnoy 1977, Nesbitt et al. 1982, Runde 1991, Correa 1992).

Comprehensive surveys in nearly entire U.S. breeding range in 1976 suggested minimum breeding population of 96,807 pairs, or about 193,600 adults (Custer and Osborn 1977, Portnoy 1977, Nesbitt et al. 1982, Texas Colonial Waterbird Society 1982)—probably an underestimate, however, given the low detectability of this dark-colored species by aerial surveys. These surveys suggest that the minimum measured population size of this species was larger in 1976 than for any other North American heron except the Cattle Egret. While this certainly was true for the areas surveyed, it may also be true in general—no heron other than these 2 have been found with a total population of ≥100,000 in the U.S. Earlier in this century, the Tricolored Heron was noted as "the most abundant heron" in Florida (Sprunt 1954: 32). In 1976, 72% of U.S. breeding population was found in Louisiana, 12% in Texas, 6.3% in Florida, and 9.7% in Atlantic coastal states north of Florida. In Suriname, numerous; colonies totaling 10,000–15,000 pairs of mixed small herons, "of which Tricolored and Little Blue Herons were the most numerous" (Haverschmidt and Mees 1994: 64). In Guyana, total population estimated at 5,000 birds (Dejonghe et al. 1992).

Trends. Probably declining as a breeding bird, perhaps rapidly, throughout North American range. In Everglades, declined from 10,000–15,000 breeding individuals in 1930s to 2,000 in 1980s (Ogden 1994). In Florida, 54% decrease in breeding pairs between 1976–1978 and 1986–1989 (Nesbitt et al. 1982, Runde 1991). In Louisiana and Texas, marked increases between 1950s and 1970s (Ogden 1978, but see Oberholser 1974), followed by probable decline thereafter.

During late 1980s, only 11,450 pairs nested in Louisiana (Martin and Lester 1990), a decline of 84% from Portnoy's (1977) survey. Although there were differences in survey methods, a close look at the studies in Louisiana suggests that the magnitude of the decline was unlikely to have been due to differing survey techniques. Marked increases in Christmas Bird Counts of wintering birds in Louisiana during 1990s, likely influenced by increases in food made available through burgeoning aquaculture industry (Fleury and Sherry 1994).

On East Coast, rapid increase in population in many states during 1940s–1970s, coinciding with rapid range expansion, including Virginia, Maryland, Delaware, New Jersey, New York, Connecticut, and Massachusetts (Kain 1987, Andrle and Carroll 1988, Sibley 1993, Veit and Petersen 1993, Bevier 1994, Robbins and Blom 1996). Rapid increases in population in Maryland; rare before 1960s, but during 1970s breeding population tripled, from about 300 to about 900. In s. New Jersey, breeding population has been declining rapidly since early 1980s. In New York, Massachusetts, and Delaware, population has been stable since mid-1970s.

On Yucatán Peninsula during 1980s, stable population of about 250 pairs nesting in Sian Ka'an Biosphere Reserve wetlands (Lopez-Ornat and Ramo 1992).

POPULATION REGULATION

Consistent reduction of broods because of starvation (Rodgers 1978a), as well as nesting failure in response to interruptions in food supply (Frederick and Collopy 1988, Frederick and Loftus 1993, Smith and Collopy 1995), suggest that food availability often limits reproduction. Little information on factors that affect postfledging and adult survival, however, which could be demographically more important.

Populations also likely limited by habitat. Significant correlations between coastal breeding abundance and amount of wetland area by state along Atlantic Coast (Custer et al. 1980). Majority of population outside of Florida seems restricted to estuarine and coastal nesting habitat (Ogden 1978). Estuarine productivity may therefore be important in regulating distribution and abundance of this species. This species has shown ability to colonize new nesting habitat when created (see Distribution, above).

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. Probably not taken in large numbers for plume trade (late 1800s, early 1900s), and not hunted in North American range today. However, large increase in aquaculture in s.-central U.S. has led to large increase in permits to kill herons and other waders (Coon et al. 1996). In Guyana, eggs and young are often taken by humans, and adults are often hunted for food (Llowe-McConnell 1967).

Pesticides and other contaminants/toxics. See Appendix 3. Generally low values of pesticides and other contaminants in this species. Moderately high levels of DDE (1.3 ppm) and PCBs (2.0 ppm) found in eggs from St. Marks, Wakulla Co., FL (Ohlendorf et al. 1979); high levels of DDE and PCBs in eggs from Louisiana, although measurement in fat makes interpretation difficult (Faber and Hickey 1973). Spalding et al. (in press) found DDE at 0.01–0.07 ppm (wet weight in brain tissue) from 7 birds in Florida Everglades.

Mercury in livers of 12 nestlings from s. Florida averaged 0.72 ppm wet weight (range 0.12–4.96), with higher values from e. Florida Bay and central Everglades (Sundlof et al. 1994); liver mercury was inversely related to body fat. In central Everglades, mean of 1.4 µg/g lead (wet weight, liver tissue) is considered high, and in extreme cases (>2 µg/g, up to 6.3 μg/g in liver) may have contributed to death of nestlings (Spalding et al. in press).

Although this species does not appear to have been at high risk of contaminant accumulation during 1970s, most of the available contaminant values are now >20 yr old, and more recent surveys should be undertaken.

Collisions with stationary/moving structures or objects. During 1,200 h of diurnal observations in Everglades, 0 of 567 Tricolored Herons were observed striking a high-voltage power line, although dead and wounded postfledging birds were sometimes found below it (PCF). These data suggest that collisions with power lines are rare in open habitat, although such collisions may increase when visibility is poor (fog, rain, crepuscular flight).

Degradation of habitat. Declining numbers in Everglades may be response to coastal degradation through reduced flow of fresh water to estuary (Frederick and Spalding 1994, McIvor et al. 1994, Ogden 1994), and this estuarine-dependent species is likely to be sensitive to reductions in estuarine productivity. This may be the most important conservation problem for the species. In Central and South America, losses of estuarine and marine swamps to commercial shrimp aquaculture and coastal development are likely to affect Tricolored Heron habitat (Bildstein 1990, Massey and Palacios 1994).

Disturbance at nest and roost sites. Rodgers and Smith (1995) found that Tricolored Herons flushed from their nests at mean distance of 30 m when approached on foot, and 12 m when approached by canoe. Bratton (1990) reported that 19 of 20 foraging groups flushed in response to approach of boat with outboard motor to within 25 m. No changes in foraging behavior or location documented in response to intensity of human visitation at Ding Darling National Wildlife Refuge, Collier Co., FL (Klein et al. 1995). Chick growth retarded in proportion to frequency of researcher visits to nest (Portraj 1978, but see Frederick and Collopy 1989b). Overflights of F-16 jets at 150 m above ground level and up to 100 decibels had no measurable impact on reproductive behavior, success, or growth rates of chicks (Black et al. 1984). At least 2 colonies of free-ranging birds in Florida are situated at tourist attractions, despite daily close approach (within 1–10 m) by large numbers of tourists on boardwalks.

Direct human/research impacts. Frederick and Collopy (1989b) found no differences in reproductive-success measures at a colony visited by researchers in an airboat at 4- and 8-d intervals in Everglades, although researcher visitation may affect nestling growth (Portraj 1978). American Crows may be attracted to disturbance caused by researchers, resulting in egg predation and consequent frequent nest failure and reduced clutch size of Tricolored Herons (Bent 1926, Bancroft et al. 1990).

MANAGEMENT

Conservation status. Classified as Migratory Bird (U.S.) and Species of Special Concern (Florida and Massachusetts). Declining rapidly in Florida, and perhaps elsewhere in se. U.S. Population probably stable on Yucatán Peninsula (Lopez-Ornat and Ramo 1992); declining in Baja California (Massey and Palacios 1994). Little other information about status outside of U.S. Migratory patterns suggest that wetland conditions in Greater Antilles, Yucatán, and Central America are important to U.S. wintering populations.

Measures proposed and taken. Identification of unprotected habitat in Florida (Cox et al. 1994) is an important preliminary conservation strategy—one that should be undertaken in other states throughout range. This species may have been positively affected throughout Gulf and Atlantic coastal range by construction and maintenance of dredge material islands (Parnell et al. 1986), and of coastal impoundments and protected islands of the National Wildlife Refuge system. Islands provide protection from mammalian predators for both roosting and breeding birds (see Breeding: nest site, above). Wintering populations may benefit strongly from aquaculture activities in Louisiana. Since the apparent take of aquaculture organisms by herons is small and largely unharvestable, Fleury (1994) has suggested that animal control measures are not necessary for herons, egrets, and ibises. Rodgers and Smith (1995) recommended setback distances for humans walking or in boats of 88 m for colonies and roosts.

Effectiveness of measures. The large increase in range and local abundance during 1950–1978 (see Demography and populations: population status, and Distribution, above) and the large number of colonies on dredge material islands suggests that the latter have benefited the species (Ogden 1978). Similarly, the large increases recorded on CBCs in Louisiana is highly correlated with increased acreage of crayfish aquaculture (Fleury and Sherry 1994), indicating that crayfish aquaculture may benefit this species. Protection of colonies in Florida apparently has not stemmed population declines there (see Demography and populations: population status, above).

APPEARANCE

MOLTS AND PLUMAGES

Although hatchling sequence, Juvenal, Definitive Basic, and Definitive Alternate plumages are well known for this species, the timing, extent, and feather replacement patterns of molts are poorly documented (Palmer 1962, McVaugh 1972).

Hatchlings. See also Breeding: young birds, above. Downy feathers cover much of body. Top of head covered with long hairlike plumes, army brown to fawn, mixed with shorter gray down on head; back has long, soft, dark gray down. Under neck, abdominal region, and femoral tract is coarse, scant, white down (McVaugh 1972).

Juvenal plumage. Prejuvenal molt sequence poorly known. Head, neck, and body completely covered with Juvenal feathers by 30 d of age, though molt into Juvenal plumage probably continues until after fledging.

Head, neck, and lesser wing-coverts deep chestnut or bright bay; narrow white stripe down front of throat; white underparts. Mantle olive, washed with chestnut. Upper surface of wings and tail dark drab to brownish olive (Palmer 1962), or deep neutral gray (Oberholser 1974). Lower back, rump, uppertail-coverts, chin, cheeks, upper throat, posterior underparts white. Breast streaked with chestnut or gray. Tail deep neutral gray.

Basic I plumage. Prebasic I molt occurs gradually during late fall and first winter. Extent of this molt unknown.

Dark feathers dull slaty on back and top of wings, much like Juvenal, possibly acquired through wear. Basic I plumage poorly known, especially degree of brown on neck.

Alternate I plumage. Prealternate I molt partial; limited to head, neck, and mantle. Occurs during first spring (9–12 mo).

Head and neck becoming much as in Definitive Alternate but plumes shorter on head, neck and back, and much more chestnut on upper wings and neck.

Definitive Basic plumage. Definitive Prebasic molt occurs Jul–Aug; extent of molt unknown, but assumed complete. Timing of plume replacement unknown. Definitive Basic Plumage worn from late summer into winter; retained in part until following late summer.

Most of head and neck, mantle, upper wing surface, and tail slaty to blackish; lesser-coverts dark neutral gray. Head plumes purplish; chin white; underside of neck white, with thin line of chestnut or rust continuing to upper breast. At dorsal base of neck, feathers becoming long, lanceolate slate and purple plumes, but shorter than in Definitive Alternate plumage. Lower back, rump, uppertail-coverts, breast, chin, and underwing-coverts white. Sexes similar.

Definitive Alternate plumage. Definitive Prealternate molt probably occurs Feb–Mar; partial molt, primarily of breeding plumes.

Definitive Alternate plumage worn late winter to Jul/Aug. Occipital plumes white; neck- and mantle-feathers mauve to violet; remainder of feathering much as in Definitive Basic. Rufous tinge more obvious on upper scapulars and back of neck; plumes of mantle longer, more filamentous, and wood brown; plumes generally longer and more deeply colored than in Definitive Basic.

BARE PARTS

Bill and gape. During courtship, bill-tip black, remaining two-thirds of bill turquoise cobalt; frequent rubbing of bill over oil gland makes soft-part colors more intense; turquoise cobalt less intense in females (Rodgers 1978a). During nonbreeding period, bill mottled yellow to brownish yellow, and sexes indistinguishable by plumage. Juveniles have mostly yellow bill, terminal third dull black. In hatchlings, light green.

Iris. In males, magenta during courtship; inner margin rose to scarlet in females (Oberholser 1974, Rodgers 1978a). During nonbreeding, inner margin on both sexes becoming pink; iris brown. In juveniles, iris yellowish white.

Bare skin on head. Bare skin on lores to eye-ring, cere, lower and upper margins of mandible. During nonbreeding season, mottled yellow to brownish yellow; during courtship, facial skin is cobalt.

Legs and feet. During breeding, legs fleshy maroon (Rodgers 1978a), orange (Oberholser 1974), or deep pink (Hancock and Kushlan 1984); grayish yellow during nonbreeding. Greenish yellow in juveniles; light green to partly yellow in hatchlings.

MEASUREMENTS

LINEAR

See Appendix 4. Males generally larger than females; South American birds tend to be smaller than others; Baja Californian birds tend to be larger than all other subspecies. For *E. t. ruficollis*: bill 88.9–103.8 mm for males, 87–98 for females. Wing-chord 247–268 mm in males, 204–264 in females. No measurements available for wingspan or total length.

MASS

See Appendix 4. Few measurements. Mean for males 415 g (*ruficollis*); range for South American females 213–344 g ($n = 8$). South American races may be smaller, but this is difficult to tell from mass data.

PRIORITIES FOR FUTURE RESEARCH

Almost nothing is known of the ecology and current status of the Tricolored Heron throughout its

Central and South American range. Although the species has been well documented in the past in the West Indies, most reports are now more than 30 years old and need to be updated. For management and conservation, the importance of estuarine productivity and function to reproduction and distribution seems critical. Though all aspects of the nesting period are quite well described and measured, almost nothing is known of the critical first year of life, including habitat preferences, development of hunting behavior, survival, and age at first breeding. Adult survival is so far unmeasured. Finally, the most recent comprehensive surveys for this species are now 20 years old, and little information exists on the current population status of this species in the United States.

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Appendix 2. Measures of reproductive success of the Tricolored Heron.

Location	Year(s)	Clutch size[1]	Nest success[2]		Young/ successful nest[5]	Loss of eggs	Hatching success[6]	Mortality of young (%)[7]	Source[8]
			Mayfield[3]	Traditional[4]					
Freshwater Everglades, FL	1986–1995	3.06–3.57	47.3–74.8	55.8–89.7	1.92–3.04		0.821–0.986		A, B
Estuarine Everglades, FL	1986–1989	1.9–3.03	5.2–66.7		1.79–2.42				C
	1990		78.5		1.6–2.2			5.5	D
Lake Okeechobee, FL	1989	3.00–3.30	53.6	64.9	2.10				E
Coastal N. Carolina	1984–1985	2.9–3.00							F
Coastal Louisiana	1977	2.53	56.7						G
	1973	3.00						22.5	H
Tampa Bay, FL	1976–1978			77.5					H
	1979–1980	2.79		63.7	1.78		0.947	25.4	M
	?				1.89				N
Interior central Florida	1960	4.10		64.2	2.80			25.4	I
	1983–1984	3.33–3.90	67.5–100		2.17–2.82	1.6–12.2		8.2–14.5	J
Coastal Florida (Atlantic)	1975	3.10		95.0	2.59	13.1	0.914	8.5	K
Coastal Florida (Gulf)	1975	3.00				23.4		28.2	R
Coastal Georgia	1955	3.13		47[7]	2.14	19	0.92	51	L
Coastal Texas	1970–1974	2.80		75.5					O
Coastal New Jersey	1975	3.60							P
Coastal Maryland	?				2.30				Q

[1] Average or mean of annual averages.

[2] Probability of raising at least 1 young to 14 d of age.

[3] Calculated using daily pro-rating of survival.

[4] Number of nests surviving/total nests.

[5] At 14 d of age.

[6] Number of eggs hatching/number of eggs surviving to hatch.

[7] To 14 d of age.

[8] Sources: A = Frederick and Collopy 1988; B = Frederick 1995; C = Frederick et al. 1993; D = Frederick et al. 1992; E = Smith 1994; F = Bjork 1986; G = Hammatt 1981; H = Rodgers 1978; I = Jenni 1969; J = Black et al. 1984; K = Maxwell and Kale 1977; L = Teal 1965; M = Rodgers 1986; N = Rodgers 1980; O = Telfair 1979; P = Burger 1978; Q = Robbins and Blom 1996; R = Girard and Taylor 1979.

Appendix 3. Geometric means or ranges of contaminant levels (ppm wet weight) found in the Tricolored Heron.

Location	Sample period	DDE	PCBs	Dieldrin	Mirex	Mercury	Lead	Tissue	Source[1]
Louisiana	1969–1970	12.311	28.51	0.63		0.09		eggs	A[2]
S. Carolina	1969–1971				0.563			muscle	B
Florida Everglades	1989 1990	0.07 0.01						brain brain	C C
S. Florida	1989–1990 1989–1990					0.72	1.4 1.4	liver liver	D C
Louisiana	1972–1973	0.42–1.2^{3}	0.31–1.40^{3}	0.0092–0.36^{3}	0.14			eggs	E
Alabama	1972–1973	0.98	1.3	0.016				eggs	E
Florida	1972–1973	0.15–1.3^{3}	0.12–2.00^{3}	0.014–0.17^{3}	0.026–0.27^{3}			eggs	E
Georgia	1972–1973	0.333–0.68^{3}	0.28–0.51^{3}	0.012	0.65			eggs	E
S. Carolina	1972–1973	0.36–0.54^{3}	0.17–0.50^{3}	0.042	0.014			eggs	E
N. Carolina	1972–1973	0.6	0.21					eggs	E
Maryland/Virginia	1972–1973	0.88	0.97	0.023	0.064			eggs	E
New Jersey	1972–1973	1.1	1.3	0.03				eggs	E

[1] Sources: A = Faber and Hickey 1973; B = Borthwick et al. 1973; C = Spalding et al. in press; D = Sunlof et al. 1994; E = Ohlendorf et al. 1979.
[2] Lipid weight basis.
[3] Range of location-specific geometric means.

Appendix 4. Linear measurements (mm) and mass (g) of adult Tricolored Herons. Data shown as mean (range; *n*).

Subspecies	*E. t. ruficollis*						*E. t. rufimentum*	*E. t. tricolor*	
Location Source[1]	E. United States A	Texas B	Baja California A	North America C	South America D	Location not given D	Trinidad D	Suriname E	Location not given D
Bill length									
Male	99 (95.2–102.3; 16)	97 (88.9–101.9)	104 (n = 9)		98 (93.8–103.8; 8)		92 (88–96; 3)		94 (84–104; 8)
Female	94 (90–97.4; 5)	93 (87.1–98.1)	99 (n = 6)		94 (87–98.4; 7)				87 (84–94; 9)
Wing-chord									
Male	259 (247–268)	253 (235–267)	269 (n = 9)		253 (248–259; 8)		229 (221–232; 3)^{2} 225–228 (n = 2)^{3}	222 (215–236; 8)	235 (216–260; 8)^{2}
Female		238 (230.1–246.1)	253 (n = 6) 250 (238–264; 5)		241 (237–249; 7)	209 (204–213; 3)	220 (217–240; 3)		216 (205–237; 9)
Mass									
Male				415 (n = 35)			295 (n = 1)^{3}	296 (242–344; 4)	
Female							334 (n = 5)^{3}	229 (213–240; 3)	

[1] Sources (except as noted): A = Palmer 1962; B = Oberholser 1974 ; C = Dunning 1993; D = Blake 1977; E = Haverschmidt and Mees 1994.
[2] Flattened wing.
[3] From ffrench 1991.

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