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Rallus longirostris

Clapper Rail

FRENCH:
Râle gris, Râle d'Eau, Pintade, Rateau
SPANISH:
Rascón picudo, Gallinuela de aqua salada, Pollo de mangle

A characteristic species of salt marshes and mangrove swamps, this large, gray to dull cinnamon buff rail breeds in tidal wetlands from the northern United States to Peru and Brazil. It varies greatly over its range, and many subspecies are recognized. Although its distribution on the West Coast of the United States is limited by habitat availability, most eastern populations are abundant, inhabiting coastal areas from Massachusetts through Central America and the Caribbean. One subspecies, the Yuma Clapper Rail (*R. l. yumanensis*), nests in freshwater marshes of the Southwest. Most races of the Clapper Rail are sedentary, but breeding populations from southern New England to the mid-Atlantic generally winter on the southern Atlantic Coast. Clapper Rails undergo erratic dispersal movements both before and after nesting, as indicated by radiotelemetry studies and by occasional inland or extralimital records.

Clapper Rails typically feed on crustaceans, but they take a variety of other foods if crustaceans are unavailable. Males average larger in size and mass than females, but the sexes are alike in plumage. Both sexes of Clapper Rail assist in incubation and brood-rearing, suggesting that the species is monogamous. Nest success is typically high in high-quality habitats; flooding and predation are the principal causes of nest failure. Pairs may renest up to 5 times after failure of

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

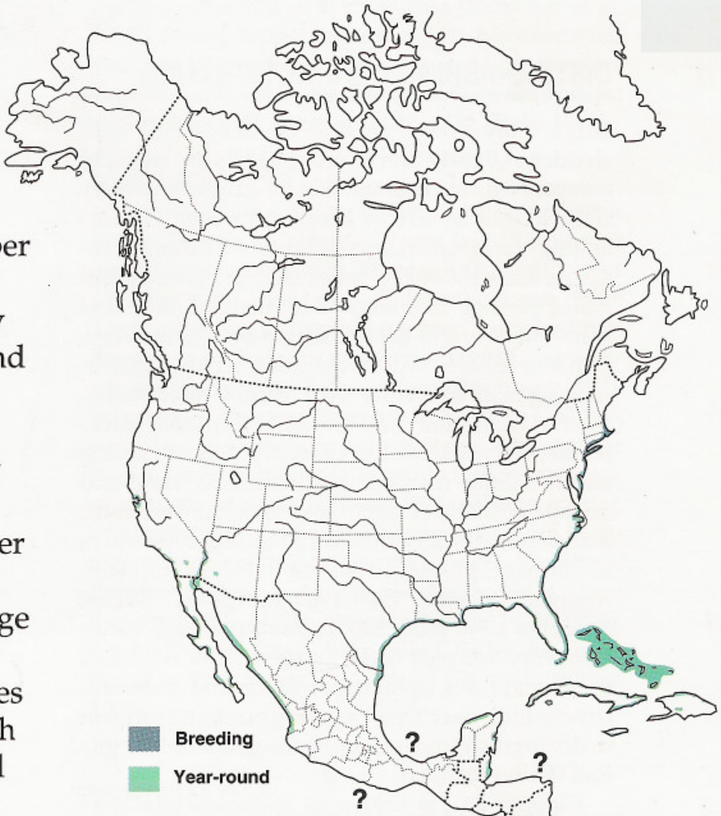

Figure 1.
Distribution of Clapper Rail in North America. This species also breeds in the eastern Caribbean and northern South America. See text for details.

Order GRUIFORMES Family RALLIDAE

previous nests, allowing populations to withstand significant losses of nests. The species is hunted locally in many Atlantic and Gulf Coast states, but little is known about adult and juvenile survival.

Clapper Rail populations in the eastern United States appear stable, although periodic storms may cause local populations to decline temporarily. The Mangrove Clapper Rail (*R. l. insularum*), California Clapper Rail (*R. l. obsoletus*), Light-footed Clapper Rail (*R. l. levipes*), and Yuma Clapper Rail (*R. l. yumanensis*) have limited habitats and consequently face threats from habitat loss, pollutants, urbanization, and exotic predators. The latter 3 subspecies are listed as Endangered by the U.S. Fish and Wildlife Service [USFWS].

Although the Clapper Rail is widely distributed and often locally abundant, little is known about many aspects of its biology because this species is difficult to observe in its dense habitats. Much study since 1980 has focused on endangered western subspecies. Its characteristic loud advertising and territorial vocalizations, often heard, give the species its name. Several other vocalizations are heard rarely, and their functions remain poorly known.

DISTINGUISHING CHARACTERISTICS

Large, gray brown to dull cinnamon rail with slender, slightly decurved bill. Body laterally compressed, and legs and toes long relative to body size. Second in size to King Rail (*Rallus elegans*) among North American rails; total adult length 32–41 cm, mass 160–400 g. Sexes alike in plumage, but males average 20% larger than females. Base and sides of bill bright flesh to bright orange in males, duller in females. Adult coloration highly variable, ranging from grayish brown to cinnamon brown. Ventral coloration uniform; darker on back. Back-feathers have blackish or dusky centers of varying width. Flanks marked with alternate white and dusky to dull black bars. Color morphs described; may pertain to individual variation, age differences in plumage, plumage wear, or hybridization with King Rail (Meanley 1969, 1985, Ripley 1977, WRE). Juveniles have paler bill. Juvenal plumage varies from very dull gray to dark gray, with nearly black flanks and sides; streaking on flanks and undertail-coverts indistinct. Downy young black and difficult to distinguish from young of King Rail or Virginia Rail (*Rallus limicola*).

Clapper Rail is similar in appearance to King Rail; often difficult to distinguish the 2 species. Generally, Clapper Rail is smaller than King Rail. In areas where both species occur (e.g., Louisiana coast, Chesapeake Bay), overall color of most Clapper Rails grayish or dull brown; King Rail more rufescent (Meanley 1985). Most Clapper Rails have grayish face and olive brown to olive russet lesser wing-coverts (bend of wing); edges of feathers of upperparts ashy gray, washed with olive or brownish, but never with lively buff tone (Oberholser 1937, Ridgway and Friedmann 1941, Stevenson and Anderson 1994). In contrast, King Rail usually has russet to chestnut lesser wing-coverts; lively buff edges of feathers of upperparts, washed with olive or brownish; and brownish face. Width of interorbital bridge narrower in Clapper Rail than in King Rail, presumably because of more developed salt gland in Clapper Rail (Olson 1997). Vocalizations of Clapper Rail are delivered more rapidly on average, although great overlap in this trait with King Rail makes it of little utility for distinguishing the 2 species (Meanley 1969). Most Clapper Rail subspecies (*yumanensis* is an exception) are restricted to salt marshes or mangrove swamps, while King Rail occurs in fresh water or brackish marshes. The large rail of inland Mexico, *R. elegans tenuirostris*, has the rufous coloration and is considered a subspecies of King Rail (Warner and Dickerman 1959, Am. Ornithol. Union 1983, Howell and Webb 1995), although sometimes considered most similar to Clapper Rail (Oberholser 1937, Williams 1989).

Hybridizes readily with King Rail in habitats of intermediate salinity on East and Gulf Coasts of U.S. (Meanley 1985). Hybrids may be intermediate in coloration and size, but individual birds from sites where hybridization occurs may show wide variation from typical Clapper Rail plumage to typical King Rail plumage (Meanley 1969).

Virginia Rail noticeably smaller, with grayer cheeks and brighter bill color. Similar in plumage to Wetmore's Rail (*Rallus wetmorei*) which overlaps in range in Venezuelan mangrove swamps, but distinguished by larger size, bolder plumage coloration, and longer 10th primary (Ripley 1977).

DISTRIBUTION

THE AMERICAS

Breeding range. Figure 1. Saline wetlands on East Coast of U.S. from Massachusetts (Veit and Peterson 1993) and Rhode Island (Enser 1992) and possibly New Hampshire (Foss 1994) south to Florida Keys (Am. Ornithol. Union 1983); on Gulf Coast from Cape Sable, FL, west to Tamaulipas, Mexico (16 km south of mouth of Rio Grande; Banks 1974). Nests inland to extent of saline wetlands (e.g., >5,700 ppm salinity; Ripley 1977) in areas such as Delaware Bay (north to Pea Patch I., New Castle Co., DE; Hess et al. in press) and Chesapeake Bay (on western shore, north to Sandy

Point State Park, Anne Arundel Co., MD; on eastern shore, north to se. Talbot Co., MD; Robbins and Blom 1996).

Range in Mexico, Central America, and South America poorly known. Recorded on Yucatán Peninsula from Quintana Roo (Chinchorro Reef), Rio Lagartos, and Belize (Ycacos Lagoon and Half Moon Cay; Am. Ornithol. Union 1983, Howell and Webb 1995, CJC). One record from Bocas del Toro, Panama (Ridgely and Gwynne 1989). Recorded from Caribbean coast of South America in La Guajira (Ríohacha, Bahía Portete, Pto. López) and coastal Nariño, Colombia (Hilty and Brown 1986). Also resident from nw. Colombia coast to Tumbes in nw. Peru (Meyer de Schauensee 1966, Hilty and Brown 1986). Occurs from Falcón and Carabobo, Venezuela, along coast of the Guianas, and casually to Santa Catarina in se. Brazil (Meyer de Schauensee 1966, Am. Ornithol. Union 1983), as well as on Trinidad (Bond 1971, Ripley 1977).

Resident in Caribbean on all main islands of Bahamas (Brudenell-Bruce 1975), Cuba and Isle of Pines (common; Garrido and Kirkconnell 1993), Jamaica (uncommon; Downer and Sutton 1990), Dominican Republic (locally on north coast and along Lake Enriquillo in interior; Dod 1981, Puerto Rico (Raffaele 1989), U.S. Virgin Is. (less numerous than on Puerto Rico; Raffaelle 1989, Evans 1990), St. Croix, Antigua, and Guadeloupe (Evans 1990).

Occurs in San Francisco and San Pablo Bays, CA (and formerly in Monterey and Tomales bays); from Santa Barbara Co. to San Diego Co., CA; locally along Pacific Coast of Baja California south to Magdalena Bay; and on s. Gulf Coast of Baja California Sur (La Paz, San José, and Espíritu Santo Is.; Am. Ornithol. Union 1983, Shuford 1993, Massey and Palacios 1994, Small 1994, Howell and Webb 1995). Resident on south end of Salton Sea, CA; lower Colorado River from Laughlin Bay, NV, to Colorado River delta in Mexico; lower Gila River, AZ; and occasionally east to Phoenix, AZ, area (Todd 1986, Rosenberg et al. 1991). Occurs on West Coast of mainland Mexico from Bahía Kino, Sonora, south to San Blas, Nayarit (Tomlinson and Todd 1973, Ripley 1977, Am. Ornithol. Union 1983, Howell and Webb 1995).

Winter range. Populations in s. and w. U.S. and farther south are resident; northeastern populations winter in southern part of breeding range (Meanley 1985). Small numbers remain as far north as Connecticut during mild winters (Root 1988, Bevier 1994). Uncommon (but regular) in New Jersey and Delaware in winter (Sibley 1993, Hess et al. in press). Detailed delineation of winter range difficult because Clapper Rails are difficult to observe and vocalization rates decline substantially in winter (see Sounds: vocalizations, below). Highest densities in winter occur from Camp Lejeune, NC, to Titusville, FL, including almost entire length of S. Carolina coast (Root 1988). Also recorded in winter in Bahamas (Cory 1888).

OUTSIDE THE AMERICAS

Not recorded.

HISTORICAL CHANGES

Arguably rare historically north of New York, but began to increase in Connecticut in 1930s and 1940s (Saunders 1950, Bevier 1994). No nesting noted until 1953 in Rhode Island (Enser 1992) and until 1955 in Massachusetts (Veit and Petersen 1993). Local loss of breeding populations has occurred in e. U.S. because of habitat loss and degradation (Meanley 1985).

Distribution of subspecies in w. U.S. much reduced since 1900 (Gill 1979, Zembal and Massey 1981, Shuford 1993, Fleischer et al. 1995). Habitat in San Francisco Bay, CA, has been reduced by 80–90%, and Clapper Rails have disappeared from Morro, Tomales, and Monterey bays. Range of Light-footed Clapper Rail (*R. l. levipes*) has been similarly reduced in s. California (Fleischer et al. 1995). Yuma Clapper Rail believed to have occurred mostly in Colorado River delta in Mexico before dam-building on lower Colorado River; now most may nest in U.S. (Ohmart et al. 1975, Todd 1986).

FOSSIL HISTORY

Fossils of rails in the *Rallus elegans-longirostris* group have been reported from late Pliocene or early Pleistocene (early Blancan); (3.5 million yr B.P.) Hagerman local fauna of Idaho (Feduccia 1968). Three other fossil species have been described that are closely related to or synonymous with *R. elegans-longirostris* complex: *Rallus philippsi* (Wetmore 1957), from upper Pliocene deposits in Mohave Co., AZ, described from right tarsometatarsus, was smaller than *R. longirostris*, but falls within lower size range of modern material (Olson 1977). *Rallus natator*, originally described as *Epirallus natator* from Pleistocene deposits in San Josecito Cavern, Aramberri Province, Nuevo León, Mexico (Miller 1942), was a large member of the complex (Olson 1973, 1974). An additional large, long-billed *Rallus* has been found in Pleistocene deposits of Bermuda (Olson 1973).

SYSTEMATICS

GEOGRAPHIC VARIATION

Individuals from northernmost and westernmost populations are larger in all measurements except culmen length, which is shortest in West Coast and southernmost forms. Bill heaviest in South American birds and most slender in birds of e. North America and the Caribbean (Olson 1997). Overall body coloration of individuals from East Coast of U.S. and Caribbean populations gray to dull gray brown or buff; northern subspecies grayer (Oberholser 1937, Ripley 1977). Birds from West Coast of U.S. and freshwater habitats buff to rich cinnamon. Individuals darker and more richly colored from north to south along coasts of e. U.S., w. Mexico, and Baja California (Ripley 1977). Most populations from East Coast of Mexico and Central America and n. Caribbean paler than mainland coastal forms (Ripley 1977). Different color morphs may complicate plumage description of subspecies. Populations from Arizona south to Nayarit, Mexico, show cline of decreasing wing length and slightly darker dorsal coloration (Ripley 1977). See Appearance, and Measurements: linear, below.

SUBSPECIES

For the King and Clapper rail as a whole (*elegans-longirostris* complex), between 20 (Peters 1934) and 27 (Ridgway and Friedmann 1941) subspecies are recognized. This account includes the subspecies in Ripley (1977), excluding the 3 subspecies currently included under King Rail (*elegans*, *ramsdeni* of inland Cuba, and *tenuirostris* of central Mexico).

Subspecies are distinguished mainly by differences in coloration of underparts and upperparts, wing length, culmen length, and overall body size. May be considerable overlap in plumage color and measurements where distributions of subspecies overlap (Heard 1983). Three groups of subspecies distinguished: *obsoletus* group of West Coast of North America, *crepitans* group of e. North America, Caribbean, and Yucatán; and *longirostris* group of South America. All resident, except where noted.

***obsoletus* group**. Four subspecies in *obsoletus* group distinguished largely by buff to cinnamon brown underparts and more richly colored plumage. Cheeks generally brownish. Subspecies in this group have also been considered separate species (Bent 1926) or subspecies of *elegans* (Peters 1934, Hellmayr and Conover 1942, Olson 1997).

R. l. obsoletus Ridgway, 1874. San Francisco Bay, CA, area (and formerly in Tomales and Monterey Bays). Largest subspecies; throat, breast, and upper abdomen ochraceous buff; flanks dark sepia to black, contrasting with white barring; cheeks brownish.

R. l. levipes Bangs, 1899. Santa Barbara, CA, to San Quintín Bay, Baja California Sur. Averages slightly smaller than *obsoletus*; breast deep cinnamon rufous; flanks and back darker in comparison to *obsoletus*.

R. l. yumanensis Dickey, 1923. Lower Colorado River (Arizona and California), Colorado River delta (Sonora and Baja California Norte), and West Coast of Mexico from Punta Sargento, Sonora, to San Blas, Nayarit. Distinguished by paler, duller underparts and grayish edging of dorsal feathers. Cheeks and postoculars bluish or ashy gray. Ripley (1977) considered *rhizophorae* Dickey, 1930 (Punta Sargento, Sonora, to central Sinaloa) and *nayaritensis* McLellan, 1927 (central Sinaloa to San Blas, Nayarit) as clinal variations of *yumanensis*. Additional specimens might confirm the validity of these subspecies (but see Banks and Tomlinson 1974).

R. l. beldingi Ridgway, 1882. Mangrove swamps from Margarita Bay on Pacific Coast to Espíritu Santo I. on Gulf Coast of Baja California Sur (includes *magdalenae* van Rossem, 1947).

***crepitans* group**. Twelve subspecies in *crepitans* group have grayish to dull cinnamon underparts and long, slender bill. Feathers of upperparts edged in various shades of gray, and cheeks grayish.

R. l. crepitans Gmelin, 1789. Breeds from s. New England to se. North Carolina; winters from breeding range to ne. Florida. Migratory, large, grayish subspecies. Underparts pale cinnamon buff; culmen long. Winters from breeding range to ne. Florida.

R. l. waynei Brewster, 1899. Se. North Carolina, where it intergrades with *crepitans*, to Volusia and Brevard Cos. in ne. Florida, where it intergrades with *scotti* in Indian River, Saint Lucie, and Martin Cos. (Stevenson and Anderson 1994). Resembles *crepitans*, but is slightly smaller and darker on upperparts. Underparts more cinnamomeous, with an ashy band across upper breast.

R. l. scottii Sennett, 1888. Jupiter Inlet, Martin Co., FL; around southern tip of Florida to Pensacola, Escambia Co., FL, intergrading with *saturatus* (see below) in w. Florida Panhandle. It has the darkest upperparts of all subspecies: blackish brown, shaded with grayish olive. Breast cinnamon, shaded with olive brown.

R. l. insularum Brooks, 1920. Florida Keys from Key Largo to Boca Grande and, presumably, Marquesas Keys (Owre 1978). Similar to *waynei* (see above), but smaller; culmen shorter; feathers of upperparts more broadly edged with grayish. Overall coloration relatively pale.

R. l. saturatus, Ridgway 1880. Gulf Coast from Florida Panhandle to Tamaulipas, Mexico. More brownish than other subspecies of eastern U.S. Closely resembles King Rail, except duller and less rufescent on underparts; grayish edging on feathers of upperparts.

This group also includes *pallidus* Nelson, 1905 (Río Lagartos, Yucatan); *grossi* Paynter, 1950 (islands on Chinchorro Reef, Quintana Roo, Mexico); *belizensis* Oberholser, 1937 (Ycacos Lagoon, Belize, and possibly Half Moon Cay, Belize); *coryi* Anonymous = Maynard, 1887 (Bahama Is.); *leucophaeus* Todd, 1913 (Isle of Pines, Cuba); *caribaeus* Ridgway, 1880 (n. Antilles, islands of Cuba, Hispaniola, Puerto Rico, to Antigua and Guadeloupe—includes *cubanus* Chapman, 1892; *vafer* Wetmore, 1928; *limnetis* Oberholser, 1937; *manglecola* Danforth, 1914; Ripley 1977); and *pelodramus* Oberholser, 1937 (Trinidad).

***longirostris* group**. Characterized by relatively small body size and short, heavy bill. Consists of 5 subspecies from South America: *margaritae* Zimmer and Phelps, 1944 (Margarita I., Venezuela); *phelpsi* Wetmore, 1941 (northern coast of Colombia and Venezuela); *longirostris* Boddaert, 1789 (coasts of Guyana, Suriname, and French Guiana); *crassirostris* Lawrence, 1871 (coastal salt marshes of e. Brazil); and *cypereti* Taczanowsky, 1877 (Ecuador and nw. Peru).

Very little divergence in mitochondrial DNA among subspecies *yumanensis*, *levipes*, *obsoletus*, *crepitans*, and *saturatus* (Fleischer et al. 1995). Subspecies *yumanensis* and *levipes* probably had common ancestor within last 50,000 yr, but minisatellite and Randomly Amplified Polymorphic (RAPD) DNA differences suggest there has been little genetic interchange recently.

RELATED SPECIES

Hybridizes with King Rail in brackish marshes where geographic ranges overlap (Meanley and Wetherbee 1962, Meanley 1969, Bledsoe 1988). Hybrids show variety of plumage intergradations (Meanley 1969), and may partly explain "color phases" of Clapper Rails. Accordingly, many taxonomists consider Clapper Rail and King Rail conspecific (Ripley 1977). Mitochrondrial DNA studies of Clapper and King rails are inconclusive regarding their specific status (Avise and Zink 1988). Wetmore's Rail similar in appearance and habitat, but considered separate species because of geographical overlap with Clapper Rail in n. South America (Ripley 1977). Clapper, King, and Wetmore's rails presently are construed as a superspecies group (Sibley and Monroe 1991).

MIGRATION

NATURE OF MIGRATION IN THIS THE SPECIES

Most populations considered nonmigratory (Meanley 1985, Eddleman 1989). Individuals from s. New England to central N. Carolina are largely migratory, although some remain on breeding areas in winter (Stewart 1954, Meanley 1985, Sibley 1993). Individuals breeding on s. Atlantic Coast of U.S. may make short-distance winter migration, as suggested by limited banding data (Hon et al. 1977). Elsewhere unclear; some individuals of most subspecies undertake erratic postbreeding movements (Crawford et al. 1983; see Demography and populations: range, below). Claim of migration for *yumanensis* along lower Colorado River and at Salton Sea, CA, based on indirect evidence (Tomlinson and Todd 1973, Smith 1974, Bennett and Ohmart 1978, Am. Ornithol. Union 1983), but could not be confirmed by radiotelemetry studies (Eddleman 1989, Conway 1990).

TIMING AND ROUTES OF MIGRATION

Timing of spring migration poorly known. Individuals begin calling in mid-to late Mar in New Jersey and Virginia (Kozicky and Schmidt 1949, MacNamara and Udell 1970, Meanley 1985, Sibley 1993, see Fig. 4). Continue to arrive through early Apr (Meanley 1985). No information on spring routes.

Fall migration begins late Aug and early Sep in Virginia and New Jersey (Stewart 1954, Mangold 1974, Sibley 1993). Timing variable depending on weather; favorable conditions include passage of cold front and a tailwind. Peak varies from year to year: Sep–Oct in New Jersey (Kozicky and Schmidt 1949), late Sep–early Oct in N. Carolina (Adams and Quay 1958). Arrival on wintering areas begins mid-Sep in S. Carolina (Stewart 1951). Fall migration on Atlantic Coast of U.S. extends through Oct and Nov (Meanley 1985, Taylor and Kershner 1986).

Route of migration probably along coast, but individuals may appear up to 330 km inland during autumn (Murray 1929, Meanley 1985). Individuals migrating along eastern shore of Delmarva Peninsula cross from Cape Charles, 30 km across mouth of Chesapeake Bay, then to Back Bay, VA, and to N. Carolina border (Meanley 1985). Individuals that breed in New Jersey and Maryland have been documented in winter as far south as central Florida and west to Florida Panhandle (Stewart 1951, Crawford et al. 1983). Specimens identified as *crepitans* (breeding in N. Carolina and north) collected from Florida at Ft. Myers, Tarpon Springs, Turkey Point (Franklin Co.), Shell Point (Wakulla Co.), and WDBO TV tower (Orange Co.; Crawford et al. 1983). Birds from s. Atlantic Coast (*waynei*) possibly partial migrants, but specimen records from Florida in "winter" are mostly from periods of postbreeding and prebreeding dispersal, and cited banding records are likely *crepitans* individuals from breeding areas farther north (Crawford et al. 1983, T. Hon pers. comm.).

Extralimital records may represent migrants or dispersing juveniles and adults. Such accidental records are from New Brunswick, Nova Scotia, Prince Edward I. (Godfrey 1986), Maine (Forbush

1925, Packard 1958), New Hampshire (Forbush 1925), and Bermuda (Spittal Pond; Amos 1991). Occasional inland records of East Coast vagrants include w. Maryland (Martin 1962); Lexington, VA; near Stapleton, NE; Raleigh, NC (McCullough 1944); central New York, Vermont, W. Virginia (Forbush 1925, Am. Ornithol. Union 1983); Pennsylvania (Philadelphia, Lancaster Co., and Latrobe, Westmoreland Co.; Russell 1994); and Lake Nasworthy, Tom Green Co., TX (Burt et al. 1987). Wanders casually to Tucson, AZ (WRE); Farallon Is., CA; n. California (Humboldt Bay); and s. Baja California (Todos Santos; Am. Ornithol. Union 1983). Regularly reported at inland sites near coastal California (Orr 1939, Zembal et al. 1985).

MIGRATORY BEHAVIOR

Poorly known. Migrates at night and sometimes strikes objects such as TV towers, wires, or tall buildings (Crawford et al. 1983, Meanley 1985). Altitude unknown, but presumed to be low, as with other rails (Forbush 1925, Meanley 1985), possibly because flight is energetically expensive for rails and flight may be less energetically costly at low altitudes (Klaassen 1996). Speed of migration poorly known; estimated at 480 km/3–4 d in N. Carolina (Adams and Quay 1958). One immature banded 26 Aug 1950 was recovered in ne. Florida 24 Sep 1950 (Stewart 1954). Individuals land in marshes during the day, but usually move on within 1 d. Sometimes grounded and disoriented during inclement weather, especially fog (Adams and Quay 1958).

CONTROL AND PHYSIOLOGY

No information.

HABITAT

BREEDING RANGE

Principal habitats are low portions of coastal wetlands dominated by cordgrass (*Spartina* sp.), pickleweed (*Salicornia* spp.), or mangroves. These are wetlands with salinity of >7,100 ppm at low tide, and >5,600 ppm at high tide (Meanley 1985). See Breeding: nest site, below. Major coastal habitat types include marshes dominated by Pacific cordgrass (*Spartina foliosa*; Foin and Benchley-Jackson 1991), Pacific cordgrass–pickleweed-mix (Harvey 1988), salt marsh cordgrass (*Spartina alterniflora*), needlerush (*Juncus roemerianus*), salt meadow cordgrass (*Spartina patens*), red mangrove (*Rhizophora* spp.), black mangrove (*Avicennia* spp.), and white mangrove (*Laguncularia* spp.; Hon et al. 1977, Owre 1978, Holliman 1981, Meanley 1985).

Habitat on East Coast of U.S. ideally has emergents and scattered shrubs bordering ditches or tidal creeks within 15 m of open water, and at least 25% of total wetland area within 15 m of a shoreline (Lewis and Garrison 1983). Preferred habitats in New Jersey are natural and ditched short-form salt marsh cordgrass (most preferred), tall-form salt marsh cordgrass, and salt meadow cordgrass (least preferred; Mangold 1974). Very few individuals recorded in salt meadow cordgrass.

Nesting habitat in San Francisco Bay, CA, characterized by presence of tidal sloughs; abundant invertebrate populations; pickleweed coverage with extensive cordgrass coverage in lower zone; and tall pickleweed, gum plant (*Grindelia cuneifolia*), and wrack in upper zone (Harvey 1988). Nesting habitat in s. California includes tall, dense Pacific cordgrass in the low littoral zone, wrack deposits in the low marsh zone, and hummocks of high marsh within the low marsh zone (Massey et al. 1984). Fringing areas of high marsh serve as refugia during high tides (Zembal et al. 1989, Shuford 1993). Although used infrequently, this habitat may be extremely important at reducing mortality during high tides.

In Arizona, found in variety of marsh types dominated by emergent plants, including southern cattail (*Typha domingensis*), bullwhip bulrush (*Juncus californicus*), three-square bulrush (*Scirpus olneyi*), and sedges (Cyperaceae; Todd 1986). Presence of emergent cover, not plant species or marsh area, is important trait of habitat in Arizona (Anderson and Ohmart 1985). Arizona habitat includes sites with high coverage by water, low stem density, and moderate water depth used for foraging during nesting season; sites with shallower water near shorelines are used for nesting (Conway et al. 1993). Ideal habitat has mosaic of emergent plant stands of different ages interspersed with shallow pools of open water.

SPRING AND FALL MIGRATION

Little information. Presumably uses salt and brackish marshes similar to breeding areas. Sometimes observed in freshwater marshes or unsuitable habitats such as rock jetties during daytime stopovers, but moves onward the next night (Glick 1963, Meanley 1985). May move overland, as indicated by the fact that birds collide with stationary objects.

WINTER RANGE

Winter habitat similar to breeding habitat. Abundance of populations on East Coast of U.S. may vary greatly in winter, depending on tide, wind, amount of ice, and temperature (Meanley 1985). Wintering birds in N. Carolina move from low marsh to mixed salt marsh cordgrass, needlerush, salt meadow cordgrass, and shrub-dominated

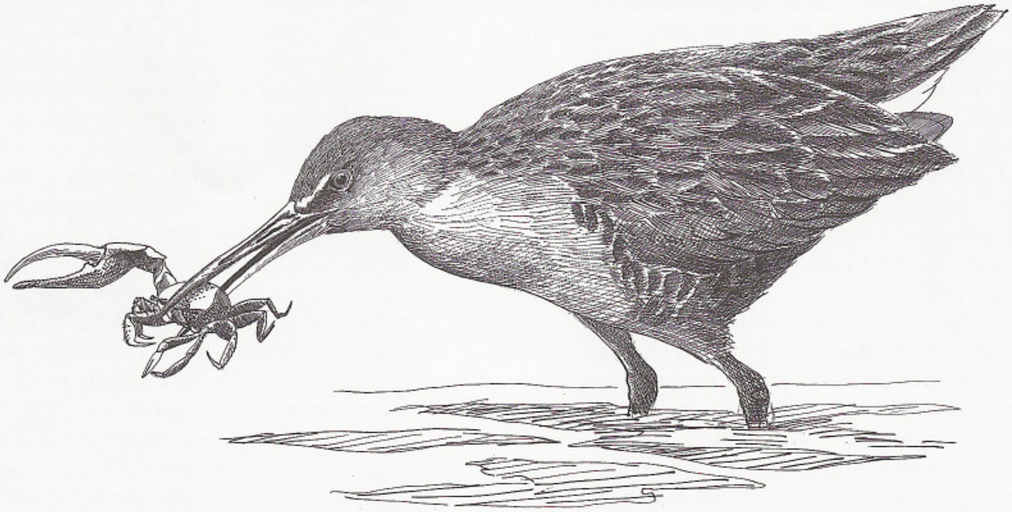

Figure 2. Clapper Rails on the East Coast feed primarily on fiddler crabs. Drawing by T. Henneberg.

habitats (Adams and Quay 1958). Often occurs near drifts of logs and wrack during windy weather (Simmons 1914). In winter, Clapper Rails in freshwater marshes in Arizona exhibit narrower habitat breadth (Anderson and Ohmart 1985, Conway et al. 1993). Habitat used in early winter (Nov–Dec) in Arizona has lower emergent stem density, basal coverage, and ground coverage; less distance to water; greater overhead coverage by vegetation, distance to adjacent uplands, distance to vegetative edges, water depth, and water coverage; and taller emergent plants than do randomly selected sites (Eddleman 1989, Conway et al. 1993).

FOOD HABITS

FEEDING

Main foods taken. Crustaceans if available (Heard 1983, Meanley 1985). Highly opportunistic, eating small crabs, slugs, minnows, aquatic insects, grasshoppers, small vertebrates, seeds (Simmons 1914), amphipods (Test and Test 1942), other bird's eggs (Segre et al. 1968), and occasionally immobilized small birds (Spendelow and Spendelow 1980, Jorgensen and Ferguson 1982). Freshwater populations on lower Colorado River eat mostly crayfish (*Procambarus clarki* and *Orconectes* sp.), clams (*Corbicula* sp.), isopods, water beetles (Hydrophilidae) and small fish; saltwater populations in mangroves on West Coast of Sonora and Nayarit, Mexico, eat crabs, marine snails, and insects (Ohmart and Tomlinson 1977). On East Coast of U.S. and in n. South America, mostly fiddler crabs (*Uca* or *Sesarma* spp.; Fig. 2; Heard 1983, Hilty and Brown 1986). Consumption of seeds and vegetation increases in winter (Martin et al. 1951).

Microhabitat for foraging. Forages within emergent vegetation or mangroves, or along edges between marsh and mudflats (Clark and Lewis 1983, Meanley 1985, Zembal and Fancher 1988). Foraging habitat on East and Gulf Coasts determined mainly by abundance of emergent vegetation or mangroves, secondarily by presence of fiddler crabs (Clark and Lewis 1983). Regularly ventures onto mudflats and algal mats with gently sloping shorelines at low tide or after wind-driven low tides in the evening (Simmons 1914, Lewis and Garrison 1983, Zembal and Fancher 1988). Forages for crabs by searching along central drains of tidal creeks at low tide (Zembal and Fancher 1988). Feeds during high tides on prey on grass stalks (Meanley 1985). In Arizona, forages at sites with high mean coverage by water, low stem density relative to other sites in marsh, and moderate water depth (about 7.5 cm)—traits of newly formed marsh areas (Eddleman 1989, Conway et al. 1993).

Food capture and consumption. Sight feeder, moving erratically in response to cues; does not often probe deep in substrate (Simmons 1914, Williams 1929, Meanley 1985, Zembal and Fancher 1988). Rails have highly developed olfactory process with many mucous cells, and have large olfactory bulb in the brain, indicating that they may be able to use smell to assist in locating prey; deserves further study (Bang and Wenzel 1985).

Surface-gleaning and shallow probing account for 90% of time spent foraging in s. California (Zembal and Fancher 1988). Searching for crabs ("crabbing"), foraging on mudflats, fishing, and scavenging account for the remaining 10% of time. Often average 675 gleans/h; sometimes up to 2,000 gleans and probes/h (Zembal and Fancher 1988).

Obtains prey after 18.2–52.9% of attempts. Success rate lowest for crabbing or casual foraging, and highest at prey concentrations. Average 250 morsels of tiny prey/h during foraging bouts (Zembal and Fancher 1988). Moves 0.2–10 m between foraging bouts; travels the most during crabbing. Crabbing bouts last 1–3.5 h (Zembal and Fancher 1988). At high tide in Virginia, may probe into fiddler crab (*Uca* spp.) burrows and moves rapidly from burrow to burrow; forages slowly and deliberately at low tide (Meanley 1985).

Swallows smaller crabs and other crustaceans whole; dismembers medium-sized crabs by shaking them, then swallows the parts whole; dismembers larger crabs and swallows parts whole, and breaks open body and consumes only flesh (Bent 1926, Meanley 1985, Zembal and Fancher 1988, WRE). Sometimes rinses clams in water to remove mud, then swallows them whole or breaks them and eats the contents (Williams 1929). Remains of prey items often found on constructed platforms in marsh or on muskrat (*Ondatra zibethicus*) houses throughout range, suggesting that some prey may be transported and eaten at central location (Meanley 1985, WRE).

Major foods in Arizona peak in abundance during time of hatching and brood-rearing (Conway 1990). Lowest food abundance in winter, and increased movements by rails at that time of year may be a response to this decline.

DIET

Major foods items. Birds from e. U.S. eat mainly fiddler crabs and other small crabs; shrimp (especially *Orchestia grillus*), amphipods, insects, snails, clams, polychaete worms (*Nereis succinea*), fish; and cordgrass, bulrush (*Scirpus* spp.), sedges, smartweed (*Polygonum* spp.), oak (*Quercus* spp.), and soybean (*Glycene max*) seeds (Martin et al. 1951, Heard 1983). Principal prey of West Coast subspecies includes crabs (*Pachygrapsus crassipes* and *Hemigrapsus oregonensis*), ribbed horse mussels (*Modiolus demissus*), spiders (Lycosidae), little macoma clams (*Macoma balthica*), California horn snails (*Certhidea californica*), salt marsh snails (*Melampus olivaceus*), crayfish (*Procambarus* sp.), beetles, other insects, isopods, pickleweed and Pacific cordgrass vegetation, seeds, and small fish (Moffitt 1941, Zembal and Fancher 1988). Diet of 278 Clapper Rails collected year-round on East Coast consisted of 96% animal prey and 4% plant items (Martin et al. 1951). Plant material is not part of summer diet, and makes up 3% of fall diet, 11% of winter diet, and 1% of spring diet (Martin et al. 1951).

Quantitative analysis. Food of 124 Clapper Rails collected in summer from range of all 5 eastern subspecies was mainly fiddler crabs (*Uca pugnax* found in 29.8% of the birds; *U. largisignalis*, 16.9%; *U. pugilator*, 4.8%; *U. rapax*, 7.2%; *U. panacea*, 8.1%; *U. speciosa*, 1.6%; *Sesarma reticulatum*, 17.7%; *S. cinereum*, 3.2%); species eaten depends on location of collection and geographic range of crab (Heard 1983). Other crabs eaten were *Aratus pisonii* (3.2% occurrence), *Eurytium limosum* (4.8%), *Panopeus herbstii* (0.7%), and *Rhithropanopeus harrisii* (0.7%). Remainder of diet included shrimp (*Palaemonetes pugio*, 0.7%); amphipods (*Orchestia grillus*, 9.7%); insects (*Orchelimum fidicinum*, 5.6%); ants (Formicidae, 0.6%; and unidentified, 5.6%); Gulf periwinkle (*Littorina irrorata*, 10.5%); southern periwinkle (*L. angulifera*, 0.6%); salt-marsh snails (*Melampus bidentatus*, 6.5%); coffee bean snail (*M. coffeus*, 3.2%); ribbed mussel (*Geukensia demissa*, 0.7%); and stout tagelus (*Tagelus plebeius*, 0.7%); clam worms (*Nereis succinea*, 7.3%); pinfish (*Lagodon rhomboides*, 0.7%); and acorns (0.7%). In Louisiana, 15 nesting birds ate fiddler crabs (*Uca* spp.; 100% occurrence, 95% volume), salt marsh snails (30%, 4%), fish (12%, <1%), and insects (6%, <1%; Roth 1972).

In S. Carolina, 284 birds collected in autumn ate fiddler crabs (*Sesarma cinereum*, 58% occurrence, 33% volume; *S. reticulatum*, 37%, 15%; *Sesarma* sp., 17%, 6%; *Uca* spp.; 45%, 14%); other crabs (18, 6); periwinkle snails (37%, 14%); moth larvae (Noctuidae; 12%, 6%); and other insects (3% volume; Oney 1951). Other small invertebrates, killifish (*Fundulus* sp.), and cordgrass made up trace of diet. Clapper Rails collected in fall in Louisiana had similar diet dominated by crabs, snails, and plant debris (Bateman 1965). One hundred birds collected at Wallops I., VA, in autumn ate crabs (50% of volume); grasshoppers and allies (Orthoptera; 35%); spiders (5%); and miscellaneous insects, periwinkle snails, and plant material; while 80 birds collected at Gargathy Bay, VA, ate grasshoppers (60% of volume), fiddler crabs (20%), snails (10%), and other insects (10%; Meanley 1985).

In Louisiana, winter diet is more varied than summer and fall diet; 103 birds ate crayfish (*Procambarus* sp., 20% volume), fiddler crabs (*Uca* spp., 5%; *Sesarma* spp., 2%), insects 29%), snails (*Polygyra* sp., 6%; others, 3%), clams (*Ragina* sp., 4%), rodents (3%), skink (*Eumeces* sp., 2%), frogs (*Pseudacris* sp., 1%; others, 2%), and plant material (cowpea [*Vigna repens*], 9%; other, 2%; Roth 1972).

In San Francisco Bay, CA, Clapper Rails collected in Feb ate ribbed horse mussels (56.5% of volume); spiders (Lycosidae, 15.0%); seeds and hulls of cordgrass (14.6%); little macoma clam (7.6%); mud crabs (3.2%); worn-out nassa (*Ilyanassa obsoletus*; 2.0%); and insects, clam worms (*Nereis* spp.), and carrion (total 1.1%; Moffitt 1941).

Considerable variation in diet of Yuma Clapper Rail during breeding season, depending on location

(Ohmart and Tomlinson 1977). Above Imperial Dam on Colorado River in sw. Arizona and se. California, diet of 9 birds was crayfish (94.7% volume), weevils (Curculionidae, 2.8%), ground beetles (Carabidae, 0.1%), other beetles (0.6%), damselfly nymphs (Odonata, 0.1%), grasshoppers (0.1%), other insects (0.8%), insect eggs (0.1%), spiders (0.6%), clams (*Corbicula* sp., 0.1%), mammal bones (0.1%), and seeds (0.1%). At mouth of Gila River in Arizona, 2 birds ate isopods (48.5% volume), clams (50.0%), and insects (1.5%). In Colorado River delta of nw. Sonora, Mexico, 4 birds ate water beetles (56.6% volume), fish (31.8%), leeches (Hirudinea, 3.8%), seeds (2.8%), twigs (2.5%), damselfly nymphs (2.0%), dragonfly nymphs (0.5%), and shrimp (Palaemonidae, 0.2%). Diet of 16 birds collected in coastal Sonora and area of San Blas, Nayarit, Mexico, was similar to that of other subspecies in mangrove wetlands (Ohmart and Tomlinson 1977).

FOOD SELECTION AND STORAGE

Opportunistic and omnivorous; food selection reflects mainly salinity of marsh type and geographic location (Heard 1983).

NUTRITION AND ENERGETICS

No information.

METABOLISM AND TEMPERATURE REGULATION

No information.

DRINKING, PELLET-CASTING, AND DEFECATION

Owing to its salt glands, capable of drinking either fresh water or seawater (Conway et al. 1988, Hammons et al. 1988). Total body water (mean 68.3% ± 2.8 SD, *n* = 16) and total body mass not affected by acclimation to seawater (Hammons et al. 1988). Mean daily water flux of freshwater-adapted birds (290 ml/kg ± 70 SD, *n* = 16) reduced after acclimation to salt water (255 ml/kg ± 20 SD, *n* = 12). Average daily water flux 71 ml/d for a 280-g individual (*n* = 8; Hammons et al. 1988). Solute concentration of salt gland secretion of birds acclimated to salt water was similar, but flow rate of secretions was only 10% that of marine gulls (Conway et al. 1988). May ingest ice during prolonged cold weather (Meanley 1969).

Regurgitates pellets consisting of fragments of crustacean exoskeletons, mollusk shells, insect exoskeletons, and seeds (Meanley 1962, Zembal and Fancher 1988). Pellets usually cast in concealed locations where birds hide and consume prey (e.g., grassy runways, bushes, clumps of grass), or at high spots such as muskrat houses (Meanley 1962).

SOUNDS

VOCALIZATIONS

Development. No information on vocal learning or sensitive periods for learning. Chicks emit peeping sounds (Adams and Quay 1958, WRE). Also capable of short squeals if exposed to sun or chills until age 6 wk (Adams and Quay 1958). Six-week-old young utter soft *chitty-chitty-chitty* sound when near parents (Meanley 1985). Seven-week-old young use both chick calls and adult call notes (Adams and Quay 1958). Fledged young capable of emitting most adult call notes, suggesting a mode of vocal development that does not involve imitation (D. E. Kroodsma pers. comm.). First evidence of Clapper vocalization (see below) at 6 mo of age (Meanley 1985).

Vocal array. Has large and varied vocal repertoire, although many vocalizations are subtle and rarely heard. As with most other rails, study of vocalizations complicated by inconsistent terminology and confusion over names of vocalizations. Most advertising and territorial vocalizations are based on 1 note that shows on a sonogram as a vertical bar with series of harmonic bands above a weak fundamental (Massey and Zembal 1987). Three sound types derived from these, including *kek*, Clapper, and *burr*. These sounds further serve as basis for most calls; differences are due to changes in intensity, duration, length of intervals between notes, and pitch. Low frequencies and buzzes of these sounds carry well through dense vegetation (Massey and Zembal 1987).

KEK. Male primary advertising call, *kek*, is simplest vocalization of Clapper Rails, consisting of 1 short, repeated note described as *kek-kek-kek*, *kik-kik-kik*, or *bup-bup-bup* (Meanley 1985, Massey and Zembal 1987). Pitch of notes varies, and call may be heard for 1–2 km. Sometimes confused with *kek* call of grackles (*Quiscalus* spp.), Red-winged Blackbird (*Agelaius phoeniceus*), or Common Moorhen (*Gallinula chloropus*; WRE). Sound spectrogram is given in Massey and Zembal 1987.

CLAPPER. Primary vocalization given by paired birds during breeding season is Clapper, or Clatter (Massey and Zembal 1987). Composed of rapidly repeated *chock-chock-chock-chock-chock-chock-chock-chock* (Simmons 1914), *cac-cac-cac* series, or slower *jupe-jupe-jupe* series; variable in pitch and speed of delivery (Meanley 1985). Delivered as single, repeated notes (numbering 12–100), complete vocalization lasts up to 10 s (Massey and Zembal 1987). Call starts at higher pitch and volume; intervals between notes stay about the same in duration. Often given as antiphonal duet by pair or by single member of pair. Sound spectrograms of single and duet Clapper are given in Massey and Zembal

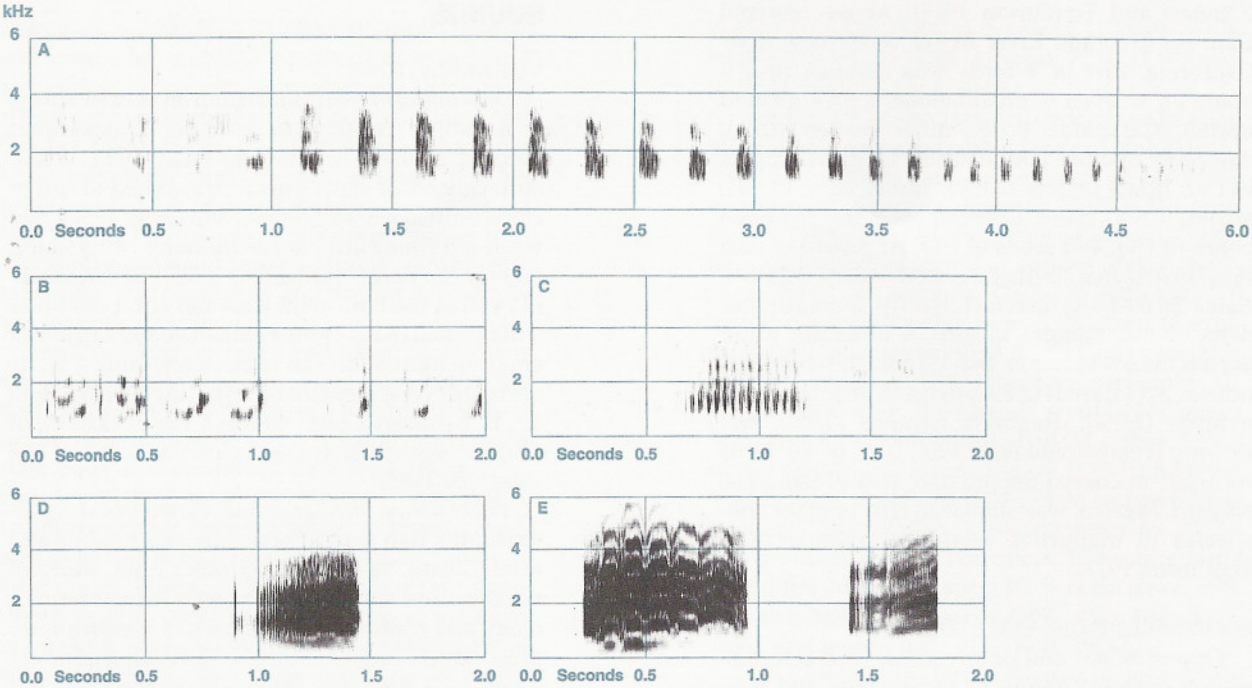

Figure 3. Selected Clapper Rail vocalizations. A. Kek-hurrah (from Crystal Beach Marsh, Mohave Co., AZ, Jul 1986). B. *Wheet* (from Crystal Beach Marsh, Mohave Co., AZ, 2 Oct 1986). C. Agitated Purr (from Mittry Lake Wildlife Management Area, Yuma Co., AZ, 15 May 1985). D. *Rack* (from Big Bend Wildlife Management Area, Dixie Co., FL, Mar 1993). E. Tremolo Call (from Crystal Beach Marsh, Mohave Co., AZ, Jul 1986). Prepared by Borror Laboratory of Bioacoustics from recordings made by Louis R. Hanebury and Vincent J. Semonsen (Kek-hurrah, *wheet*, Tremolo), and WRE (others). Sonograms were prepared on a Kay Elemetrics DSP 5500 Sonagraph with an effective band-width of 600 Hz (100 pt. transform size).

1987. The Kek-hurrah is similar in pattern to Clapper, consisting of 2–6 drawn-out *kek*s and a trilled, descending *krrrr* (Eddleman 1989; see Fig. 3A).

KEK-BURR. Given by female. Differs from Kek-hurrah (see above) in consisting of ≥1 evenly spaced, distinctive *kek*s followed by a trilled *brrrr*; or the *brrrr* may be given without introductory note(s) (Zembal and Massey 1985). Sound spectrogram is given in Zembal and Massey 1985. Has been described or noted in Clapper Rails from California, Arizona, and Florida, and in King Rail (Zembal and Massey 1985, Bailey 1977, Zembal and Massey 1985, Eddleman 1989, WRE). Descriptions of Kek-burr and Kek-hurrah in Todd (1986) are reversed.

WHEET. Rapid series of *wyeek* or *wheet* sounds (Eddleman 1989, see Fig. 3B); rarely heard.

PURR. Members of both sexes of pairs emit *purr* vocalization during nesting season (Smith 1974, Meanley 1985, Massey and Zembal 1987, Eddleman 1989). This is a low-pitched, low-volume call that sounds much like purr of a cat. If intruder or member of other pair is nearby, louder version of vocalization—Agitated Purr—may be given (Tomlinson and Todd 1973, Massey and Zembal 1987, Eddleman 1989; see Fig. 3C). Low-pitched, soft trill (*churr*) rarely given (Massey and Zembal 1987).

ALARM CALLS. Several alarm or agitation calls given by either sex in different contexts. Agitated Kek (also termed Jeer-kek [Todd 1986], *gip-gip-gip*, or *gup-gup-gup* [Meanley 1985]) is higher pitched and faster than *kek* (Tomlinson and Todd 1973, Smith 1974, Massey and Zembal 1987, Eddleman 1989). Chase Squeal, or *kak*, resembles squawk of a chicken and is given by birds involved in territorial disputes (Massey and Zembal 1987, Eddleman 1989). Flushed birds or birds in traps, in situations where behavior alternates between aggression and flight, may emit Screech, or Shriek (Massey and Zembal 1987).

OTHER VOCALIZATIONS. Birds in hand or (presumably) seized by predator give raucous *rack* vocalization, sounding like *rack-k-k-rack-k-k*, and repeated incessantly (Meanley 1985, Eddleman 1989, Fig. 3D). Bird under extreme duress may combine this vocalization with Tremolo Call: *rack-k-k, rack-k-k, raa-ha-ha-ha-*, speeding up with the end phrases (Eddleman 1989, Fig. 3E). Birds in traps may emit Burp Call, which sounds like low *kek* (Eddleman 1989).

If disturbance occurs within 15 m of bird, both sexes may give Hoo Call, sounding like *oom-oom-oom*, and similar to sound of a distant Great Horned Owl (*Bubo virginianus*; Tomlinson and Todd 1973, Smith 1974, Holliman 1978, Meanley 1985, Eddleman 1989). Adults with young produce calls that sound like cluck of chicken, or *woof-woof-woof* (Meanley 1985, Duhsé 1988).

Phenology. Exact phenology variable among sites and years (Eddleman 1989). Vocalizations involved with breeding are highly seasonal. *Kek* calls peak in Virginia between second week of Apr and second week of May; heard less often thereafter (Meanley 1985). Peak in Mar in Texas, then tapering off at start of nesting season (Simmons 1914). *Kek* given mostly Feb–Jun, *kek-burr* heard only in May–Jun, and *purr* in Apr–late May in Arizona (Smith 1974). Peak of spring vocalization at 2 Arizona sites in 1985–1987 varied from late Feb to mid-Jul among years (Eddleman 1989). Peak of *kek* vocalization in Mar–Jun and Clapper vocalization in mid-Feb–mid-Apr in California (Zembal and Massey 1987). In autumn, peak of vocalizations (mainly Clapper and Kek-hurrah) from mid-Jul to mid-Oct in Arizona and in Sep–Oct in California (Zembal and Massey 1987, Eddleman 1989); may represent addition of calling juveniles or gonadal recrudescence. Calls associated with aggression (Agitated Kek, Chase Squeal) increase at end of breeding season and in autumn because of frequent interactions among juveniles (Zembal and Massey 1987). Response to tape playback highly seasonal in Arizona, averaging 40% of birds during Mar–Apr, 20% May–Jul, 7% Aug–Oct, and 10% Nov–Feb (Conway et al. 1993). However, these estimates are from populations that had been repeatedly presented with playback recordings; response rate is probably higher when birds are not habituated to recordings. Other estimates of 70–95% response rate are based on estimates of calling by unknown numbers of birds (Smith 1974, Bennett and Ohmart 1978).

Daily pattern of vocalizing. Depends on call type and weather. Generally, most calling occurs in evening and early morning (Smith 1974, Zembal and Massey 1987, WRE). In morning, calling period shorter, individual birds do not call as often, and more difficult to distinguish pairs and individuals (Zembal and Massey 1987). Heavy rain, high winds (>16 km/h), and extreme high tides depress vocalizing activity (Smith 1974, Zembal and Massey 1987). In spring in Arizona, responds well to tape playback for only 0.5 h after sunrise, especially when temperature is <21°C (Smith 1974). As temperatures warm in summer, birds respond best to tape playback for about 3.5 h after dawn. *Kek* vocalization given mostly in late afternoon and evening, but may be given all night when single males are attempting to attract mates in spring (Todd 1986, Massey and Zembal 1987, WRE). Clapper vocalization given at any time of day, but especially in evening (Massey and Zembal 1987). More calling at night in late summer and early fall in Virginia (Meanley 1985).

Places of vocalizing. Poorly described. Usually vocalize from the ground in dense vegetation, but a few birds vocalize from sites up to 3 m above ground or above water level in tall emergent plants (WRE). Advertising males vocalize from small area at sites with high density of conspecifics; but vary their location frequently in low-density populations, suggesting that unmated males move in and out of substandard habitats (Zembal and Massey 1987). Single males that do not attract mates call from 1–3 sites for periods of up to 4 wk before moving to other areas (WRE).

Repertoire and delivery of songs. No information, because of difficulty of making repeated observations on individuals. Delivers Clapper vocalization with bill open, and entire body shakes during vocalization (Todd 1986). Vocalizing birds hold body in varied postures. Rate of delivery of *kek* 70–125/min.

Social context and presumed functions. In general, more vocalizations given by birds in populations of higher density, indicating increased interactions among birds (Zembal and Massey 1987).

KEK. Delivered by unmated males, presumably to attract females (Massey and Zembal 1987, Eddleman 1989). Often given incessantly for many hours during spring. Tempo increases in response to external stimuli such as other calling birds, tape playback, or presence of humans. Ceases when male is mated.

CLAPPER. Given by both sexes; appears to function as greeting when separated members of pair meet, as means of communicating location of mate in dense vegetation, as nest exchange vocalization, during precopulatory period, or in response to loud noises or vocalizations of other pairs (Zembal and Massey 1985). May function for territorial defense.

KEK-HURRAH. May be abbreviated version of Clapper, given by single birds of either sex, possibly given by unmated males in summer, or may be "subsong" given by maturing juveniles. Heard more often in some populations than in others (Todd 1986). *Wheet* always followed by Clapper or Kek-hurrah; possibly an indication of a high level of agitation (Eddleman 1989).

KEK-BURR. Primary advertising call of female; functions to attract males (Zembal and Massey 1985). May be given by unmated females, females that have lost their mates, or females calling to straying males (Zembal and Massey 1985). Playback of Kek-burr attracts both mated and unmated males (Eddleman 1989).

PURR. Serves as contact call between members of pair; given by both sexes, especially near nests or when pair responds to minor disturbances (Massey and Zembal 1987). Agitated Purr given in response to disturbance when adult is close to nest. *Churr* heard rarely; function unknown, possibly given by female calling to nearby mate (Zembal and Massey 1987, WRE).

OTHER VOCALIZATIONS. Several calls indicate agitation or alarm, possibly given in different contexts. Agitated Kek is emitted by disturbed individuals or birds under stress (Massey and Zembal 1987). Examples include juveniles involved in chase sequences as they leave natal territories, and adults when humans are detected near nest (Simmons 1914, Meanley 1985, Massey and Zembal 1987). Chase Squeal is given by bird initiating chase; sometimes followed by Clapper if mate appears or Agitated Kek if an unrelated bird is being chased (Massey and Zembal 1987). *Rack* and Tremolo Call is given only by birds in the hand; indicate very high level of distress (Eddleman 1989).

Single sharp *kek* given by adult in Florida caused chicks to stop moving (Duhsé 1988). Low clucking sound given by brooding parents may function to keep brood together. Function of Burp Call unknown, but may be for pair contact (Smith 1974) or alarm or agitation call (Eddleman 1989). Hoo Call given by startled birds, as low-level agitation call, or as investigatory vocalization (Bennett and Ohmart 1978, Todd 1986, Eddleman 1989). May also be used by young birds to keep family unit together (Holliman 1978).

NONVOCAL SOUNDS

Adults sometimes communicate with young using a low clicking or *shirring* sound apparently made by snapping bill (Nicholson 1927, Duhsé 1988). These sounds are barely audible, but they travel 5–7 m through dense vegetation and are used to call chicks for feeding or for safety.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Prefers walking or running to other forms of locomotion (Ripley 1977, Meanley 1985). Walks upright unless forced to crouch to avoid vegetation (Todd 1986). Confines most activity to dense vegetation, thus appearing "wary" or "secretive." Walking is slow and deliberate; often darts head (Ripley 1977, Todd 1986). Holds feathers compacted, neck outstretched, and tail erect, and moves in irregular path. May jerk tail up and down when walking, especially if agitated. Uses runways of muskrats or other marsh species (Simmons 1914). Occasionally climbs into tall emergent plants, shrubs, or trees, especially in response to tape playback (Ripley 1977, Todd 1986). Leaves chickenlike tracks, spaced about 25 cm apart (Oberholser 1974).

Flight. Seldom flies during summer or winter. When flushed, short-distance flight is slow and labored, with legs dangling below body (Ripley 1977). If distance of flight is >80 m, however, may attain flight speed nearly equal to that of shorebird or duck, suggesting good capability for migratory flight (Meanley 1985, Todd 1986). Short, rounded wings result in high wing-loading; landings appear clumsy. See also Migration: migratory behavior, above.

Swimming and diving. Swims well, sitting high on water and holding head and neck up (Ripley 1977). Swimming used for locomotion only to cross channels or escape immediate threat, especially at high tide (Sibley 1955, Meanley 1985, Todd 1986). Dives only if wounded or in response to immediate threat (Ripley 1977). Holds onto submersed vegetation in such cases. Uses wings for propulsion underwater.

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. Often bathes in shallow pools, especially at low tide (Meanley 1985). One pair in Florida observed taking daily baths at dusk (Duhsé 1988). Bathes by dipping head first, immersing body up to back and breast (Williams 1929). May bathe more thoroughly by ducking and raising head, at the same time raising and lowering body. Preens after bathing for up to 30 min; often preens at dusk (Meanley 1985).

Sleeping, roosting, sunbathing. Often roosts at high tide during day (Zembal et al. 1989). Birds fitted with radio transmitters in Arizona settled at one location about 0.5 h after sunset and rarely moved until about 0.5 h before sunrise the next day, regardless of season (Eddleman 1989). Seeks shelter behind drifted wrack or other objects during cold weather (Simmons 1914).

Daily time budget. Activity diurnal; active for 75 to >90% of day; peaks in early morning and late evening (Roth et al. 1972, Zembal et al. 1989, WRE). No difference in activity among time periods throughout day in Arizona, except for reduction in activity before sunset (Eddleman 1989). Within-day movements greatest in winter and early breeding season, and least during brood-rearing ($p < 0.05$); average 140 m/movement in Jan–Feb ($n = 88$), 155 m/movement in Mar–Apr ($n = 151$), 111 m/movement in May–Jul (n = 495), 121 m/movement in Aug–Oct (n = 305), and 161 m/movement in Nov–Dec (n = 57; Conway et al. 1993). Immatures in late summer and fall move the farthest (Zembal et al. 1989).

AGONISTIC BEHAVIOR

Physical interactions. Little studied. Male-male interactions consist of attempting to peck each other and flapping wings (WRE). Territorial interactions include chasing intruders (Williams 1929).

Communicative interactions. Attacking birds in territorial interactions chase intruders and give Clapper vocalization when intruder has left territory (Williams 1929). Nesting adults give Agitated Kek (see Sounds: vocalizations, above) if threatened at nest sites (WRE).

SPACING

Territoriality. Territorial during nesting season, but more tolerant of incursions into territory in late summer when juveniles become independent (Zembal et al. 1989). Territory established by male giving *kek* call; defense by *kek* and Clapper calls and by chases (Meanley 1985, Zembal et al. 1989, WRE). Defends territory against all other calling Clapper Rails except mate and brood, but may tolerate silent or passive individuals in the territory (Johnson 1973). Nature of interspecific territoriality poorly known, but is known to defend against Laughing Gulls (*Larus atricilla*; Segre et al. 1968). Size of breeding territory estimated at 0.12–3.59 ha in Arizona (Smith 1974, Bennett and Ohmart 1978, Todd 1986), but often forage off territory (WRE). Smallest territory size in Virginia 0.1 ha (Meanley 1985). Nests placed a minimum of 13 m apart in New Jersey if a barrier such as a dense patch of vegetation was between them, at least 23 m apart otherwise (Kozicky and Schmidt 1949). A total of 92% of nests were >45 m apart. May be territorial to some extent in winter; chases sometimes observed (Williams 1929). Appears to use same territory in subsequent breeding seasons in Arizona (CJC).

Individual distance. No information.

SEXUAL BEHAVIOR

Mating system and sex ratio. Monogamous, because both sexes are needed to complete incubation (Oney 1954, Meanley 1985, Eddleman 1989). Sex ratio of trapped birds in Arizona is 2 males: 1 female, but trapping techniques probably biased toward males (Eddleman 1989). However, evidence of unmated males and the extremely short time between initiation of Kek-burr and paired Clapper at specific sites suggests skewed sex ratio. Sex ratio of birds shot in N. Carolina was 71 males: 29 females in 1955 and 50:50 in 1956; reason for variation unknown (Adams and Quay 1958). Sex ratio of 146 birds shot in Louisiana did not differ from 1:1 (Sharp 1976).

Pair bond. Mate attraction involves use of *kek* call by male; details of courtship unknown (Ripley 1977, Meanley 1985). Symbolic nest-building may be part of courtship, although context of observation not clear (Meanley 1985). At least 2 displays given by male are for maintenance of pair bond (Meanley 1985). First, male lowers tail to horizontal position, extending white undertail-coverts and pointing bill toward ground and holding it slightly open, then slowly moving it from side to side. Second, male stretches neck with bill open, approaches female, and pursues her for up to 1 m. Both displays last <1 min (Meanley 1985). Courtship-feeding of female by male occurs during egg-laying and incubation. Pair bond presumably lasts for duration of breeding season; rate of selecting same mate in subsequent years unknown (WRE). However, 1 mated pair in Arizona maintained adjacent home ranges during postbreeding period (WRE). Both sexes attempt to attract new mate if mate is killed (Zembal and Massey 1985, WRE).

Extra-pair copulations. No information. Probably occur, because mated males actively seek unmated females giving advertising call (Zembal and Massey 1985, WRE).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Tend to form loose colonies, although this tendency may be associated with quality of habitat and not sociality (Simmons 1914). Social groups rarely form outside the family unit, and usually only at high tide when individuals concentrate on high ground (Stone 1937).

Play. No information.

Nonpredatory interspecific interactions. Responds to alarm calls or actions of other species to avoid predators (Todd 1986). Competes with Laughing Gulls for nest sites on East Coast; often fights with gulls and eats gull eggs (Segre et al. 1968). Lays in gull nests, or gulls may lay in Clapper Rail nests if gull colonies are nearby, but no parasitic eggs hatch. Laughing Gulls attack incubating rails (Segre et al. 1968).

PREDATION

Kinds of predators. Predation on chicks not studied, but probably very high (Meanley 1985). Fish Crows (*Corvus ossifragus*) eat rail eggs, and Laughing Gulls puncture eggs and eat rail chicks (Fargo 1927, Bongiorno 1968, Segre et al. 1968). Most important nest predator in Georgia was raccoon (*Procyon lotor*; Oney 1954). Norway rat (*Rattus norvegicus*) and red fox (*Vulpes vulpes*) are important predators of eggs in San Francisco Bay, CA (DeGroot 1927, Harvey 1988, U.S. Dept. of the Interior 1991).

Avian predators documented to have taken adult Clapper Rails include Great Blue Heron (*Ardea herodias*), Bald Eagle (*Haliaeetus leucocephalus*), Northern Harrier (*Circus cyaneus*), Harris' Hawk (*Parabuteo unicinctus*), Red-shouldered Hawk (*Buteo lineatus*), Red-tailed Hawk (*B. jamaicensis*), Ferruginous Hawk (*B. regalis*), White-tailed Hawk (*B. albicaudatus*), Peregrine Falcon (*Falco peregrinus*), Prairie Falcon (*F. mexicanus*), Barn Owl (*Tyto alba*), Great Horned Owl, Short-eared Owl (*Asio flammeus*), and Common Raven (*Corvus corax*; Bent 1926, DeGroot 1927, Fargo 1927, Cottam and Nelson 1937, Baldwin 1940, Stevenson and Meitzen 1946, Johnston 1956a, Meanley 1985, Willey 1986, Eddleman 1989, Zembal et al. 1989, U.S. Dept. of the Interior 1991). Most important mammalian predator of adults probably is the raccoon (Oney 1954, Bateman 1965, Holliman 1981, Eddleman 1989). Introduced red fox preys on adult *obsoletus* in San Francisco Bay, CA, and is thought to be severe threat to this race (U.S. Dept. of the Interior 1991). Other mammals that prey on Clapper Rails include mink (*Mustela vison*), coyote (*Canis latrans*), opossum (*Didelphis marsupialis*), and domesticated dogs (*Canis familiaris*) and cats (*Felis domesticus*; Bent 1926, Oney 1954, MacNamara and Udell 1970, Eddleman 1989, U.S. Dept. of the Interior 1991). Rattlesnake (*Crotalus* sp.) also known to have taken Clapper Rail in S. Carolina (Grant 1970).

Manner of predation. Little information on predation at nests. Nest predation seems to be highest on Gulf Coast (Eddleman and Conway 1994). Adult most often taken on ground when foraging in edges of mudflats, when away from usual dense cover, and at high tide (Arnett 1951, Todd 1986, WRE). In Arizona, predation peaks in late summer–early fall, when coyotes and raccoons move into marshes, and in midwinter, when avian predators are at greatest density (Eddleman 1989).

Response to predators. Avian predators near nests late in incubation period evoke Screech (see Sounds: vocalizations, above) and flights up to 1.5 m high (Zembal and Massey 1987). Adults emit sharp *kek* to warn chicks of predators. Adults escape from avian predators by seeking cover in dense herbaceous vegetation or diving underwater (Lima 1993). Usually walk into vegetation if threat is moderate; if threat is immediate, run while holding tail and head straight out and body horizontal (Todd 1986). May rapidly jerk conspicuous tail up and down to signal predator that it has been detected (Alvarez 1993).

BREEDING

PHENOLOGY

Pair formation. Males begin advertising in Feb in Arizona; pair formation begins shortly thereafter (WRE). Pairs begin to form in late Mar in Texas (Simmons 1914). Adults arrive in New Jersey and Virginia in early Apr; pair formation begins almost immediately (Mangold 1974, Meanley 1985). Timing unknown for other populations.

Nest-building. Nesting in San Francisco Bay, CA, begins in late Mar; peaks in late Apr–mid-May (DeGroot 1927, Harvey 1988). First nests in Arizona recorded 13 Mar; peak initiation mid-May (Eddleman 1989). In Trinidad, breeds Apr–Dec (mostly May–Jun; Hilty and Brown 1986). First nests in e. Florida in Mar (Nicholson 1927). Initiates first nests in Louisiana the last week in Mar; peak mid-Apr–mid-May (Sharp 1976). Earliest nest in N. Carolina 1 Apr; peak late Apr (Adams and Quay 1958). Nest initiation begins in Virginia in latter half of May to early Jun (Stewart 1951, Meanley 1985). First nests initiated in New Jersey in early Apr; peaks 27 Apr–1 Jun and 1–20 Jul (Mangold 1974). Peak in New York in second week of May (MacNamara and Udell 1970).

First brood per season. Figure 4. Peak based on egg dates varies with subspecies and location (Western Foundation of Vertebrate Zoology [WFVZ] records, nest card records from Cornell Laboratory of Ornithology; WRE); from earliest to latest (subspecies, location—mean date [SD], *n*): *levipes*, s. California—20 Apr ± 18.4, 209; *obsoletus*, San Francisco Bay, CA—1 May ± 24.8, 275; *yumanensis*, sw. Arizona and se. California—11 May ± 29.8, 11; *scotti*, Florida—4 May ± 25.1, 35; *waynei*, s. Atlantic Coast of U.S.—17 May ± 19.3, 120; *crepitans*, n. Atlantic Coast of U.S.—23 Jun ± 24.3, 579.

Second brood per season. Second nests in San Francisco Bay, CA, initiated late Jun–early Jul; eggs begin to hatch in Jul (DeGroot 1927, Harvey 1988). Hatching date for second brood of 1 pair in New Jersey on 20–29 Jul (after first nest hatched between 10 and 19 Jun; Ferrigno 1990). Small numbers of nests occur into Aug in most locations (WRE).

NEST SITE

Selection process. Nests placed to avoid flooding by tides, yet in dense enough cover to be hidden from predators and to support the relatively large nest (Storey et al. 1988). Nest-site selection thus involves a compromise between sites at higher elevation with less dense cover and sites at lower elevation with denser cover.

Microhabitat. Nests placed in clumps of vegetation or forks of shrubs from just above ground

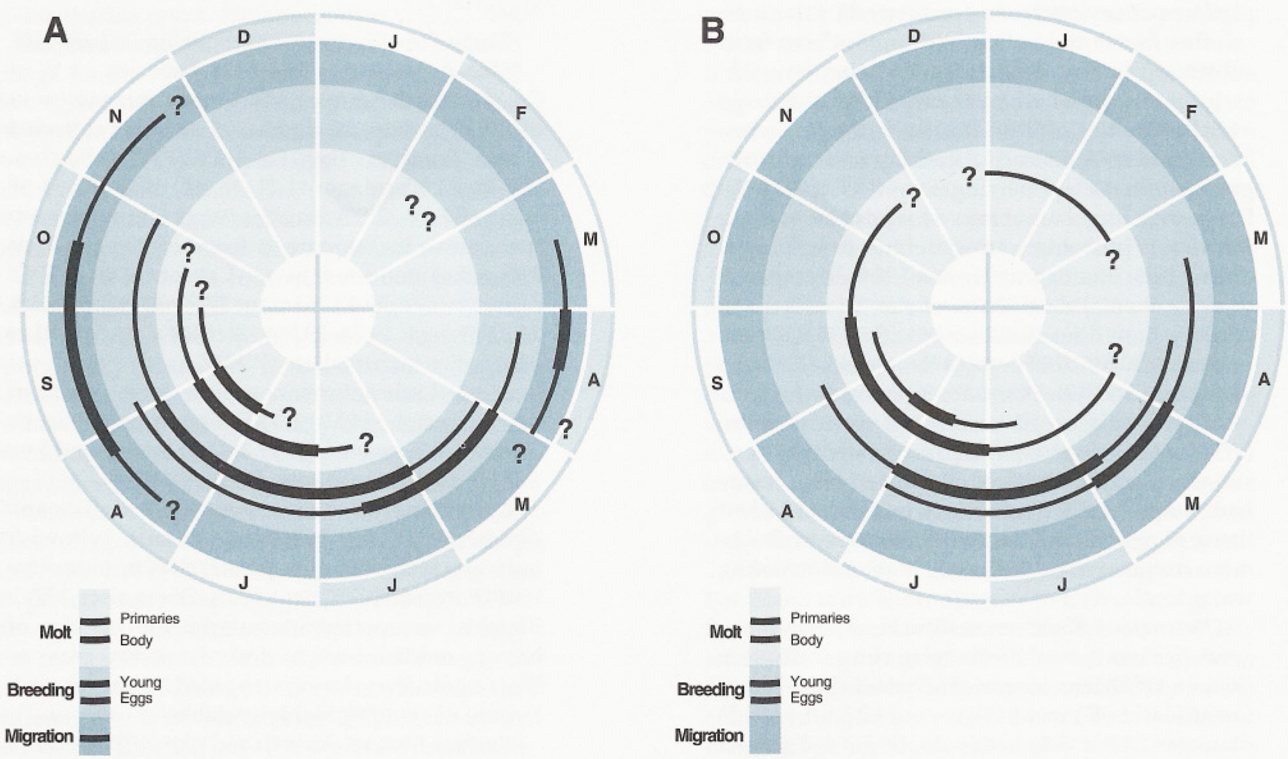

Figure 4. Annual cycle of breeding, molt, and migration of the Northern Clapper Rail (A) in Virginia, and breeding and molt of the Yuma Clapper Rail (B) in sw. Arizona. Thick lines show peak activity; thin lines, off-peak.

surface in marsh habitat to 1.5 m above substrate in mangroves. Nests in se. California and sw. Arizona placed in clumps of emergent plants, in base of shrubs, or in clumps of downed dead vegetation near uplands (Eddleman 1989). Clapper Rails nesting in mangroves in Mexico and the Caribbean placed nests an average of 73.6 cm ± 28.1 SD above ground (range 30–150, *n* = 19; WFVZ records). In San Francisco Bay, CA, places nests on raised ground near tidal sloughs in low marsh (Harvey 1988, Shuford 1993). Early nests placed under dense vegetation, under wrack or debris, or under gum plant bushes. Vegetation recorded at 45 nests in San Francisco Bay, CA, was pickleweed (at 96% of nests), Pacific cordgrass (45%), and salt grass (*Distichlis spicata*, 18%; Harvey 1988). Most nests in New Jersey placed on ground among plant stems (Kozicky and Schmidt 1949). Vegetational type at 56 nests was salt marsh cordgrass >61 cm tall (73.2%), high-tide bush (*Iva frutescens*; 14.3%), salt marsh cordgrass–salt meadow cordgrass mix (7.1%), salt marsh cordgrass <61 cm tall (3.6%), and black rush (*Juncus gerardi*; 1.8%).

Site characteristics. Grass height is a major proximate cue used in site selection, because of need for nest concealment (Adams and Quay 1958, Sharp 1976, Storey et al. 1988). Nest sites vary depending on stage of nesting season; earlier nests placed on higher sites because of shorter available grasses at lower sites. Substrate height above mean high water (MHW) 1.9 cm ± 1.8 SD at 16 early nests, 3.7 cm ± 1.8 SD at 16 late nests; grass height 72.8 cm ± 3.2 SD at early nests, 91.6 cm ± 6.1 SD at late nests; grass height above MHW 75.0 cm ± 2.8 SD at early nests, 87.6 cm ± 5.0 SD at late nests (Storey et al. 1988). Implies that later nests are placed at lower sites, but in taller grass to avoid flooding and take advantage of denser cover. Similarly, first nests in N. Carolina placed in needlerush (higher sites) in early Apr, later in needlerush-cordgrass mix, then in cordgrass (lower sites) by late Apr (Adams and Quay 1958).

Nests on East and West Coasts often placed near edges of tidal sloughs; 60% of 50 nests in s. California were within 7.8 m of a slough edge, 80% of 79 nests in Virginia were within 4.6 m, and 71% of 63 nests in New Jersey were within 3.7 m (Kozicky and Schmidt 1949, Stewart 1951, Massey et al. 1984). No such relationship found in Alabama or Louisiana, where nests were dispersed in large patches of tall salt marsh cordgrass (Holliman 1978, Sharp 1976).

NEST

Construction process. Male performs most nest-building (Meanley 1985). Process of nest construction not described. Egg-laying often begins before nest is completed.

Structure and composition matter. Nests tall and cryptic to avoid tidal flooding and protect eggs from predation (Storey et al. 1988). Nest is a bulky platform of dry cordgrass, pickleweed, salt grass, or other marsh vegetation built up 8–15 cm from substrate (Shuford 1993). In San Francisco Bay, CA, early nests consist of layer of pickleweed twigs over broken bits of dead Pacific cordgrass stems; later nests are constructed entirely of dead cordgrass, often attached to living stems (DeGroot 1927). Dome over top of nest may or may not be present; function is probably concealment or to hold eggs during tidal inundation (Kosten 1984). In response to experimental destruction of dome in 15 nests, adults rebuilt dome in 12 nests within 24 h. Dome present in 90.5% of 63 nests in New Jersey (Kozicky and Schmidt 1949). Dome absent in many Arizona nests, probably because overhead cover is dense (WRE). Nests may have ramp from water surface or substrate to rim; 68.4% of 63 nests in New Jersey had ramps, but 50% of 6 nests in Arizona lacked these ramps (Eddleman 1989). Ramps probably more common in habitats with high or fluctuating water levels.

Dimensions. Eighteen nests in New Jersey averaged 26.7 cm (range 10–50) from rim to substrate (Kosten 1982). Dimensions of 63 nests in New Jersey (mean [cm] ± SD): inside diameter 14.2 ± 1.8, outside diameter 23.6 ± 3.2, inside depth 5.3 ± 1.4, nest height above substrate 22.9 ± 8.0, nest rim to top of dome 18.3 ± 3.5 (Kozicky and Schmidt 1949). Measurements at 45 nests in San Francisco Bay, CA, (mean [cm] ± SD): outside diameter 21.1 ± 2.8, nest height above substrate 17.9 ± 6.3, height of dome 57.1 ± 15.2 (Harvey 1988). Dimensions of nests and nest bowls in Arizona (mean [cm] ± SD): inside diameter 14.7 ± 4.1 (n = 15), outside diameter 26.5 ± 3.0 (n = 12), inside depth 4.3 ± 2.6 (n = 16), nest height above substrate 19.3 ± 20.8 (n = 18), width of ramp 10.7 ± 3.2 (n = 3), length of ramp 37.7 ± 26.5 (n = 3; Eddleman 1989).

Microclimate. No information.

Maintenance or reuse of nests, alternate nests. Builds up nest during periods of high water (Jackson 1983). Male adds material to nest while female continues to incubate; female tucks material under eggs and into nest. Such augmented nests may measure up to 31 cm in diameter, 19.5 cm from rim to bottom, and 41 cm from mean water level. Egg nest may be used to brood young, but it is not used for second clutch (Blandin 1963).

Nonbreeding nests. Up to 6 brood platforms constructed after hatching for brooding chicks (Adams and Quay 1958). Differ from primary nest in lacking a dome and being capable of floating at high tide. One pair in Florida constructed crude roost platform each evening to brood chicks (Duhsé 1988). Often uses dead mats of emergent vegetation for loafing and casting pellets after feeding; these sites may appear similar to nests (WRE).

EGGS

Shape. Subelliptical to long subelliptical or ovate.

Size. Largest eggs laid by subspecies on West Coast of North America. Mean measurements (mm) of 165 eggs from 20 clutches of *obsoletus* collected at San Francisco Bay, CA, in WFVZ collection: length 44.30 (range 41.71–45.80), breadth 31.58 (range 30.69–32.50). Smallest eggs laid by *yumanensis;* mean measurements (mm) of 30 eggs from 6 clutches collected in se. California in WFVZ collection: length 40.26 (range 37.91–41.86), breadth 28.87 (range 28.26–29.76). Size of eggs of other subspecies intermediate (WFVZ data).

Mass. Little information. One fresh egg from Arizona weighed 19.0 g (WRE). Eggs from n. Atlantic Coast of U.S. may weigh 18–20 g at laying, and lose 2–2.5 g during incubation (Ripley 1977).

Color. Ground color creamy white, dull cream, pinkish, very pale buff, pinkish buff, yellowish buff, greenish buff, glossy buff, clay, or pale olive buff (Forbush 1925, Bent 1926, Oberholser 1974). Blotched or spotted irregularly with shades of brown, reddish brown, drab, lavender, gray, or lilac; spots may be concentrated at larger end. Degree of spotting highly variable.

Surface texture. Smooth and glossy (Bent 1926).

Eggshell thickness. Mean eggshell thickness in clutches collected in 1863–1947 averaged 0.241–0.244 mm from N. Carolina to Florida (n = 156 clutches), and 0.258–0.260 mm from New Jersey and Virginia (n = 82 clutches; Klaas et al. 1980). Similar measurements on clutches collected after 1947 were 0.242–0.257 mm for 16 clutches collected from N. Carolina to Florida and 0.255–0.262 mm for 40 clutches collected from New Jersey and Virginia. No difference in eggshell thickness between time periods, but shells of New Jersey and Virginia eggs were thicker than those of N. Carolina to Florida (Klaas et al. 1980). Mean empty shell weight of 165 eggs from 20 clutches of *obsoletus* from San Francisco Bay, CA, in WFVZ collection 1.832 g (range 1.658–2.013); mean empty shell weight of 30 eggs from 6 clutches of *yumanensis* from se. California in WFVZ collection 1.332 g (range 1.142–1.507).

Clutch size. See Demography and populations: measures of breeding activity, below.

Egg-laying. Little information. Birds at 4 New Jersey nests laid average of 0.9 egg/d (Kozicky and Schmidt 1949). Egg-laying rate at 1 nest in Louisiana 7/8 d (Bateman 1965). Eggs are laid before 08:00 in New Jersey (Schmidt and McLain 1951).

INCUBATION

Onset of broodiness and incubation in relation to laying. In many nests, incubation begins before end of egg-laying, resulting in asynchronous hatching (Meanley 1985).

Incubation patch. No information.

Incubation period. Averages 20 d in New Jersey (range 18–22, *n* = 6; Kozicky and Schmidt 1949). Averages 21 d in N. Carolina (Adams and Quay 1958). Extremes of 23 and 29 d reported in San Francisco Bay, CA (Applegarth 1938, Zucca 1954, Johnston 1956b). Incubation period at 7 nests in Arizona 23–28 d (Eddleman 1989); varies because incubation begins before last egg is laid.

Parental behavior. Incubation by both sexes, on basis of marking and radiotelemetry data (Oney 1954, Eddleman 1989). Male incubates at night and sporadically during day; female does most diurnal incubation, and relieves male after sunrise. Disturbance of incubating adults produces responses including aimless flight, "broken wing" displays, aggressive distraction displays, and bewilderment (Nicholson 1927, MacNamara and Udell 1970). These displays reach peak during hatching (Kozicky and Schmidt 1949). Incubating adult retrieves eggs displaced from nest using bill (Pettengill 1938, Kosten 1982). Experimental displacement of eggs 1 m from nest showed that adults retrieved eggs in 15 out of 18 trials; stage of nesting cycle made no difference in behavior (Kosten 1982). Rare individuals (4 of 200) had to be lifted off nest to examine eggs (Zembal and Massey 1983).

Hardiness of eggs against temperature stress; effect of egg neglect. Eggs in 1 nest in New Jersey hatched successfully after submersion during high tide (Kozicky and Schmidt 1949). Eggs submersed up to 45 cm deep during high tide are still capable of hatching (Oney 1954).

HATCHING

Preliminary events and vocalizations. Head tucked under right wing in egg; egg tooth by side of flank under section of egg covered with wreath of spots (larger end; Simmons 1914). Pipping begins about 48 h before hatching (Kozicky and Schmidt 1949).

Shell-breaking and emergence. Hatching lasts 24–48 h; duration may depend on whether incubation begins before egg-laying is completed (Kozicky and Schmidt 1949, Johnston 1956b). One clutch in Virginia hatched during 37-h period. A few young die during hatching; young from 0.8% of 513 eggs died during this time in New Jersey (Kozicky and Schmidt 1949).

Parental assistance and disposal of eggshells. Eggshells left in nest, eaten by adult, ground into small pieces, or dropped up to 6 m from nest (Simmons 1914, Meanley 1985).

YOUNG BIRDS

Condition at hatching. Covered with wet, long, black down; bill color pied, ranging from pinkish white with black base to blackish with pinkish white area around nostrils and tip; irides dark brown (Simmons 1914, Adams and Quay 1958, Meanley 1985). Stomach and cloaca rich orange pink or salmon (Simmons 1914). Eyes open, and emit faint cheeps. Length 75–80 mm (Adams and Quay 1958). Semiprecocial; incapable of moving from nest for at least 1 h after hatching and brooded by adult for several days (Meanley 1985).

Growth and development. Egg tooth shed 4–6 d after hatching (Meanley 1985). Most growth in first 3 wk, but young able to swim and dive for short periods (Adams and Quay 1958). Bill coloration darkens in basal half by third week; still covered with black down at this time. Feathers appear in all except capital, caudal, and alar tracts by week 5; bill becoming uniformly light gray. All tracts have growing feathers by week 6, and irides become olive drab. See Appearance: molts and plumages, below.

Chick behavior. Chicks flushed from egg nest in Louisiana ran a short distance to cover, then gave faint peeping sounds (Bateman 1965). Young follow adults during foraging bouts (Zembal and Fancher 1988). Forage independently on small prey soon after hatching. Begin to feed farther from adults as fledging age approaches (Meanley 1985).

PARENTAL CARE

Brooding. First-hatched chicks are led from nest by one parent while other parent continues incubating newly hatched chicks and remaining eggs (Kozicky and Schmidt 1949, Adams and Quay 1958). Brooded continually for first few days, on original nest, brood nest, or floating debris. One brood brooded by both parents for first 7 d in Florida; only 1 chick seen with 1 parent thereafter (Duhsé 1988). Adult covered chicks each night on newly constructed brood nest. Adults divided brood after first week, each parent tending half the brood (Duhsé 1988).

Feeding. See Food habits: diet, above. Chicks eat fragments of prey broken up by adults; foods do not differ from those eaten by adults (Adams and Quay 1958, Zembal and Fancher 1988). Adults sight prey, become motionless, and young race in to eat prey the adult has sighted (Zembal and Fancher 1988). Parental care usually extends until fifth or sixth week after hatching (Adams and Quay 1958, Zembal and Fancher 1988), but brooding may continue until eighth to tenth week (MacNamara and Udell 1970). At high tide, broods forage along narrow ditches with water 15–20 cm deep (Meanley 1969). Chicks stay in edge of vegetation during this time. Family groups forage in loosely organized unit, often dispersed over an area 15 m across (Adams and Quay 1958). Family unit maintained by peeps of chicks and subdued clucks of adult.

Table 1. Nest success (% nests hatching at least 1 chick) of Clapper Rail in North America.

Location	Number of nests	Nest success (%)	Source
San Francisco Bay, CA	50	56.0	Harvey 1988
Georgia	50	42.3	Oney 1954
N. Carolina	26	42.0	Adams and Quay 1958
Virginia	79	94.0	Stewart 1951
New Jersey	61	89.3	Kozicky and Schmidt 1949
New Jersey		87.1	Mangold 1974
New York	80	87.6	MacNamara and Udell 1970

Carrying of young. Adults carry chicks <2 wk old during high water or across open water or to move away from human intrusion (Tomkins 1937, Pettengill 1938).

COOPERATIVE BREEDING

Little studied; not known to occur (WRE).

BROOD PARASITISM

No information.

FLEDGLING AND IMMATURE STAGE

Growth. Independent of adult by week 6 after hatching (Adams and Quay 1958). Primaries about half grown by age 7 wk, three-fourths by age 8 wk. Bill and legs uniformly gray at 8 wk. Sheaths on primaries still visible on basal 1 cm, legs beginning to show orange at joint of tarsus and tibiotarsus; bill shows slight orange color at base, flank markings indistinct; some individuals capable of flight at 9 wk. All individuals can fly at age 10 wk; no sheaths remain on primaries, orange color expanding on bill and legs, flank barring becoming more distinct, iris becoming orange brown. After age 10 wk, individuals becoming indistinguishable from adults, but fleshy parts are somewhat duller in juvenile.

Association with parents or other young. Apparently not associated with parents or broodmates after fledging (WRE).

Ability to get around, feed, and care for self. Tidal sloughs important for escape from predators (Harvey 1988).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding. Unknown; presumed to be 1 yr.

Clutch. Mean clutch size differs among subspecies ($p = 0.0001$), on basis of data from completed clutches in WFVZ collection and nest card records at Cornell Laboratory of Ornithology. Differences explained mainly by the larger clutches of Clapper Rails on East and Gulf Coasts of U.S. ($p < 0.05$). Clutch size for nests of different subspecies (mean ± SD, range, n): *obsoletus* (San Francisco Bay, CA), 8.3 ± 1.7, 4–14, 179; *levipes* (s. California and Baja California Norte), 7.3 ± 1.2, 5–11, 94; *yumanensis* (lower Colorado River and Salton Sea, CA), 6.7 ± 0.8, 5–8, 15; *yumanensis* (West Coast of Mexico), 5.5 ± 0.9, 3–7, 22; *beldingi* (Baja California Sur), 6.4 ± 1.0, 5–8, 9; *crepitans* (n. Atlantic Coast of U.S.), 9.2 ± 1.6, 4–16, 455; *waynei* (s. Atlantic Coast of U.S.), 9.4 ± 1.9, 5–15, 75; *scotti* (s. and w. Florida), 7.3 ± 2.0, 2–11, 19; *insularum* (Florida Keys), 6.5, 6–7, 2; *saturatus* (Gulf Coast of U.S.), 9.5 ± 1.5, 7–14, 20; and *caribaeus* (Jamaica), 6.5, 6–7, 2. Similarly, clutch size increases with latitude ($p = 0.0133$) at rate of 0.174 egg for every 1° of latitude (WRE).

One clutch from San Francisco Bay, CA, with 21 eggs probably represented a dump nest (DeGroot 1927). In Virginia, clutches in 149 first nests averaged 9.0 ± 0.2 (range 4–12), but 16 second clutches averaged only 5.6 ± 1.1 (range 3–9; Stewart and Meanley 1960). Clutch size averaged 7.9 in 42 first nests in S. Carolina, 6.7 in 15 second nests, and 6.2 in 6 third nests (Blandin 1963). No appreciable decrease in clutch size in second nests in Georgia (Oney 1954).

Reproductive success. Nest success (nests hatching ≥1 young) variable, but often high in good habitat (Table 1). Egg success also high; 87.3% of 513 eggs hatched in New Jersey (Kozicky and Schmidt 1949). An average of 8.1 eggs ± 0.7 SD hatched/successful nest in New Jersey ($n = 242$ nests), 11.2 ± 2.0 SD ($n = 174$ pairs) chicks hatched/pair and (12.8 ± 3.2 SD) chicks hatched/ha (36.8-ha study area; Mangold 1974).

Nest success estimates are based on proportions of nests found (Table 1). Mayfield daily nest survival for 145 nests in New Jersey from nest card records from Cornell Laboratory of Ornithology 0.994063 (95% confidence interval [CI], 0.991988–0.995841;

WRE). For 21-d incubation period (not including laying period), nest success is 88.2% (95% CI, 84.4–91.6%).

Most nest failures attributed to flooding by high tides or high winds, but predation also a factor; in s. California, 9 nests lost to high tides and 6 to predation (Zembal and Massey 1983). Eggs often lost to predation by Norway rats in San Francisco Bay, CA (Harvey 1988). Isolation of nesting areas from the mainland may determine success, because predators have poor access to isolated habitats (Meanley 1985).

Chick mortality high in first few weeks; observed brood size is low relative to number hatched and often decreases rapidly after hatching (Duhsé 1988). Age ratios in fall populations are variable; 3 juveniles/adult in Virginia (Meanley 1985), 2 in Louisiana (Sharp 1976), 4.9–5.8 juveniles/adult in N. Carolina, (Adams and Quay 1958).

Number of broods normally reared per season. Birds with failed nesting attempts renest up to 5 times; some evidence suggests up to 7 attempts (Blandin 1963), suggesting high reproductive potential despite losses to flooding and predation. About 50% of pairs in San Francisco Bay, CA, renest following nest failure (DeGroot 1927). Second nests after successful first nest documented in New Jersey, S. Carolina, and Florida (Blandin 1963, Duhsé 1988, Ferrigno 1990). Second nest placed on average 17 m from first nest ($n = 21$; Blandin 1963).

LIFE SPAN AND SURVIVORSHIP

After-hatch-year male banded 24 May 1971 8 km SSE of Tuckerton, NJ, was shot 5 Dec 1977 6.4 km south of Tuckerton, making it at least 7 yr 6 mo old (Clapp et al. 1982). Annual survival rates of adults fitted with radio transmitters ranged from 49 to 67% in Arizona (Eddleman 1989). Composite annual survival rate for all years (1985–1987) was 26%, but effects of radio transmitters may have depressed survival. Most adult mortality occurred during fall and winter.

DISEASE AND BODY PARASITES

Diseases. Poorly known. One of 9 birds necropsied from Arizona died from ideopathic hepatitis caused by disease or ingestion of a toxin (Eddleman 1989). Six individuals died during a botulism outbreak in San Francisco Bay, CA, in 1974 (USFWS 1974).

Body parasites. Forty-six species of internal parasites reported: 35 trematodes, 6 cestodes, 4 nematodes, and 1 acanthocephalan (Bateman 1965, Heard 1968, Deblock and Heard 1969, Byrd and Heard 1970, Heard 1970, Nickol and Heard 1970, Bates and Meade 1972, Brooks and Heard 1977, Taft and Heard 1978, Underwood and Dronen 1986, Wong and Anderson 1990). Type host for nematode parasite *Ancyracanthus heardi* (Wong and Anderson 1990) and trematode parasites *Levinsiella byrdi* (Heard 1968), *Longiductotrema floridensis*, *Maritrema prosthometra* (Deblock and Heard 1969), *Renicola ralli*, *R. glandoloboides* (Byrd and Heard 1970), and *Notocotylus schmidti* (Brooks and Heard 1977). Effects of parasites on individuals unknown.

CAUSES OF MORTALITY

See Behavior: predation, above. Ribbed horse mussels and other bivalves clamp onto Clapper Rail toes or bills, which prevents birds from feeding and causes them to starve (DeGroot 1927, Zembal and Fancher 1988). Storms devastate local breeding and wintering populations (see Population regulation, below; see also Conservation and management: effects of human activity, below). Susceptible to prolonged cold, especially unusually cold periods (Simmons 1914).

RANGE

Initial dispersal from natal site. Juveniles become independent at about 5–6 wk, then move erratically (Meanley 1985). Often chased by territorial adults (Zembal and Massey 1987). Natal dispersal patterns and degree of philopatry unknown.

Fidelity to breeding site and winter home range. More than 17% of 191 birds banded on nesting areas in New Jersey were recaptured in subsequent years (Mangold 1974). Adults in Arizona and s. California that have established home range usually move little (Eddleman 1989, Zembal et al. 1989). Fidelity to winter home range unknown.

Dispersal from breeding site or colony. Highly vagile; individuals sometimes appear far from typical habitats (Crawford et al. 1983). However, poorly described. Occurrences of *obsoletus*, *levipes*, and *yumanensis* in atypical habitats summarized by Leipsic-Baron (1992). Most movements made by young birds, but dispersal in sw. Arizona occurred in 4 different ways: dispersal by juveniles, movement to new sites by males that had failed to attract a mate, movements from breeding areas by post-breeding adults, and movements to new areas by birds in late winter (Eddleman 1989). These dispersal movements allow birds to find new or ephemeral habitats, such as on lower Colorado River in the past (Ohmart et al. 1975). Fall dispersal also occurs in San Francisco Bay, CA, area (Linsdale 1936, Orr 1939). Has been suggested as a mechanism for occupying ephemeral habitat, new habitat, or habitats in which local extinction has occurred (Orr 1939, Remsen and Parker 1990). Dispersal distances of 3 individuals from s. California were minimum of 23.5, 32.2, and 12.9 km, respectively (Zembal et al. 1985). One banded male dispersed from Upper Newport Bay, CA, to Seal Beach National Wildlife Refuge, CA, between 5 Oct and 29 Dec 1982, a distance of 21.7 km.

Home range. During breeding season, banded birds in S. Carolina occur in range with diameter of 183–274 m (Blandin 1963). Mean maximum movement of birds occurring along canals in Louisiana was 154 m ± 37 SD during Aug and 487 m ± 467 SD in Dec–Feb (Roth et al. 1972). Daily home range of 3 breeding adults in Louisiana averaged 0.44 ha, and total breeding-season home range averaged 0.53 ha (Sharp 1976). Home range in Arizona shows great seasonal variation: for males—largest (24.0 ha ± 15.7 SD, $n = 6$) in Jan–Feb and smallest (3.6 ha ± 2.8 SD, $n = 9$) during incubation; for females—largest (21.0 ha ± 8.7 SD, $n = 8$) in Aug–Oct, and smallest (2.2 ha ± 1.8 SD, $n = 4$) during incubation (Eddleman 1989). Home ranges in s. California ranged from 0.4 to 1.7 ha, and adults generally used only a small portion of their entire range within a day (Zembal et al. 1989). Home range boundaries of adjacent individuals overlap considerably (Zembal et al. 1989, WRE).

POPULATION STATUS

Numbers. Density in ideal habitat 2.2–4.7 individuals/ha in Georgia (Oney 1954), 3.2/ha in New Jersey, and 8.4/ha in Virginia (Mangold 1977). Number of active nests ranged from 1.0 to 1.6/ha during 6-yr study in New Jersey (Mangold 1974). Nest density at Chincoteague, VA, was 4.2/ha (Stewart 1951). Density was 0.9–1.6/ha in San Francisco Bay, CA (Harvey 1988); density in s. California ranges from 0.12 pair/ha at Anaheim Bay to 2.0 individuals/ha in Upper Newport Bay (Zembal and Massey 1987). Density in habitats of different quality ranges from 0.09 to 0.79 individual/ha in Arizona (Smith 1974).

Trends. Few data available, except for endangered western subspecies, which have declined greatly during past 100 yr (see Conservation and management: effects of human activity, below). On basis of limited Breeding Bird Survey data, Clapper Rail populations showed no increasing or decreasing trend from 1966 to 1994 (Sauer et al. 1996). However, populations appear to have declined at rate of 8.2% in U.S. during 1966–1979 ($p < 0.01$). Declines appear greatest in Texas and Louisiana. Clapper Rails occurred on only 20 routes with usable data during this time, so this trend should be interpreted with extreme caution. Distribution of Clapper Rails in Maryland largely unchanged during past century, although numbers have probably been reduced because of habitat loss (Robbins and Blom 1996).

POPULATION REGULATION

Along Atlantic Coast, Clapper Rail population limited by nesting losses of eggs and young caused by high tides in association with storms (Bent 1926, Kozicky and Schmidt 1949, Adams and Quay 1958). Ability to repeatedly renest allows populations in good habitat to recover rapidly (Blandin 1963). Storms affecting major wintering areas on s. Atlantic Coast may cause direct mortality of large numbers of adults (Ferrigno 1990). Breeding populations were at record lows in New Jersey in 1990 after Hurricane Hugo struck a major Clapper Rail wintering area in Oct 1989. Flooding also believed to be important factor for population regulation in coastal Texas (Simmons 1914). Sand deposition after Hurricane Frederic in 1979 affected salt marsh cordgrass distribution, and therefore Clapper Rail distribution (Holliman 1981). Populations probably recover after cordgrass reinvades such areas. Elevated beaches or tree lines may protect salt marshes from storm damage.

Other factors affecting populations in New Jersey include territoriality (in dense populations), predation, interspecific competition with Laughing Gulls, pesticides, winter kill, and habitat loss (Ferrigno 1990). Nest predation by raccoons, mink, or opossums is an important limiting factor in Georgia, Louisiana, and Texas (Simmons 1914, Oney 1954, Bateman 1965); and probably also elsewhere (Sharp 1976, Eddleman and Conway 1994). Populations of *obsoletus* in San Francisco Bay, CA, have declined mainly because of predation on adults by introduced Norway rats and red foxes (Harvey 1988). Predation is principal cause of mortality in adult *yumanensis* in sw. Arizona (Eddleman 1989). Availability of quality habitat is a principal limiting factor for West Coast subspecies (Eddleman et al. 1988, Fleischer et al. 1995). Nest-site availability thought to limit *levipes* populations in s. California (Zembal and Massey 1983).

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. Extremely abundant in early 1900s, and hunted for food and profit; tens of thousands of birds taken in 2 d in 1896 in New Jersey (Forbush 1925), and as many as 200 birds/d taken by many market hunters in San Francisco Bay, CA (U.S. Dept. of the Interior 1991). Annual harvest in Virginia in 1922 estimated at 25,000 birds (Forbush 1925). Currently on list of game birds in all coastal eastern states from Rhode Island to Texas, except New York (Eddleman and Conway 1994). Assessment of number taken per year unreliable. Past estimates were based on number taken by waterfowl hunters, which may represent only 60%

of harvest and group Clapper Rail with King and Virginia rails (Banks 1979, Martin 1979). These data show combined harvest of 100,983/yr from 1964 to 1986 (95% CI, 74,100–127,400). State estimates of harvest (1987–1988 in Louisiana, 1990–1991 for other states) available only for Louisiana (20,000), Virginia (9,549), Texas (1,200), New Jersey (800), and Maryland (200; Eddleman and Conway 1994).

Harvest size highly dependent on timing of fall migration in north, because few birds may be available for hunting in years when migration begins before 1 Sep. Hunting pressure heaviest in New Jersey, S. Carolina, and Georgia. Season opening dates ranged from 19 Aug (Virginia) to 19 Sep (Louisiana) in 1990. Bag limits liberal (10–15 daily), but few hunters take Clapper Rails (Eddleman and Conway 1994). Hunting season lasts 2.0–2.5 mo in most states.

Effects of harvest unknown, but probably minimal because of small number of hunters, timing of seasons after peak of migration, difficulty of hunting rails, and tendency of rails to run rather than flush (Eddleman et al. 1988). Most state biologists responding to survey indicated little need for change in existing regulations, although 3 indicated that reducing bag limits might be warranted because of lack of information about population biology (WRE).

Clapper Rails occasionally caught and killed in traps set for fur-bearing animals such as mink or muskrats (Simmons 1914, Eddleman et al. 1988). This probably has little effect on populations, however. Eggs once gathered in large numbers for food in southern states (Forbush 1925).

Pesticides and other contaminants/toxics. Coastal wetlands in which Clapper Rails occur serve as settling basins for a wide variety of toxic materials (Eddleman et al. 1988). Specific effects of most of these materials on Clapper Rails unknown. Captives fed DDT are relatively resistant to it; show no immediate effects (Van Velzen and Kreitzer 1975). Long-term reproductive effects unknown.

Eggs collected in New Jersey, Virginia, and S. Carolina in 1972–1973 had residues of DDE and PCBs (ranging from 0.10 to 1.3 ppm), but showed no eggshell thinning (Klaas et al. 1980). Mercury contamination in breast muscle of 93.5% of birds collected near Brunswick, GA, exceeded Food and Drug Administration's tolerance level of 0.5 ppm (ranging from 0.01 to 9.45 ppm wet weight; Odom 1975). Residues of DDD, DDT, DDE, dieldren, heptachlor epoxide, and PCBs were found in body tissues of 27 birds from Louisiana, but all were below levels that might cause concern (Roth 1972). Mercury levels in *obsoletus* eggs from San Francisco Bay, CA, were higher than those from N. Carolina, and within the range associated with developmental abnormalities in other birds (Lonzarich et al. 1992). Selenium levels were also elevated in *obsoletus* eggs, but lower than values causing reproductive effects in American Coots (*Fulica americana*). Two of 7 eggs of *levipes* from s. California analyzed in 1983 had DDE levels of 9.6 and 6.8 ppm, respectively—within the range that causes poor reproduction in other species (Eddleman et al. 1988). Several compounds found in chlordane (oxychlordane, heptchlor epoxide, trans- and dis-nonachlor, MC-2, and MC-5) were detected in *levipes* eggs in s. California (Jarman 1991). MC-2 bioaccumulated to greatest degree. Selenium accumulates in sediments and crayfish prey of *yumanensis* in backwater habitats on lower Colorado River in Arizona and California (mean liver selenium level 25.3 ppm dry weight ± 5.9 SD, $n = 5$; Rusk 1991). This level unlikely to cause adult mortality, but conveys moderate to high risk of hatching defects in chicks.

Collisions with stationary/moving structures or objects. Sometimes collides with TV towers, lighthouses, telephone wires, or fences (Emerson 1904, Forbush 1925, Murray 1929, Taylor and Kershner 1986, Allen and Ramirez 1990). Timing of strikes corresponds with fall migration, spring migration, or fall dispersal (Orr 1939). Sometimes hit by vehicles if roads bisect marshes (Zembal et al. 1989). Vehicle collisions accounted for 1.5% of 156 recoveries of birds banded in New Jersey (Ferrigno 1990).

Degradation of habitat. Interference with tidal flow is the most common mode of habitat degradation for Clapper Rails (Meanley 1985, Eddleman and Conway 1994). Effects of this problem include drying of habitats such that high marsh or terrestrial plants replace low marsh plants favored for nesting and foraging by Clapper Rails, lowering of salt content, invasion of habitat by common reed (*Phragmites australis*), or permanent flooding of marshes by construction of impoundments. Nonetheless, large areas of suitable habitat remain on East Coast. Wetlands of Baja California are largely intact, although threatened by resort and industrial development planned by international companies and salt evaporation pond development (Massey and Palacios 1994).

Loss and degradation of habitat because of urbanization in coastal California has been severe (Eddleman et al. 1988); <33% of original habitat in range of *levipes* remains intact in s. California, although more remains in Mexico. About 80–90% of the original 73,500 ha of marsh in San Francisco Bay, CA, has been filled, destroyed, or diked, and much of the remainder is degraded (U.S. Dept. of the Interior 1991). Former habitat of *yumanensis* mostly in Colorado River delta, because most wetlands on lower part of river were ephemeral (Ohmart et al. 1975). Much of habitat today consists of marshes formed behind dams from Needles, CA, to Mexican border. Most water reaching Colorado River delta in n. Mexico comes from floodwater, irrigation runoff, and municipal sewage effluent, but these sources do maintain >5,800 ha of *yumanensis* habitat (Glenn et al. 1996). Much of this habitat is threatened by water diversion to Gulf of California and future disposal of salt into the sources of water from desalinization plant.

Direct human/research impacts. Introduction of exotic mammals such as red foxes, rats, dogs, and cats is a major factor in the decline of *obsoletus* since 1970, and to a lesser extent, *levipes*. Harnesses used for attaching radio transmitters may affect survival by interfering with ability to fly (WRE). Nest traps caused 56% of trapped birds to desert nests (Blandin 1963).

MANAGEMENT

Conservation status. Stable in eastern U.S., provided that wetland degradation ceases. Protected status accorded to Clapper Rails in New York because of lack of information on effects of hunting (WRE). Status and biology of *insularum* of Florida Keys least known among North American subspecies; status of Central and South American taxa unknown or poorly known (Ripley 1977). Monitoring programs used for other bird species are not effective for wetland species such as Clapper Rails, and valid information on status must await development and implementation of new monitoring techniques (Eddleman and Conway 1994).

Three taxa of Clapper Rail—*obsoletus*, *levipes*, and *yumanensis*—are classified as both state and federally Endangered (Arizona Game and Fish Dept. 1988, California Dept. of Fish and Game 1989, USFWS 1989). Initially, *levipes* and *obsoletus* populations declined because of overhunting (Leipsic-Baron 1992). With protection, *obsoletus* rebounded in numbers, but *levipes* did not. Past wetland loss and degradation has been severe in coastal California and in Colorado River ecosystem, and all 3 subspecies have declined since 1900 as result of habitat loss. In addition, nearly all habitats of these taxa have contaminants either in water inflows or in sediments. Low fertility and egg-hatching success in northern populations of *levipes* may be result of contaminants or inbreeding (Eddleman et al. 1988, Fleischer et al. 1995). Very little genetic variation detected in *levipes* populations, but effects of inbreeding have not been assessed. Numbers estimated at 300–600 pairs in U.S. (Small 1994). Numbers of *obsoletus* estimated at 4,000–6,000 birds in mid-1970s, 1,000 in mid-1980s, <700 by 1988, <500 by 1991, and by 1996 <300 (U.S. Dept. of the Interior 1991). Remaining *yumanensis* number about 700 (Shuford 1993, Small 1994). Estimates of genetically effective population size based on mitochondrial DNA microsatellites for *levipes* (N_e = 174–283) and *yumanensis* (N_e = 824; Fleischer et al. 1995) lend credence to call-survey estimates.

Measures proposed and taken; effectiveness of measures. Continued implementation of wetland protection laws is the most effective conservation technique for Clapper Rails (Eddleman and Conway 1994). Most habitat management programs for coastal subspecies have involved preservation or restoration of tidal flow (Shisler and Schulze 1976, Ferrigno et al. 1987). Tidal restoration of salt hay impoundments, in which areas diked for hay production in New Jersey salt marshes have had tidal flow restored, has improved some marshes for Clapper Rail (Ferrigno et al. 1987). Open marsh water management, used in many eastern salt marshes to control mosquitoes, consists of connecting existing pools in salt marshes to allow fish to move between pools and eat mosquito larvae (Shisler and Schulze 1976, Erwin et al. 1994). Effects of open marsh water management on rails poorly known, although spoil from the ditches may provide additional nest sites for Clapper Rails. Management for *levipes* in s. California is same as management for Pacific cordgrass (Foin and Benchley-Jackson 1991): Techniques include keeping salt marshes open to tidal flow, restoring potential remaining wetland areas, and expanding efforts to improve habitat where there is the greatest potential for cordgrass enhancement. Habitat acquisition for *obsoletus* in s. San Francisco Bay, CA, has helped slow population decline (U.S. Dept. of the Interior 1991).

Improved harvest assessment for hunted subspecies is possible with implementation of migratory bird permit requirement for hunting Clapper and other rails (Tautin et al. 1989). Translocations among *levipes* populations in s. California and from *yumanensis* to *levipes* populations have been suggested to increase genetic variation of *levipes* (Fleischer et al. 1995). Control of nonindigenous predators (red fox) undertaken to increase numbers of *obsoletus*, and estimates of population in s. San Francisco Bay, CA, doubled in 1993 (from 300 to 600) after predator removal in 1992 (Takekawa 1993). Predator control (domestic cats) also resulted in increased number of *levipes* at Seal Beach National Wildlife Refuge, CA.

Recommendations for stabilization and increase of *yumanensis* populations include: increased consideration of the subspecies in management of federal and state wildlife refuges; continued population monitoring; year-round management based on the assumption of year-round residency by the subspecies; water level manipulations on diked impoundments; restoration of wetlands in Colorado

River delta; maintenance of irrigation drain water to Cienega de Santa Clara; and careful monitoring of river management and mitigation projects conducted in the habitat (Eddleman 1989, Glenn et al. 1996). Maintenance of existing marshes and creation of new marsh habitats using dikes, impoundments, and reliable sources of water would provide improved nesting and foraging areas for this subspecies (Eddleman and Conway 1994).

APPEARANCE

MOLTS AND PLUMAGES

Considerable variation in plumage color within many subspecies; described as color phases or morphs; not related to age, sex, or adventitious coloring (Oberholser 1937). Five color morphs are light gray, dark gray, light brown, dark brown, and gray-breasted (upperparts like dark brown morph). Possible other explanations for color morphs include different hormonal levels in different birds (Ripley 1977), hybridization with King Rail (Ripley 1977, Meanley 1985), or previously undescribed variations in plumage progression (WRE). Clarification of color morphs and their significance will depend on detailed study of birds of different age, sex, and genetic background. Feathers from head and neck have tips extended; oval in cross section (Brush 1967). Function of tipping unknown.

Molt and plumage descriptions based on *crepitans* from Atlantic Coast of U.S., with supplementary information on *yumanensis* from Arizona. Color terminology follows Ridgway 1912 for *crepitans* and Smithe 1975–1981 for *yumanensis*, based on the literature and examination of living specimens. Additional plumage descriptions are presented in Bent 1926, Oberholser 1937, Ridgway and Friedmann 1941, and Ripley 1977.

Hatchlings. Covered with jet black down with greenish gloss above; blackish-brown below, with slight greenish gloss anteriorly, but abdomen dark blackish clove brown (Oberholser 1937). Individuals have 1–30 white neossoptiles in anterior abdominal region of ventral tract (Wetherbee and Meanley 1965). Presence of these neossoptiles once thought to be a trait that differed between Clapper and King rails, but reflects individual variation (Ripley 1977).

Juvenal plumage. Prejuvenal molt complete; plumage acquired in first 6–8 wk. Juvenal feathers appear at 4 wk after hatching, first in auricular area, then in ventral and femoral tracts. By age 5 wk, feathers appear in all except capital, caudal, and alar tracts. All tracts have growing feathers by age 6 wk. Plumage begins to be replaced by Basic I plumage shortly after completion of Prejuvenal molt, so molt may appear to be continuous with Prebasic I molt.

Juvenal plumage similar to Basic I for *crepitans* (see below), but lower back, rump, and uppertail-coverts more uniformly olive brown to sepia, with margins reduced or obscure (Ridgway and Friedmann 1941). Greater and median upperwing-coverts more generally tipped with narrow whitish band and subterminally crossed by narrow white bar. Grayish below, but paler than adult. Abdomen more extensively white; side and flanks mouse gray to deep mouse gray, barred irregularly with grayish white; sides washed with pale cinnamon buff; thighs white anteriorly, deep mouse gray posteriorly. Juvenal plumage in *yumanensis* similar, but differs greatly from cinnamon buff underparts and brownish upperparts of adult. Some individual juveniles have blackish feathers along sides and flanks; similar to Juvenal plumage of Virginia Rail.

Basic I plumage. Prebasic I molt partial; does not include rectrices or remiges. Commences when flight-feathers are about half unsheathed (Meanley 1985). Completed between late Aug and Nov on Atlantic Coast of U.S., and between 1 Aug and 31 Oct in Arizona (Oberholser 1937, WRE). Upperparts from forehead to uppertail-coverts, including upperwing-coverts, buffy olive brown to light sepia; feathers of back and rump, and some of upperwing-coverts, conspicuously margined with neutral gray to olive gray, the margins most pronounced on interscapulars, scapulars, and upper back, and the brownish centers of the feathers usually darkest on scapulars (Ridgway and Friedmann 1941). Remaining upperwing-coverts dark buffy brown to olive brown or umber, narrowly edged with slightly paler shade. Rectrices dark olive brown. Superciliary line white, often washed with buffy; lores deep mouse gray with faint brownish tinge; eyelids whitish or pale buffy; cheeks, auriculars, and side of occiput neutral gray to deep neutral gray, washed lightly with brownish in some individuals. Chin and upper throat white; side of neck and lower throat grayish hair brown to dusky grayish buffy brown in some individuals. In other individuals, these areas pale cinnamon buff, slightly clouded with grayish. Breast like lower throat, but paler, less grayish. Abdomen whitish to pale buffy white, sides and flanks barred with dusky drab and white, the white bars about one-third to one-half the width of the dark bars. Crissum like flanks; thighs like abdomen, but washed or barred with dusky drab. Longer undertail-coverts almost entirely white, the others dusky drab barred with white. Underwing-coverts Dresden brown to Prout's brown, crossed by narrow white bars. Considerable variation in overall plumage color among different subspecies (see Systematics: geographic variation, above).

Alternate I plumage. Prealternate I molt poorly described. Oberholser (1937) states that Clapper Rails molt only once per year, but year-round trapping in Arizona indicated a second peak in body molt in Oct and a lesser peak in Jan–Feb (WRE). Part of this molt may involve completion of Prebasic molt, but at least some body molt was repeated on retrapped individuals, indicating Prealternate molt. Not known if this molt represented Prealternate I, Definitive Prealternate, or both. Involves head, neck, back, ventrum, leg, tail-coverts, and wing-coverts, and apparently is prolonged through late fall–winter. Similar to Basic I plumage, but Juvenal flight-feathers and possibly tail retained. Body plumage and remiges become much faded and frayed by end of breeding season.

Definitive Basic plumage. Definitive Prebasic molt complete; occurs after breeding (see Fig. 4). All remiges and all rectrices lost simultaneously; loss of remiges precedes loss of rectrices by a few days (WRE). Duration of flightless period about 1 mo in *crepitans*, 3.5 wk in *yumanensis* (Meanley 1985, WRE). Body molt begins about 6 wk before molt of flight-feathers, commencing on head and neck and progressing to all other body regions within 1 mo (Eddleman 1989). Individuals molt wing- and tail-feathers between 10 Jul and 15 Sep. Plumage indistinguishable from Basic I, as far as known.

Definitive Alternate plumage. Definitive Prealternate molt partial; probably similar to Prealternate I molt (needs more study). Definitive Alternate plumage does not differ from Alternate I.

BARE PARTS

Color terminology for *yumanensis* based on Smithe 1975–1981.

Bill and gape. *crepitans*. Bill gray brown along culmen and ventral part of lower mandible; orange yellow or orange red from base to nares on upper mandible and on upper part of lower mandible (Meanley 1985). Color less intense in immature in early fall: light yellowish, straw yellow, or flesh. Gape in adult is orange red, yellowish in juveniles and fall immatures.

yumanensis. Dorsal surface of upper mandible and ventral surface of lower mandible dark grayish brown, sepia, or raw umber in adult; side of bill burnt orange, chrome orange, or orange rufous (WRE). Juvenile bill similar in color to adult bill on top and bottom; side is natal brown or sepia at first, changing by fall to cinnamon drab, smoke gray, or fawn color, then to true cinnamon, light russet vinaceous, or orange rufous. Gape duller than in *crepitans* and shows little variation with age (WRE).

Iris. *crepitans*. Reddish orange in adult (Meanley 1985). Eye color dark brown at hatching; turns olive brown or olive drab at about 6 wk; dull brown or orange brown by early fall (Adams and Quay 1958, Meanley 1985).

yumanensis. Amber, raw sienna, Pratt's rufous, or kingfisher rufous in adult (WRE). Sepia or fuscous in younger chicks, gradually changing to shades of olive (dark brownish olive, olive brown, olive green, or grayish olive), then cinnamon brown, and finally becoming like adult in late summer and early fall.

Legs and feet. *crepitans*. Light yellow or pinkish in adults; heel area brighter in some individuals (Meanley 1985). Duller in immature.

yumanensis. Leading edge of tarsus sayal brown, true cinnamon, verona brown, or robin rufous in adult, fading to verona brown or ground cinnamon on trailing edge (WRE). Darker in immatures; light drab or drab gray on leading edges, sepia or dark drab on trailing edge. Toes somewhat darker shade than tarsus.

MEASUREMENTS

LINEAR

Males average larger than females in all measurements (see Appendix). Considerable geographic variation in size, but exact patterns difficult to delineate because of lack of data from large portions of range. Wing longer in subspecies on West Coast of U.S.; shortest in subspecies in tropical areas. Bill tends to be longest in northern, central Caribbean, and Mexican subspecies and smallest in South American birds. Tarsus longer in West Coast and central Caribbean subspecies; shortest in South American forms. Measurements of North American subspecies given in Appendix.

MASS

Little information for most subspecies; most data are from breeding birds or hunter-killed birds taken in autumn (see Appendix). Mass shows considerable variation among sexes, subspecies, and times of year. Mass lowest after stresses of breeding and Prebasic molt and greatest during midwinter (Eddleman 1989). Mass of male *yumanensis* in Arizona (mean [g] ± SD): 270.9 ± 31.8 (range 207–319, n = 19) during early breeding season (Mar–Apr); 257.9 ± 31.9 (range 166–336, n = 58) during late breeding season (May–Jul); 268.2 ± 38.9 (range 206–344, n = 17) during postbreeding season (Aug–Oct); and 311.7 ± 24.6 (range 259–347, n = 14) during winter (Nov–Feb; WRE). Suggests that mass data must be interpreted in light of time of year.

PRIORITIES FOR FUTURE RESEARCH

Research needs for the habitat and harvest management of the Clapper Rail have been summarized by Eddleman and Conway (1994). They include research on methods for assessing relative abundance, distribution, and population trends using tape playback or call counts; additional banding programs to determine survival rates, local population sizes, and migration patterns; additional research on habitat manipulations and the effects of habitat management practices; the development of methods to assess harvest; and investigations of basic biology, with emphasis on variation in population parameters, calling behavior (using consistent terminology for the various vocalizations), external age and sex determination, postbreeding biology, and winter biology.

Information on distribution, especially outside the United States, is needed, as well as clarification of the taxonomic status of several subspecies. Additional material is needed to determine the validity of several subspecies from the Caribbean and adjacent mainland areas that are described from < 10 specimens. Several taxonomic questions might be answered by detailed study of molts and plumages using captives or conducted in conjunction with intensive trapping and marking of a local population. The nature of geographic variation in measurements and plumage is poorly known and needs clarification (Kale 1978). At least one researcher has questioned the validity of all subspecies in the eastern United States (Heard 1983). Most study of Clapper Rails in the Americas since 1980 has focused on endangered western taxa (*obsoletus*, *levipes*, *yumanensis*) or on populations on the northern Atlantic Coast; additional work is needed on all aspects of the biology of birds in other portions of the geographic range, especially those found mainly in mangrove habitats (Kale 1978, Owre 1978). Contaminants accumulate in most habitats used by Clapper Rails (Eddleman et al. 1988); additional study of the effects of these potential toxins on reproduction and mortality is essential to conservation programs for this species.

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REFERENCES

Adams, D. A., and T. L. Quay. 1958. Ecology of the Clapper Rail in southeastern North Carolina. J. Wildl. Manage. 22: 149–156.

Allen, G. T., and P. Ramirez. 1990. A review of bird deaths on barbed-wire fences. Wilson Bull. 102: 553–558.

Alvarez, F. 1993. Alertness signalling in two rail species. Anim. Behav. 46: 1229–1231.

American Ornithologists' Union. 1983. Checklist of North American birds. 6th ed. Am. Ornithol. Union, Washington, D.C.

Amos, E. J. R. 1991. The birds of Bermuda. Corncrake, Warwick, Bermuda.

Anderson, B. W., and R. D. Ohmart. 1985. Habitat use by Clapper Rails in the lower Colorado River Valley. Condor 87: 116–126.

Applegarth, J. H. 1938. The ecology of the California Clapper Rail on the south arm of San Francisco Bay. M.S. thesis, Stanford Univ., Palo Alto, CA.

Arizona Game and Fish Department. 1988. Threatened native wildlife in Arizona. Arizona Game and Fish Dept. Publ., Phoenix.

Arnett, J. H., Jr. 1951. Great Blue Heron captures Clapper Rail. Cassinia 38: 32–33.

Avise, J. C., and R. M. Zink. 1988. Molecular genetic divergence between avian sibling species: King and Clapper Rails, Long-billed and Short-billed Dowitchers, Boat-tailed and Great-tailed Grackles, and Tufted and Black-crested Titmice. Auk 105: 516–528.

Bailey, S. F. 1977. "Ornithological mystery story" revisited—the plot thickens. Am. Birds 31: 1051–1056.

Baldwin, W. P. 1940. Bald Eagle robbing Marsh Hawk. Auk 57: 413.

Bang, B. G., and B. M. Wenzel. 1985. Nasal cavity and olfactory system. Pp. 195–225 *in* Form and function in birds. Vol. 3 (A. S. King and J. McLelland, eds). Academic Press, New York.

Banks, R. C. 1974. Clapper Rail in Tamaulipas, Mexico. Wilson Bull. 86: 76–77.

Banks, R. C. 1979. Human related mortality of birds in the United States. U.S. Fish and Wildl. Serv. Spec. Sci. Rept.—Wildl. No. 215.

Banks, R. C., and R. E. Tomlinson. 1974. Taxonomic status of certain Clapper Rails of southwestern United States and northwestern Mexico. Wilson Bull. 86: 325–335.

Bateman, H. A., Jr. 1965. Clapper Rail (*Rallus longirostris*) studies on Grand Terre Island, Jefferson Parish, Louisiana. M.S. thesis, Louisiana State Univ., Baton Rouge.

Bates, B. H., Jr., and T. G. Meade. 1972. Helminth parasites of the King Rail, *Rallus elegans* Aud., and Clapper Rail, *Rallus longirostris* Boddaert, of the Bolivar Peninsula, Texas. Proc. Helminth. Soc. Wash. 39: 146–147.

Bennett, W. W., and R. D. Ohmart. 1978. Habitat requirements and population characteristics of the Clapper Rail (*Rallus longirostris yumanensis*) in the Imperial Valley of California. Univ. of California, Lawrence Livermore Lab., Livermore, CA.

Bent, A. C. 1926. Life histories of North American marsh birds. U.S. Natl. Mus. Bull. 135.

Bevier, L. R., ed. 1994. The atlas of breeding birds of Connecticut. State Geol. Nat. Hist. Surv. Connecticut Bull. no. 113.

Blandin, W. W. 1963. Renesting and multiple brooding studies of marked Clapper Rails. Proc. Ann. Conf. Southeast. Game & Fish Comm. 17: 60–68.

Blandin, W. W. 1965. Marsh hen investigation. Ann. Progr. Rep., Proj. W-31-R. S. Carolina Wildl. Resour. Dept., Columbia.

Bledsoe, A. H. 1988. Status and hybridization of Clapper and King Rails in Connecticut. Conn. Warbler 8: 61–65.

Bond, J. 1971. Birds of the West Indies. 2nd ed. Houghton Mifflin Co. Boston, MA.

Bongiorno, S. F. 1968. Egg puncturing behavior in Laughing Gulls. Auk 85: 697–699.

Brooks, D., and R. W. Heard, III. 1977. Parasites of the Clapper Rail, *Rallus longirostris* Boddaert. III. Description of *Notocotylus schmidti* sp. n. (Digenea: Notocotylidae). Proc. Biol. Soc. Wash. 44: 63–65.

Brudenell-Bruce, P. G. C. 1975. The birds of the Bahamas—New Providence and the Bahama Islands. Taplinger Publ. Co., New York.

Brush, A. H. 1967. Additional observations on the structure of unusual feather tips. Wilson Bull. 79: 322–327.

Burt, D. B., D. Burt, T. C. Maxwell, and D. G. Tarter. 1987. Clapper Rail (*Rallus longirostris*) in west-central Texas. Tex. J. Sci. 39: 378.

Byrd, E. L., and R. W. Heard, III. 1970. Two new kidney flukes of the genus *Renicula* Cohn, 1904, from the Clapper Rail *Rallus longirostris*. J. Parasitol. 56: 493–497.

California Department of Fish and Game. 1989. List of the state and federal endangered and threatened animals of California. California Dept. Fish and Game, Sacramento.

Clapp, R. B., M. K. Klimkiewicz, and J. H. Kennard. 1982. Longevity records of North American birds: Gaviidae through Alcidae. J. Field Ornithol. 53: 81–124.

Clark, J. D., and J. C. Lewis. 1983. A validity test of a habitat suitability index model for Clapper Rail. Proc. Ann. Conf. Southeast. Assoc. Fish Wildl. Agen. 37: 95–102.

Conway, C. J. 1990. Seasonal changes in movements and habitat use by three sympatric species of rails. M.S. thesis, Univ. of Wyoming, Laramie.

Conway, C. J., W. R. Eddleman, S. H. Anderson, and L. R. Hanebury. 1993. Seasonal changes in Yuma Clapper Rail vocalization rate and habitat use. J. Wildl. Manage. 56: 282–290.

Conway, G. L., M. R. Hughes, and R. R. Moldenhauer. 1988. Extra-renal salt excretion in Clapper and King rails. Comp. Biochem. Physiol. A Compar. Physiol. 91: 671–674.

Cory, C. B. 1888. The birds of the West Indies, including the Bahama Islands, the Greater Antilles, excepting the islands of Tobago and Trinidad. Auk 5: 48–82.

Cottam, C., and A. L. Nelson. 1937. Winter nesting and winter food of the Barn Owl in South Carolina. Wilson Bull. 49: 283–285.

Crawford, R. L., S. L. Olson, and W. K. Taylor. 1983. Winter distribution of subspecies of Clapper Rails (*Rallus longirostris*) in Florida with evidence for long-distance and overland movements. Auk 100: 198–200.

Deblock, S., and R. W. Heard, III. 1969. Contribution a l'etude des Microphallidae Travassos, 1920 (Trematoda). XIX. Description de *Maritrema prosthometra* n. sp. et de *Longiductotrema* nou. gen. parasites d'Oiseaux Ralliformes d'Amerique du Nord. Ann. Parasit. 44: 415–424.

DeGroot, D. S. 1927. The California Clapper Rail: its nesting habits, enemies, and habitat. Condor 29: 259–270.

Dod, A. S. 1981. Guia de campo para las aves de la Republica Dominica. A. S. Dod, Santo Domingo.

Downer, A., and R. L. Sutton. 1990. Birds of Jamaica: a photographic field guide. Cambridge Univ. Press, Cambridge, U.K.

Duhsé, R. J. 1988. Observing the secretive Clapper Rail. Florida Wildl. Sept–Oct 1988: 31–33.

Eddleman, W. R. 1989. Biology of the Yuma Clapper Rail in the southwestern U.S. and northwestern Mexico. Final Rept., Intra-Agency Agreement No. 4-AA-30-02060, U.S. Bur. Reclam., Yuma Proj. Off., Yuma, AZ.

Eddleman, W. R., and C. J. Conway. 1994. Clapper Rail. Pp. 167–179 *in* Management of migratory shore and upland game birds in North America (T. C. Tacha and C. E. Braun, eds.). International Association of Fish and Wildlife Agencies, Washington, D.C.

Eddleman, W. R., F. L. Knopf, B. Meanley, F. A. Reid, and R. Zembal. 1988. Conservation of North American rallids. Wilson Bull. 100: 458–475.

Emerson, W. O. 1904. Destruction of birds by wires. Condor 6: 37–38.

Enser, R. W. 1992. The atlas of breeding birds in Rhode Island. Rhode Island Dept. of Environ. Manage., Providence.

Erwin, R. M., J. S. Hatfield, M. A. Howe, and S. S. Klugman. 1994. Waterbird use of saltmarsh ponds created for open marsh water management. J. Wildl. Manage. 58: 516–524.

Evans, P. G. H. 1990. Birds of the eastern Caribbean. Macmillan Press, Ltd., London.

Fargo, W. G. 1927. Feeding station habit of Fish Crow. Auk 44: 566–567.

Feduccia, J. A. 1968. The Pliocene rails of North America. Auk 85: 441–453.

Ferrigno, F. 1990. Clapper Rail nesting survey. P. R. Proj. No. W-58-R-14, Job II-A. New Jersey Div. Fish., Game, Wildl., Trenton.

Ferrigno, F., J. K. Shisler, J. Hansen, and P. Slavin. 1987. Tidal restoration of salt hay impoundments. Pp. 284–296 *in* Waterfowl and wetlands symposium (W. R. Whitman and W. H. Meredith, eds.). Delaware Dept. Nat. Resour. Environ. Control., Dover.

Fleischer, R. C., G. Fuller, and D. B. Ledig. 1995. Genetic structure of endangered Clapper Rail (*Rallus longirostris*) populations in southern California. Conserv. Biol. 9: 1234–1243.

Foin, T. C., and J. L. Benchley-Jackson. 1991. Simulation model evaluation of potential recovery of endangered Light-footed Clapper Rail populations. Biol. Cons. 58: 123–148.

Forbush, E. H. 1925. Birds of Massachusetts and other New England states. Vol. I. Waterbirds, marshbirds, and shorebirds. Mass. Dept. of Agric., Boston.

Foss, C. R. 1994. Atlas of breeding birds in New Hampshire. Chalford Publ. Co., Dover, NH.

Garrido, O., and A. Kirkconnell. 1993. Checklist of Cuban birds. Published by the authors, Havana.

Gill, R., Jr. 1979. Status and distribution of the California Clapper Rail (*Rallus longirostris obsoletus*). Calif. Fish Game 65: 36–49.

Glenn, E. P., C. Lee, R. Felger, and S. Zengel. 1996. Effects of water management on the wetlands of the Colorado River Delta, Mexico. Conserv. Biol. 10: 1175–1186.

Glick, B. 1963. An unusual location for a Clapper Rail. Wilson Bull. 75: 93.

Godfrey, W. E. 1986. The birds of Canada. Rev. ed. Natl. Mus. Nat. Sci., Ottawa.

Grant, G. S. 1970. Rattlesnake predation on the Clapper Rail. Chat 34: 20–21.

Hammons, R. L., M. R. Hughes, and R. R. Moldenhauer. 1988. Body water and water flux in fresh water and sea-water acclimated Clapper Rails, *Rallus longirostris*. Comp. Biochem. Physiol. A Comp Physiol. 91: 539–541.

Harvey, T. E. 1988. Breeding biology of the California Clapper Rail in south San Francisco Bay. Trans. West. Sect. Wildl. Soc. 24: 98–104.

Heard, R. W., III. 1968. Parasites of the Clapper Rail, *Rallus longirostris* Boddaert. I. The current status of the genus *Levinseniella* with the description of *Levinseniella byrdi* n. sp. (Trematoda: Microphallidae). Proc. Helminthol. Soc. Wash. 35: 62–67.

Heard, R. W. 1970. Parasites of the Clapper Rail, *Rallus longirostris* Boddaert. II. Some trematodes and cestodes from *Spartina* marshes of the eastern United States. Proc. Helminthol. Soc. Wash. 37: 147–153.

Heard, R. W. 1983. Observations on the food and food habits of Clapper Rails (*Rallus longirostris* Boddaert) from tidal marshes along the East and Gulf Coast of the United States. Gulf Res. Repts. 7: 125–135.

Hellmayr, C. E., and B. Conover. 1942. Catalogue of birds of the Americas and the adjacent islands in Field Museum of Natural History. Part I, No. 1. Field Mus. Nat. Hist. Zool. Ser. Publ. 514.

Hess, G. K., R. L. West, M. V. Barnhill, and L. M. Fleming. In press. Birds of Delaware. Univ. of Pittsburgh Press, Pittsburgh, PA.

Hilty, S. L., and W. L. Brown. 1986. A guide to the birds of Columbia. Princeton Univ. Press, Princeton, NJ.

Holliman, D. C. 1978. Clapper Rail (*Rallus longirostris*) studies in Alabama. Northwest Gulf Sci. 2: 24–34.

Holliman, D. C. 1981. A survey of the September 1979 hurricane damage to Alabama Clapper Rail habitat. Northwest Gulf Sci. 5: 95–98.

Hon, T., R. R. Odom, and D. P. Belcher. 1977. Results of Georgia's Clapper Rail banding program. Proc. Ann. Conf. Southeast. Assoc. Fish Wildl. Agen. 31: 72–76.

Howell, S. N. G., and S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford Univ. Press, New York.

Jackson, J. A. 1983. Adaptive response of nesting Clapper Rails to unusually high water. Wilson Bull. 95: 308–309.

Jarman, W. M. 1991. Identification and levels of organochlorine compounds in birds and marine mammals (*Falco peregrinus anatum, Falco mexicanus, Rallus longirostris levipes*). Ph.D. thesis, Univ. of California, Santa Cruz.

Johnson, R. W. 1973. Observations on the ecology and management of the Northern Clapper Rail, *Rallus longirostris crepitans* Gmelin, in Nassau County, New York. Ph.D. thesis, Cornell Univ., Ithaca, NY.

Johnston, R. F. 1956a. Predation by Short-eared Owl on a *Salicornia* salt marsh. Wilson Bull. 68: 91–102.

Johnston, R. F. 1956b. The incubation period of the Clapper Rail. Condor 58: 166.

Jorgensen, P. D., and H. L. Ferguson. 1982. Clapper Rail preys on Savannah Sparrow. Wilson Bull. 94: 215.

Kale, H. W., II. 1978. Florida Clapper Rail. Pp. 112–113 *in* Rare and endangered biota of Florida. Volume II—Birds. (H. W. Kale, II, ed.). Univ. Presses of Florida, Gainesville.

Klaas, E. E., H. M. Ohlendorf, and E. Cromartie. 1980. Organochlorine residues and shell thicknesses in eggs of the Clapper Rail, Common Gallinule, Purple Gallinule, and Limpkin (Class Aves), eastern and southern United States, 1972–74. Pestic. Monitor. J. 14: 90–94.

Klaassen, M. 1996. Metabolic constraints on long-distance migration in birds. J. Exp. Biol. 199: 57–64.

Kosten, P. A. 1982. Egg retrieval by Clapper Rails. J. Field Ornithol. 53: 274–275.

Kosten, P. A. 1984. Dome rebuilding by Clapper Rails. J. Field Ornithol. 55: 386.

Kozicky, E. L., and F. W. Schmidt. 1949. Nesting habits of the Clapper Rail in New Jersey. Auk 66: 355–364.

Leipsic-Baron, T. 1992. Anthropogenic influences on the biogeography of Clapper Rails in California. M.S. thesis, Univ. of California, Los Angeles.

Lewis, J. C., and R. L. Garrison. 1983. Habitat suitability index models: Clapper Rail. U.S. Fish Wildl. Serv. FWS/OBS-83/10.

Lima, S. L. 1993. Ecological and evolutionary prospectives of escape from predatory attack: a survey of North American birds. Wilson Bull. 105: 1–47.

Linsdale, J. M. 1936. Occurrence of the California Clapper Rail away from marshes. Condor 38: 216.

Lonzarich, D. G., T. E. Harvey, and J. E. Takekawa. 1992. Trace element and organochlorine concentrations in California Clapper Rail (*Rallus longirostris obsoletus*) eggs. Arch. Environ. Contam. Toxicol. 23: 147–153.

MacNamara, E. E., and H. F. Udell. 1970. Clapper Rail investigations on the south shore of Long Island. Proc. Linnean Soc. N.Y. 71: 120–131.

Mangold, R. E. 1974. Clapper Rail studies. 1974 Final Report, U.S. Fish and Wildlife Service Accelerated Research Program Contract No. 14-16-0008-937, Trenton, NJ.

Mangold, R. E. 1977. Clapper Rail (*Rallus longirostris*). Pp. 84–92 *in* Management of migratory shore and upland game birds in North America (G. C. Sanderson, ed.). International Association of Fish and Wildlife Agencies, Washington, D.C.

Martin, A. C., H. S. Zim, and A. L. Nelson. 1951. American wildlife and plants. U.S. Dept. Interior, Washington, D.C.

Martin, A. J. 1962. Clapper Rail in western Maryland. Maryland Birdlife 18: 92.

Martin, E. M. 1979. Hunting and harvest trends for migratory game birds other than waterfowl: 1964–76. U.S. Fish & Wildl. Serv. Spec. Sci. Rept.—Wildl. No. 218.

Massey, B. W., and E. Palacios. 1994. Avifauna of the wetlands of Baja California, Mexico: Current status. Stud. Avian Biol. 15: 45–57.

Massey, B. W., and R. Zembal. 1987. Vocalizations of the Light-footed Clapper Rail. J. Field Ornithol. 58: 32–40.

Massey, B. W., R. Zembal, and P. D. Jorgensen. 1984. Nesting habitat of the Light-footed Clapper Rail in southern California. J. Field Ornithol. 55: 67–80.

McCullough, N. 1944. Clapper Rail at Raleigh. Chat 8: 60.

Meanley, B. 1962. Pellet casting by King and Clapper rails. Auk 79: 113.

Meanley, B. 1969. Natural history of the King Rail. N. Am. Fauna 67.

Meanley, B. 1985. The marsh hen: A natural history of the Clapper Rail of the Atlantic coast salt marsh. Tidewater Publ., Centreville, MD.

Meanley, B., and D. K. Wetherbee. 1962. Ecological notes on mixed populations of King Rails and Clapper Rails in Delaware marshes. Auk 79: 453–457.

Meyer de Schauensee, R. 1966. The species of birds of South America and their distribution. Acad. Nat. Sci., Philadelphia, PA.

Miller, L. 1942. Two new bird genera from the Pleistocene of Mexico. Univ. of Calif. Publ. Zool. 47: 43–46.

Moffitt, J. 1941. Notes on the food of the California Clapper Rail. Condor 43: 270–273.

Murray, J. L. 1929. A dead Clapper Rail found at Lexington, in the valley of Virginia. Auk 46: 106–107.

Nicholson, D. J. 1927. Late nesting of Wayne's Clapper Rail. Auk 44: 98.

Nickol, B. B., and R. W. Heard, III. 1970. *Arhythomorphynchus frassoni* from the Clapper Rail, *Rallus longirostris*, in North America. J. Parasitol. 56: 204–206.

Oberholser, H. C. 1937. A revision of the Clapper Rails (*Rallus longirostris* Boddaert). Proc. U.S. Nat. Mus. 84(3018): 313–354.

Oberholser, H. C. 1974. The bird life of Texas. 2 vols. Univ. of Texas Press, Austin.

Odom, R. R. 1975. Mercury contamination in Georgia rails. Proc. Ann. Conf. Southeast. Assoc. Game & Fish Comm. 28: 649–658.

Ohmart, R. D., and R. E. Tomlinson. 1977. Foods of western Clapper Rails. Wilson Bull. 89: 332–336.

Ohmart, R. D., W. O. Deason, and S. J. Freeland. 1975. Dynamics of marsh land formation and succession along the lower Colorado River and their importance and management problems as related to wildlife in the arid Southwest. Trans. N. Am. Wildl. Nat. Resour. Conf. 40: 240–251.

Olson, S. L. 1973. A classification of the Rallidae. Wilson Bull. 85: 381–416.

Olson, S. L. 1974. The Pleistocene rails of North America. Condor 76: 169–175.

Olson, S. L. 1977. A synopsis of the fossil Rallidae. Pp. 339–373 *in* Rails of the world (S. D. Ripley, ed.). David R. Godine, Publ. Boston, MA.

Olson, S. L. 1997. Towards a less imperfect understanding of the systematics and biogeography of the Clapper and King rail complex (*Rallus longirostris* and *R. elegans*). Pp. 93–111 *in* The era of Allan R. Phillips: A Festschrift. Mus. Southwest. Biol., Albuquerque, NM.

Oney, J. 1951. Fall food habits of the Clapper Rail in Georgia. J. Wildl. Manage. 15: 106–107.

Oney, J. 1954. Clapper rail survey and investigation study. Final Rept., Fed. Aid Proj. W-9-R. Georgia Game and Fish Comm., Atlanta.

Orr, R. T. 1939. Fall wanderings of Clapper Rails. Condor 41: 151–152.

Owre, O. T. 1978. Mangrove Clapper Rail. Pp. 113–114 *in* Rare and endangered biota of Florida. Vol. II—Birds. (H. W. Kale, II, ed.). Univ. Presses of Florida, Gainesville.

Packard, C. M. 1958. Clapper Rail in Cumberland County. Maine Field Nat. 14: 20.

Peters, J. L. 1934. Check-list of the birds of the world. Vol. II. Harvard Univ. Press, Cambridge, MA.

Pettengill, O. S., Jr. 1938. Intelligent behavior in the Clapper Rail. Auk 55: 411–415.

Raffaele, H. A. 1989. A guide to the birds of Puerto Rico and the Virgin Islands. Princeton Univ. Press, Princeton, NJ.

Remsen, J. V., Jr., and T. A. Parker, III. 1990. Seasonal distribution of the Azure Gallinule (*Porphyrula flavirostris*) with comments on vagrancy in rails and gallinules. Wilson Bull. 102: 380–399.

Ridgely, R. S., and J. A. Gwynne, Jr. 1989. A guide to the birds of Panama, with Costa Rica, Nicaragua, and Honduras. 2nd ed. Princeton Univ. Press, Princeton, NJ.

Ridgway, R. 1912. Color standards and color nomenclature. R. Ridgway, Washington, D.C.

Ridgway R., and H. Friedmann. 1941. The birds of North and Middle America. U.S. Natl. Mus. Bull. 50, Pt. 9.

Ripley, S. D. 1977. Rails of the world. David R. Godine, Publ. Boston, MA.

Robbins, C. S., and E. A. T. Blom. 1996. Atlas of the breeding birds of Maryland and the District of Columbia. Univ. of Pittsburgh Press, Pittsburgh, PA.

Root, T. 1988. Atlas of wintering North American birds. Univ. of Chicago Press, Chicago, IL.

Rosenberg, K. V., R. D. Ohmart, W. C. Hunter, and B. W. Anderson. 1991. Birds of the lower Colorado River Valley. Univ. of Arizona Press, Tucson.

Roth, R. R. 1972. The daily and seasonal behavior patterns of the Clapper Rail (*Rallus longirostris*) with notes on food habits and environmental pollutant contamination. M.S. Thesis, Louisiana State Univ., Baton Rouge.

Roth, R. R., J. D. Newsom, T. Joanen, and L. L. McNease. 1972. The daily and seasonal behavior patterns of the Clapper Rail (*Rallus longirostris*) in the Louisiana coastal marshes. Proc. Ann. Conf. Southeast. Assoc. Game Fish Comm. 26: 136–159.

Rusk, M. K. 1991. Selenium risk to Yuma Clapper Rails and other marsh birds of the lower Colorado River. M.S. thesis, Univ. of Arizona, Tucson.

Russell, K. 1994. The Clapper Rail in Pennsylvania. Penna. Birds 8: 88–89.

Sauer, J. R., B. G. Peterjohn, S. Schwartz, and J. E. Hines. 1996. The North American Breeding Bird Survey home page. Version 95.1. Patuxent Wildl. Res. Center, Laurel, MD.

Saunders, A. A. 1950. Changes in the status of Connecticut birds. Auk 67: 253–255.

Schmidt, F. V., and P. A. McLain. 1951. The Clapper Rail in New Jersey. Proc. Northeast. Fish and Wildl. Conf. 7: 164–172.

Segre, A., J. P. Hailman, and C. G. Beer. 1968. Complex interactions between Clapper Rails and Laughing Gulls. Wilson Bull. 80: 213–219.

Sharp, T. L. 1976. Productivity and distribution of the Clapper Rail in a Louisiana salt marsh. M.S. thesis, Louisiana State Univ., Baton Rouge, LA.

Shisler, J. K., and T. L. Schulze. 1976. Some aspects of open marsh water management procedures on Clapper Rail production. Trans. Northeast. Sec. Wildl. Soc. 32: 101–104.

Shuford, W. D. 1993. The Marin County breeding bird atlas. Bushtit Books, Bolinas, CA.

Sibley, C. G. 1955. The responses of salt marsh birds to extremely high tides. Condor 57: 241–242.

Sibley, C. G., and B. L. Monroe, Jr. 1991. Distribution and taxonomy of the birds of the world. Yale Univ. Press, New Haven, CT.

Sibley, D. 1993. The birds of Cape May. Cape May Bird Observ., Cape May, NJ.

Simmons, G. F. 1914. Notes on the Louisiana Clapper Rail (*Rallus longirostris saturatus*) in Texas. Auk 31: 363–384.

Small, A. 1994. California birds: Their status and distribution. Ibis Publ. Co., Vista, CA.

Smith, P. M. 1974. Yuma Clapper Rail study, Mohave County, Arizona, 1973. Progress Rept., Proj. W-54-R-6, Job II-5.9. Calif. Dept. Fish and Game, Sacramento, CA.

Smithe, F. B. 1975–1981. Naturalists' color guide. 3 parts. Am. Mus. Nat. Hist., New York.

Spendelow, J. A., and H. R. Spendelow, Jr. 1980. Clapper Rail kills birds in a net. J. Field Ornithol. 51: 175–176.

Stevenson, H. M., and B. H. Anderson. 1994. The birdlife of Florida. Univ. of Florida Press, Gainesville.

Stevenson, J. O., and L. H. Meitzen. 1946. Behavior and food habits of Sennett's White-tailed Hawk in Texas. Wilson Bull. 58: 198–205.

Stewart, R. E. 1951. Clapper Rail populations of the Middle Atlantic states. Trans. N. Am. Wildl. Conf. 16: 421–430.

Stewart, R. E. 1954. Migratory movements of the Northern Clapper Rail. Bird-Banding 25: 1–5.

Stewart, R. E., and B. Meanley. 1960. Clutch size of the Clapper Rail. Auk 77: 221–222.

Stone, W. 1937. Bird studies at old Cape May. Delaware Valley Ornithol. Club, Philadelphia, PA.

Storey, A. E., W. A. Montevecchi, H. F. Andrews, and N. Sims. 1988. Constraints on nest site selection: A comparison of predator and flood avoidance in four species of marsh-nesting birds (Genera: *Catoptrophorus*, *Larus*, *Rallus*, and *Sterna*). J. Comp. Psychol. 102: 14–20.

Taft, S. J., and R. W. Heard, III. 1978. Aspects of the larval development of *Ophthalmophagus* sp. (Trematoda: Cyclocoelidae). J. Parasitol. 64: 597–600.

Takekawa, J. 1993. The California Clapper Rail: Turning the tide? Tideline 13(2): 1–3, 11.

Tautin, J., S. M. Carney, and J. B. Bortner. 1989. A national migratory gamebird harvest survey: a continuing need. Trans. N. Am. Wildl. Nat. Resour. Conf. 54: 545–551.

Taylor, W. K., and A. Kershner. 1986. Migrant birds killed at the vehicle assembly building (VAB), John F. Kennedy Space Center. J. Field Ornithol. 57: 142–154.

Test, F. H., and A. R. Test. 1942. Food of the California Clapper Rail. Condor 44: 228.

Todd, R. L. 1986. A saltwater marsh hen in Arizona: A history of the Yuma Clapper Rail (*Rallus longirostris yumanensis*). Completion Rept. Arizona Game and Fish Dept., Fed. Aid Proj. W-95-R, Phoenix.

Tomkins, I. R. 1937. Wayne's Clapper Rail carries its young. Wilson Bull. 49: 296–297.

Tomlinson, R. E., and R. L. Todd. 1973. Distribution of two western Clapper Rail races as determined by responses to taped calls. Condor 75: 177–183.

Underwood, H. T., and N. O. Dronen. 1986. *Neocy-*

clustera ralli Gen. ET SP. N. (Cestoidea: Dilepididae) and other endohelminths from Clapper Rails, *Rallus longirostris*, from a marsh in Galveston County, Texas. Proc. Helminthol. Soc. Wash. 53: 59–62.

U.S. Department of the Interior. 1991. The California Clapper Rail: A beleaguered bird faces new threats. Endangered Spp. Techn. Bull. 16: 1–6.

U.S. Fish and Wildlife Service. 1974. Monthly activity report, November 1974. Region 1, Portland, OR.

U.S. Fish and Wildlife Service. 1989. Endangered and threatened wildlife and plants. 50 CFR 17.11 and 17.12. U.S. Govt. Print. Off., Washington, D.C.

Van Velzen, A., and J. F. Kreitzer. 1975. The toxicity of p.p'-DDT to the Clapper Rail. J. Wildl. Manage. 39: 305–309.

Veit, R. R., and W. R. Peterson. 1993. Birds of Massachusetts. Massachusetts Aud. Soc., Lincoln, MA.

Warner, D. W., and R. W. Dickerman. 1959. The status of *Rallus elegans tenuirostris* in Mexico. Condor 61: 49–51.

Wetherbee, D. K., and B. Meanley. 1965. Natal plumage characters in rails. Auk 82: 500–501.

Wetmore, A. 1957. A fossil rail form the Pliocene of Arizona. Condor 59: 267–268.

Willey, G. W. 1986. Great Blue Heron takes Clapper Rail. Maryland Birdlife 42: 4.

Williams, L. 1929. Notes on the feeding habits and behavior of the California Clapper Rail. Condor 31: 52–56.

Williams, S. O., III. 1989. Notes on the rail *Rallus longirostris tenuirostris* in the highlands of central Mexico. Wilson Bull. 101: 117–120.

Wong, P. L., and R. C. Anderson. 1990. *Ancyracanthopsis winegarsi* N. Sp. (Nematoda: Acuarioides) from *Pluvialis squatarola* (Aves: Charadriidae) and *Ancyracanthus heardi* N. Sp. from *Rallus longirostris* (Aves: Rallidae) and a review of the genus. Can. J. Zool. 68: 1297–1306.

Zembal, R., and J. M. Fancher. 1988. Foraging behavior and foods of the Light-footed Clapper Rail. Condor 90: 959–962.

Zembal, R., and B. W. Massey. 1981. A census of the Light-footed Clapper Rail in California. West. Birds 12: 87–99.

Zembal, R., and B. W. Massey. 1983. The Light-footed Clapper Rail: Distribution, nesting strategies, and management. Cal-Neva Wildl. Trans. 1983: 97–103.

Zembal, R., and B. W. Massey. 1985. Function of a rail mystery call. Auk 102: 179–180.

Zembal, R., and B. W. Massey. 1987. Seasonality of vocalizations by Light-footed Clapper Rails. J. Field Ornithol. 58: 41–48.

Zembal, R., J. M. Fancher, C. S. Nordby, and R. J. Bransfield. 1985. Intermarsh movements by Light-footed Clapper Rails indicated in part through regular censusing. Calif. Fish and Game 71: 164–171.

Zembal, R., B. W. Massey, and J. M. Fancher. 1989. Movements and activity patterns of the Light-footed Clapper Rail. J. Wildl. Manage. 53: 39–42.

Zucca, J. J. 1954. A study of the California Clapper Rail. Wasmann J. Biol. 12: 135–153.

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Appendix. Linear measurements (mm) and mass (g) of adults of North American Clapper Rail subspecies. Data are shown as mean ± SD (range; *n*). From Oberholser 1937, except as noted.

Subspecies	*crepitans*	*waynei*	*scottii*	*insularum*	*saturatus*	*obsoletus*	*levipes*	*yumanensis*[1]
Wing-chord length								
Male	151.1 (142.5–159.5; 21)	145.1 (135–151; 15)	146.0 (135–155; 23)	144.8 (140–148; 4)[2]	150.4 (140.5–163; 23)	161.7 (153.5–170; 29)	161.9 (154.5–167; 10)	154.1 ± 4.7 (141–164; 65)
Female	146.8 (135.5–160; 17)	138.4 (129.5–146.5; 16)	137 (128.5–145; 18)	133.8 (129.5–136.5; 4)	141.3 (131–154; 16)	151.6 (147–161; 24)	147.3 (138–155.5; 12)	141.6 ± 3.4 (133–146; 30)
Bill length								
Male	63.3 (55–69.5; 21) 65.7 ± 1.9 (62–70; 17)[3]	62.2 (54–67.5; 15)	61.6 (56–66; 23)	60.6 (59–61.5; 4)[2]	61.7 (54–69; 23) 61.4 ± 3.0 (54–68; 64)[4]	60.3 (52–61; 29)	58.9 (56–61; 10)	61.0 ± 2.8 (50–67; 94)
Female	59.6 (53.5–67; 17) 58.4 ± 2.4 (54–63.5; 48)[3]	58.7 (53–62.5; 16)	55.9 (51.5–60; 18)	55 (53–59; 4)	59.9 (55.5–64; 16) 57.9 ± 2.8 (50–62; 101)[4]	55 (49–61; 24)	54.2 (51.5–58; 12)	55.6 ± 2.5 (50–62; 47)
Tail length								
Male	64.6 (55–69; 21)	61.9 (57.5–72; 15)	63.3 (56.5–72; 23)	57.5 (51–64; 4)[2]	63.6 (58–68; 23)	73.1 (68–80; 29)	66.7 (62.5–69; 10)	66.6 ± 5.2 (54–82; 66)
Female	61.9 (55–69.5; 17)	59.9 (56–63.5; 16)	59.2 (54.5–63.5; 18)	58 (57–60; 4)	60.9 (56–66; 16)	65.3 (60–76; 24)	62.6 (57–67; 12)	60.8 ± 3.7 (56–69; 29)
Tarsus length								
Male	51.7 (48–56; 21)	48.2 (46.5–53.5; 15)	49.8 (42–55.5; 23)	50.4 (47–54; 4)[2]	50.9 (47–55; 23)	56.7 (52–61; 29)	56.9 (53–60.5; 10)	49.6 ± 2.4 (45–55.5; 29)
Female	48.1 (41–56; 17)	46.7 (43.5–50; 16)	45.6 (42–51; 18)	45.1 (44–47; 4)	47.7 (42–52.5; 16)	51.1 (45–63; 24)	49.5 (47–51; 12)	45.5 ± 3.0 (43.0–49.5; 23)
Middle–toe length								
Male	48.8 (45.5–53.5; 21) 64.0 ± 1.8 (60–67; 17)[3, 5]	45.4 (40–48; 15)	45.5 (39.5–49; 23)	45.2 (45–45.5; 4)[2]	47.6 (43–52.5; 23) 50.7 ± 2.5 (46–56; 35)[4]	51.3 (47–56; 29)	51.2 (50–54; 10)	50.8 ± 2.8 (41–57; 96)
Female	45.9 (40–52; 17) 56.8 ± 2.1 (49–62; 48)[3, 5]	44.4 (41.5–47.5; 16)	41.9 (37–45; 18)	40.5 (39–42; 4)	43.9 (37–47; 16) 44.8 ± 2.4 (40–50; 48)[4]	47.4 (44–51.5; 24)	44.9 (41–48; 12)	44.8 ± 2.3 (41–50; 32)
Mass								
Male	351.0 (286.5–394.5; 14)[6]	337 (275–375; 17)[7]	290.2 ± 15.5 (263–310; 11)[8]			321.7 ± 35.5 (180–400; 109)[4]		269.0 ± 35.8 (194–347; 109)
Female	278.1 (235.9–330.4; 6)[6]	272 (200–400; 33)[7]	247.3 ± 30.1 (199–314; 14)[8]			256.6 ± 34.3 (180–320; 157)[4]		209.5 ± 35.3 (160–310; 49)

[1] WRE and R. E. Tomlinson unpubl. data; Arizona, California, and n. Sonora.
[2] Ridgway and Friedmann 1941.
[3] Mangold 1974; New Jersey.
[4] Bateman 1965; Grand Terre Is., LA; mass from hunter-killed birds in autumn.
[5] Measurement includes claw.
[6] Meanley 1985; Accomac Co., VA.
[7] Blandin 1965; Beaufort Co., SC.
[8] WRE and M. L. Legare, Big Bend Wildlife Management Area, Dixie Co., FL, breeding season 1992–1993.

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