TOWARDS A LESS IMPERFECT UNDERSTANDING OF THE SYSTEMATICS AND BIOGEOGRAPHY OF THE CLAPPER AND KING RAIL COMPLEX (*RALLUS LONGIROSTRIS* AND *R. ELEGANS*)

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ABSTRACT.–In eastern North America and Cuba, King and Clapper rails (*Rallus elegans* and *R. longirostris*) are fresh and salt water counterparts that differ in plumage, size, development of the salt gland and width of the interorbital bridge, and in certain aspects of behavior. King Rails are capable of inhabiting salt marshes but seldom do so when Clapper Rails are present and may be excluded from eastern salt marshes by Clapper Rails. On the other hand, Clapper Rails are not known to invade freshwater marshes. The two species hybridize readily, but only in areas where ecological conditions are intermediate, a specific instance of which in Florida is described in detail. Hybrids do not occur outside these areas of intermediate salinity and nowhere is there a hybrid zone in which no pure parental types occur. King and Clapper rails are therefore best treated as separate species. Morphology, distribution, and paleontology are used to reconstruct a hypothetical evolutionary history of the complex. *Rallus longirostris* falls into two subspecies-groups—a heavy-billed *longirostris* group in South America and a slender-billed crepitans group in the West Indies and coastal marshes of eastern North America and Yucatan. All other North American populations of the complex on the Pacific coast of California and Baja California, and in central and western Mexico, are regarded as relicts of an original widespread North American King Rail stock that were isolated following desertification of the American west and should be treated as subspecies of *Rallus elegans.*

Two large forms of *Rallus* have been recognized in North America ever since the Reverend John Bachman persuaded his friend Audubon that the large, reddish, freshwater birds were a different species from the smaller, grayish birds of the salt marshes (see the history in Meanley 1969:4-6). Audubon (1834, 1835) named the freshwater inhabiting King Rail as *Rallus elegans*. The Clapper Rails now take the name *Rallus longirostris* Boddaert (1783).

Although the very close relationship between King and Clapper rails is commonly acknowledged, they have most often been kept as separate species. Bull (1964:173) considered that the two "form a superspecies, at least," and perhaps he can be credited with originating that perplexing phrase. "At least a superspecies" was later echoed throughout the 6th edition of the A. O. U. Check-list (American Ornithologists' Union, 1983), although I am still at a loss to understand precisely what this means. Predictably, in that work the King and Clapper rails were said to "constitute a superspecies," as also may be inferred from the treatment of these taxa in Mayr and Short (1970).

Rallus elegans is generally distributed in freshwater marshes throughout the United States east of the plains. It also occurs in freshwater habitats in Cuba. This of itself defies most definitions of subspecies, which are supposed to designate within-species variants that replace each other geographically. How can *Rallus elegans* in North America be a subspecies of *R. longirostris*, which surrounds it, and at the same time be in Cuba, where it is likewise surrounded by *R. longirostris*? Clearly we are dealing here with some historical factors that transcend those responsible for what we normally consider to be subspecies.

An unnamed species of this complex is known from abundant bones dating well back into the Pleistocene of Bermuda (Olson 1977). I believe that this is a flightless derivative of *R. elegans* (see discussion of osteology).

The race *tenuirostris* from fresh-water marshes of central Mexico was first described by Ridgway (1874) as a variety of *elegans*, and was almost invariably listed as such until the revision of Oberholser (1937). Even after this, other authorities continued to place this form in *elegans*, as was done most recently in the 6th A. O. U. Check-list (A.O.U. 1983).

The large rails of the coastal marshes of California and Baja California have a checkered taxonomic history. The first of these populations to be named (*obsoletus*) was described from the San Francisco Bay area by Ridgway (1874) as a variety of *elegans.* In the early literature, the races named later from southern California (*levipes* Bangs 1899) and Baja California (*beldingi* Ridgway 1882) were treated either as distinct species or as subspecies of *elegans* or of *obsoletus*, never of *longirostris.* Peters (1934) listed all of these taxa as subspecies of *elegans*. When van Rossem (1947:52) described another race from Baja California as *Rallus longirostris magdalenae*, he did so "in the interest of conformity to current usage," although stating his preference for the arrangement "whereby the western rails are treated as races of *Rallus elegans.*"

The writers who associated these western rails with *elegans* did so for one simple reason—they look like *elegans.* They are richly tawny below with rusty wings, the races *levipes* and *beldingi* (including *magdalenae*) from southern California and Baja California being perhaps the most intensely "King Rail-like" of any of the populations of this complex.

Relatively late in the taxonomic history of the group, three very similar populations were named within less than a decade from very few specimens taken in the lower Colorado basin of California, Arizona, and Sonora, and from mangrove swamps along the eastern side of the Gulf of California in Mexico: *yumanensis* Dickey (1923), *nayaritensis* McLellan (1927), and *rhizophorae* Dickey (1930). These are relatively brightly colored below and on the wings and consequently were originally associated either with *elegans* or *obsoletus.* The margins of the dorsal feathers are decidedly grayish, however, which is more suggestive of Clapper Rails. To a lesser extent this applies to the race *obsoletus* as well, which also has some grayish in the dorsum.

In his influential revision of all of the North American and West Indian forms of this complex, Oberholser (1937) recognized *elegans* as a full species because of the the problem of explaining the Cuban population of King Rail being separated from that of the mainland by several intervening subspecies of *longirostris.* His solution, however, was to recognize in this species only nominate *elegans* and the Cuban subspecies *ramsdeni.* All of the other taxa he considered to be subspecies of *longirostris.* This would have had a certain logic in making *longirostris* apply to salt-water populations and *elegans* to fresh-water ones, were it not for the fact that *tenuirostris* is a fresh-water race.

Oberholser's classification (1937) was followed by Ridgway and Friedmann (1941). Hellmayr and Conover (1942) reversed the trend and returned the controversial western taxa to *elegans*, but then the 5th A.O.U. Check-list (A. O. U., 1957) once again made them subspecies of *longirostris.*

Warner and Dickerman (1959:50) gave new locality records for *tenuirostris* and stated that "inclusion of *tenuirostris* in *Rallus longirostris* obscures obvious similarities to *R. e. elegans*. The same, of course, might be said of *R. l. beldingi*, and perhaps of the other populations of large rails of northwestern Mexico and southwestern United States ....*Rallus longirostris* from Yucatan and Quintana Roo do not bear close color resemblance to *R. elegans* of the highlands of Mexico and eastern North America."

Dickerman (1971), in giving additional distributional records of various rails from Mexico, reversed his previous stance by merging the entire complex under the specific name *longirostris* because "species differences . . . break down as one examines specimens from throughout the range of the entire complex," and because of Meanley's (1969) record of interbreeding between Clapper and King Rails. Ripley (1977) was perhaps the most influential author to treat the King Rail as no more than a subspecies of *Rallus longirostris*, in which he has been followed by others (e.g. Heard 1982).

Although the situation remains complicated, I believe that the forms *elegans* and *longirostris* in eastern North America and Cuba do not behave as geographical subspecies and, in spite of frequent hybridization, should still be maintained as distinct species. Here I shall review new and previous evidence bearing on this question and attempt to provide a speculative evolutionary history of the complex that I hope will provide a new background against which additional research and experimentation may be conducted.

MORPHOLOGY

Adult plumage. – The several races of *R. longirostris* in eastern North America vary considerably in overall coloration, from light to dark. All forms, however are more subdued in coloration than *elegans*, in which the overall hue is brownish, the wings rich chestnut-red, the cheeks light brown, the breast rich cinnamon, and the dorsal feathers edged with light tawny-olive. Clapper Rails are always grayer in appearance, with the cheeks gray, the wings dull olive brown, and the edging of the dorsal feathers varying from brownish-gray to a light, almost greenish-gray, but not like the tawny color of King Rails. The breast may be richly colored in some races, especially at the outset of the breeding season, but is never as rich cinnamon-brown as in *elegans.*

On this basis the birds of the Pacific coast salt marshes and lower Colorado Basin, which include some of the most richly rufous-colored of all the forms in this complex, would have to be classified with King Rails, which they much more closely resemble in coloration. As mentioned, the *yumanensis* group of southeastern California, southwestern Arizona, northwestern Sonora, and mangrove areas of the west coast of Mexico is perplexing because it combines the rufous tendencies of the *elegans* style of coloration with decidedly grayish edging to the dorsal feathers. Nevertheless, the plumage differences outlined above are usually all that we have to go on in identifying skins of each of these species and their probable hybrids in eastern North America.

Natal plumage. – Wetherbee and Meanley (1965) noted an interesting difference in the downy plumage of neonatal King and Clapper rails. Chicks of *elegans* are entirely glossy black, whereas in those of *longirostris* there is a patch of white neossoptiles in each ventral pteryla, just below the wings. This white patch was also present in nearly fully developed embryos from a clutch of eggs belonging to a mixed King/Clapper pair (Wetherbee and Meanley 1965).

Wetherbee and Meanley (1965:500) hypothesized a genetic parallel between the condition in the rails and one observed in domestic fowl (*Gallus gallus*): "In homozygous blackish varieties of chickens, chicks with some white in the neonatal down become all black at maturity and chicks with no white in the neonatal down become 'broken' in color of plumage at maturity. Phaeomelanins (red-brown) can be expressed in the later ontogeny of solid black chicks, but phaeomelanin genes are cryptomeric in the later ontogeny of white-spotted black chicks." Thus, if the same were true for *Rallus*, this could explain the reddish color in *elegans* as opposed to its absence in *longirostris.*

Ripley (1977:126) considered that this character was not constant, and indeed in the USNM collections there are several downy chicks attributed to *R. longirostris*, one of which (USNM 298880) is associated with an adult specimen that is definitely *longirostris*

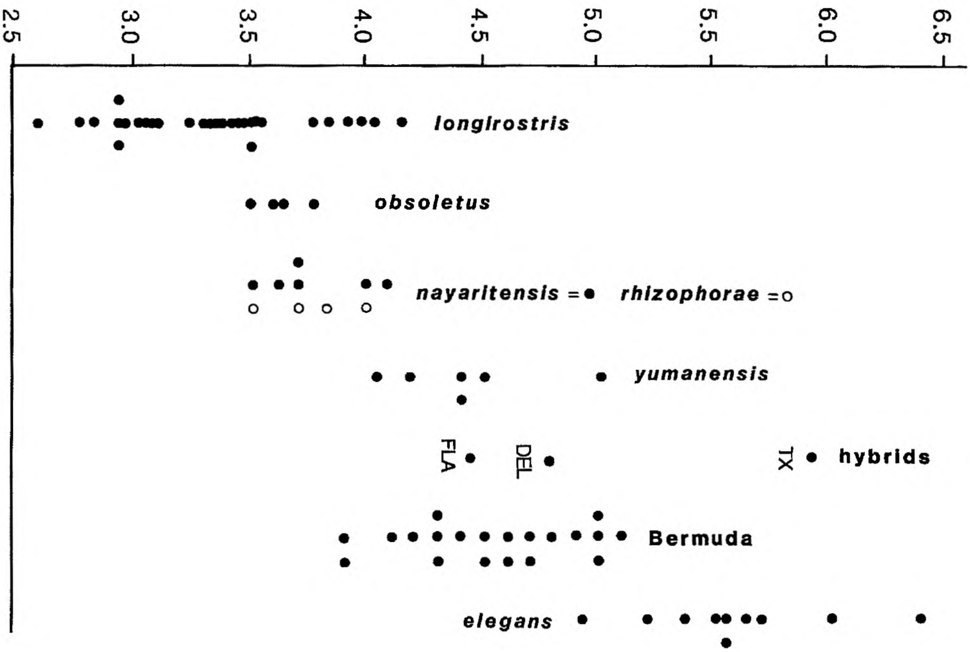

FIG. 1. Scatter diagram showing measurements (mm) of interorbital bridge width in specimens of the *Rallus longirostris/elegans* complex. Hybrids from Florida (FLA) and Delaware (DEL) have the expected intermediate width, whereas the suspected hybrid from Texas (TX), which is virtually identical in plumage, falls within the range of *elegans*. All salt marsh and mangrove-dwelling forms have narrow interorbital bridges, regardless of apparent derivation from *elegans*. Populations with intermediate widths include one (*yumanensis*) that breeds in freshwater but winters in saline habitat, and another (unnamed, flightless Bermuda species) believed to be an *elegans* derivative living in an environment with somewhat increased salt loads.

(USNM 298957), that lack any white neossoptiles. It is possible that some of these are misidentified or that the white down may have been lost in preparation. Regardless, the character was expressed as described by Wetherbee and Meanley in most specimens of chicks of both species from eastern North America that I examined. Of further interest is that the natal down in the populations of the Pacific region appears to corroborate the appearance of the adults as being like King Rails. Ten downy young that I examined at the Museum of Vertebrate Zoology were entirely black and showed no sign of the white neossoptiles of *longirostris* (*obsoletus* MVZ 25377, 25500, 25501 100402 106803; *levipes* MVZ 3702-4, 53275-6). A downy young (Bell Museum, University of Minnesota 12878) collected 22 July 1956 in Jalisco, Mexico, and thus referable to the subspecies *tenuirostris,* although rather large, is still completely downy and lacks the white neossoptiles. Thus, on the basis of natal down these subspecies would have to be considered King Rails, not Clappers.

Size. – Considering only birds in eastern North America, although there is considerable overlap, King Rails average larger in wing and tarsus length but not in culmen (see measurements in Ridgway and Friedmann 1941). In skeletons it can be seen that the wing and leg bones of *longirostris* are more slender than in *elegans*. The rostrum of *elegans*, while about the same length as in *longirostris* is usually broader and heavier and not as decurved. The cranium is somewhat higher and broader in *elegans*. Although lack of sufficient series of skeletons of *elegans* is an impediment to better documentation of the differences, it is safe to say that on the whole *elegans* is a larger, studier bird than *longirostris*. As an example, among a series of 22 skeletons of *R. l. scottii* that I assembled from north Florida was one exceedingly large male (skull length 96.2 mm). When compared to a large male *elegans* with a skull of nearly equal length (95.0 mm), the skeletal elements of the specimen of *longirostris* were noticeably smaller and more slender in all dimensions.

Cranial osteology and salt glands. – In one of the studies instigated by Pierce Brodkorb (Olson 1994) to discern osteological differences between closely related species, Fehon (1952) could find only one "qualitative" difference between King and Clapper Rails, though it is an easily quantifiable one. He found that the width of the interorbital bridge was narrow in *longirostris* and wide in *elegans*. I found no overlap between the species in the east in this measurement (FIG. 1).

Bock (1958) showed in plovers that the degree of ossification of this area of the skull is a result of the relative development of the supraorbital nasal glands. The interorbital bridge is wide when these glands are small, and narrow when they are large. The nasal glands function solely to excrete sodium chloride and are well-developed in marine and coastal birds (Schmidt-Nielsen et al. 1958; Schmidt-Nielsen 1959). As might be expected, the nasal glands of *longirostris* are much enlarged, whereas in *elegans* they are reduced (FIG. 2).

Experiments in ducks and gulls indicate that increased salt stress results in hypertrophy of the nasal glands (Holmes et al. 1961, Schmidt-Nielsen and Kim 1964, Barnes and Nudds 1991). Bock (1958) concluded that the reduction of bone in the supraorbital area of marine plovers was a purely environmental manifestation correlated with the development of the salt glands. Ripley (1977) likewise considered that the width of the interorbital bridge in King and Clapper rails was environmentally controlled.

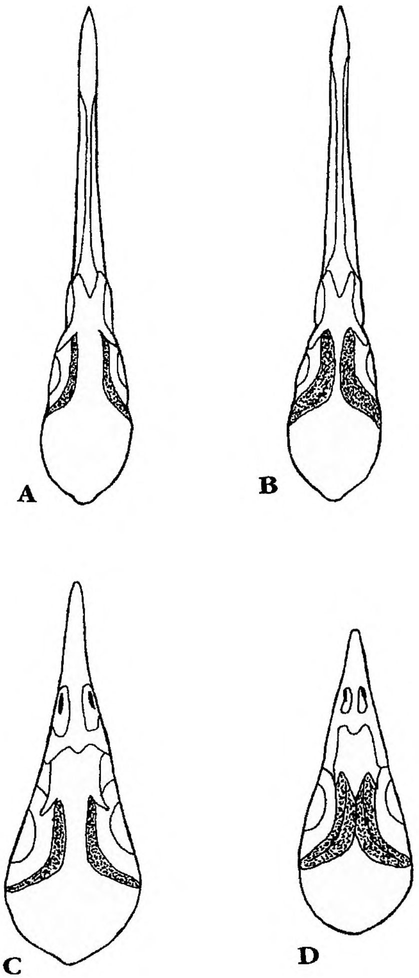

FIG. 2. Diagram of skinned heads of adult (above) and young (below) King and Clapper rails to show the difference in the development of the salt glands (stippled): A, King Rail *Rallus elegans* (Cameron Parish, Louisiana, 5 January 1965); B, Clapper Rail *R. longirostris* (Chincoteague, Virginia, 18 April 1967); C, King Rail *R. elegans* (USNM 511049, Arkansas, 2.5 weeks old); D, Clapper Rail *R. longirostris* (USNM 225972, Haiti, less than one week old). Not to scale (chicks enlarged about 2X).

That this is not entirely the case has been demonstrated experimentally. I obtained specimens of a number of Clapper Rails that had been reared in captivity (from eggs taken in Virginia) until maturity. During this time the birds received only fresh water to drink and commercial poultry food to eat, so they may be considered to have been free of salt stress throughout their development. At the age of one year or more, these birds were killed for analysis in connection with another study and frozen. I obtained the heads, preserved them in alcohol, removed the salt glands and weighed them, and then cleaned and

TABLE 1
WIDTHS (MM) OF INTERORBITAL BRIDGE

	n	range	mean
Captive males	6	3.1-4.2	3.7
Wild males	11	3.2-4.1	3.5
Captive females	5	3.1-3.8	3.4
Wild females	16	2.8-4.0	3.2

Widths (mm) of interorbital bridge in captive Clapper Rails (*Rallus longirostris*) raised entirely on fresh water, versus wild-taken birds.

examined the skulls (now in USNM).

The salt glands in the captive birds were very noticeably atrophied, as borne out by visual comparison with wild-caught Clapper Rails and by weighing. The average mass of the salt glands in 21 captive Clapper Rails was 0.014 g, which was even less than in King Rails (mean 0.033 g, n = 3), and far less than in wild-taken Clapper Rails (mean 0.076 g, n= 8). However, the width of the interorbital bridge in the captive specimens, reared on fresh water, showed no significant differences from those of wild Clapper Rails (Table 1). Studies in other birds have confirmed that the size of the salt glands becomes quickly reduced when dietary salt levels decrease under both natural and experimental conditions (e. g. McArthur and Gorman 1978). However, in Clapper Rails, although the size of the salt gland itself may be environmentally determined, the underlying osteology must have some hereditary component. In experiments on salt-tolerance in chicks of Mallards and Black Ducks (*Anas platyrhynchos* and *A. rubripes*) it was found that "the functional capacity of the salt gland was partially dependent upon a genetic component" (Barnes and Nudds 1991:96). In rails, the width of the interorbital bridge would probably be subject to rapid selection over time in any population that habitually resorted to saline environments, but the fact that this condition does have a genetic basis in Clapper Rails in eastern North America makes it potentially useful in identifying hybrids.

A bird undoubtedly of hybrid parentage from Florida had an interorbital bridge width that is exactly intermediate between measurements of King and Clapper rails (FIG. 1). One of Meanley's birds from Taylor's Gut, Delaware, is in plumage clearly a hybrid and also has an interorbital bridge that is intermediate in width (FIG. 1). Another specimen from Texas in nearly identical plumage had an interorbital width similar to that of King Rails (see discussion of hybridization).

From measurements of skeletons I was able to determine that the interorbital bridge of the salt marsh dwelling subspecies *obsoletus* is narrow (FIG. 1), as in *longirostris*, despite its actually being an *elegans* derivative according to my belief. This is not unexpected because it has obviously long been restricted to environments with high salt loads.

Of considerable interest in this connection are the subspecies of the *yumanensis* group, of which only two skeletons were available. In order to obtain additional data, I took 16 study skins of 3 subspecies and made a slit in the top of the head through which I measured the interorbital width with needlepoint dial calipers. The widths in both *rhizophorae* and *nayaritensis*, which are resident in coastal mangroves and under constant salt stress, are narrow (FIG. 1). The subspecies *yumanensis*, however, breeds in freshwater marshes of the Colorado Basin, which it vacates after the breeding season, presumably wintering in mangroves along with the more southern races (Tomlinson and Todd 1973, Banks and Tomlinson 1974). In this subspecies the interorbital bridge width is almost perfectly intermediate between King and Clapper rails (FIG. 1). If this form were purely of *longirostris* derivation, it is difficult to imagine why the bridge would be wider if the birds spend the winter on salt water. Thus, on this basis and on the reddish plumage, it is probably safe to assume that *elegans* is involved in the derivation of *yumanensis.*

In the flightless Pleistocene species from Bermuda, the average width of the interorbital bridge also falls almost exactly between the averages of *R. longirostris* and *R. elegans.* At the time this species lived on Bermuda, the island may have been ten times larger than at present and probably had an extensive area of open marshy habitat in the center, sufficient to sustain an endemic crane and an endemic duck (Wetmore 1960). These environments may have been brackish, or even if mostly freshwater would have been subject to influxes of salt from sea spray. I interpret this largest Bermuda rail as being a King Rail derivative that lived in an environment with salt loads intermediate between those encountered by *R. elegans* and *R. longirostris.*

BEHAVIOR

Assessments of behavior are often necessarily subjective, yet in the case of King and Clapper rails provide further suggestive evidence that these are distinct species. Meanley (1969:63) stressed the consistently different behavior of incubating birds. Incubating King Rails "seldom flush until an intruder is within 10 feet or less of the nest" and as incubation proceeds they become more tenacious and may boldly defend the nest. "In contrast to this type of behavior, the Clapper Rail is usually gone before the intruder gets near the nest. At Chincoteague, Virginia, I have examined some 200 Clapper Rail nests, and only on some half dozen occasions has an incubating bird remained while approached to within 10 feet. This appears to be a striking behavioral difference between these two closely related species." Additional observations confirmed these differences (Meanley 1985).

Another possible difference that Meanley (1969:73) noted between individuals of the two species held in outdoor cages through a Maryland winter is so peculiar that I quote his observations in full. "During alternate periods of freezing and thawing, spherical chunks of ice, up to the size of a baseball, stuck to the tails of the Clapper Rails, and smaller particles stuck to their breasts. Strangely, particles of ice virtually never adhered to any part of the plumage of the King Rails." Because Clapper Rails live in salt marshes and move out of the northern parts of their range in winter, they may seldom encounter ice in their environment, whereas King Rails much more likely would. Perhaps there is some underlying difference in feather structure between the two that might explain this.

Meanley (1969:75, 78) also emphasized the adaptability of the King Rail to a wide variety of habitats and that it "is more diversified in its choice of food" than the Clapper Rail and is "apparently more of a vegetarian." Clapper Rails live in a world of abundant food, being heavily dependent on crustaceans, particularly fiddler crabs (*Uca*), marine snails, especially periwinkles (*Litorina*), and marine worms (Meanley 1985, Heard 1982).

ECOLOGY

Ecological differences between *elegans* and *longirostris* are one of the primary considerations in attempting to assess their relationships. Most field identifications are based upon whether a bird is found in salt marsh (Clapper Rail) or freshwater (King Rail) environments. The exceptions to this deserve scrutiny. In many places, King Rails have been noted in salt marsh areas usually typical of Clapper Rails. Meanley (1969) discusses the occurrence of King Rails in salt or brackish tidal habitats in Virginia, Maryland, Delaware, Georgia, South Carolina, Florida, and Louisiana, to which may be added Texas (Williams 1938), Alabama (Stewart 1965), and North Carolina (Funderburg 1949). King Rails have been reported actually breeding in salt marshes in Virginia (Montagna and Wimsatt 1942) and North Carolina (Duvall 1937), and within 150 yards of salt marsh on Long Island, New York (Latham 1954). In all these instances, King Rails were found in Clapper Rail habitat, but the opposite seems never to occur.

As already noted, the *elegans*-like subspecies *tenuirostris* and *yumanensis* breed in freshwater habitats, although the latter winters in saline areas. Willett (1906) records an instance of the subspecies *levipes*, otherwise a salt-marsh inhabitant, breeding in a freshwater marsh in Los Angeles County. Dickerman (1971) gives a record of *rhizophorae*, a coastal mangrove form, collected with a specimen of *tenuirostris* at Laguna San Felipe, Puebla, Mexico, in a freshwater environment.

All of these instances of salt-marsh subspecies occurring in freshwater marshes involve populations that I, and others in the past, have thought to be related to *elegans*. I have not uncovered any instance of a true Clapper Rail, *Rallus longirostris*, actually inhabiting a freshwater marsh (there are inland records, but so far as I am aware, only of obvious migrants found in parking lots or that struck TV towers, etc.).

HYBRIDIZATION

Several instances have been published of King and Clapper rails being found in the same marsh, of observations of mixed mated pairs, and of specimens identified as hybrids. Hybridization probably occurs much more frequently than has been reported. King and Clapper rails have been seen together in tidal marshes in Virginia and Maryland and specimens of each species were collected in a pond in Cameron Parish, Louisiana, where freshwater and salt marshes were separated by only a few hundred yards (Meanley and Wetherbee 1962). The last situation is very similar to that where a specimen virtually identical to a known hybrid from Florida was obtained in Jefferson County, Texas, 26 April 1988 (MSB 18286, male with testes 8 x 15 mm, flat skin and skeleton). This, however, has a wide interorbital bridge, that falls within the range of *Rallus elegans* (FIG. 1). The habitat here consisted of a freshwater pond separated from salt marsh by a coastal dune (information fide R. W. Dickerman).

Tomkins (1958) observed King and Clapper rails in view at the same time near Savannah, Georgia, in a "brackish area, a place of transition from fresh to salt." Such transitional areas are, I believe, essential in permitting hybridization to occur in these two species.

Meanley and Wetherbee (1962; summarized also in Meanley,1969 1985) detailed the habitats and salinities along an area of Delaware Bay where rails of these species occurred. In the area of lowest salinity (3700-4380 ppm), where, however, salt meadow grasses (*Spartina patens* and *Distichlis spicata*) predominated, only King Rails were found. A little over 6 km seaward where salinities were highest (7480-7600 ppm) and taller salt-marsh vegetation occurred (*Spartina alterniflora* and *Scirpus robustus*), only Clapper Rails were found. Halfway between, where salinities were intermediate (5670-7190 ppm), but the vegetation was essentially like that where only Clapper Rails lived, both species occurred together. A nest of a mixed pair was discovered and the eggs were incubated artificially, although the embryos died before hatching. Although no specimens identified as hybrids were obtained at that time, those obtained later were said to show "wide variation" (Meanley 1985:130). At least one of these (USNM 530151, 23 Aug 1963) is in intermediate plumage and has an intermediate width of the interorbital bridge and is thus certainly a hybrid.

Bledsoe (1988) identified a skin of a hybrid picked up in October in a backyard in New Haven, Connecticut, this being an obvious migrant or wanderer. Thus the title of his paper is somewhat misleading because we cannot know where this instance of hybridization actually occurred, nor can we infer anything about the ecological conditions that may have contributed to it.

Meanley (1989) reported a specimen that he identified as a hybrid from a brackish marsh on the Rappahannock River in Virginia. Many more specimens in museum collections, none with habitat notations, appear likely to be hybrids, although these are almost always identified as *Rallus longirostris.* Numerous specimens from the Louisiana delta, adjacent Mississippi, and elsewhere fall into this category. A series of large *Rallus* from the Ramsden collection (USNM) labelled "Guantanamo, Cuba," consists of specimens of *Rallus elegans* (including the type of *R. e. ramsdeni* Riley, 1913), *R. longirostris*, and at least two apparent hybrids (USNM 453188, 453201). Perversely, the more King Rail-like of these two was labelled as *R. longirostris* and vice versa. Habitats in the Guantanamo area probably include intermediate conditions of salinity that permit hybridization even in this disjunct Cuban population of *elegans.*

King and Clapper rails appear to be able to hybridize only in areas that either are transitional between salt and fresh water, as in the extensive marshes along a gradient that Meanley studied in Delaware, or in areas of ecological "breakdown" where one habitat is replacing another. I studied the effects of such an instance of ecological instability on hybridization in these species along the Gulf Coast of northern Florida at Shell Point, Wakulla County. This occurrence is particularly illustrative of the conditions that may lead to hybridization, however temporary.

In this case the original habitat was salt marsh, dominated by needlerush (*Juncus roemerianus*), in which an elevated dirt roadbed, 2-3 m above mean water level, had cut off a section (FIG. 3). Although still connected to salt marsh by ditches and culverts, by 1965 this hydrologically semi-isolated area of marsh and shallow open water had become largely fresh in character, the main pool having large masses of filamentous green algae growing in it with large stands of cattail (*Typha*) bordering it. On the landward portion of the saltmarsh side was a large mudflat dominated by pokeweed (*Phytolacca*), indicating that, even here, perhaps some artificial elevation had created less saline conditions.

This entire area was flooded by hurricane tides in September 1965. Afterwards I found a few dead warmouth Sunfish (*Chaenobryttus* = *Lepomis gulosis*, Centrarchidae), a freshwater species that had presumably been killed by the influx of salt water on the fresh side, and the pokeweed on the saltmarsh side was killed off, never to recolonize. A survey of the fish fauna of the marshes on either side of the road conducted 16 March 1966 disclosed mostly euryhaline killifish (Cyprinodontidae) on the "fresh" side, augmented by a few typically salt-marsh species on the other side. Two cyprinodonts (*Jordanella floridae* and *Fundulus chrysotus*) and one poeciliid (*Heterandria formosa*) are in large measure inhabitants of fresh water, however, and were not found in the salt marsh. By autumn of 1967, considerable crepuscular splashing in the main pool on the fresh side led me to make a perfunctory ichthyological survey with rod and reel that yielded several large-mouthed bass (*Micropterus salmoides*, Centrarchidae) from 0.5 to 1 kg, thus indicating that the marsh had regained its former freshness.

The history of the rail specimens collected here follows. The first was a male (USNM 525882, left testis 6 x 19 mm and grayish in color) taken 17 June 1965 along the paved road bordering the eastern side of the freshwater marsh and preserved as a study skin only. This is a typical King Rail in all aspects of the plumage. A second specimen (H_1 in Fig. 3), a male with gonads in similar condition, was collected 18 June 1965 among the pokeweeds on the salt-marsh side and preserved as a study skin (USNM 525869). This is

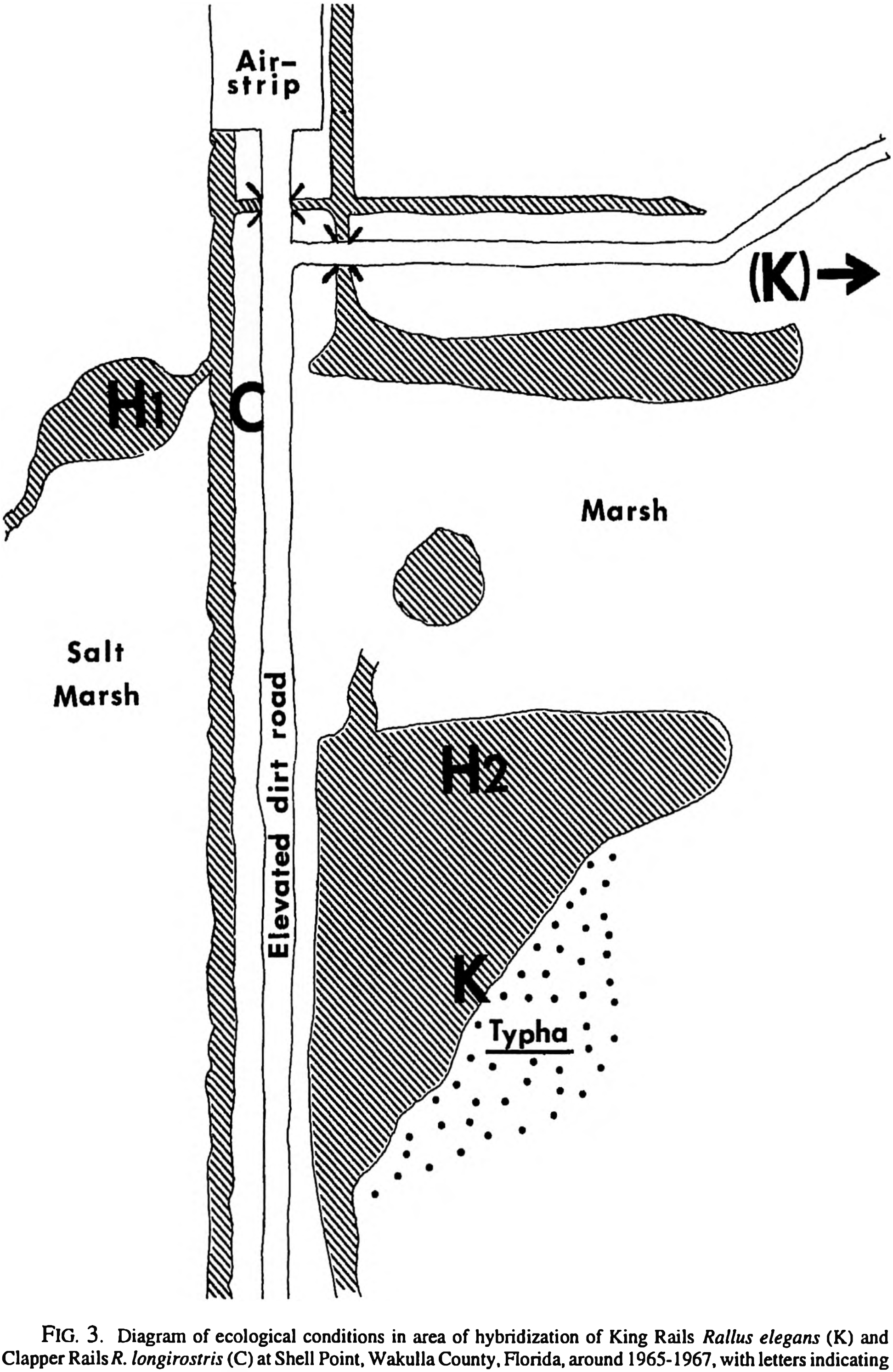

FIG. 3. Diagram of ecological conditions in area of hybridization of King Rails *Rallus elegans* (K) and Clapper Rails *R. longirostris* (C) at Shell Point, Wakulla County, Florida, around 1965-1967, with letters indicating specimens collected (H_1 and H_2 are hybrids discussed in the text). Hatched areas indicate open water and mud flats.

perfectly intermediate between King and Clapper Rails in plumage. Another specimen (USNM 525870, female with ovary 7 x 20 mm, largest follicle 2 mm) was taken 16 March 1966 along the road on the salt-marsh side and is a typical Clapper Rail.

No more specimens came to hand here until 18 May 1967 when Fred Shanholtzer collected two adults and one downy young from the pool on the fresh side. I obtained the adults from him and prepared them as complete skeletons with flat skins. The first adult (USNM 525886, a male with enlarged testes 12 x 22 mm) is pure *elegans* in plumage and osteology. The second (USNM 525887; H_2 in Fig. 3) was also a male (with dark testes 7 x 14 mm that were apparently regressing) that in every aspect of plumage and osteology is clearly a hybrid. The long bones are intermediate between the large, stout King Rail and smaller more slender Clapper Rail. More importantly, the interorbital bridge at 4.4 mm is almost exactly intermediate between the minimum for *elegans* and the maximum for *longirostris* (Fig. 1). A chick with this hybrid adult was killed by the same charge of shot, although the specimen cannot be traced with certainty. A skin (TTRS 3181) of a downy chick with the same collection data except having the date 13 May rather than 18 May may be the individual in question. This specimen is entirely black, without white neossoptiles.

Summary of ecology and hybridization. – The King Rail is an adaptable species that is capable of living in either salt or freshwater environments, as shown by several reported instances of King Rails being found in salt marshes. If, as supposed here, the Pacific coast populations are derived from King Rails, this provides further evidence of the adaptability of the species. However, because King Rails do not normally inhabit salt marsh environments when Clapper Rails are present, we must assume that Clapper Rails are capable of excluding King Rails. For whatever reason, Clapper Rails do not occur in fresh-water marshes, presumably because they are excluded by King Rails or because they are physiologically intolerant or cannot adapt to a less abundant and more varied food supply. In their respective habitats, King Rails are generally scarcer than Clapper Rails and the species is thought to be in a decline, with numerous seemingly suitable fresh-water marshes being unoccupied. Thus physiological and feeding constraints are more likely to explain the absence of Clapper Rails from freshwater marshes than exclusion by King Rails.

When ecological distinctions break down, as along rivers and estuaries where conditions change gradually from salt to fresh, or where human activity such as diking causes salt marsh to turn fresh, intermediate conditions of salinity permit the two species to come together and here they hybridize freely. This may happen at any point where the ranges of the two species coincide and intermediate conditions occur, but these points can in no way be considered "hybrid zones" as there is no place known where only hybrids occur in the absence of any pure parental types. The same factors that restrict the King and Clapper rails to their respective habitats would presumably apply to their hybrids, which would be at a selective disadvantage in either a purely fresh or purely salt environment. Thus, although evidently fertile and potentially capable of backcrossing, there is no hybrid introgression outside the ecologically intermediate areas that permit hybridization to occur in the first place.

Thus, under normal conditions King and Clapper rails are functioning as perfectly good species and ought be be classified as such.

OUTLINE OF DISTRIBUTION AND SYSTEMATICS WITHIN *RALLUS LONGIROSTRIS*

A brief review of the systematics of the widespread Clapper Rail is necessary for a discussion of the possible evolutionary history of the entire complex. The type locality of *Rallus longirostris* is Cayenne, and this form and the subspecies *R. l. crassirostris*

FIG. 4. Heads of study skins of Clapper Rails *Rallus longirostris* to contrast the longer, more slender bill of North American and West Indian birds as represented by the subspecies *R. l. insularum* of Florida (far left), with the shorter, heavier bill in various populations from mainland South America: from left to right—*crassirostris, phelpsi, wetmorei,* and *cypereti.*

Lawrence (1871) inhabit coastal mangroves from Guyana to southeastern Brazil. To the west the distribution is extremely spotty. Subspecies have been named from Trinidad (*pelodramus* Oberholser 1937), Isla Margarita (*margaritae* Zimmer and Phelps 1944), the adjacent mainland Peninsula de Araya in the state of Sucre, Venezuela (*dillonripleyi,* Phelps and Hostos 1987), and disjunctly in the western Venezuelan provinces of Carabobo and Falcon where there is a population, *R. l. phelpsi* (Wetmore 1941), that extends over to the Goajira Peninsula. The seemingly very distinct species *Rallus wetmorei* (Zimmer and Phelps 1944) is also known from the western coast of Venezuela and has been listed from some of the same localities as *R. l. phelpsi* (Phelps and Phelps 1958). This form is unique in being entirely dark brownish below, with no barring on the venter or underwings. In view of its co-occurrence with *R. l. phelpsi,* from which it does not differ in size or shape, one wonders if *R. wetmorei* might be an aberrant color phase, similar, for example, to the so-called Cory's Least Bittern, which is a rare chestnut-plumaged form of *Ixobrychus exilis.* A very disjunct race is *R. l. cypereti* Taczanowski (1877) is known from Ecuador and Peru, with sight records from southernmost Nari–o, Colombia (Hilty and Brown 1986). Strangely, there are no records of the species from the Pacific coast of Colombia north of here, or from the Caribbean coast west of the Goajira Peninsula.

All of the South American subspecies of *Rallus longirostris* have relatively shorter and noticeably heavier bills than do birds from the West Indies and North America (FIG. 4). Indeed, in the southernmost race of the West Indies, *R. l. manglecola* Danforth (1934), the bill is as long as or longer than in most of the northern races. Thus *Rallus longirostris* falls into two well-defined subspecies-groups that are sharply defined both morphologically and geographically (Fig. 5). The stout-billed South American birds may be known as the *longirostris* subspecies-group. The oldest name among the slender-billed forms of Clapper Rail is *crepitans* Gmelin (1789), so the North American and West Indian birds may be known as the *crepitans* subspecies-group. Genetic studies to determine whether these two groups may be specifically distinct would be highly desirable.

Various nominal subspecies of Clapper Rails, much in need of revision, are found in mangrove swamps virtually throughout the West Indies and the Bahamas. The species has obviously spilled over from here to occupy parts of the Yucatan Peninsula south to Belize. I have no idea what to make of a single individual, apparently not assignable to any known subspecies, that was taken on a freshwater pond near the coast in eastern Bocas del Toro Province on the Caribbean coast of Panama (Ridgely and Gwynne 1989). Forms generally similar to those of the West Indies continue north in mangroves in southern Florida, from which they then extend in salt marshes north to Connecticut and westward to southern Texas and Tamaulipas, Mexico (Banks 1974, Howell and Webb 1995). The east coast populations are in part migratory and not only move southward, but some must also cross overland to winter on the Gulf coast (Crawford, Olson, and Taylor 1983).

FOSSIL RECORD

Apart from the as yet undescribed flightless derivative of *Rallus elegans* from the Pleistocene of Bermuda, discussed elsewhere in this paper, the main value of the fossil record in this group is in documenting the former presence of large forms of *Rallus* in western North America in places where no such birds occur today.

The earliest record for the group is the nominal species *Rallus phillipsi* Wetmore (1957), named for the honoree of the present volume, based on a tarsometatarsus from a lake deposit rich in fossils of waterfowl and waders (Bickart 1990) in the Mio-Pliocene of Arizona dated at 5.5 million years BP (Becker 1987). Measurements of the holotype fall within the lower end of the size range of *Rallus longirostris* (Olson 1977), as do those of additional specimens referred by Bickart (1990). Smaller average size would not be unexpected in an older form of this group, considering that all other members of the genus *Rallus* are smaller. A rail the size of *Rallus longirostris/elegans* has also been reported from the fossiliferous Hagerman beds in Idaho (Feduccia 1968), dated at about 3.5 million years BP in the Pliocene (Becker 1987).

A single very large tarsometatarsus, originally described as a new genus and species, *Epirallus natator* L. Miller (1942), from the late Pleistocene San Josecito cave fauna in Nuevo Leon, Mexico, was referred to the *Rallus longirostris/elegans* complex (Olson 1974), although it was slightly larger than any specimens of *R. elegans* then available. No more fossils of large *Rallus* have subsequently been found at the site, however (Steadman et al. 1994).

HYPOTHETICAL HISTORY OF THE *RALLUS LONGIROSTRIS/ELEGANS* COMPLEX

It is uncertain when and where the large rails of this complex originated. No species of *Rallus* of this size occurs in the Old World, so the complex is doubtless New World in origin and would necessarily be derived from some smaller form of *Rallus*. It has often been noted that the King Rail is very similar in plumage to the Virginia Rail (*Rallus limicola*) from which we might easily infer a North American origin for the larger birds, were it not for the fact that *R. limicola* also occurs widely in South America.

Some form of *Rallus* of this size existed in North America as long ago as 5.5 million years in the latest Miocene (*Rallus phillipsi*). It is also possible that the complex was already in South America before the beginning of the Pleistocene. It is tempting to regard *Rallus longirostris cypereti* in Peru and Ecuador as a relict from a time these rails were distributed continuously around northern South America. Because they are not in

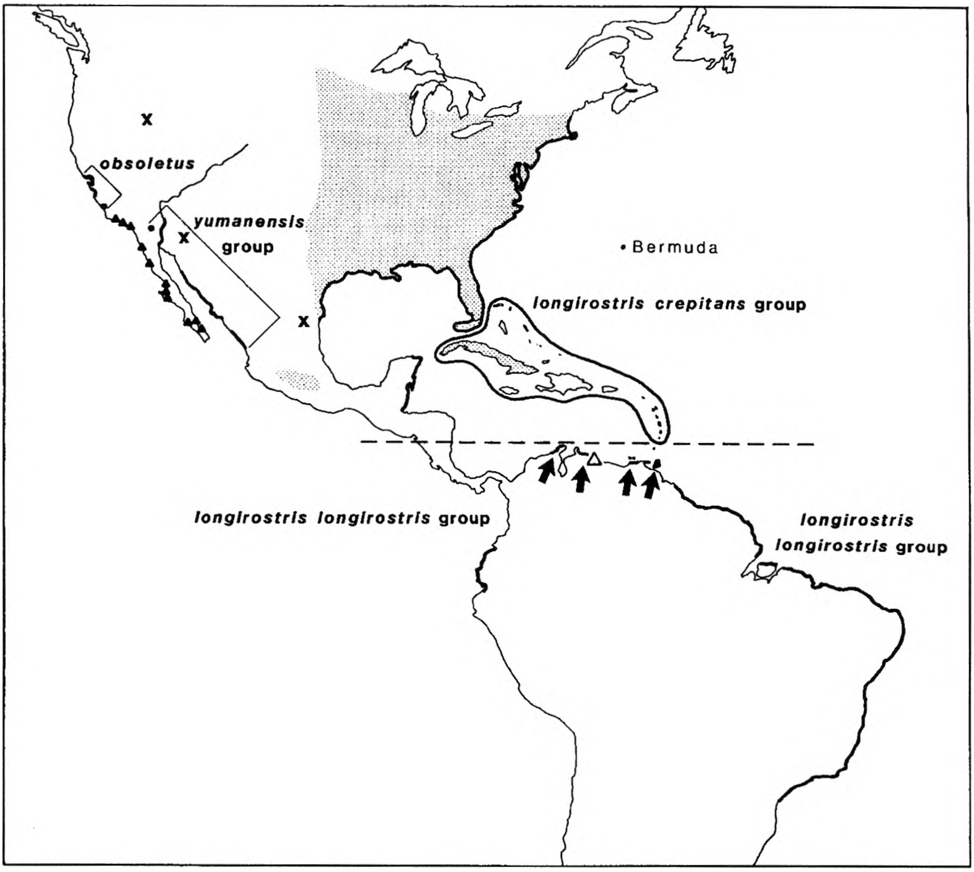

FIG. 5. Map showing generalized distribution of various forms of the *Rallus longirostris/elegans* complex. Fossil records of members of this complex are indicated by X. Fresh-water populations of King Rail are shown in stipple in eastern North America (*elegans*), Cuba (*ramsdeni*), and central Mexico (*tenuirostris*). The California and Mexican populations are postulated here to be derivatives of *elegans*, with the exceptionally richly colored *beldingi* group (*levipes, magdalenae, beldingi*) indicated by dark triangles. The heavy line along the coasts of eastern North America, Yucatan, West Indies, and South America shows the distribution of true Clapper Rails, with the two major subspecies groups divided by the dashed line. Arrows indicate small disjunct populations in Trinidad and Venezuela, and the open triangle is for *Rallus wetmorei*.

Panama we would have to assume that this was prior to the isthmian connection at the end of the Pliocene.

Other species in the genus *Rallus* are inhabitants of freshwater marshes, so mangrove-dwelling would be a secondary adaptation. For the sake of argument then, we can hypothesize that the large *Rallus* complex arose in freshwater marshes in North America. From here it spread into South America either directly or stepping-stone fashion through the Antilles.

The cause of the subsequent isolation that produced the separate lineages of *elegans* and *longirostris* is unclear. Throughout most of the Pleistocene, the original inhabitant of North America is assumed to have been the King Rail, which once probably ranged from coast to coast in marshes both fresh and salt, at least as far south as central Mexico. This species also colonized Cuba and during a low sea stand of the Pleistocene gave rise to a flightless species in Bermuda.

Pleistocene desertification of the American west resulted in loss of wetland habitats suitable for King Rails although scattered fossils indicate that large rails of this complex once occurred here in areas where they no longer found. As a result of habitat loss, relict populations of King Rails were stranded in the saltwater habitats in California and western Mexico and freshwater marshes of central Mexico.

Clapper Rails meanwhile were adapting to strictly salt-water habitats in South America and in mangrove swamps in the West Indies. They were isolated in the West Indies long enough to become recognizably distinct from South American birds in bill shape. Perhaps during high sea-level stands habitats would have been reduced, particularly on the smaller islands of the Lesser Antilles, so that gene flow between South American and Antillean Clapper Rails was restricted.

Low sea-level stands, perhaps the most extreme one during the last Wisconsinan glaciation (peak at 17,000 years BP), would have greatly facilitated passage of Clapper Rails out of the West Indies to the Yucatan and Florida peninsulas. In North America they then spread out along the coasts, displacing the resident King Rails in salt marshes so that in eastern North America the King Rail became restricted to fresh-water habitats, although it may still occur in salt marshes in the east when Clapper Rails are absent. The two species readily hybridize and probably did so at their initial contact, but eventually Clapper Rails predominated in salt marshes in a situation perhaps analogous to that of the Blue-winged Warbler (*Vermivora pinus*) which is hybridizing with and then swamping out and replacing the Golden-winged Warbler (*V. chrysoptera*) in much of its range in eastern North America (Confer 1992).

Hybridization still occurs between King and Clapper rails, but only in scattered areas of ecological intermediary, etc., where habitats are neither salt nor fresh in nature. There is never a hybrid zone between the two species in which there are no pure parental types. The fact that a similar situation between King and Clapper Rails exists in Cuba suggests that the origin of the Antillean group of subspecies of Clapper Rails was to the south and east of Cuba.

There is still the complicating factor of how to explain the grayish Clapper-like dorsal coloration of *obsoletus* in northern California, and particularly the populations of the *yumanensis* group. One possibility is that this grayish coloration simply arose independently of that in Clapper Rails and is not indicative of any relationship. Another possibility is that these are representatives of the ancestral type from which both King and Clapper Rails sprang. If so, it would be difficult to explain their geographically intermediate position between the richly reddish King Rail-like birds from the Los Angeles area south through Baja California and also those in the freshwater habitats of central Mexico.

The birds of the *yumanensis* group in particular are reminiscent of hybrids between the two species and perhaps a hybrid origin of these populations should also be entertained. The subspecies *yumanensis* (sensu stricto) is best known from freshwater marshes formed by dams along the lower Colorado Basin and in the Salton Sea in California (Tomlinson and Todd 1973)—habitats that are largely man-made and probably existed to a more limited extent prior to the present century. The birds completely vacate these areas after the breeding season, presumably to winter mainly in mangrove swamps along the Pacific coast of Mexico among resident populations of similar forms (*rhizophorae* and *nayaritensis*). Tomlinson and Todd (1973) also found that *yumanensis* occurred in salt and brackish environments in the delta of the Colorado River in Mexico, which, however, is subject to winter desiccation. This must have been the original habitat of these birds if they were present in the Colorado drainage prior to dam construction.

Perhaps large rails had disappeared from this area entirely during Pleistocene desertification. The Colorado River delta may then have been colonized simultaneously in geologically recent times by both King and Clapper rails, as both species are known to wander widely. If a hybrid population formed here, there would not have been the adverse selection pressure of adjacent populations of pure parental stock such as occur where the birds hybridize in the east. Periodic drying of the Colorado delta would have forced this population into migrating to more stable environments and the birds then "discovered" the mangroves of western Mexico, typical habitat for Clapper Rails, where they then established resident populations. The main difference between *yumanensis* and the resident forms *rhizophorae* and *nayaritensis* is the longer wing of *yumanensis*, associated with its migratory habits. Color differences are very slight, so that Ripley (1977), not without some justification, merged the three under the name *yumanensis*. The original brackish environment coupled with the lack of influx of pure parental types may have favored the persistence of essentially hybrid populations without their being swamped out. Also, if pure *longirostris* is incapable of colonizing freshwater marshes, a hybrid population would have been in a better position to take advantage of the man-made environments created later along the Colorado River.

Long-distance wandering by both King and Clapper rails is probably more frequent than usually realized. There have been numerous inland records of Clapper Rails and because birds of the northeastern subspecies have been taken on several occasions on the northern Gulf Coast of Florida (Crawford, Olson, and Taylor 1983), they probably cross overland regularly. Hubbard (1972) recorded a King Rail from El Paso, Texas. R. C. Banks and I examined a specimen (ARIZ 16196) that we identified as *yumanensis*, taken 26 September 1990 at Tucson, Arizona.

A hybrid origin for any of the subspecies of this complex is likely to remain highly speculative for a long time. Meanwhile, because we can be certain that *Rallus elegans* is involved in the origin of the *yumanensis* group, until a hybrid origin can be proven, the *yumanensis* group and all other western populations of large *Rallus* should be considered as subspecies of *elegans*, not of *longirostris*.

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