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Rallus limicola

FRENCH:
Râle de Virginie
SPANISH:
*Rascón de agua,
Gallineta, Kidika*

Virginia Rail

The Virginia Rail is a secretive freshwater marsh bird that is more often heard than seen. A brief glimpse of a reddish bill and legs, banded black-and-white flanks, and a short, upturned tail is often all that is afforded observers. A habitat generalist, this species probes mudflats and shallow water with its long, slightly decurved bill searching for invertebrates, small fish, and the occasional seed. Vagrancy and generalist habits allow it to exploit a highly ephemeral niche. A laterally compressed body, flexible vertebrae, and modified feather tips in anterior regions of the head (to prevent feather wear) are adaptations for passing through dense marsh vegetation. Virginia Rails are agile on their feet and most often escape danger by running, but they may also dive and swim, using their wings to propel themselves underwater.

Within its range the Virginia Rail is restricted to isolated wetland areas, but can be locally abundant if habitat conditions are favorable. Like other North American rails, it is monogamous, territorial, and fecund. Duetting *grunt* vocalizations—specialized calls used in pair-bonding—signal the start of the nesting season each spring. Adults build numerous "dummy" nests within their territories in addition to their primary nest. Precocious young may leave the nest immediately after hatching, and both parents share in caring for them. Virginia Rails undergo two annual molts, including a simultaneous wing
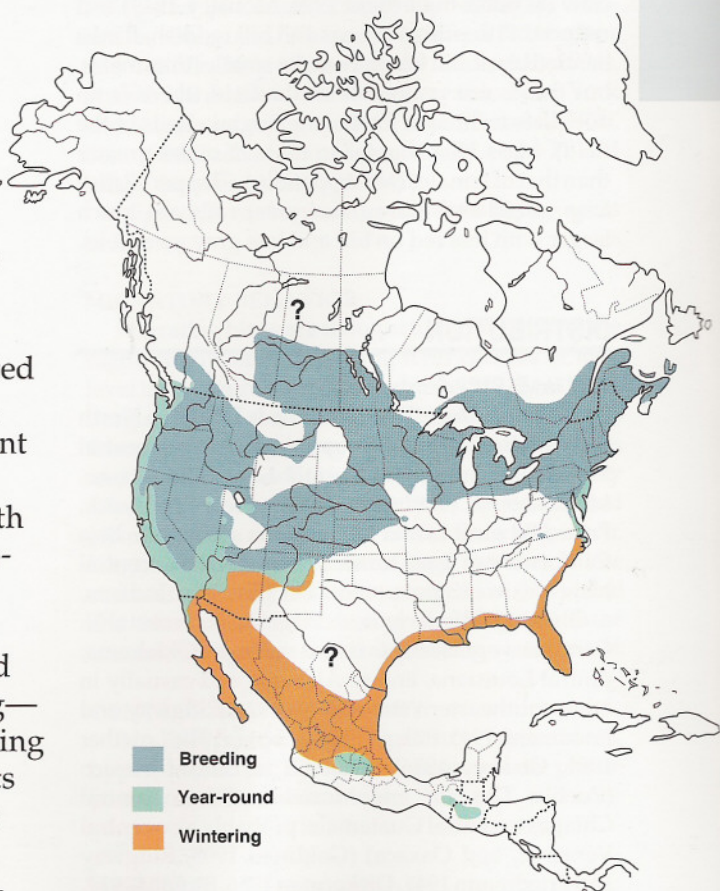
The Birds of North America

Life Histories for the 21st Century

Figure 1.

Distribution of the Virginia Rail in North America. It breeds and winters very locally in areas of suitable habitat, and is rare in the central and southern United States.

and tail molt in late summer that renders them flightless.

Although the Virginia Rail is considered a game species throughout North America, hunters seldom take it. Wetland loss has caused population declines, but the species is now considered relatively stable (Conway et al. 1994). It often coexists with Soras (*Porzana carolina*) in marshes throughout its range. Comparisons between these two rails are common and allow insights into evolutionarily-recent life history adaptations.

Because it is difficult to observe and attracts little interest from hunters, the Virginia Rail has been little studied. Detailed information on many aspects of its life history is still lacking.

DISTINGUISHING CHARACTERISTICS

Small (22–27 cm total length), dorsally compressed, reddish bird with gray cheeks and a long, slightly decurved bill. Wings chestnut-colored with a 1-mm claw on outer digit (Bent 1926, Mousley 1940) and reduced 11th primary. Legs and bill reddish, flanks banded black and white. Females smaller than males, but this is not noticeable in the field (there is no adequate technique for sexing Virginia Rails in the field). Mass 55–124 g; mean mass of males greater than that of females (see Appendix). Clapper (*Rallus longirostris*) and King (*R. elegans*) rails are much larger with less red on bill and less gray on cheeks.

DISTRIBUTION

THE AMERICAS

Breeding range. Figure 1. Breeds locally in North America from s. British Columbia, se. Alberta, central Saskatchewan, central Manitoba, sw. Ontario, ne. Minnesota, se. Ontario, s. Quebec, New Brunswick, Prince Edward I., and Nova Scotia south to n. Baja California (at least formerly), s. Arizona, central New Mexico, Kansas, n. Iowa, n. Illinois, n. Indiana, n. Ohio, s. Pennsylvania, e. Virginia, and coastal N. Carolina; very locally in n. and se. Texas, Oklahoma, central Louisiana, and n. Alabama and casually in other southeastern states (Bent 1926, Ridgway and Friedmann 1941, Billard 1948, Robbins 1949, Lowther 1961, Godfrey 1986). Resident in central Mexico (Puebla, Tlaxcala, and México and from central Chiapas to central Guatemala; probably also central Veracruz, and Oaxaca) (Goldman 1908, Ridgway and Friedmann 1941, Dickerman 1966, Binford 1972, Am. Ornithol. Union 1983, Howell and Webb 1995). Resident in South America from sw. Colombia to Ecuador and w. Peru and in s. Chile and s. Argentina (Bent 1926). Has been reported at elevations up to

2,370 m (Goldman 1908, Griese et al. 1980) but generally breeds in marshlands where spring air temperatures are warmer (mean $\geq 5.6°C$) than in Sora breeding marshes (Griese et al. 1980).

Winter range. Figure 1. Winters predominantly along the East, West, and Gulf coasts, with large interior populations. From sw. British Columbia south through s. Baja California and central Mexico (recorded south to Jalisco and Veracruz). Along the Gulf Coast and coastal New England south locally through s. Florida, rarely in Cuba (Bond 1947), and in interior North America north to Montana, Colorado, Wyoming, Nebraska, Illinois, Michigan, and s. Ontario. Breeding populations in Central and South America are nonmigratory (Bent 1926, Ridgway and Friedmann 1941, Billard 1948, Dickerman 1971, Griese et al. 1980, Am. Ornithol. Union 1983, Root 1988, Howell and Webb 1995). Observations of wintering birds as far north as Maine (Beston 1954, Werner 1955, Robbins 1967), Wisconsin (Degner 1963, Dunwiddie 1963), and Minnesota (Tanner and Hendrickson 1954, Glassel 1959). Limited wintering occurs along the Great Lakes. Scarce but frequent in Bermuda Aug–Apr (Amos 1991). Based on Christmas Bird Count data, Root (1988) found the highest density in the lower Colorado River Valley. Winter distribution frequently follows major drainage systems, water-storage impoundments, irrigation districts, wet meadows, and irrigated hay fields. Environmental factors affecting winter distribution include availability of freshwater marshes and warm (> -7°C) temperatures (Root 1988). Occasionally winters in areas surrounding warm springs in otherwise frozen marsh conditions.

OUTSIDE THE AMERICAS

Casual or accidental in Greenland.

HISTORICAL CHANGES

No recent changes in distribution are known, but few data owing to species' reclusive habits. See Demography and Populations: population status.

FOSSIL HISTORY

Very limited. Earliest definitive rail fossils come from the late Oligocene to early Miocene of Europe (Olson 1985). Fossil record tells us little about early history of the family, but fossil rails occur fairly regularly in various younger Tertiary deposits from Europe, Asia, and North America (Olson 1985). The genus *Rallus* exhibits much more specialized forms than other genera in the family and appears to have specialized and radiated in the New World (Olson 1973). *Rallus* has been traced from the primitive genus *Canirallus* (Olson 1973). *R. prenticei* was considered a slightly larger ancestor of *R. limicola* from

the Pliocene (Feduccia 1968, but cf. Olson 1974). Left humerus, ulnae, tarsometatarsi, and tibiotarsus of *R. limicola* from Middle Pleistocene, Arredondo Clay and Reddick beds from Haile, Alachua Co., and Reddick, Marion Co., FL (Olson 1977: 349). Holotype is discussed in Brodkorb (1957) and Ligon (1965).

SYSTEMATICS

Formerly called *Rallus virginianus* (Audubon 1842).

GEOGRAPHIC VARIATION

No distinct geographic variation in size, color, or vocalizations. Olson (1974) suggested that the species averaged larger during the Pleistocene than at present. Eastern and western specimens are similar in size (Ridgway and Friedmann 1941, contra Dickey 1928). Meyer de Schauensee (1966) suggested variation in size and plumage color among populations in South America, but this was based on few data.

SUBSPECIES; RELATED SPECIES

Only 1 recognized subspecies (*Rallus limicola limicola*) in North America (Am. Ornithol. Union 1957, but see Dickey 1928, Dickerman 1966). Clapper Rail is similar in appearance with black-and-white banded flanks, short upturned tail, superciliary line, decurved bill, and reddish legs and bill, but much larger. Water Rail (*R. aquaticus*) from Europe and Great Britain is very similar in size, plumage, and habit but has a slate-gray breast.

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Most populations migrate; some are resident in Arizona (Conway 1990) and probably other parts of southern breeding range. Arrival dates on breeding grounds thought to be influenced by spring weather and emergent plant phenology (Walkinshaw 1937, Pospichal and Marshall 1954, Kaufmann 1989). Fall migration is variable, also influenced by weather conditions (Walkinshaw 1937, Pospichal and Marshall 1954). Seasonal changes in movements and habitat occur, possibly in response to changes in food availability, predation pressure, or competing species (Conway 1990). Vocalizations are rare and difficult to evoke in Aug and Sep; cannot be used to assess migration chronology.

TIMING AND ROUTES OF MIGRATION

Exhibits irregular irruptions which may be adaptive for a species that inhabits ephemeral habitats.

Fall departure dates vary with latitude and elevation (see Fig. 4); in Iowa, 7 radio-marked adults dispersed from their breeding territory between 19 Jul and 1 Aug (Johnson and Dinsmore 1985). Most birds leave northern breeding areas late Sep to mid-Oct and begin to arrive on wintering grounds in Sep (Cooke 1914). Birds in the central U.S. concentrate on larger marshes prior to fall migration (Pospichal and Marshall 1954). In Kansas, birds present through Oct, although vocalizations end in late Sep (Baird 1974). In Ohio and Michigan, depart mid-Sep to 1st wk Oct, but recorded as late as 18 Oct (Walkinshaw 1937, Trautman 1940, Andrews 1973). In Colorado, fall migration peaks between 2d wk Aug and 3d wk Sep (Griese et al. 1980). Birds may leave as late as Nov in southern part of breeding range. Leave winter grounds by early Apr. Arrive southern breeding grounds in early Apr, northern breeding grounds late Apr to mid-May (Conway and Eddleman 1994). Can arrive as early as late Mar (Cooke 1914). Arrive in Colorado early Apr (Glahn 1974, Griese et al. 1980), in Kansas 3d wk Apr (Baird 1974), and in Connecticut, Iowa, Michigan, Minnesota, Ohio, and Wisconsin between 3d wk Apr and 1st wk May (Conway and Eddleman 1994). Birds have arrived at breeding areas in New York and Kansas as early as 10–17 Mar (Crandall 1920, Bent 1926, Tacha 1975). Males usually arrive 7–10 d before females (Audubon 1842).

Migration routes and important staging areas unknown.

MIGRATORY BEHAVIOR

Migrating birds are thought to fly low during the night, singly, often following river courses or low, level land (Audubon 1842, Forbush 1912, Bent 1926, Barger 1957). Audubon (1842) observed birds, thought to be migrating, flying < 1 m above rivers and level ground. Spring migrants are adversely affected by storms (Kaufmann 1989). Speed, method of orientation, and degree of flocking unknown. Virginia Rails concentrate on large marshes in late summer and early fall prior to migration (Pospichal and Marshall 1954, Griese et al. 1980), but these concentrations may reflect decreasing water levels.

CONTROL AND PHYSIOLOGY

No information on migratory restlessness, hyperphagia, fat deposition, response to photoperiod, or roles of hormones.

HABITAT

BREEDING RANGE

Breeds predominantly in freshwater wetlands, but nests have been reported in salt marshes (Griffing

1881, Taylor 1971). Uses drier areas of marsh than Sora. Inhabits stands of robust emergent vegetation (e.g., cattails [*Typha*] and bulrush [*Dvitpud*]) within freshwater and brackish marshes and wetlands, and occasionally coastal salt marshes (Fig. 2; Horak 1964, Weller and Spatcher 1965, Post and Enders 1970, Johnson 1984, Sayre and Rundle 1984, Eddleman et al. 1988, Manci and Rusch 1988, Gibbs et al. 1991). Prefers freshwater marshes in early stages of succession (Pospichal and Marshall 1954); most common in moist-soil emergent wetlands and along seasonal or semipermanent ponds and lakes in the midwestern U.S. (Fredrickson and Reid 1986).

Shallow water, emergent cover, and substrate with high invertebrate abundance are thought to be the most important features of Virginia Rail habitat (Berger 1951, Andrews 1973, Baird 1974, Glahn 1974, Tacha 1975, Griese et al. 1980, Rundle and Fredrickson 1981, Sayre and Rundle 1984, Fredrickson and Reid 1986, Gibbs et al. 1991; also see Fig. 2). In Maine, wetlands used by breeders have a greater abundance of emergent vegetation than unused wetlands (Gibbs et al. 1991). In Iowa and Arizona, uses relatively homogeneous stands of emergent vegetation compared to other rails (Johnson 1984, Conway 1990). In other areas, seems to prefer heterogeneous stands with more vegetative edge (Allen 1934, Pospichal and Marshall 1954, Glahn 1974, Sayre and Rundle 1984).

Needs standing water, moist-soil, or mudflats for foraging; avoids dry stands of emergents (Johnson 1984, Fredrickson and Reid 1986, Manci and Rusch 1988, Gibbs et al. 1991). Will use deep-water habitats, but prefers shallow and intermediate water depths (0–15 cm) with muddy, unstable substrates for foraging (Billard 1948, Pospichal and Marshall 1954, Irish 1974, Tacha 1975, Griese et al. 1980, Rundle and Fredrickson 1981, Sayre and Rundle 1984, Johnson and Dinsmore 1986). If adequate upright emergent cover exists, will occupy deeper water habitats where there is substantial collapsed or floating vegetation that gives the birds a substrate upon which to walk and forage (Sayre and Rundle 1984, Johnson and Dinsmore 1985).

A moderate cover:water ratio within wetlands is important; Virginia Rails are often absent from wetlands lacking adequate shallow-water pools or mudflats. An equal mixture of emergent vegetation and flooded openings increases macroinvertebrate production (Voigts 1976, Kaminski 1979, Nelson and Kadlec 1984), and Virginia Rails may use interspersion as a proximate cue in selecting habitats rich in macroinvertebrates (Kaminski and Prince 1981, Reid 1985). Most common in wetlands with 40–70% upright emergent vegetation interspersed with open water, mudflats, and/or matted vegetation (Krapu and Green 1978, Fredrickson and Reid 1986).
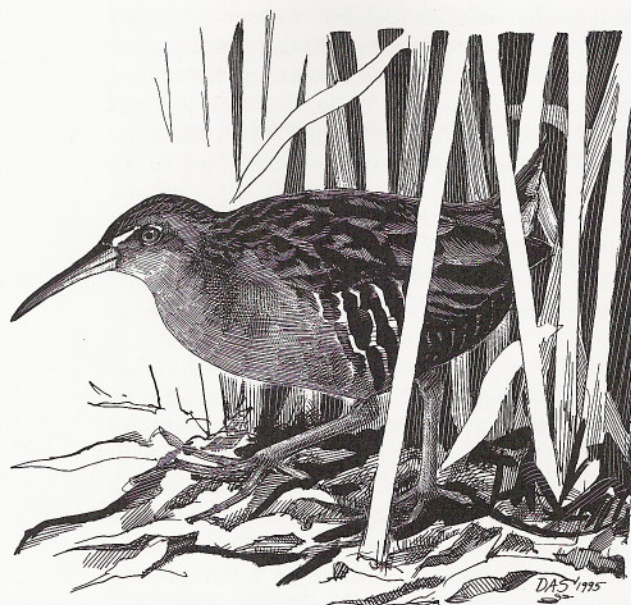

Figure 2. Primarily a bird of freshwater marshes, the Virginia Rail prefers a mixture of emergent vegetation and flooded openings which boost insect abundance. This rail is most common in wetlands in which at least half the area consists of upright emergent vegetation interspersed with open water, mudflats, and/or matted vegetation. Drawing by David Sibley.

Avoids emergent stands with high stem densities or large amounts of residual vegetation (Johnson 1984, Conway 1990). These features, common in older marshes, can impede the birds' movement. Vegetation height is not considered important for optimal Virginia Rail habitat as long as there is adequate overhead cover. Birds will move into regrowing marshes as soon as there is adequate cover.

Wetland size may be important (Gibbs et al. 1991, but see Brown and Dinsmore 1986). In Maine, inhabits large wetlands more commonly than small ones; wetland use correlated with shoreline length, but area of emergent and Ericaceous vegetation within a wetland was considered more important (Gibbs et al. 1991). Within a wetland complex, prefers littoral sites (Weller and Spatcher 1965, Zimmerman 1977, Johnson and Dinsmore 1986, Swift 1989) and sites of relatively high pH and conductivity (Gibbs et al. 1991). In Maine, uncommon in glacial wetlands (Gibbs et al. 1991), preferring beaver (*Castor canadensis*)- or human-created wetlands with fertile soil, heterogeneous topography, and more understory herbs. See also Breeding: nest site.

SPRING AND FALL MIGRATION

Flooded annual grasses or forbs with shallow water (< 10 cm) for optimal foraging in the central U.S. (Sayre and Rundle 1984, Fredrickson and Reid 1986). Migrating birds require a variety of water depths, robust vegetative cover, and short-stemmed seed-producing plants (Andrews 1973, Rundle and Fredrickson 1981). Optimal wetland habitat for migrants includes a diversity of plant species with annuals predominating (Fredrickson and Reid 1986).

WINTER RANGE

Includes both freshwater and salt marshes, generally similar to breeding habitat. Slight shifts in microhabitat use during winter in Arizona; winter birds used areas farther from open water, with more bare ground basal coverage and taller mean emergent height (Conway 1990).

FOOD HABITS

FEEDING

Main foods taken. Breeding season: small aquatic invertebrates, mainly beetles, snails, spiders, true bugs, and diptera larvae. Winter: invertebrates, a variety of aquatic plants, and seeds of emergent plants.

Microhabitat for foraging. Forages mainly in shallow water or on mudflats. Prefers unstable, moist, silty substrate. Generally more open areas compared to nesting microhabitat. Will forage in adjacent upland habitats in some areas (Walkinshaw 1937, Pospichal and Marshall 1954, Horak 1970).

Food capture and consumption. Feeds standing up, probing mud and shallow water with its long, decurved bill; rapid, uninterrupted, methodical foraging, primarily at dawn and dusk (Gillette 1897). Also probes with bill under mats of vegetation and floating vegetation (Kaufmann 1989). Long toes allow Virginia Rails to forage on top of floating marsh vegetation within deeper-water habitats. Birds will climb vegetation in pursuit of food.

DIET

Major food items. Animal foods predominate (85–97% of diet in summer; Martin et al. 1951, Horak 1970). Diet includes slugs, snails, small fish, insect larvae, aquatic invertebrates, caterpillars, beetles, flies, earthworms, amphipods (*Gammarus* spp.), crayfish, frogs, and small snakes (Audubon 1842, Shaw 1887, Forbush 1925, Cahn 1915, Richter 1948, Pospichal and Marshall 1954, Brocke 1958). Mainly adult insects, insect larvae, worms, other invertebrates (Horak 1970). Beetles, snails, spiders, true bugs, and diptera larvae are the items taken most frequently; various crustaceans, dragonfly and damselfly nymphs, ants and other Hymenoptera, grasshoppers and crickets, bryozoans, and small fish (Martin et al. 1951). Also eats a variety of aquatic plants and seeds of emergent plants (Fassett 1940, Pospichal and Marshall 1954, Irish 1974). Seeds of marsh plants (wildrice, bulrush, spikerush, sedge, buttonbush, cyperus, pondweed, cowlily, smartweed, cordgrass, marestail, burreed) are consumed more commonly in fall (32%) and winter (21%) than in spring (12%) and summer (3%) (Martin et al. 1951).

Quantitative analysis. In Iowa, insects comprised nearly 62% of diet of 37 breeding birds, based on percent volume of gizzard and proventriculus contents of collected birds. Adult insects: Hydrophilidae (13.7%), Odonata (12.1%), Dytiscidae (4.6%), Coleoptera (2.4%), Diptera (0.2%), Curculionidae (trace), Notonectidae (trace), unknown (2.0%). Insect larvae: Diptera (22.0%), Hydrophilidae (2.0%), Dytiscidae (trace), unknown (1.5%). Vegetation: *Lemna* (12.8%), *Carex* (1.7%), *Polygonum* (trace), *Setaria* (trace), *Scirpus* (trace), *Agropyron* (trace), unknown seeds (0.9%). Crayfish: Decapoda (9.1%). Unknown animal (9.0%). Snails: *Helisoma* (3.9%), *Physa* (trace), unknown snail (2.1%) (Horak 1970).

Consumes a much higher percentage of animal foods than does sympatric Sora; Virginia Rail gizzards contained 2.6% grit by volume (Horak 1970). Similar results from 7 Virginia Rails in Minnesota based on the percent of individual birds containing items in their gizzard: insects: Coleoptera adult (29%), Diptera pupa (14%), Lepidoptera adult (14%), Curculianidae adult (14%), unidentifiable insects (71%); snails: *Physa* (14%), unidentifiable snails (57%); seeds: *Scirpus acutus* (29%), *S. fluviatilis* (14%), *Cyperaceae* unidentifiable (14%), *Leersia oryzoides* (14%), *Bidens* sp. (14%), *Chenopodium* sp. (14%), unidentifiable Compositae (29%), miscellaneous seed coats (29%); leafy material: *Lemna minor* (43%), unidentifiable leafy material (29%) (Pospichal and Marshall 1954).

FOOD SELECTION AND STORAGE

No information on recognition or choice of food items or caching, but Virginia Rails have a highly developed olfactory process, a large number of nasal glands and ducts in their olfactory chamber, and a large olfactory bulb in their brain; thus they have probably retained a keen sense of smell. Experimental research needs to address the ability of this species to recognize and locate food by smell.

NUTRITION AND ENERGETICS

Daily food intake, and nutritional and caloric value of foods not known. Virginia Rail has a long caeca, which allows increased absorption of nutritive food. Captive birds are easy to maintain on a diet of hard-boiled egg yolks, horsemeat dog food, vegetable dog food, and vitamins (Kaufmann 1977, 1987). Wild-caught birds would not eat dog food unless mixed with live invertebrates (Kaufmann 1987).

METABOLISM AND TEMPERATURE REGULATION

Few data. Kaufmann (1987) stated that "chicks appear to depend upon their parents for warmth and dryness for an extended period or time."

DRINKING, PELLET-CASTING, AND DEFECATION

Few data on drinking and defecation. For first week after hatching, chick dips bill into water, then tips bill up to drink; older chicks and adults do not tip bill up (Kaufmann 1987). Young chicks usually defecate over water (Nice 1962, Kaufmann 1987). In captivity, brooding parents sometimes eat their chicks' feces (Kaufmann 1989). No documented cases of pellet-casting, but other rails cast pellets of exoskeletons and other difficult-to-digest items.

SOUNDS

VOCALIZATIONS

Development. Few data. Chicks peep from egg during hatching (Kaufmann 1987). Immediately after hatching, and for several weeks thereafter, they can emit strong 1- to 2-syllable calls and call repeatedly when separated from their brood (Walkinshaw 1937, Nice 1962). Young captive birds call regularly: 66 calls/min at 9 d, constant vocalizations at 11 d (Nice 1962). No data on when young begin to call like adults; no information on vocal learning or sensitive periods for learning.

Vocal array. Chicks emit *pee-eep* calls (Walkinshaw 1937). See Kaufmann 1983 for description and sonograms of vocal array.

Four primary adult vocalizations (Brewster 1902, Allen 1934, Walkinshaw 1937, Callin 1968). Antiphonal, duetting *grunt* (Fig. 3A), given by pairs, is the most frequently given call (Brewster 1902, Walkinshaw 1937, Thorpe 1972, Irish 1974, Ripley 1977). Infrequent *tick-it* call (Fig. 3B) is heard for brief period in spring, probably given by males only (Bent 1926, Glahn 1974, Irish 1974). *Kicker* call (Fig. 3C; Brewster 1902, Reynard and Harty 1968, Bollinger and Bowes 1973, Reynard 1974) is given very infrequently in early spring; probably functions as a primary breeding call (Callin 1968, Post and Enders 1970). In Arizona, *kicker* appeared to be equivalent to *kek-burr* given by female Clapper Rails (Zembal and Massey 1985). A sharp piercing or rasping *kiu* call (Forbush 1912, Burtch 1917, Pospichal and Marshall 1954, Kaufmann 1983, Orman and Swift 1987). Adults also give several low-pitched, quiet calls around the nest and directed toward the brood (Walkinshaw 1937, Kaufmann 1983).

Few data on duration, repetition, cadence, or geographic variation in calls. In Minnesota, both sexes of a captive pair gave 1–9 *grunts*/h before egg-laying and 0–5/h during laying and incubation (Kaufmann 1989). Six calls/h, unelicited, in an area with 3.6 birds/ha in Colorado (Glahn 1974).

Phenology. Birds vocalize most frequently early in breeding season, but response rate to broadcast vocalizations was higher postlaying than prelaying
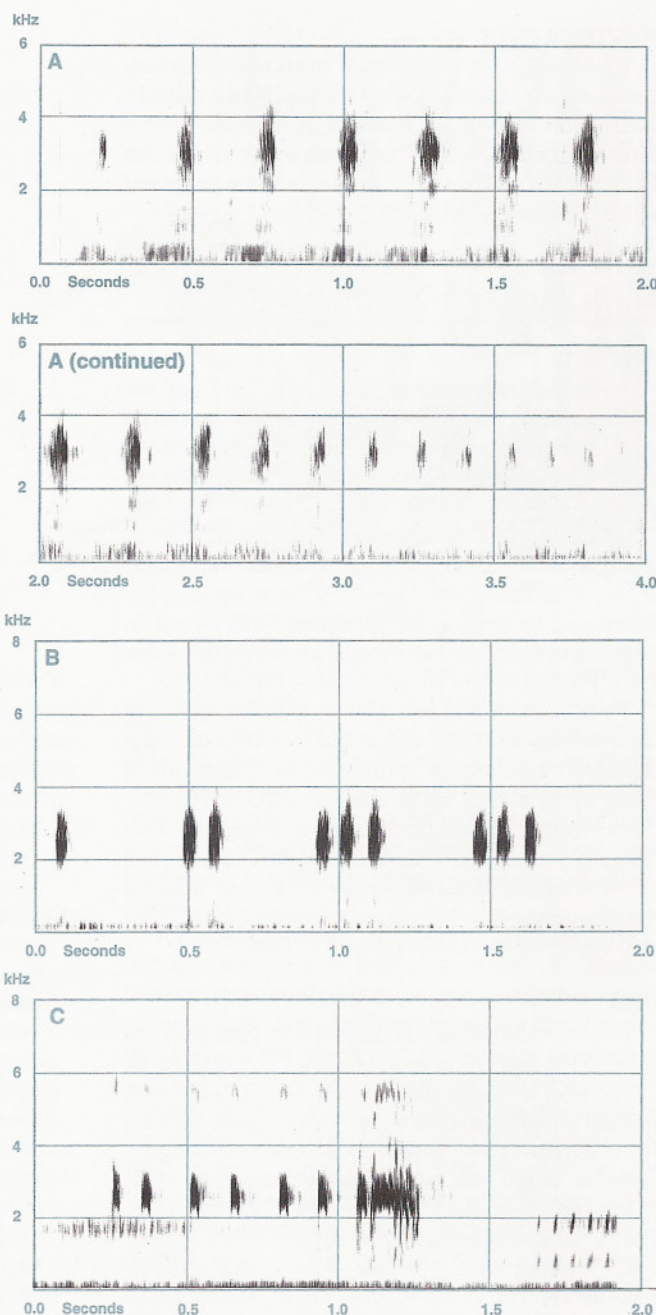

Figure 3. Primary adult vocalizations of the Virginia Rail. A: *Grunt* Call; B: *Tick-it* Call; and C: *kicker* Call. From the collection of the Library of Natural Sounds (LNS), Cornell Laboratory of Ornithology (A: LNS #38198, recorded in Tioga Co., NY, 7 May 1947; B: LNS #45631, recorded in Plumas, CA, 8 June 1989; and C: LNS #2882, recorded in Pennsylvania, 25 March 1966). Prepared by the Borror Laboratory of Bioacoustics, The Ohio State University.

(Johnson and Dinsmore 1986). Migrants seldom vocalize during the first 1–3 wk after arrival on breeding grounds (Walkinshaw 1937, Pospichal and Marshall 1954, Tanner and Hendrickson 1954,

Andrews 1973, Baird 1974, Glahn 1974, Kaufmann 1989; but see Griese et al. 1980). *Tick-it* calls are monotonously repeated throughout the day during a brief period each spring. *Kicker* calls are rare and heard only during a similar period each spring. *Grunt* calls are heard more frequently as spring progresses and rapidly become common as birds are paired.

Peaks in vocalization frequency vary annually (Tacha 1975, Johnson and Dinsmore 1986) and latitudinally: last week in Apr through second week in May in Colorado and Kansas (Glahn 1974, Griese et al. 1980, Zimmerman 1984), third week of May in Wisconsin and Maine (Manci and Rusch 1988, Gibbs and Melvin 1993), throughout May in Ohio and Iowa (Andrews 1973, Johnson and Dinsmore 1986), late Apr to mid-Jun in Kansas (Tacha 1975), and mid-Apr in Arizona (CJC). A second peak in vocalization frequency is reported in several studies and may coincide with hatching (Kaufmann 1971, Glahn 1974, Gibbs and Melvin 1993). Calling frequency is reduced during poor weather (Tacha 1975, Gibbs and Melvin 1993). Vocalization frequency declines after Jul (Brewster 1902, Glahn 1974, Irish 1974). Vocalizations are rare and difficult to evoke in Aug and Sep; also rare during migration and on wintering grounds.

Daily pattern of vocalizing. Individuals vocalize most frequently during the 2–3 h surrounding dawn and dusk. Occasionally vocalize through the night, especially at the height of breeding season.

Places of vocalizing. Few data. Birds vocalize on the ground or from a low perch within dense vegetation, not during flight. Incubating birds vocalize from nest in response to mate or neighbors; one adult vocalized 3 times during 1 h of incubation (Walkinshaw 1937). Birds may vocalize from roost at night.

Repertoire and delivery of songs. More diverse repertoire for both sexes during courtship and early breeding season. No known age, individual, or geographic variation in repertoire. Repertoire size is difficult to determine under field conditions because of difficulty in observing individuals within their dense habitat. Individuals respond readily to neighbors' vocalizations. *Grunts* are given in response to *grunts* (Kaufmann 1989), and *kicker* and *tick-it* calls are given in response to each other. Birds frequently give *tick-it* calls repetitively for hours.

Social context and presumed functions of vocalizations. SOCIAL CONTEXT. *Grunts* are thought to function in pair communication, territorial defense, and neighbor recognition. They are frequently given during hostile interactions before and after chasing or aggressive displays, in response to *grunts* of other territorial males, and in response to *grunts* given by mate (Kaufmann 1983, 1989). *Tick-it* calls are thought

to function in courtship as solicitation calls by unpaired males holding a territory and seeking a mate (Burtch 1917, Bent 1926, Irish 1974). *Kicker* calls probably function as solicitation calls by unpaired females; they are usually given briefly and attract other individuals (presumably males) to the area rapidly.

Tick-it calls are often heard in the same area repeatedly for numerous days during the spring until a *kicker* call is eventually heard. Not long after *kicker* call is heard for the first time, paired *grunts* are the only calls heard in that area. *Kicker* calls were never heard later than the first week in Jun in most of range (Reynard and Harty 1968, Post and Enders 1970) but were recorded as late as the end of Jun in northern extent of range (Callin 1968). *Kiu* call is thought to be an alarm call given near the nest by both sexes (Kaufmann 1983, Orman and Swift 1987). Vocalization rate is positively correlated with breeding density (Kaufmann 1971, Glahn 1974).

ASSOCIATION BETWEEN CALLS AND COURTSHIP DISPLAYS. The actual courtship period is brief and can be identified by the short duration of the *tick-it* calls in spring (Bent 1926, Glahn 1974, Irish 1974). Both members of pair give nasal peeps and low, guttural growls prior to and during copulation (Kaufmann 1983). As the pair bond forms, the pair exchange calls (Kaufmann 1989).

It is thought that either sex may initiate a *grunt* duet; it is joined by the other member of the pair shortly thereafter (Kaufmann 1971, Thorpe 1972, Glahn 1974). Pairs perform duets of *grunts* throughout the breeding season, and individuals readily respond to *grunt* calls of birds on neighboring territories. Individuals appear to recognize their mate's *grunt*. *Grunts* appear to function primarily for pair bonding and territorial defense early in the breeding season and for mate location later in the breeding season. There may be 2 types of *grunt* vocalizations; one that functions in pair communications and one that functions in territorial disputes. Pairs may give a low clucking call at incubation change-overs (Walkinshaw 1937).

NONVOCAL SOUNDS

Little information. Birds possibly produce a "clacking" sound by repeatedly bringing their mandibles together rapidly (Irish 1974).

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Walks and runs on ground. All rails have strong legs, with the highest leg-muscle to flight-muscle ratio of any birds (25-15% of body weight, respectively). Long toes allow

birds to walk on floating marsh vegetation, and laterally compressed bodies allow them to walk through dense understory marsh vegetation. Occasionally climb up stems of emergent plants and shrubs while foraging, occasionally using claw at tip of wing (Forbush 1925, Walkinshaw 1937, Nice 1962). Tail normally fanned and erect while walking, exposing banded black-and-white undertail-coverts.

Flight. Seldom flies except during migration. Flight muscles are poorly developed. Flight involves rapid wingbeats on short, rounded wings. Often drops to ground, abruptly and ungracefully, after short flight. Very flexible vertebrae facilitate movement through dense marsh understory vegetation, but may reduce efficiency in flight.

Swimming and diving. Can dive and swim, using wings for propulsion underwater; probably does so only to foil potential predators (Forbush 1925). After a dive, pokes head, or sometimes only bill and eyes (Forbush 1925, Pospichal and Marshall 1954), slightly above water surface, keeping body underwater.

SELF-MAINTENANCE

Pairs engage in allo- and autopreening. Roost each night in same spot, occasionally vocalizing during the breeding season but seldom moving. Actively forage at dawn and dusk but remain active throughout the day. Modified feather tips in anterior region of head lessen feather wear when passing through dense vegetation. Nasal valves of mucous-laden skin protect inner membrane from abrasions that can be caused by dense, coarse marsh vegetation.

AGONISTIC BEHAVIOR

Breeding pairs are monogamous and territorial. As pair bonds are formed, pairs engage in precopulatory chases, exchanges of calls, and vigorous defense of their territory (Audubon 1842, Nice 1962, Kaufmann 1988, 1989). Males probably perform the majority of territorial defense (71% of territorial chases in 5 captive pairs; Kaufmann 1989). A mated pair in captivity defended its territory up to 7 wk before nesting (Kaufmann 1989), but territory defense may be rare within several weeks of territory establishment (Johnson and Dinsmore 1985). Parents protect young aggressively and approach intruders closely with regular rasping calls, head and neck bowed and outstretched (Allen 1934, Pospichal and Marshall 1954). Both sexes engage in nest defense and continue to defend their young after they leave the nest, but the female is usually more aggressive (Weber 1909, McLean 1916, Burtch 1917, Mousley 1940, Pospichal and Marshall 1954, Wiens 1966, Ripley 1977). In pens with Soras and other Virginia Rails, males direct more aggressive chases toward conspecifics than toward male Soras (Kaufmann 1989).

Kaufmann (1983) identified 4 displays associated with hostile interactions: (1) birds may engage in fights by jumping into the air, pecking and clawing their opponent's breast; (2) incubating adults may leap at, peck, or strike severely and utter low *grunts* at potential intruders (Burtch 1917, Walkinshaw 1937); (3) captive males may often "attack an opponent's back, raking it with his claws, striking with the edges of his wings, and repeatedly pecking the head", forcing his subordinate under water; (4) when fleeing, birds may jump or turn abruptly and stand motionless to avoid detection (Walkinshaw 1937).

SPACING

Territoriality. Territorial defense is vigorous during establishment and pair formation. Once the nesting season has begun, pairs defend the area around their nest vigorously but do not defend their territory boundaries as aggressively. Territory size is difficult to measure. Territories often overlap Sora territories. Chicks are brooded by their parents as a family group within the breeding territory for 3–4 wk (Johnson and Dinsmore 1985, Kaufmann 1987, 1989), after which adults shift their home range out of their territory as young become independent (Johnson and Dinsmore 1985). Winter territories are loose or nonexistent. Some evidence of dominance hierarchies, but few empirical data.

Individual distance. Distances between adjacent Virginia Rail nests in Minnesota average 46 m (Pospichal and Marshall 1954). Adjacent Virginia Rail nests in Iowa known to be as close as 17.4 m (Tanner and Hendrickson 1954); as little as 1.5 m between Virginia Rail and Sora nests in Connecticut and Minnesota (Billard 1948, Pospichal and Marshall 1954). Virginia Rails frequently forage alongside conspecifics and Soras.

SEXUAL BEHAVIOR

Mating system. Few data. Considered socially monogamous, but extent of extra-pair fertilizations unknown.

Pair bond. Mated pairs perform allopreening, precopulatory chases, courtship displays, copulations, and exchanges of calls (Audubon 1842, Kaufmann 1988, 1989). Male performs courtship display to female, running around female with wings raised above body and flitting his tail, bowing in front of her at each pass (Audubon 1842). Mated pairs perform courtship feeding (Kaufmann 1983). Actual courtship period is brief and can be identified by the short duration of *tick-it* calls in spring (Bent 1926, Glahn 1974, Irish 1974). Copulations have been observed as many as 20 d prior to laying of first egg. The pair bond breaks down before dispersal, shortly after young fledge (Johnson and Dinsmore

1985), but adults may return to a nest site the following year if habitat conditions are stable (Mousley 1931, Pospichal and Marshall 1954).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Solitary during breeding season. Aggregations observed during migration probably a response to drying of suitable habitat and concurrent concentration of aquatic inverte-brates rather than social aggregations. Tolerance of Soras appears liberal (Pospichal and Marshall 1954).

Play. No information. See Breeding: young birds; growth and development.

Nonpredatory interspecific interactions. Allo-preening between pair members and preening of young by adults are common during the breeding season (Kaufmann 1988). Allopreening is also common during the winter and not restricted to pair members (Kaufmann 1988).

PREDATION

Rate of predation probably high on both young and adults.

Kinds of predators and manner of predation. Documented nest predators include snakes, muskrat (*Ondatra zibethica*), weasels (*Mustela erminea* and *M. frenata*), raccoon (*Procyon lotor*), hawks, blackbirds, and wrens (Gillette 1897, Allen 1934, Walkinshaw 1937, Pospichal and Marshall 1954, Tanner and Hendrickson 1954). Likely nest predators include skunk (*Mephitis* spp.), mink (*Mustela vison*), crows, and Yellow-billed Cuckoo (*Coccyzus americanus*) (Randall 1946, Billard 1948, Pospichal and Marshall 1954, Tanner and Hendrickson 1954, Andrews 1973, Tacha 1975). Pike (*Esox* spp.), bass (*Micropterus* spp.), Sandhill Cranes (*Grus canadensis*), and frogs prey on young chicks (Forbush 1925, Cramer 1932), and mink (Audubon 1842, Billard 1948, Baird 1974, Tacha 1975), coyote (*Canis latrans*), feral house cats (Pos-pichal and Marshall 1954, Robbins 1967), Great Egret (*Egretta alba*; Campbell and Wolf 1977), Northern Harrier (*Circus cyaneus*; Audubon 1842), and owls (CJC) prey on adults and juveniles.

Response to predators. Birds perform distraction displays and submerge bodies underwater. Adults perform distraction displays around nest: wings lowered, body forward, they run in tight circles (Burtch 1917, Walkinshaw 1937). Adults give alarm calls around nest when approached by humans, especially during the 1–3 d surrounding hatching.

BREEDING

PHENOLOGY

Pair formation. Little information. Males arrive on breeding grounds first (see Migration). Pairs
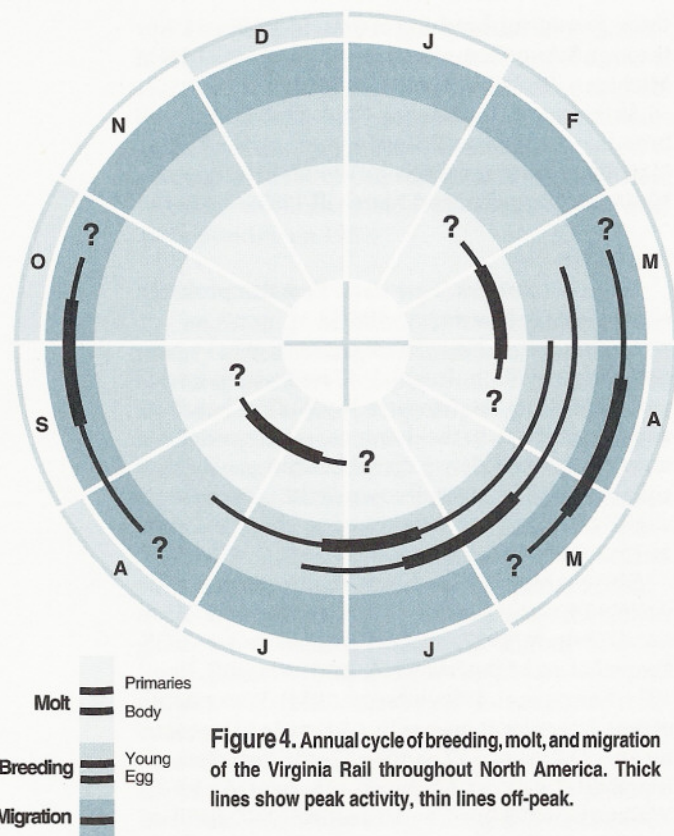

Figure 4. Annual cycle of breeding, molt, and migration of the Virginia Rail throughout North America. Thick lines show peak activity, thin lines off-peak.

associate soon after female arrival and are thought to stay together through the nesting cycle. Either member of an eventual pair may initiate bond (Kaufmann 1989). Both birds stand quietly side by side for episodes of up to 0.5 h for a period of 1–2 wk. As pair bond forms, pair engages in auto- and allopreening, precopulatory chases, copulations, exchanges of calls, courtship feeding, and defense of territory (Kaufmann 1989). A captive male carried food to his mate at least 13 times during 2 wk prior to laying, traveling 1–5 m each time (Kaufmann 1989). Copulations were observed 20 d before laying of first egg and ceased after last egg was laid (Kaufmann 1989).

Nest-building. Begins with laying of first egg (Short 1890, Kaufmann 1989), shortly before egg-laying (Gentry 1882, Shaw 1887), or > 1 wk before egg-laying (Mousley 1940). Construction is thought to take 3–4 d, but material is continually added (Pos-pichal 1952). In ne. U.S., nest-building normally begins in early May (Wood 1937, Billard 1948); in Minnesota, 11–20 May (Pospichal and Marshall 1954).

First brood per season. Figure 4. In Minnesota, hatch 7–12 Jun (Pospichal and Marshall 1954). In Arizona, downy young seen as early as 1 Apr (Anderson and Ohmart 1984).

Nest card data from throughout North America shows first eggs are laid from first week in Apr

through mid-Jul; hatching of first chicks from 1 Apr through 3 Aug. Completed clutch as late as 31 Jul in Michigan (Walkinshaw 1937).

Later broods per season. Pairs probably have 2 broods in some areas (Pospichal and Marshall 1954). Hatching of presumed second broods in Minnesota: 10–19 Jul (Pospichal and Marshall 1954).

NEST SITE

Selection process. Few data. Females probably select nest site (Kaufmann 1989).

Microhabitat. Nests in robust emergent vegetation (e.g., cattails, bulrush). Will nest within a wide variety of emergents (reviewed by Walkinshaw 1937 and Horak 1964), so the dominant plant species in a marsh is not considered a good indication of habitat suitability. Nests are well concealed; built touching, slightly submerged below, or a short distance (< 15 cm) above water surface.

Site characteristics. Nests at sites with a wide variety of water depths, ranging from 0 to 71 cm (Walkinshaw 1937, Billard 1948, Tanner 1953, Pospichal and Marshall 1954, Andrews 1973, Baird 1974, Griese et al. 1980, Johnson 1984). Water depth at nest, however, is normally < 30 cm. In Minnesota, mean = 21.2 cm (*n* = 12, range = 12–44; Pospichal and Marshall 1954); in Michigan, 18 cm (16, 10–25; Walkinshaw 1937); in Connecticut, 6.6 (0–15.2; Billard 1948), and in Colorado, 8.2 cm (Griese et al. 1980). In Michigan, mean height above water surface (to nest rim) = 14 cm (16; Walkinshaw 1937). Nests are most often placed near a border between vegetative types (Allen 1934) but not near open water (Andrews 1973, but see Pospichal and Marshall 1954). In Colorado, nests ranged from 1,120 to 2,730 m elevation (Griese et al. 1980).

NEST

Construction process. Both sexes construct nest(s), which are completed within 1 wk (Pospichal and Marshall 1954, Kaufmann 1989). Adults may add material to the nest throughout laying and incubation, especially if water levels rise (Walkinshaw 1937).

Structure and composition matter. Nests are loosely woven baskets, usually well concealed, often with a vegetation canopy constructed above the nest bowl (Beattie 1899, Walkinshaw 1937, Post and Enders 1970). Canopies are constructed by bending adjacent vegetation over the top of the nest bowl (Kaufmann 1989). Loosely formed ramps are sometimes built from substrate to nest rim (Post and Enders 1970, Kaufmann 1987). Birds use the most abundant emergent plants at the nest site (usually cattails or bulrush) for construction (Walkinshaw 1937, Billard 1948, Horak 1964, Kaufmann 1989).

Dimensions. Inside diameter: mean = 11.7 cm (*n* = 12, range = 10–13); outside diameter: 17.3 cm (12, 14–20); height of nest lip above substrate 12.8 cm (12, 5–21) (Minnesota; Pospichal and Marshall 1954). Inside diameter: mean = 12 cm (*n* = 16); outside diameter: 15 cm (16); depth of nest from nest rim to bottom of interior: mean = 3 cm (16, 1–6) (Michigan; Walkinshaw 1937).

Microclimate. No data.

Maintenance or reuse of nests, alternate or nonbreeding nests. Adults may add material to the nest throughout the nesting cycle; they often build "dummy," or brood, nests near the active nest (Walkinshaw 1937, Billard 1948, Pospichal and Marshall 1954, Kaufmann 1989). These dummy nests may number as many as 5/active nest and are probably used for feeding, brooding, resting, or as alternates in case of flooding, destruction, or predation (Walkinshaw 1937, Billard 1948, Pospichal and Marshall 1954, Kaufmann 1989). Nest desertion is not uncommon (Pospichal and Marshall 1954).

EGGS

Shape. Oval to short oval.

Size. Mean length: 32.06 mm (*n* = 20 clutches, 175 eggs, range = 29.41–34.32); mean breadth: 23.77 mm (*n* = 20 clutches, 175 eggs, range = 22.43–25.48); mean empty shell weight of pre-1947 eggs from sample drawn throughout North American range: 0.725 g (*n* = 15 clutches, 128 eggs, range = 0.616–0.807); all means and ranges are based on clutch averages (Western Foundation of Vertebrate Zoology [WFVZ]). Mean length: 32.34 mm (97 eggs); mean breadth: 23.49 mm (97 eggs) (Michigan; Walkinshaw 1937). Mean length: 31.2–33.0 mm; mean breadth: 22.9–24.4 mm (Forbush 1912, 1925).

Mass. Precocious young, high ratio of egg to female body mass. Mean mass of newly laid egg = 9.19 g (74 eggs, 9 clutches; 7.15–11.3), about 12–14 % of female mass; range of pipped eggs = 6.9–9.6 g (74 eggs, 9 clutches; Walkinshaw 1937).

Color. Variable. Creamy white to buff, sparingly and irregularly spotted with brown, lilac, and gray, often more spotting at larger end. Paler, less heavily marked, less glossy, and with smaller spots than Sora eggs (Walkinshaw 1937, Harrison 1979).

Eggshell thickness. Pre-1947 eggs from sample drawn throughout North American range: 0.185 mm (*n* = 10 clutches, 89 eggs, range = 0.170–0.202; WFVZ).

Clutch size. Mean = 8.5 eggs (*n* = 115 clutches from across North American range), range = 4–13; Walkinshaw 1937, Ripley 1977, Kaufmann 1989). In Minnesota, first clutch: 6 eggs (2, 4–8) in 1950 and 8.2 eggs (6, 5–11) in 1951; second clutch: (2, 5–9) in 1951; overall mean = 7.5 eggs (Pospichal and Marshall 1954). Clutch size may vary geographically, with more eggs in northern areas, but data are limited (Walkinshaw 1937).

Egg-laying. Begins with onset of nest construction (Short 1890, Kaufmann 1989), shortly after nest construction begins (Gentry 1882, Shaw 1887), or after nest is complete (Mousley 1940). Nesting females lay 1 egg/d (Gentry 1882, Mousley 1940, Pospichal and Marshall 1954, Kaufmann 1989), usually early in morning (Walkinshaw 1937, Pospichal and Marshall 1954, Kaufmann 1989). No information on parental behavior during laying. Estimates of egg-hatching success are few; 95.6% in Connecticut (Billard 1948). In Iowa, egg-laying peaks in mid-May (Johnson and Dinsmore 1986). In New York, egg-laying has been recorded as early as 17 Apr (Orman and Swift 1987).

INCUBATION

Onset of broodiness and incubation in relation to laying. Incubation usually begins 1–2 d (range 0–5 d) before last egg is laid (Bent 1926, Walkinshaw 1937, Mousley 1940, Kaufmann 1989).

Incubation patch: No data.

Incubation period. Normally 19 d, range 18–20 d (Walkinshaw 1937, Wood 1937, Mousley 1940, Billard 1948, Pospichal and Marshall 1954, Ripley 1977). Peak incubation is late May through mid-Jun.

Parental behavior. Both sexes incubate (Walkinshaw 1937, Kaufmann 1989), with change-overs occurring every 1–2 h. In 4 pairs, however, 60–80% of incubation was by female, and female bouts averaged longer than male bouts (119.7 min, n =10 vs. 71.3 min, n =13, respectively); longest bout lasted > 3 h (Kaufmann 1989). Pairs have fairly stable daily rhythms (Kaufmann 1989, CJC). Feeding of incubating partner observed (Walkinshaw 1937). Pair thought to exchange calls when initiating change-overs.

Hardiness of eggs. No data.

HATCHING

Two of 190 eggs were infertile in Iowa (Tanner and Hendrickson 1954).

Preliminary events and vocalizations. Eggs are pipped about 48 h before they hatch (Walkinshaw 1937). Small projection appears where eggshell is broken outward; chick utters soft peeping cries from within egg (Kaufmann 1987). Chick seems to make little progress during first 36 h of pipping (Walkinshaw 1937).

Shell-breaking and emergence. Chick breaks entirely through eggshell after 36–48 h, emerges within 1–1.5 h (Walkinshaw 1937, Kaufmann 1987). Interval between hatching of eggs is not as variable as in Sora; mean = 2.0 d (n = 23 eggs; range = 1–5 d; Kaufmann 1989). Hatching has been described as synchronous, or nearly so (within 48 h) (McLean 1916, Burtch 1917, Bent 1926, Walkinshaw 1937, Mousley 1940, but see Pospichal and Marshall 1954).

Parental assistance and disposal of eggshells. Both parents are present during hatching (Pospichal and Marshall 1954). Shells of first-hatching eggs are usually carried 1–3 m from nest and dropped; shells of later-hatching eggs are pecked into fragments in nest and partly eaten; tiny fragments of eggshell are found buried in nest lining of all successfully hatched nests (Kaufmann 1989).

YOUNG BIRDS

Condition at hatching. In one study, approximately 15% of young had unabsorbed yolk sacs at hatching; sacs were absorbed within 1–2 d (Pospichal and Marshall 1954). Young are precocial. For newly hatched young, mean mass = 5.4 g (n = 3 young, 1 clutch; range = 5.0–5.8), 7.7 g (3 young, 1 clutch; 7.5–8.1), 7.4 g (1) (Walkinshaw 1937). At 1 day old, mean mass = 7.3 g (8, 6.2–8.5) and mean culmen length = 8 mm (8, 7–9) (Pospichal and Marshall 1954). Mass = 6.3 g for a 1-day-old bird (Post and Enders 1970).

Newly hatched chicks are completely covered in glossy black natal down, except slightly bare on crown (Nice 1962, Kaufmann 1987). Bill is buff with a 1-mm-wide black band near its center, approximately 1–2 mm from base of bill (Walkinshaw 1937, Nice 1962). White egg tooth is present near tip of upper mandible (Walkinshaw 1937); it is retained for several days or up to 2 wk. Legs and feet fuscous (Walkinshaw 1937). Eyes open at hatching.

Chicks are weak and wet immediately after emergence; can hold head upright for only a few seconds (Kaufmann 1987); yawn within minutes (Nice 1962); may flee nest immediately if approached by humans. Develop quickly compared to Soras (Nice 1962). Preen within 1–4 h, snap and eat within 1–2 h, sit upright, crouch, and scratch head within 4–6 h (Nice 1962, Kaufmann 1987). Siblings frequently preen themselves and each other as early as 1 d of age in the nest (Kaufmann 1987, 1988). Use claws on wings to grasp vegetation and pull forward (Kaufmann 1987). Strong on feet by 11 h (Nice 1962); by end of first day, running down nest ramp, drinking, defecating, and swimming (Kaufmann 1987). Bathing at 2–7 d (Nice 1962, Kaufmann 1987). Escape is slow and uncoordinated, but young can scramble out of nest and swim almost immediately after hatching if prompted by parental warning (Burtch 1917, Nice 1962). Probably unable to find food independent of parents for several days.

Departure from the nest. Precocial chicks leave the nest within 3–4 d after hatching and can feed on their own by day 7 (Gillette 1897, McLean 1916, Kaufmann 1987, 1989). Chicks follow parents out of the nest but frequently lag behind, occasionally stopping to preen, feed, or rest and returning to the nest without a parent (Kaufmann 1987). Adults may bring chicks back to the nest during the night for

several days (Walkinshaw 1937). Both sexes continue to defend their young after they leave the nest (Weber 1909, McLean 1916, Burtch 1917, Mousley 1940, Pospichal and Marshall 1954, Wiens 1966, Ripley 1977).

Growth and development. See Nice 1962 for sketches of 1- to 31-d-old birds. Young grow rapidly; tarsometatarsi and toes reach adult size by 3–4 wk (Kaufmann 1987). Young probably gain approximately 1.5–3 g body mass/d (Pospichal and Marshall 1954, Kaufmann 1987). Culmen length reaches 25 mm by 3 wk. Juvenal plumage emerges at 2–3 wk (Nice 1962, Kaufmann 1987). No data on control of body temperature.

Young can emit *pee-eep* calls immediately after hatching if flushed from nest (Walkinshaw 1937). Beg at 10 d, probe at 14–16 d, exhibit aggression at 16–22 d, nest-building behavior at 23 d, washing food at 16–28 d, sunning at 30 d, play-fighting at 31 d (Nice 1962, Kaufmann 1987). Begging is much less frequent and social preening more fre-quent compared to Soras (Nice 1962, Kaufmann 1987). Oiling first observed at 18 d (Kaufmann 1987).

Chicks can walk almost immediately after hatching and are strong on feet and walking well by 11 h (Nice 1962); can jump 30–40 cm at 3 wk and can fly at 4 wk (Kaufmann 1987) or 6–7 wk (Billard 1948). In Iowa, nearly all juveniles could fly by mid-Aug (Tanner and Hendrickson 1954). Chicks can swim as soon as dry (approximately 2–4 h) (Walkinshaw 1937, Nice 1962, Kaufmann 1987).

PARENTAL CARE

Nest sanitation. Few data. Adults probably use their bills to remove broken or rotten eggs (Kaufmann 1989). Chicks leave nest to defecate (Kaufmann 1987). Nice (1962) observed captive chicks returning to the same place to defecate and suggested that this behavior is an adaptation to keep the nest platform clean.

Brooding. One parent broods hatchlings while the other completes incubation of the clutch (Pospichal and Marshall 1954, Kaufmann 1989). Brooding parent may feed and brood chicks on brood nest while occasionally bringing food to incubating mate (Kaufmann 1989). After all eggs hatch, brooding mate brings food to mate at nest, and that mate passes it to a chick, but as chicks grow older, they rush from nest to accept food from approaching adult (Kaufmann 1989). Females brood chicks 67% of time (range = 50–90%, $n = 4$ pairs; Kaufmann 1989). Proportion of food brought to the nest by each sex of brooding pair varies among pairs (Kaufmann 1989).

Both male and female parents brood the chicks immediately after departure from nest, occasionally dividing up large broods (Kaufmann 1987, 1989).

Chicks are brooded constantly by parents for first 4–7 d, then less and less during the following 2 wk (Kaufmann 1989). Parents brood chicks as a family group within the breeding territory for 3–4 wk (Kaufmann 1987, 1989), after which parents expand movements beyond their territory as young become independent (Johnson and Dinsmore 1985). Brooding parents frequently preen chicks. The bond between brood mates may last longer than that between young and parents (Pospichal and Marshall 1954, Nice 1962).

Feeding. Both parents feed chicks immediately after hatching (Pospichal and Marshall 1954, Kaufmann 1989). Minimal begging behavior; young peep loudly and peck parent's bill to stimulate feeding (Kaufmann 1987). Young learn to feed themselves at 3–7 d and are capable of foraging independently within 7 d after hatching (Pospichal and Marshall 1954, Kaufmann 1987). In captivity, brooding parents continue to feed chicks for > 1 mo (Kaufmann 1987). No data on direct or indirect method of feeding, food of young, or rate of feeding.

Parental carrying of young. Parents observed carrying young nestlings in bill (Burtch 1917, Bent 1926, Walkinshaw 1937, Kaufmann 1987, 1989), but frequency is unknown. Parents also carry eggs in bill occasionally, moving clutch to alternate nests (Kaufmann 1989).

COOPERATIVE BREEDING
Not observed.

BROOD PARASITISM

Few data. Inter- and intraspecific egg parasitism documented (Allen 1934, Tanner and Hendrickson 1954), but frequency is unknown owing to difficulty of finding and monitoring nests. One nest was parasitized by a Sora in Iowa (Tanner and Hendrickson 1954), and a Virginia Rail reportedly laid in a Sora nest (Miller 1928). One record of parasitism by Brown-headed Cowbird (*Molothrus ater*), from Ontario in 1971 (8 Virginia Rail eggs, 1 cowbird egg; Friedmann et al. 1977). Virginia Rails reportedly will reject cowbird eggs from their nest.

FLEDGLING STAGE

Growth. Few data. Attain adult body proportions by 3–4 wk and adult body mass by 6 wk (Pospichal and Marshall 1954, Kaufmann 1987). Mass 25.5 g at 10 d, 30.8 g at 14 d, and 50.0 g at 21 d ($n = 1$; Pospichal and Marshall 1954); captive birds 43 g at 3 wk and 65 g at 5 wk (Nice 1962). One captive chick steadily increased in mass and tarsometatarsus to 39 g and 30 mm at 24 d (Kaufmann 1987). Culmen length 16 mm at 10 d, 18 mm at 14 d, and 25 mm at 21 d ($n = 1$; Pospichal and Marshall 1954).

Association with parents or other young. Limited

data. Young may attain independence about the same time they learn to fly. First aggressive interaction between captive parents and young occurred 4–8 wk after hatching, although one male did not chase his young until they were 59 d old (Kaufmann 1989).

Ability to get around, feed, and care for self. Few data. Young can probably get around, feed, and care for themselves within 1 mo after hatching.

IMMATURE STAGE
No data.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY
Age at first breeding. Both sexes can breed in their first year (Pospichal and Marshall 1954).

Clutch. Some evidence that clutch size varies geographically and annually (Walkinshaw 1937, Pospichal and Marshall 1954, Kaufmann 1989). Mean clutch size from nests throughout North America : 8.5 eggs (4–13 eggs, $n = 115$; Kaufmann 1989). Pairs may nest twice in a breeding season (Pospichal and Marshall 1954), especially in southern part of breeding range, but empirical data are limited.

Annual and lifetime reproductive success. Limited information. Estimates of annual nesting success (≥ 1 young leaves nest successfully) are few; 53% from throughout North America using Mayfield estimates from nest card programs (Conway et al. 1994). Previous estimates (50–78%) are based on ratios of successful versus total nests found and hence are biased upwardly (Conway et al. 1994).

Many nests do not successfully hatch all eggs. In Minnesota, mean brood size was 4 and 4.4 chicks/brood for 2 yr (Pospichal and Marshall 1954). No data on brood or juvenile survival. No data on proportion of females successfully nesting each year. Relationship between age and breeding success unknown.

Number of broods normally reared per season. Probably only 1 in most areas (but see Pospichal and Marshall 1954), but data are lacking.

Proportion of total females that rear at least one brood to nest-leaving or independence. No data.

LIFE SPAN AND SURVIVORSHIP
Chick mortality is probably high prior to fledging; most broods are small (range 2–5) relative to published estimates of clutch size (Hunt 1908, Allen 1934, Lowther 1961, Wiens 1966, Irish 1974). Daily survival rate (MICROMORT; Heisey and Fuller 1985) of 36 radio-marked birds in Arizona: 0.998 ± 0.001 (SE); annual survival rate 0.526±0.195 (SE) in Arizona for all age/sex classes and seasons combined

(Conway et al. 1994). Although seasonal survival probabilities did not differ statistically, mortality was highest in winter (Conway et al. 1994). Annual survival probability of 88 banded birds in Arizona using capture-recapture (JOLLY; Pollock et al. 1990) was 0.532 ± 0.128 for all age/sex classes combined (Conway et al. 1994).

DISEASE AND BODY PARASITES
Diseases. No information.

Body parasites. No evidence of external body parasites, but in Minnesota, 6 of 7 birds examined contained at least 1 internal parasite (Pospichal and Marshall 1954). Parasites included Nematodes, Cestodes, and Trematodes (Pospichal and Marshall 1954). *Lynchia holoptera* was recorded from a nest of an unidentified *Rallus* sp. (Hicks 1959).

CAUSES OF MORTALITY
Not known. Predation on young and adults is probably high (see Predation, above).

RANGE
Initial dispersal from natal site. Broods appear to stay in vicinity of nest for first week after hatching, but can undergo large movements soon thereafter if habitat conditions or water levels deteriorate. Natal dispersal/philopatry unknown.

Fidelity to breeding site and winter home range. Adults will return to nest in the same location in successive years if habitat conditions remain stable (Mousley 1931, Pospichal and Marshall 1954, CJC). One adult in Arizona returned to the same location on breeding grounds for 4 consecutive yr (CJC). Fidelity to wintering grounds unknown.

Dispersal from breeding site. Frequency and distance of dispersals from breeding sites unknown, although rails are known to disperse long distances. Vagrancy, plasticity, and generalist habits allow this species to exploit a highly ephemeral niche.

Home range. Home range size varies seasonally (Conway 1990) and with habitat quality. Estimates of average home range size are limited. In Iowa, 0.18 ± 0.02 (SE) ha during the breeding season (Johnson and Dinsmore 1985); in Arizona, 1.64 ± 1.48 ha during the breeding and 2.41 ± 1.84 ha during the winter (Conway 1990). In Iowa, male and female home range sizes did not differ, and home ranges of pairs overlapped extensively (Johnson and Dinsmore 1985).

POPULATION STATUS
Numbers. Density of breeding birds depends on habitat quality, but Virginia Rails tend to occur at lower densities than do Soras (Pospichal and Marshall 1954). Densities vary from 0.1 to 8.9 pairs/ha (Neilson 1925, Tanner and Hendrickson 1954,

Post and Enders 1970, Glahn 1974, Tacha 1975, Griese et al. 1980, Johnson 1984, Manci and Rusch 1988). Highest density of Virginia Rails: 25 pairs/ha in Michigan (Berger 1951).

Availability of adequate food and nesting cover probably determines territory size and breeding density. Estimates of breeding density ranged from 0.2 to 4.7 birds/ha in Colorado, based on response to broadcast tapes (Griese et al. 1980); 0.9/ha in Iowa (Tanner and Hendrickson 1954); 8.6/ha in Kansas (Tacha 1975); and 3.6/ha in Colorado (Glahn 1974). Virginia Rails commonly occur in very small marshes but are more common in marshes >1 ha in size (Brown and Dinsmore 1986).

Trends. Populations in the ne. U.S. are thought to have declined in the early 1900s (Forbush 1912), but populations have been difficult to monitor. Grinnell and Miller (1944) stated that habitat loss reduced Virginia Rail populations. Based on Breeding Bird Survey (BBS) data, Virginia Rail populations declined 2.2%/yr (P < 0.05, n = 93) throughout North America from 1982 to 1991 (Conway et al. 1994). Declines were greatest in central U.S. Although there are problems and biases associated with interpreting Virginia Rail population trends from BBS data, these data may be the best available and may even underestimate negative trends (Conway et al. 1994). Populations in the lower Colorado River Valley apparently increased substantially in the late 1970s (Anderson and Ohmart 1984).

POPULATION REGULATION

Little known. Spring temperatures may influence breeding and wintering distribution, and consequently may regulate populations (Griese et al. 1980). Seral stage of marsh succession is probably the most influential factor affecting presence/absence and abundance (Conway and Eddleman 1994). Competition with other rails (e.g., Soras and King and Clapper rails) may influence density and habitat breadth, but studies have been correlative and conflicting (Pospichal and Marshall 1954, Horak 1970, Glahn 1974, Irish 1974, Conway 1990).

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. Thirty-seven states and 1 province (Ontario) consider Virginia Rail a game species, and bag limits are liberal, but few hunters take rails (Conway et al. 1994). Hunting pressure is highest on the birds' wintering grounds along s. Atlantic and Gulf coasts (Horak 1964, Andrews 1973). There are no national surveys specifically designed to estimate numbers of hunters or harvested birds. Hunting pressure on Virginia Rails has probably decreased since the early part of this century (Conway and Eddleman 1994). Surveys of waterfowl hunters suggested that the annual rail harvest varied greatly during 1964–1986 (Conway and Eddleman 1994), averaging 13,374 hunters and 100,983 rails other than Soras taken annually (U.S. Fish and Wildl. Serv. 1988). In coastal states, however, most harvested rails were probably Clapper Rails. Both Soras and Clapper Rails are more popular with hunters than are Virginia Rails. Only 0.9% of waterfowl hunters from 3 eastern flyways harvested rails other than Soras during 1964–1975 (Martin 1979).

In all but 1 state, the rail hunting season is in the fall, and in most states (22/35), seasons are from early Sep through early to mid-Nov. Daily bag and possession limits are set at 25 birds in most (30/35) states (Conway and Eddleman 1994).

Effects of harvest on Virginia Rail populations are not known, but annual harvest is probably within sustainable levels, at least on a national scale (Eddleman et al. 1988, U.S. Fish and Wildl. Serv. 1988). Of 1,688 Virginia Rails banded prior to 1950, none were reported harvested by hunters (U.S. Fish and Wildl. Serv. 1988). In 1992, five states and provinces indicated a need for decreased season lengths or bag limits, whereas 25 states/provinces reported no need for such changes (Conway and Eddleman 1994).

Pesticides and other contaminants/toxics. Rails are susceptible to toxic bioaccumulation. Of 75 rails examined in Georgia, 95% had high mercury levels, but only 1 Virginia Rail, an adult, was included in the sample (Odom 1975); the bird was struck by a car in 1973 and had liver mercury levels that were higher than expected (0.40 parts per million [ppm] fresh wet weight) but still within established limits.

Collisions with stationary/moving structure or objects. Frequently collides with utility wires and television towers while flying low at night on migration (Forbush 1912, Tordoff and Mengel 1956). Frequently hit by vehicles (especially young birds) while crossing roads bisecting marshlands.

Degradation of habitat. Many nests are lost or deserted owing to flooding in some areas (Walkinshaw 1937, Tanner and Hendrickson 1954, Post and Enders 1970, Griese et al. 1980). Changing water levels adversely affect rails by increasing nest loss, disrupting breeding activities, increasing chick mortality, restructuring location of optimal foraging sites, and increasing rail movements (Baird 1974, Tacha 1975, Griese et al. 1980).

Disturbance at nest and roost sites. Young will fledge immediately after hatching if disturbed (Pospichal and Marshall 1954).

Human/research impacts. No information.

MANAGEMENT

Conservation status. Although Virginia Rails are declining in many areas, no conservation programs are specifically aimed at or proposed for this species. Virginia, Indiana, and Ohio classify Virginia Rail as a "species of special interest" because of lack of adequate information. Current monitoring programs do not adequately survey Virginia Rail populations. Alternative monitoring programs that use response to broadcast tape recordings are most effective at monitoring rails and other marsh birds and should be implemented nationally (Manci and Rusch 1988, Gibbs and Melvin 1993, Conway and Eddleman 1994).

Measures proposed and taken, and their effectiveness. Few if any management activities have been implemented specifically for rails, but rails have responded well to some waterfowl management programs (Rundle and Fredrickson 1981). Activities that increase wetland cover of emergent perennial vegetation, while retaining 30–60% of the wetland in open water or mudflat, will provide both optimal nesting and foraging habitat for Virginia Rails.

Shallow flooding of areas with heterogeneous topography, or partial drawdowns of more homogeneous human-made wetlands, concentrate invertebrate prey (Fredrickson and Reid 1986, Eddleman et al. 1988), resulting in ideal foraging conditions for breeding rails.

Shallow flooding of wetland complexes in early fall has been suggested for managing migrant rails in Missouri (Fredrickson and Reid 1986). Fall flooding stimulates growth and productivity of many invertebrate species (Reid 1985). Flooding too deeply, however, reduces habitat quality for Virginia and other rails (Fredrickson and Reid 1986, Eddleman et al. 1988).

Fall or winter drawdowns maintained through Aug can also provide attractive fall habitat for migrating rails (Johnson 1984). Overly aggressive drawdown/flooding strategies, however, can increase turbidity and reduce seed stocks, thereby preventing establishment of persistent emergents and increasing open water areas (Weller et al. 1991) which reduce benefits to rails.

Managers should encourage a diversity of emergent vegetation and seed-producing annuals well interspersed with aquatic bed vegetation (Cowardin et al. 1979) and open water. Management activities that eliminate ground topographic diversity (e.g., grading) reduce vegetation/water interfaces preferred by foraging rails (Sayre and Rundle 1984, Eddleman et al. 1988).

APPEARANCE

MOLTS AND PLUMAGES

Hatchlings. Completely covered in glossy black natal down with metallic dark green gloss, except slightly bare on crown (Nice 1962, Oberholser 1974, Kaufmann 1987).

Juvenal plumage. Prejuvenal (postnatal) molt complete. Begins to emerge at 2–2.5 wk on breast area of ventral tract and expands anteriorly and posteriorly until fully emerged by 3.5 wk (Pospichal 1952, Kaufmann 1987). Ventral tract varies among individuals; sooty black to dirty white. Crural tract emerges several days after ventral, followed by femoral, spinal, and capital during week 3 (Kaufmann 1987). Alar and caudal tracts emerge at 3–4 wk. Wing-coverts acquire reddish-brown adult color by 4 wk of age (Billard 1948). Full Juvenal plumage attained by 6 wk (Pospichal 1952).

Plumage similar to nuptial adults (Definitive Alternate plumage) but duller blackish-brown above with less contrasted light edgings and edgings more rufescent. Underparts, except middle of breast and abdomen, marked profusely with fuscous, fuscous black, or grayish olivaceous brown, this color almost solid on sides of breast. Sides of head grayish olivaceous brown (Oberholser 1974).

Basic I plumage. Prebasic I (Postjuvenal) molt partial. Occurs Jul to Oct (Forbush 1925) when birds are 12–14 wk old (Billiard 1948, Pospichal 1952, Kaufmann 1987). In Iowa, nearly all juveniles had molted into reddish brown Basic I plumage by mid-Sep (Tanner and Hendrickson 1954).

Plumage similar to Definitive Alternate but somewhat darker (Oberholser 1974); perhaps slightly duller than Definitive Basic (Forbush 1925).

Alternate I plumage. Prealternate I (Prenuptial) molt partial. Occurs in Mar and includes body feathers and some wing-coverts. Plumage similar to Definitive Alternate plumage but includes Juvenal flight feathers (Oberholser 1974).

Definitive Basic plumage. Definitive Prebasic (Postnuptial) molt complete. Includes simultaneous replacement of rectrices and remiges. Occurs prior to fall migration, usually Jul–Aug (Forbush 1925, Billard 1948, Andrews 1973); early Jul through mid-Aug in s. Arizona (CJC).

Plumage similar to Definitive Alternate but darker and more richly colored (Oberholser 1974).

Definitive Alternate plumage. Definitive Prealternate (Prenuptial) molt partial. Similar to Prealternate I molt.

Upperparts, including tail, fuscous black to fuscous, feathers edged very narrowly on crown, hindneck, and sometimes rump, broadly elsewhere, with umber or light brownish olive. Remiges fuscous; lesser and most median wing-coverts russet to

brown; most of wing-coverts russet; scapulars and tertials edged light brownish olive. Supraloral stripe dull buffy white, sides of head dull neutral gray, from lores to ear-coverts deep mouse gray; chin white; throat, foreneck, and breast brownish or between cinnamon and fawn color. Flanks, sides, and undertail-coverts very dark to pale, slightly olivaceous brown, barred with white; lining of wing is hair brown mottled white (Oberholser 1974). Sexes generally similar.

BARE PARTS

Bill and gape. Pale pink at hatching with narrow black band just distal of nares and white egg tooth at tip of upper mandible (Kaufmann 1987). Black band expands with development: by 2 wk, central third of both mandibles are black and egg tooth is absorbed; at 3 wk, entire lower mandible is black; at 1 mo, entire bill is black (Kaufmann 1987). Tip of bill and small area around nasal septum are often the last to lose the white/pink coloration. In Arizona, bill color of downy chick (51 g) = 89 Munsell number with white on bill tip and nasal septum (26 May 1987; CJC). At 3 mo, center of lower mandible is brownish red (Kaufmann 1987). Adult bill is generally reddish brown; brownish on maxilla and dull orange red on mandible, fading to dusky at tip (Ridgway and Friedmann 1941). Lower mandible is more reddish in spring (Kaufmann 1989).

Iris. Black at hatching, changing to dark olive during third week, olive brown by fourth week, brown by eighth week (Kaufmann 1987). Reddish brown to russet in adult. Juveniles can be distinguished from adults by iris color. In Arizona, juvenile Munsell color = 49, 29, 49, 50, 28, 146 (dates = 8 Jul, 26 May, 12 Jun, 18 Jun, 7 Jul, 8 Jul, and weights = 50.5, 51, 56, 56, 64, and 68 g, respectively) (1987; CJC).

Bare skin on head. Chicks have dark bluish-black skin around eyes and most of head (Kaufmann 1987).

Legs and feet. Color changes gradually from dark brownish black at hatching to dusky brown at 2–3 mo (Kaufmann 1987). Dusky brownish red in adult (Ridgway and Friedmann 1941).

MEASUREMENTS

Linear measurements and mass are given in the Appendix. Males average larger and heavier than females, but an adequate sexing technique based on morphological measurements has not been developed. There is considerable overlap in morphological measurements between the sexes.

PRIORITIES FOR FUTURE RESEARCH

Standardized national population surveys should be implemented immediately to better assess seasonal distributions and population and habitat trends (Conway and Eddleman 1994). Pesticide accumulation in wetlands is a potential hazard to Virginia Rails (Odom 1975) because they feed on substrate invertebrates. Pesticides can also reduce the invertebrate prey base available to rails (Eddleman et al. 1988). Basic information on biology, natural history, and habitat needs is limited for this species. Experimental research needs to address the olfactory ability of rails to recognize and locate food.

Priorities should be to (1) estimate adult and brood survival, nesting success, site fidelity, and recruitment, (2) examine environmental factors affecting survival, nest success, site fidelity, and recruitment, (3) examine effects of common wetland management programs on Virginia Rails, and (4) evaluate effectiveness of vocalization surveys for estimating population density or indexing population trends.

ACKNOWLEDGMENTS

REFERENCES

Allen, A. A. 1934. The Virginia Rail and the Sora. Bird Lore 36: 196–204.

American Ornithologists' Union. 1957. Check-list of North American birds. 5th ed. Am. Ornithol. Union, Washington, D.C.

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

Amos, E. J. R. 1991. A guide to the birds of Bermuda. E. J. R. Amos, Corncrake, Bermuda.

Anderson, B. W., and R. D. Ohmart. 1984. Vegetation management study for the enhancement of wildlife along the lower Colorado River. Bur. Reclamation, Boulder City, NV.

Andrews, D. A. 1973. Habitat utilization by Soras, Virginia Rails, and King Rails near southwestern Lake Erie. Master's thesis, Ohio State Univ., Columbus.

Audubon, J. J. 1842. The birds of America. Vol. 5. J. J. Audubon, New York.

Baird, K. E. 1974. Field study of the King, Sora, and Virginia Rails at Cheyenne Bottoms in west-central Kansas. Master's thesis, Fort Hays Kansas State College, Fort Hays.

Barger, N. R. 1957. Virginia Rail. Wisconsin Conserv. Bull. 22(10): 35–36.

Beattie, F. N. 1899. Nesting of the Virginia Rail. Oologist 16: 184.

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

Berger, A. J. 1951. Nesting density of Virginia and Sora Rails in Michigan. Condor 53: 202.

Beston, H. 1954. Virginia Rail captured at Nobleboro. Bull. Maine Audubon Soc. 10(2): 31.

Billard, R. S. 1948. An ecological study of the Virginia Rail and the Sora in some Connecticut swamps, 1947. Master's thesis, Iowa State College, Ames.

Binford, L. C. 1972. Virginia Rail and Cape May Warbler in Chiapas, Mexico. Condor 75: 350–351.

Bollinger, R. C., and E. Bowes. 1973. Another chapter in the "ornithological mystery story." Am. Birds 27: 741–742.

Bond, J. 1947. Field guide to birds of the West Indies. Macmillan Co., New York.

Brewster, W. 1902. Voices of a New England marsh. Bird Lore 4: 43–56.

Brocke, R. H. 1958. A Virginia Rail defies a record winter. Jack-Pine Warbler 36: 100.

Brodkorb, P. 1957. New passerine birds from the Pleistocene of Florida. J. Paleont. 31: 129–138.

Brown, M., and J. J. Dinsmore. 1986. Implications of marsh size and isolation for marsh bird management. J. Wildl. Manage. 50: 392–397.

Burtch, V. 1917. The summer life of the Virginia Rail. Bird Lore 19: 243–248.

Cahn, A. R. 1915. Notes on a captive Virginia Rail. Auk 32: 91–95.

Callin, E. M. 1968. Vocalization of the Virginia Rail: a mystery solved. Blue Jay 26: 75–77.

Campbell, E. G., and G. A. Wolf. 1977. Great Egret depredation on a Virginia Rail. West. Birds 8: 64.

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

Conway, C. J., and W. R. Eddleman. 1994. Virginia Rail. Pp. 460–501 *in* Management of migratory shore and upland game birds in North America (T. C. Tacha and C. E. Braun, eds.). Intl. Assoc. Fish and Wildlife Agen.

Conway, C. J., W. R. Eddleman, and S. H. Anderson. 1994. Nesting success and survival of Virginia Rails and Soras. Wilson Bull. 106: 466–473.

Cooke, W. W. 1914. Distribution and migration of North American rails and their allies. Bull. U.S. Dept. Agric. 128.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. FWS/OBS–79/31, U.S. Fish Wildl. Serv., Office Biol. Serv., Washington, D.C.

Cramer, W. S. 1932. Virginia Rail in the stomach of a green frog. Auk 49: 80.

Crandall, L. S. 1920. Early Virginia Rail in New York. Auk 37: 452.

Degner, E. 1963. The sad tale of the rails. Passenger Pigeon 25(3): 106.

Dickerman, R. W. 1966. A new subspecies of the Virginia Rail from Mexico. Condor 68: 215–216.

Dickerman, R. W. 1971. Notes on various rails in Mexico. Wilson Bull. 83: 49–56.

Dickey, D. R. 1928. A race of Virginia Rail from the Pacific coast. Condor 30: 322.

Dunwiddie, A. 1963. Another note on wintering rails. Passenger Pigeon 25(3): 107.

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.

Fassett, N. C. 1940. A manual of aquatic plants. McGraw-Hill, New York.

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

Forbush, E. H. 1912. A history of the game birds, wild-fowl and shore birds of Massachusetts and adjacent states. Mass. State Board of Agric., Boston.

Forbush, E. H. 1925. Birds of Massachusetts and other New England states. Pt. 1. J. S. Cushing Co.-Berwick and Smith Co., Norwood, MA.

Fredrickson, L. H., and F. A. Reid. 1986. Wetland and riparian habitats: a nongame management overview. Pp. 59–96 *in* Management of nongame wildlife in the midwest: a developing art (J. B. Hale, L. B. Best, and R. L. Clawson, eds). North Central Section of the Wildlife Soc., Chelsea, MI.

Friedmann, H., L. F. Kiff, and S. J. Rothstein. 1977. A further contribution to knowledge of the host relations of parasitic cowbirds. Smithson. Contrib. Zool. 235.

Gentry, T. R. 1882. Nests and eggs of birds of the United States.

Gibbs, J. P., J. R. Longcore, D. G. McAuley, and J. K. Ringelman. 1991. Use of wetland habitats by selected nongame water birds in Maine. Fish Wildl. Res. Rep. 9, U.S. Fish Wildl. Serv.

Gibbs, J. P., and S. M. Melvin. 1993. Call-response surveys for monitoring breeding waterbirds. J. Wildl. Manage. 57: 27–34.

Gillette, D. C. 1897. Notes on the Virginia and Sora Rails. Oologist 14: 21–23.

Glahn, J. F. 1974. Study of breeding rails with recorded calls in north-central Colorado. Wilson Bull. 86: 206–214.

Glassel, R. A. 1959. Wintering Virginia Rails in Minnesota. Flicker 31(1): 23.

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

Goldman, E. A. 1908. The Virginia Rail breeding in Mexico. Condor 10: 181.

Griese, H. J., R. A. Ryder, and C. E. Braun. 1980. Spatial and temporal distribution of rails in Colorado. Wilson Bull. 92: 96–102.

Griffing, M. B. 1881. Virginia Rail. Ornithol. and Oologist 6: 59.

Grinnell, J., and A. H. Miller. 1944. The distribution of the birds of California. Cooper Ornithol. Club, Berkeley, CA.

Harrison, H. H. 1979. A field guide to western birds' nests. Houghton Mifflin Co., Boston.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. J. Wildl. Manage. 49: 668–674.

Hicks, E. A. 1959. Check-list and bibliography on the occurrence of insects in birds' nests. Iowa State College Press, Ames.

Horak, G. J. 1964. A comparative study of Virginia and Sora Rails with emphasis on foods. Master's thesis, Iowa State Univ., Ames.

Horak, G. J. 1970. A comparative study of the foods of the Sora and Virginia Rail. Wilson Bull. 82: 207–213.

Howell, S. N. G., and S. Webb. 1995. The birds of Mexico and northern Central America. Oxford Univ. Press, Oxford.

Hunt, C. J. 1908. *Rallus virginianus* a Delaware Valley breeder. Auk 25: 81.

Irish, J. 1974. Postbreeding territorial behavior of Soras and Virginia Rails in several Michigan marshes. Jack-Pine Warbler 52: 115–124.

Johnson, R. R. 1984. Breeding habitat use and postbreeding movements by Soras and Virginia Rails. Master's thesis, Iowa State Univ., Ames.

Johnson, R. R., and J. J. Dinsmore. 1985. Brood-rearing and postbreeding habitat use by Virginia Rails and Soras. Wilson Bull. 97: 551–554.

Johnson, R. R., and J. J. Dinsmore. 1986. The use of tape-recorded calls to count Virginia Rails and Soras. Wilson Bull. 98: 303–306.

Kaminski, R. M. 1979. Dabbling duck and aquatic invertebrate responses to manipulated wetland habitat. Ph.D. diss., Michigan State Univ., East Lansing.

Kaminski, R. M., and H. H. Prince. 1981. Dabbling duck and aquatic macroinvertebrate responses to manipulated wetland habitat. J. Wildl. Manage. 44: 1–15.

Kaufmann, G. W. 1971. Behavior and ecology of the Sora, *Porzana carolina*, and Virginia Rail, *Rallus limicola*. Ph.D. diss., Univ. of Minnesota, Minneapolis.

Kaufmann, G. W. 1977. Breeding requirements of the Virginia Rail and the Sora in captivity. Avic. Mag. 83: 135–141.

Kaufmann, G. W. 1983. Displays and vocalizations of the Sora and the Virginia Rail. Wilson Bull. 95: 42–59.

Kaufmann, G. W. 1987. Growth and development of Sora and Virginia Rail chicks. Wilson Bull. 99: 432–440.

Kaufmann, G. W. 1988. Social preening in Soras and in Virginia Rails. Loon 60: 59–63.

Kaufmann, G. W. 1989. Breeding ecology of the Sora, *Porzana carolina*, and the Virginia Rail, *Rallus limicola*. Can. Field-Nat. 103: 270–282.

Krapu, G. L., and R. K. Green. 1978. Breeding bird populations of selected semipermanent wetlands in south-central North Dakota—1977. Am. Birds 32: 110–112.

Ligon, J. D. 1965. A Pleistocene avifauna from Haile, Florida. Bull. Fla. State Mus. Biol. Sci. 10: 127–158.

Lowther, J. K. 1961. Virginia Rail (*Rallus limicola limicola* Vieillot) breeding at Vermilion, Alberta. Auk 78: 271.

Manci, K. M., and D. H. Rusch. 1988. Indices to distribution and abundance of some inconspicuous waterbirds on Horicon marsh. J. Field Ornithol. 59: 67–75.

Martin, A. C., H. S. Zim, and A. L. Nelson. 1951. American wildlife and plants. McGraw-Hill, New York.

Martin, E. M. 1979. Hunting and harvest trends for migratory game birds other than waterfowl: 1964–76. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Wildl. 218.

McLean, D. D. 1916. Nesting habits of the Virginia Rail in Mariposa County, California. Condor 18: 229.

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

Miller, R. F. 1928. Virginia Rail lays in Sora's nest. Oologist 45: 132.

Mousley, H. 1931. Notes on the home life of the Virginia Rail. Can. Field-Nat. 45: 65–66.

Mousley, H. 1940. Further notes on the nesting habits of the Virginia Rail. Wilson Bull. 52: 87–90.

Neilson, J. A. 1925. Bird notes from Wheatland, Wyoming. Condor 27: 72–73.

Nelson, J. W., and J. A. Kadlec. 1984. A conceptual approach to relating habitat structure and macroinvertebrate production in freshwater wetlands. Trans. N. Am. Wildl. Nat. Resour. Conf. 49: 262–270.

Nice, M. M. 1962. Development of behavior in precocial birds. Trans. Linn. Soc. N.Y. 8: 1–211.

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 and Fish Comm. 28: 649–658.

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: a monograph of the family Rallidae (S. D. Ripley, ed.). M. F. Feheley Publ., Toronto.

Olson, S. L. 1985. The fossil record of birds. Pp. 79–238 *in* Avian biology, vol. 8 (D. S. Farner, J. R. King, and K. C. Parkes, eds.). Academic Press, Orlando, FL.

Orman, S., and B. Swift. 1987. Early nesting of a Virginia Rail in New York. Kingbird 37: 211.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildl. Monogr. 107: 1–97.

Pospichal, L. B. 1952. A field study of Sora Rail (*Porzana carolina*) and Virginia Rail (*Rallus limicola*) populations in central Minnesota. Master's thesis, Univ. of Minnesota, St. Paul.

Pospichal, L. B., and W. H. Marshall. 1954. A field study of Sora Rail and Virginia Rail in central Minnesota. Flicker 26: 2–32.

Post, W., and F. Enders. 1970. Notes on a saltmarsh Virginia Rail population. Kingbird 20: 61–67.

Randall, T. E. 1946. Virginia Rail, *Rallus limicola limicola*, Vieillot, nesting in Alberta. Can. Field-Nat. 60: 135.

Reid, F. A. 1985. Wetland invertebrates in relation to hydrology and water chemistry. Pp. 72–79 *in* Water impoundments for wildlife: a habitat management workshop (M. D. Knighton, ed.). For. Serv. Gen. Tech. Rept. NC–100, U.S. Dept. Agric., St. Paul, MN.

Reynard, G. B. 1974. Some vocalizations of the Black, Yellow, and Virginia Rails. Auk 91: 747–756.

Reynard, G. B., and S. T. Harty. 1968. Ornithological "mystery" song given by male Virginia Rail. Cassinia 50: 3–8.

Richter, C. 1948. Virginia Rail catches frog. Passenger Pigeon 10: 32.

Ridgway, R., and H. Friedmann. 1941. The birds of North and Middle America. Bull. U.S. Natl. Mus. 50: 1–254.

Ripley, S. D. 1977. Rails of the world: a monograph of the family Rallidae. M. F. Feheley Publ., Toronto.

Robbins, C., Jr. 1967. Virginia Rail on Christmas count. Maine Field Nat. 23: 13.

Robbins, C. S. 1949. Distribution of North American birds. Aud. Field Notes 3: 238–239.

Root, T. 1988. Atlas of wintering North American birds: an analysis of Christmas Bird Count data. Univ. of Chicago Press, Chicago.

Rundle, W. D., and L. H. Fredrickson. 1981. Managing seasonally flooded impoundments for migrant rails and shorebirds. Wildl. Soc. Bull. 9: 80–87.

Sayre, M. W., and W. D. Rundle. 1984. Comparison of habitat use by migrant Soras and Virginia Rails. J. Wildl. Manage. 48: 599–605.

Shaw, S. A. 1887. Nesting of the Virginia Rail in New Hampshire. Ornithol. and Oologist 12: 131–132.

Short, E. H. 1890. Breeding of the Virginia Rail. Oologist 7: 229–230.

Swift, B. L. 1989. Avian breeding habitats in Hudson River tidal marshes. Final Rep., New York Dept. Environ. Conser., Delmar.

Tacha, R. W. 1975. A survey of rail populations in Kansas, with emphasis on Cheyenne Bottoms. Master's thesis, Fort Hays Kansas State College, Fort Hays.

Tanner, W. D. 1953. Ecology of the Virginia and King Rails and the Sora in Clay County, Iowa. Ph.D. diss., Iowa State Univ., Ames.

Tanner, W. D., and G. O. Hendrickson. 1954. Ecology of the Virginia Rail in Clay County, Iowa. Iowa Bird-Life 24: 65–70.

Taylor, J. W. 1971. The Virginia Rail. Virginia Wildlife 32(9): 27.

Thorpe, W. H. 1972. Duetting and antiphonal song in birds: its extent and significance. E. J. Brill, Leiden, Netherlands.

Tordoff, H. B., and R. M. Mengel. 1956. Studies of birds killed in nocturnal migration. Univ. Kans. Publ. Mus. Nat. Hist. 10: 1–44.

Trautman, M. B. 1940. The birds of Buckeye Lake, Ohio. Misc. Publ. Mus. Zool. Univ. Mich. 44.

U.S. Fish and Wildlife Service. 1988. Final supplemental environmental impact statement: issuance of annual regulations permitting the sport hunting of migratory birds. SEIS 88, U.S. Government Printing Office, Washington, D.C.

Voigts, D. K. 1976. Aquatic invertebrate abundance in relation to changing marsh vegetation. Am. Midl. Nat. 93: 313–322.

Walkinshaw, L. H. 1937. The Virginia Rail in Michigan. Auk 54: 464–475.

Weber, J. A. 1909. The Virginia and Sora Rails nesting in New York City. Auk 26: 19–22.

Weller, M. W., G. W. Kaufmann, and P. A. Vohs, Jr. 1991. Evaluation of wetland development and waterbird response at Elk Creek Wildlife Management Area, Lake Mills, Iowa, 1961 to 1990. Wetlands 11: 245–262.

Weller, M. W., and C. E. Spatcher. 1965. Role of habitat in the distribution and abundance of marsh birds. Iowa Agric. and Home Econ. Exp. Sta. Spec. Rep. 43.

Werner, I. A. 1955. Virginia Rail winter record. Bull. Maine Audubon Soc. 11(2): 30.

Wiens, J. A. 1966. Notes on the distraction display of the Virginia Rail. Wilson Bull. 78: 229–231.

Wood, H. B. 1937. Incubation period of Virginia Rail. Auk 54: 535–536.

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

Zimmerman, J. L. 1977. Virginia Rail (*Rallus limicola*). Pp. 46–56 *in* Management of migratory shore and upland game birds in North America (G. C. Sanderson, ed.). Intl. Assoc. Fish and Wildl. Agen., Washington, D.C.

Zimmerman, J. L. 1984. Distribution, habitat, and status of the Sora and Virginia Rail in eastern Kansas. J. Field Ornithol. 55: 38–47.

Appendix. Length (mm) and mass (g) measurements of Virginia Rails. Data shown as mean ± SD (range; n). All measurements are for after-hatching-year/after-second-year (AHY/ASY) adult birds only. All museum measurements for males are larger than for females ($P < 0.001$). Sources: A = CJC, unpubl. data of measurements taken from museum skins at 7 collections; B = Ridgway and Friedmann 1941; C = Godfrey 1986; D = CJC, unpubl. data of measurements from live birds collected in Lower Colorado River Valley; E = Kaufmann 1987 (includes both juveniles and adults in autumn; no SD reported); F = Post and Enders 1970 (May and June only).

Location/ Source	United States A	B	Canada C	S. Arizona D	Iowa, Minnesota E	New York F
Depth of bill						
Females	5.1[1] ± 0.3 (4.3-5.8; 36)					
Males	5.5 ± 0.4 (4.8-6.1; 45)					
Both sexes				6.3 ± 0.6 (5-8; 106)		
Bill length						
Females	35.7[2] ± 1.7 (32.1-39.1; 40)	40.2[3] (36-42.5; 19)				
Males	40.2[2] ± 3.4 (33.3-57.9; 47)	41.7[3] (36.5-44.5; 26)	39.9[2] (35.3-41.8)			
Both sexes				38.8 ± 2.9 (32.2-46; 110)		
Wing						
Females	100.1[4] ± 3.5 (89-106.1; 29)	101.2 (95-105.5; 19)	98.1 (94.2-102.2)			
Males	106.3 ± 3.2 (99.2-112.6; 47)	105.9 (94-113; 26)	105.4 (101-107.9)			
Both sexes				107.1[3] ± 4.9 (95-118; 108)		
Tail						
Females	40.6 ± 3.0 (32-47.5; 40)	45.0 (38-47.5; 19)				
Males	43.8 ± 2.4 (39-49.5; 47)	44.3 (38.5-54; 26)	44.5 (40-48.6)			
Both sexes				45.6 ± 3.6 (34-58; 104)		
Tarsus						
Females	32.4 ± 1.3 (29.6-34.9; 36)	34.1 (31-37.5; 19)				
Males	35.1 ± 1.9 (29.1-38.7; 43)	35.4 (31.5-39; 26)	36.4 (33.1-38.2)			
Both sexes				42.6[6] ± 2.6 (35-48; 110)	34.2 (31.4-36.0; 34)	
Longest toe						
Females	34.1 ± 2.1 (30.3-39.2; 40)	34.3 (32-37.5; 19)				
Males	36.6 ± 1.8 (33-40.1; 47)	36.7 (34.5-39.5; 26)				
Both sexes				35.3 ± 2.6 (29-41; 110)		
Metatarsus-midtoe						
Females	71.2[4] ± 2.8 (66-77.4; 21)					
Males	77.7 ± 3.4 (69.1-84; 42)					
Both sexes				76.0 ± 4.3 (67-85; 107)		
Mass						
Females	69.3 ± 6.7 (63.8-76.8; 3)					
Males	89.4 ± 10.9 (79.2-104; 6)					
Both sexes				84.1 ± 14.5 (55-124; 147)		87.0 ± 9.6 (15)

[1] At distal end of nasal groove.
[2] Exposed culmen.
[3] Flattened.
[4] Distance from behind metatarsus joint to end of toe pad on middle toe.
[5] Culmen.
[6] Measured from behind joint to bend of metatarsus.

The Birds of North America

The Birds of North America series provides comprehensive, authoritative summaries of current knowledge of the breeding bird species of North America. Each of these accounts includes a major bibliography of references as well as unpublished information. Their purpose is to enable informed conservation management of our native birds and to define directions for future research. Accounts are published separately to insure timely availability of their contents.

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