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OBSERVATIONS ON THE FOOD AND FOOD HABITS OF CLAPPER RAILS (*RALLUS LONGIROSTRIS* BODDAERT) FROM TIDAL MARSHES ALONG THE EAST AND GULF COASTS OF THE UNITED STATES

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ABSTRACT The feeding habits of five nominal subspecies of clapper rails (*Rallus longirostris* Boddaert) collected in tidal marshes along the Gulf and Atlantic coasts of the United States are compared. Data on the food from the stomachs of 183 rails were analyzed and the earlier literature critically reviewed. During the warmer months (May through early fall), crabs, predominantly *Uca* spp., comprised the major part of the food items found. Limited data on a few rails collected during late fall and winter, when *Uca* spp. are not usually available, indicate that snails then become a major part of the clapper rail's diet during that part of the year. Earlier studies, which describe the food or feeding habits of clapper rails, are reviewed and the food habits and trophic relationships of some other tidal marsh consumers are discussed. Data from this and previous studies indicate that clapper rails are opportunistic omnivores, and occupy a relatively broad niche within tidal marsh ecosystems. A comparison of available data of the food of five clapper rail subspecies of the eastern United States indicates no distinct differences in their feeding behavior. Differences in the kinds of food eaten appear to simply reflect the types of marsh habitat (fresh, brackish, polyhaline) or geographical location (temperate, subtropical, tropical) in which a particular clapper rail population occurs. The food habits of the king rail are compared with those of the clapper rail and problems concerning the taxonomic status of the "subspecies" of *Rallus longirostris* are briefly discussed.

INTRODUCTION

The purpose of this report is to review and compare the feeding habits of the five nominal subspecies of clapper rails (*Rallus longirostris* Boddaert) endemic to the salt marshes and mangrove swamps of the Atlantic and Gulf coasts of the United States. The information presented here is based on food data obtained in conjunction with a study of clapper rail parasites (Heard 1968a, b, 1970, Deblock and Heard 1969, Byrd and Heard 1970, Nickol and Heard 1970, Brooks and Heard 1977) and a critical review of the published literature. An overview of the trophic relationships of clapper rail subspecies occurring in tidal salt marshes of the eastern United States will be presented. The diets of the king rail and the clapper rail will be compared and discussed. Taxonomic uncertainties concerning the subspecies of the clapper rail also will be briefly discussed.

Historical

The clapper rail, often called the mud or marsh hen, is abundant in the salt marsh and mangrove swamps of the Atlantic and Gulf coasts of the United States. This species and its eggs were a source of food and "sport" to residents along the eastern coast of the United States during the 18th and 19th centuries (Audubon 1840, Bent 1926). Clapper rails are still hunted along much of the Atlantic and Gulf coasts (Oney 1954, Adams and Quay 1958, Bateman 1966, Smith 1967). References to the earlier literature on the food, systematics, natural history, behavior, ecology, and parasites of *Rallus longirostris* subspecies are given by Bent (1926), Oberholser (1937), Adams and Quay (1958), Bateman (1965), Heard (1970), and Holliman (1978). Bent (1926) summarized observations by Audubon (1840) and Simmons (1914) on the food and feeding habits of clapper rails. Howell (1928, 1932), Oney (1954), and Bateman (1965) gave additional, more detailed data on the diet of this marsh bird.

There are currently five recognized subspecies of *R. longirostris* known to occur on the Atlantic and Gulf coasts (Ripley 1977). These are the northern clapper rail *R. longirostris crepitans* Gmelin, Wayne's clapper rail *R. longirostris waynei* Brewster, the Florida clapper rail *R. longirostris scotti* Sennett, the mangrove clapper rail *R. longirostris insularum* Brooks, and the Louisiana clapper rail *R. longirostris saturatus* Ridgway (Oberholser 1937, Ridgway and Friedman 1941, Ripley 1977).

Figure 1 presents a map giving the general ranges for these five subspecies. The northern clapper rail *R. longirostris crepitans* is a resident of the more temperate *Spartina-Juncus* marshes. This form is the only one of the five east coast subspecies known to migrate substantial distances. From April to August it nests in marshes from New England southward into Virginia. During the colder months (from late fall to mid-spring) a large part of the population migrates along the Atlantic coast as far south as central Florida (Howell 1932, Stewart 1954). Wayne's clapper rail *R. l. waynei* occurs in *Spartina-Juncus* marshes along the Atlantic coast from North Carolina to east central Florida. Although part of the population shifts southward a few miles during the winter, this "subspecies" is not considered migratory (Oney 1954). The Florida clapper rail *R. l. scotti* occurs along the southern Atlantic coast and the Gulf coast of Florida (Howell 1932) in both *Spartina-Juncus* marshes and mangrove habitats. The mangrove clapper rail *R. l. insularum*

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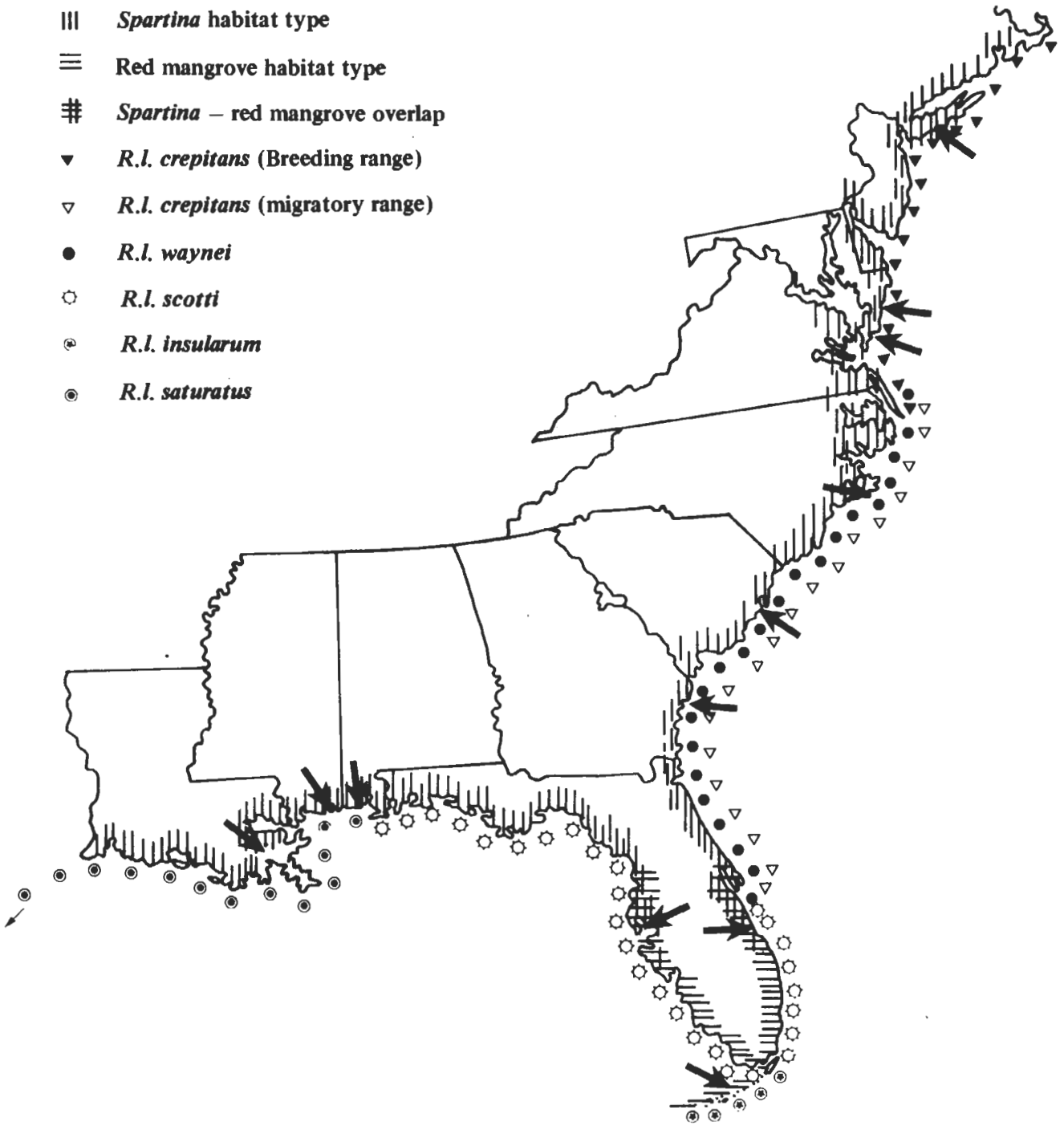

Figure 1. Map showing distribution of the five nominal subspecies of *Rallus longirostris* occurring in salt marshes along the eastern United States. Arrows indicate collecting areas sampled during the present study.

is apparently confined to the polyhaline mangrove swamps of the Florida Keys (Howell 1932, Oberholser 1937). The Louisiana clapper rail *R. l. saturatus*, occurs along the Gulf coast from Alabama to Texas (Howell 1928). Like the Florida clapper rails, this subspecies occurs in *Spartina-Juncus* marshes in the northern Gulf and in mangrove areas in the southern part of its range.

There is relatively little information available on the food and feeding habits of these five "subspecies." Audubon (1840) observed *R. l. crepitans* eating crabs, snails, aquatic insects, small fishes and plants, but he did not specifically identify the food organisms. Stone (1937) mentions that a meadow vole was found in the stomach of a specimen collected at Cape May, New Jersey. In a study of mixed

populations of King and northern clapper rails in Delaware, Meanley and Wetherbee (1962) reported the red-jointed fiddler crab *Uca minax*, and a clam, *Macoma baltica*, as important foods. Information on the food of "*Rallus longirostris*," the northern clapper rail, presented by Martin, Zim, and Nelson (1951) probably refers to *R. l. crepitans.* Howell (1932) lists eight species of crabs and snails from the stomachs of 22 *R. l. waynei* collected in northeast Florida. Oney (1954) examined the contents of 284 stomachs from *R. l. waynei* killed by hunters on the Georgia coast. He found over 30 genera of food organisms and, of the total volume, crabs comprised 74%, snails 14%, and insects 9%. The semi-terrestrial grapsid crab, *Sesarma cinereum*, accounted for 33% of the total volume of food recovered. Adams and Quay (1958) and Shanholtzer (1973) mentioned fiddler crabs (*Uca* spp.) as food for *R. l. waynei.* Howell (1932) listed four species of decapod crustaceans and one species of insect from eight stomachs of *R. l. scotti* collected in western Florida. No studies have been published on the food of the mangrove clapper rail, although Forbush and May (1955) stated that "it probably differs somewhat from other races of clapper rail in feeding habits on account of its quite different environment, the ecological factors in the mangrove swamp being unlike those of the salt marshes of the Atlantic coast." Simmons (1914) made general observations on the diet of *R. l. saturatus* from the Texas coast. Howell (1928) gave information on the food of Louisiana clapper rails from Alabama. In a comprehensive study, Bateman (1965) examined the stomachs of 103 *R. l. saturatus* collected at Grand Terre Island, Louisiana, and identified nine genera of food organisms. *Uca* sp., *Littorina* sp. and *Sesarma* sp. occurred most frequently (74%, 49%, and 38%, respecitvely). Holliman (1978) found *Uca* remains and seeds in the stomachs of seven birds collected on the coast of Alabama, and in the same study he also observed a single bird feeding on an unidentified fish.

MATERIALS AND METHODS

Clapper rails from 11 localities (Table 1 and Figure 1) were collected by hand (immature birds and molting adults at high tide only) or with a shotgun. Birds were collected during both high and low tides; however, most of the specimens of *R. l. crepitans* were collected during high tide. Stomachs were removed and examined for food organisms as soon as possible (within 6 hours of collection). Identifications to lowest possible taxon were made with the aid of a dissecting microscope having a magnification range of 6X–50X. Only stomach contents that were reasonably intact or that had diagnostic parts were identified.

RESULTS

Table 1 gives the localities, season, and number of birds of each subspecies examined. Sixty-three (33%) of the 187 stomachs examined were empty. The stomachs of 30 (75%) of the 40 *R. l. crepitans* examined were empty. Nearly all the specimens of this subspecies were collected during high tide, and many were alive for several hours after being collected. These factors probably account for the high percentage of empty stomachs. From 0% to 32% of the stomachs of the other subspecies were empty. Table 2 presents a

TABLE 1.

Number of clapper rails of each subspecies examined during this study with relation to locality and season collected.

Subspecies	State	County	Season	Number of birds examined
R. l. crepitans	New Jersey	Cape May	summer	20
	Maryland	Worcester	summer	10
	Virginia	Accomac	summer	10
R. l. waynei	North Carolina	Carteret	summer	20
			fall	5
			winter	5
	South Carolina	Charleston	summer	5
	Georgia	Chatham	summer	15
			fall	15
			winter	10
R. l. scotti	Florida	Pinellas	summer	12
		Indian River	summer	10
R. l. insularum	Florida	Monroe	summer	10
R. l. saturatus	Alabama	Mobile	summer	10
	Mississippi	Jackson	summer	10
			fall	5
			winter	5
	Louisiana	Jefferson	summer	10
			Total	187

listing of the food organisms found, the percent of stomachs containing each food item, and the total number of birds with empty stomachs.

The food of all five subspecies was essentially the same. Crabs were found in approximately 90% of all the stomachs containing food. The predominant crab genus was *Uca*, occurring in approximately 80% of the stomachs of *R. l. crepitans* and *R. l. insularum* and in approximately 70% of the stomachs of *R. l. waynei, R. l. scotti* and *R. l. saturatus. Sesarma* species were in approximately 20% of the stomachs of all "subspecies" except *R. l. insularum.*

Mollusks were the next most common food group, occurring in over 25% of the stomachs of *R. l. insularum* and *R. l. saturatus* and in over 15% of the stomachs of the other subspecies. *Littorina irrorata* was the most frequently occurring mollusk species followed by *Melampus bidentatus.*

Other food items occurred less frequently. Insects made up a small part of the diet in all five subspecies but were most frequent in *R. l. insularum* and *R. l. waynei.* Amphipods were found in a few stomachs of all subspecies except *R. l. saturatus.* Plant material was present in some stomachs of *R. l. waynei, R. l. insularum,* and *R. l. saturatus.* Polychaetes were identified occasionally among the food items of *R. l. waynei* and *R. l. saturatus.* Shrimp and fish remains were found only in the stomach contents of *R. l. saturatus.*

DISCUSSION

Table 3 lists the food organisms or types which have been reported in previous studies for the five eastern subspecies of *R. longirostris.* Some of the specific names for the food organisms listed by Howell (1932) are now out of date or appear to have been confused with other closely related forms. In Table 3, suggested corrections and additions to the scientific names appear in brackets following the original designation. In cases when only the genus name was given and only one species of the genus is present in the salt marsh habitat, the full scientific name is added. Questionable records are followed by a question mark in brackets. Howell's report of "*Palaemonetes exilipes*" in the diet of *R. l. scotti* from the northwestern coast of Florida probably refers to *P. pugio*, a brackish-water species common in the salt marshes of that area. The name *P. exilipes* has been confused with those of two freshwater prawns, *P. kadiakensis* and *P. paludosus*; it is now considered a synonym of the latter (Holthuis 1952). "*Uca pugnax rapax*" is now considered *Uca rapax* (Tashian and Vernberg 1958). Howell's (1932) records of *Uca* ("*pugnax*") *rapax, Sesarma recordii,* and *Neopanope packardii* as food of *R. l. waynei* in northeastern Florida are questionable. These three species of crabs are more characteristic of southern Florida and are not known to occur in northeastern Florida (Tashian and

TABLE 2.

Food from stomachs of *Rallus longirostris* collected during the present study giving the % occurrence of each food item for the five subspecies examined.

	"Subspecies"	*crepitans*	*waynei*	*scotti*	*insularum*	*saturatus*	All
Food Items	No. stomachs with food	10	51	18	10	35	124
ARTHROPODA		100.0	100.0	94.4	90.0	74.0	91.1
CRUSTACEA		90.0	96.1	94.4	90.0	74.0	89.5
DECAPODA		90.0	94.1	88.9	90.0	74.0	87.9
Uca		80.0	68.6	66.7	80.0	71.4	71.0
U. pugnax		80.0	52.9	11.1	–	–	29.8
U. longisignalis		–	–	38.9	–	40.0	16.9
U. pugilator		–	11.8	–	–	–	4.8
U. rapax		–	–	16.7	60.0	–	7.2
U. panacea		–	–	–	–	28.6	8.1
U. speciosa		–	–	–	20.0	–	1.6
Sesarma		20.0	21.6	27.8	–	14.3	18.5
S. reticulatum		20.0	21.6	27.8	–	11.4	17.7
S. cinereum		–	5.9	–	–	2.9	3.2
Aratus pisonii		–	–	11.1	20.0	–	3.2
Eurytium limosum		–	2.0	16.7	–	5.7	4.8
Panopeus herbstii		–	2.0	–	–	–	0.7
Rhithropanopeus harrisii		–	–	–	–	2.9	0.7

TABLE 2. (Continued)

Food from stomachs of *Rallus longirostris* collected during the present study giving the % occurrence of each food item for the five subspecies examined.

Food Items	"Subspecies"	*crepitans*	*waynei*	*scotti*	*insularum*	*saturatus*	All
	No. stomachs with food	10	51	18	10	35	124
SHRIMPS		–	–	–	–	2.9	0.7
Palaemonetes pugio		–	–	–	–	2.9	0.7
AMPHIPODS		10.0	15.7	16.7	10.0	–	10.5
Orchestia grillus		10.0	15.7	16.7	–	–	9.7
Orchestia sp. (undescribed)		–	–	–	10.0	–	0.7
INSECTS		10.0	15.7	5.6	20.0	2.9	10.5
Orchelimum fidicinum		–	11.8	–	–	2.9	5.6
unidentified insects		10.0	7.8	5.6	10.0	–	5.6
ants		–	–	–	10.0	–	0.6
MOLLUSKS		20.0	17.6	16.7	30.0	28.6	21.8
Littorina		10.0	5.9	5.6	10.0	25.7	12.1
L. irrorata		10.0	5.9	5.6	–	25.7	10.5
L. angulifera		–	–	–	10.0	–	0.6
Melampus		20.0	13.7	11.1	20.0	5.7	12.1
M. bidentatus		10.0	13.7	–	–	5.7	6.5
M. coffeus		–	–	11.1	20.0	–	3.2
Guekensia demissa (juv)		–	–	5.6	–	–	0.7
Tagelus plebeius (juv)		–	–	5.6	–	–	0.7
POLYCHAETES		–	15.7	–	–	2.9	7.3
Nereis succinea		–	15.7	–	–	2.9	7.3
FISH		–	–	–	–	5.7	1.6
Lagodon rhomboides		–	–	–	–	2.9	0.7
unidentified remains		–	–	–	–	2.9	0.7
PLANT MATERIAL		–	5.9	–	20.0	17.1	8.7
Unidentified		–	3.9	–	20.0	17.1	6.5
Acorns (live oak)		–	2.0	–	–	–	0.7
	No. empty stomachs	30	24	4	–	5	63

Vernberg 1958, Abele 1972, 1973). The record of *U. rapax* probably refers to the closely related *U. pugnax* and that of *S. recordii* to the closely related *S. cinereum*. *Neopanope packardii* was probably a misidentification of *Eurypanopeus depressus* or *Panopeus herbstii* which are superficially similar. *Uca pugnax*, *S. cinereum*, *E. depressus* and *Panopeus herbstii* are common in the salt marsh habitats of northeastern Florida.

Data from this study and from those of Oney (1954) and Bateman (1965) indicate that crabs of the genera *Uca* and *Sesarma* are the most commonly occurring food organisms in the diet of clapper rails from the Atlantic and Gulf coasts. *Uca* spp. were the most frequently encountered crabs in this study and in Bateman's (1965) study of *R. l. saturatus*. In Oney's (1954) study of *R. l. waynei*, however, *S. cinereum* was the most common crab found. Both seasonal and tidal factors may explain this difference. During the colder months *Uca* spp. are inactive and remain in their burrows (Teal 1958), where they are not readily accessible to clapper rails. Oney's observations were made on birds killed by hunters during the fall, and some of these specimens may have been collected during cold periods, when *S. cinereum* would be more easily obtained than *Uca*. Tides may also affect the relative availability of *S. cinereum* and *Uca* spp. Almost all marsh hen hunting in Georgia is done during very high tides when rails have less cover and when hunters can take their boats into the marshes (Oney 1954). *Sesarma cinereum* is more terrestrial than *Uca* spp. and *S. reticulatum*, living primarily in upper intertidal and supratidal areas or in association with large rafts of dead *Spartina*. During high tides it generally stays out of the water on top of *Spartina* rafts or along shore, where it is the most abundant crab present and is more vulnerable to predation. Observations made during this study indicate that clapper

TABLE 3.

A synoptic listing of food items previously reported from the five subspecies of *Rallus longirostris* from salt marshes along the Atlantic and Gulf coasts of the United States. Suggested corrections and additions to scientific names are in brackets. The reference or references for each food item follow it (separated by a hyphen).

Rallus longirostris crepitans

Crabs: "crabs"–Audubon (1840); *Uca minax*–Meanley and Wetherbee (1962).

Mollusks. "snails"–Audubon (1840); *Macoma baltica*–Meanley and Wetherbee (1962).

Insects: "aquatic insects"–Audubon (1840).

Vertebrates: fishes (minnows, fry)–Audubon (1840); *Microtus* [=*M. pennsylvaniaensis*]–Stone (1937).

Vegetation: unidentified plant material–Audubon (1840).

Rallus longirostris waynei

Crabs: "crabs"–Oney (1954); *Callinectes* sp. [=*Callinectes sapidus*]–Oney (1954); *Eurytium limosum*–Oney (1954); *Panopeus herbstii*–Howell (1932), Oney (1954); Pinnotheridae (unidentified)–Oney (1954); *Sesarma cinereum*–Oney (1954); *Sesarma reticulatum*–Howell (1932), Oney (1954); *Uca* (sp. or spp.)–Adams and Quay (1958); Oney (1954); *Uca pugilator*–Oney (1954); *Uca pugnax*–Shanholtzer (1973); *Uca pugnax rapax* [=*Uca pugnax?*]–Howell (1932).

Shrimp: *Penaeus setiferus*–Oney (1954); *Palaemonetes* sp. [=*Palaemonetes pugio*]–Oney (1954).

Mollusks: *Ilyanassa* (=*Nassarius*) *obseleta*–Howell (1932), Oney (1954); *Littorina irrorata*–Howell (1932), Oney (1954); *Melampus* sp. [=*M. bidentatus*]–Oney (1954); Molulidae [sic.?] (clams)–Oney (1954); *Polygyra* sp.–Oney (1954).

Marine worms: *Nereis* sp. [=*Nereis succinea?*]–Oney (1954).

Insects: *Acantodaphallus* sp.–Oney (1954); Acrididae (unidentified)–Oney (1954); *Anisolabis* sp.–Oney (1954); *Apis mellifera*–Oney (1954); Balattidae (unidentified)–Oney (1954); *Crematogaster* sp.–Oney (1954); *Gambrus bituminosus*–Oney (1954); Gryllidae (unidentified)–Oney (1954); *Gryllus assimilis*–Oney (1954); *Hylobius pales*–Oney (1954); Hymenoptera (unidentified)–Oney (1954); Ichneumonidae (unidentified)–Oney (1954); *Leptoglossus phyllopus*–Oney (1954); *Metanoplus* sp.–Oney (1954); *Neoconocephalus triops*–Oney (1954); *Scapteriscus* sp.–Oney (1954); *Schistocerca americana*–Oney (1954).

Spiders: *Clubiona* sp.–Oney (1954); *Lyeosa* sp.–Oney (1954).

Vertebrates: *Fundulus* sp.–Oney (1954); Poecillidae (unidentified)–Oney (1954).

Plant material: *Spartina alterniflora*–Oney (1954).

Rallus longirostris scotti

Crabs: *Callinectes sapidus*–Howell (1932); *Neopanopeus packardii* [?]–Howell (1932); *Rhithropanopeus harrisii*–Howell (1932); *Sesarma ricordi* [=*Sesarma cinereum?*]–Howell (1932); *Uca pugnax* [=*Uca longisignalis*]–Howell (1932).

Shrimp: *Palaemonetes exilipes* [=*Palaemonetes pugio*]–Howell (1932).

Insects: "grasshoppers"–Howell (1932); *Anisotabis maritima* Howell (1932); "beetles" [Coleoptera]–Howell (1932); "butterfly cocoons"–Howell (1932).

Rallus longirostris insularum

(No previous food records)

Rallus longirostris saturatus

Crabs: "crabs"–Simmons (1914), Howell (1928); *Panopeus* sp. [=*Panopeus herbstii*]–Bateman (1965); *Sesarma* sp.–Bateman (1965); "Fiddler or fighting crabs" [=*Uca* (sp. or spp.)]–Simmons (1914).

Hermit crabs: *Clibanarius* sp. [=*Clibanarius vittatus*]–Bateman (1965).

Shrimp: "shrimp"–Howell (1928).

Mollusks: "clams"–Bateman (1965); "slugs"–Simmons (1914); "snails"–Simmons (1914); *Littornia* sp. [=*Littorina irrorata*]–Bateman (1965); *Melampus* sp. [=*M. bidentatus*]–Bateman (1965); *Odistoma* sp. [=Hydrobiidae?]–Bateman (1965).

Marine worms: "marine worms"–Howell (1928, 1932).

Insects: "aquatic insects"–Simmons (1914); "grasshoppers"–Simmons (1914); *Sphenophorus* sp.–Bateman (1965); Tettigoniidae (unidentified)–Bateman (1965); *Belostoma* sp.–Bateman (1965).

Vertebrates: fishes (minnows, fry)–Howell (1928), Bateman (1965); diamondback terrapin [=*Malachemys terrapin*]–Simmons (1914).

Plant material: unidentified plant material–Bateman (1965); seeds–Simmons (1914).

rails feed throughout the tidal cycle, although apparently most feeding occurs during low tide. Birds collected at low tide during the warmer months had been feeding largely on *Uca* spp. and to a lesser extent on *S. reticulatum*. In Georgia, during this study, the three birds that had been feeding on *S. cinereum* were collected at high tide.

My findings agree with those of Oney (1954) and Bateman (1965) in that marsh snails of the genera *Littorina* and *Melampus* appear to be the second most abundant component of the marsh hen's diet. Seasonal observations on *R. l. waynei* and *R. l. saturatus* indicate that these mollusks may be major food items during cold periods when *Uca* and other marsh crabs are less accessible.

Salt marshes support relatively large numbers of insects (Davis and Gray 1966). Oney (1954) reported a much greater number of insects from the stomachs he examined than did Bateman (1965), earlier workers, and this study. Again, tide conditions may have influenced Oney's data, since high tides reduce the cover, thereby concentrating many of the insect species and making them more vulnerable to predation.

Polychaete worms were not often found in the gut and stomach contents of clapper rails examined during this study or those from earlier studies; however, they may be more important in the diet of clapper rails than this or previous studies indicate, especially during the cold months. *Nereis* (*Neanthes*) *succinea*, a relatively large worm with distinctive mouth parts, is the only form that has been identified from the rail stomachs examined. It is possible, however, that the macerated remains of smaller polychaetes, lacking hard

mouth parts, could have been overlooked. On numerous occasions during low tides, I have observed Wayne's clapper rails feeding along mud banks and in creek beds in *Spartina-Juncus* marshes. The rails were often actively probing in the substrata with their bills. On several occasions I sieved the mud-sand sediment from areas where the birds had been probing and found small, fragile polychaetes, principally *Scolopis fragilis* and *Heteromastis filaformis.*

Vertebrates have rarely been reported in the stomach contents of clapper rails; however, indirect data from a study of helminth parasites of the clapper rail indicate that fish are of some importance in their diets (Heard 1970, unpublished data). I removed a 5-cm-long pinfish, *Lagodon rhomboides*, from the bill of an adult *R. l. saturatus* collected at Dauphin Island, Alabama. Pinfish are wide, heavy-bodied fish, and it seems doubtful that a clapper rail could swallow a 5-cm specimen without first tearing it apart. Holliman (1978) also observed a clapper rail in the same general area of Dauphin Island feeding on an unidentified fish. The only published record of a mammal in the diet of clapper rails is that of Stone (1937) who reported that a meadow vole (*Microtus* sp.) was recovered from the stomach of *R. l. crepitans* collected in New Jersey. Sibley (personal communication, 1962) has observed California clapper rails (*R. l. obsoletum*) feeding on "small mice" in the marshes of San Francisco Bay.

Plant matter, principally seeds, is eaten by clapper rails, but it apparently is not an important part of their overall diets. Martin, Zim, and Nelson (1951) presented seasonal data based on the examination of 278 clapper rails, which indicated a larger consumption of plant food during the winter. In seasonal food studies of king rails, Martin, Zim, and Nelson (1951) and Meanley (1956, 1969) also reported a higher percentage of plant food from the stomachs of birds collected during the winter months, a situation which Meanley (1969) attributed largely to the scarcity of animal food during the winter.

All five subspecies of clapper rails studied ate basically the same kinds of food organisms—crabs, snails, and to a lesser extent, insects, polychaetes, bivalves, fishes, and plant material. There are some differences in dietary composition due to zoogeography and habitat type (*Spartina-Juncus* or mangrove).

The more temperate *Spartina* marshes of the east coast and of the northern Gulf coast are interrupted by the more tropical mangrove regions of southern Florida. Accordingly, some endemic salt marsh animals such as *Uca minax*, *Sesarma cinereum, S. reticulatum, Littorina irrorata, Geukensia* (=*Modiolus*) *demissa*, and *Orchestia grillus* apparently have disjunct ranges on the Gulf and Atlantic coasts (Williams 1965, Abele 1973, Abbott 1974, Bousfield 1973). The mud fiddler crab *Uca pugnax* is confined to the salt marshes of the Atlantic seaboard, whereas its ecological cognate, *U. longisignalis*, is endemic to the salt marshes of the Gulf of Mexico (Salmon and Atsaides 1968). These two species appear to occupy similar niches within their respective ranges.

Other food organisms of clapper rails, including *Uca pugilator, U. speciosa, U. rapax, Eurytium limosum, Rhithropanopeus harrisii, Panopeus herbstii, Melampus bidentatus,* and *Nereis* (*N.*) *succinea*, occur in both salt marsh and mangrove habitats (Crane 1975, Morrison 1958, 1964, Pettibone 1963, W. E. Odum 1971, Heard, unpublished observations). The range of the xanthid marsh crab *E. limosum* apparently extends no further northward than South Carolina (Williams 1965). *Uca rapax* is now known to occur on the Atlantic coast north of central Florida (Tashian and Vernberg 1958). Thurman (1973) reported that in the Gulf *Uca rapax* was apparently absent from the coasts of eastern Alabama and northwestern Florida. He also reported that *U. speciosa* occurred along the Gulf coast from Mississippi to the southern tip of Florida. *Uca pugilator* has a continuous range from New England into west Florida. A recently described cognate species, *U. panacea*, previously thought to be *U. pugilator*, replaces it west of Pensacola (Thurman 1973, Novak and Salmon 1974). *Nereis* (*N.*) *succinea, Melampus bidentatus, Panopeus herbstii*, and *Rhithropanopeus harrisii* occur throughout the coastal region of the southeastern United States; however, *R. harrisii,* a low-salinity species, apparently does not occur in the polyhaline waters of the Florida Keys.

Aratus pisonii, Littorina angulifera, and *Melampus coffeus* are tropical forms closely associated with mangrove habitats (Rathburn 1918, Morrison 1964, Hartnoll 1965, Abbott 1974, Thomas 1974). Accordingly, they only occurred in the stomachs of clapper rails collected from areas in or adjacent to mangrove swamps along the southern half of peninsular Florida.

Habitat variation also occurs within the tidal marshes or mangrove swamps in the same geographical area (e.g., an estuarine system). For example, along the southeastern Atlantic seaboard the lower reaches of estuaries are generally characterized by extensive *Spartina* marshes with an associated mesohaline fauna made up of species such as *Uca pugnax, U. pugilator, Eurytium limosum, Orchestia grillus, Melampus bidentatus, Modilus demissus*, and *Littorina irrorata*. In contrast, in the oligohaline upper reaches of these estuaries, *Spartina* marshes are largely replaced by *Juncus* marshes. Some of the characteristic organisms occurring in this type of habitat are *Uca minax, R. harrisii, Polymesoda carolinae, Cyrenoidea floridana, Orchestia uhleri,* and *Detracia floridana*. Similar conditions occur in other tidal

marshes and mangrove swamps along the Atlantic and Gulf coasts. Since clapper rails occur in the tidal marshes and mangrove swamps throughout the eastern United States it can be assumed that their food varies accordingly.

Trophic level

It is virtually impossible with the data now available to assign salt marsh consumers such as the clapper rail to specific or well-defined trophic levels. This is due to several factors: (1) feeding habits which are incompletely documented; (2) omnivorous feeding habits; (3) the still uncertain trophic position of "organic detritus" and (4) the seasonal availability of various food organisms.

Both *Spartina-Juncus* and mangrove systems have been described as having food webs largely based on detritus (E. P. Odum 1961, 1971, Teal 1958, 1962, Odum and de la Cruz 1967, W. E. Odum, 1971, Wass and Wright 1969, Day et al. 1973, Thomas 1974). The definitions, significance, origins, and overall conceptual problems concerning "organic detritus" in marine and estuarine systems have been discussed by Darnell (1964, 1967a, 1967b), Newell (1965), E. P. Odum (1971), Mann (1972), and Saunders (1972). Darnell (1967b) defined organic detritus as "all types of biogenic material in various stages of microbial decomposition which represent potential energy sources for consumer species." As understood by W. E. Odum (1971), the definition "includes materials which are sorbed upon the basic particle, bacteria, fungi, and protozoa, along with adsorbed dissolved organic and inorganic compounds. The entire particle and its sorbed load should be considered as a single unit. . .a small ecosystem within a larger system."

Although incompletely known, the food webs and energy flow models proposed for *Spartina-Juncus* systems (Teal 1962) and for mangrove systems (W. E. Odum 1971, W. E. Odum and Heald 1972) appear to be relatively similar. On this basis, and on the similarity of the types of food eaten, it can be assumed that clapper rails associated with both these habitats generally have similar trophic relationships. In his energy flow model for a Georgia salt marsh ecosystem, Teal (1962) categorized clapper rails as "secondary consumers" (primary carnivore).

In view of the data now available on estuarine food webs and in terms of the second law of thermodynamics as applied to biological systems by Linderman (1942), clapper rails would necessarily occupy a trophic level higher than that of a secondary consumer. Darnell (1964, 1967a, 1967b) and E. P. Odum (1971, p. 74) have pointed out that the "detritus consumer" (detritovore) is quite different trophically from the "primary consumer" or "herbivore" of the grazing food chain. The primary consumer derives its energy directly from plant matter (i.e., first trophic level) while the detritus consumer may obtain its energy from food material derived from as many as three or more trophic levels. The foods eaten by clapper rails cover a wide trophic spectrum and it would seem from the trophic data now available that the clapper rail's overall trophic position would be that of a secondary carnivore.

Based on unpublished studies and observations on the foods of salt marsh consumers, I have found that vertebrates such as the seaside sparrow *Ammospiza maritima*, sora rail *Prozana carolina*, rice rat *Oryzomys palustris*, and raccoon *Procyon lotor* have diets that are generally similar or overlap considerably that of the clapper rail during all or part of the year. Though niche-partitioning occurs among these and other salt marsh omnivores, it has not been well documented and remains a fertile area for further ecological research. A complex of subtle temporial and spatial factors, in conjunction with predator-prey size and size classes, must be understood before any meaningful description of food-resource partitioning among salt marsh omnivores and carnivores can be presented.

It should be noted that clapper rails serve as a food source for other vertebrate predators. These include the alligator, marsh hawk, mink, otter, and man (Smith 1967, Bateman 1965, Heard, unpublished observ.).

Comparison with food habits of the king rail

Whether or not the king rail *Rallus elegans* Audubon, a predominantly freshwater form, is conspecific with the similar and closely related *R. longirostris* Boddaert, has been debated since the writings of Wilson and Audubon (Audubon 1840, Bull 1964, Mayr and Short 1970). Because the king rail's range overlaps that of the clapper rail, a comparison of these two birds' food habits was made. Since Bent's (1926) review, a number of authors have reported these two forms occurring together in brackish tidal marshes (Oberholser 1937, 1938, Lowery 1955, Tomkins 1958, Meanley and Wetherbee 1962, Meanley 1965, 1969), and in Delaware Bay they have been observed interbreeding (Meanley and Wetherbee 1962). Oberholser (1937) discussed the systematic position of these two rails and concluded, ". . .it seems best, at least for the present, to consider these birds as representing two species, *Rallus elegans* consisting of two subspecies, and *Rallus longirostris*, made up altogether of 25 races (=subspecies)."

Because the king rail's range overlaps that of the clapper rail, a comparison of their food habits was made to determine if any important differences could be detected with the limited amount of published data available. King rails are primarily associated with freshwater habitats; however, they appear to have the same kind of omnivorous feeding habits as do clapper rails from tidal marshes. Meanley (1956, 1965, 1969) gave information on the food of king rails collected from a number of different habitats in the eastern half of the United States. As in the case of the clapper rail, his data indicate that the composition of the king rail's diet simply reflects the presence of the most common organisms of food size characteristic of the particular habitat from

which the birds were collected. Typical foods of king rails from freshwater areas were crayfish, frogs, insects, fishes, and plant seeds. Part of Meanley's observations, however, were made in a brackish marsh area on Delaware Bay where mixed populations of king and clapper rails occurred. In this estuarine habitat the diet of both species of rails was essentially the same, consisting largely of a fiddler crab (*Uca minax*) and a clam (*Macoma baltica*). I have also observed king and clapper rails feeding together during the winter months on small fishes and invertebrates in brackish marshes near Ocean Springs, Mississippi.

Taxonomic problems in the clapper rail complex

The taxonomic status of the "subspecies" of *Rallus longirostris* is unclear. The definitions of terms such as "geographic races," "subspecies," and even "species" are complex and accordingly more difficult to properly define and conceptualize (Mayr 1970, Scudder 1974). The taxonomy of the clapper rail and its "subspecies" is an example of this kind of systematic problem.

Although the five nominal subspecies of *R. longirostris* investigated during this study appear to breed in more or less specific geographical areas, interbreeding undoubtedly occurs in the areas of overlap in North Carolina, Florida, and Alabama. Many of 25 "subspecies" reviewed by Oberholser (1937) were described from relatively few specimens. In fact, a number of the "subspecies" descriptions were based on less than ten birds, and in the cases of *R. l. crassirostris* Lawrence, *R. l. belizensis* Oberholser, and *R. l. nayaritensis* McLellan, only a single specimen was studied (Oberholser 1937). The "subspecies" of clapper rails were separated by Oberholser (1937) primarily on subtle differences in their color patterns or on minor differences in body measurements. I have observed considerable variation in color patterns and body sizes of adult birds of the same sex collected together. Such variation was particularly evident in the clapper rails I examined from Tampa Bay, a transition-area where both mangrove and *Spartina* marshes occur. In the mesohaline marshes at Cape Romane, South Carolina, young-of-the-year birds (12–16 weeks old) were distinctly larger and heavier than adults taken in the collecting sites from other states. Additionally, the ranges of the five subspecies from the eastern United States, with the possible exception of *R. l. insularum,* do not appear to be clearcut or, as for *R. l. scotti* and *R. l. saturatus,* to relate to the basic *Spartina-Juncus* or mangrove habitat types.

The information available on the food and feeding habits of clapper rails, king rails, and their nominal subspecies occurring along the Atlantic and Gulf coasts of the United States indicates that there are no distinct differences in their feeding behavior. Differences in kinds of food eaten simply appear to reflect the types of marsh habitat (fresh, brackish, polyhaline) or geographical location (temperate or tropical) where a particular clapper rail population occurs. Accordingly, the clapper rail should be classified trophically as an opportunistic omnivore having a relatively broad niche within the marsh ecosystem in which it resides.

The facts that clapper and king rails interbreed and have the same feeding habits where their populations overlap (Meanley and Wetherbee 1962, Meanley 1965, Meanley 1969, present study) justify considering them as subspecies of *Rallus longirostris,* a designation given them by Mayr and Short (1970) and followed by Wass (1972) and Ripley (1977). If this reasoning is followed, the other forms which have been considered subspecies of the clapper rail (sensu Ripley 1977) might then fall into the category of "geographical races." Recognizing their close similarity, Bull (1964) considered the king and clapper rail to form a "superspecies"; however, such a designation, unless concisely defined, has dubious taxonomic merit. Ripley (1977) considered the king rail a "subspecies" of *R. longirostris;* however, he also recognized all of the other named "subspecies" as valid taxons. Additional research using refined ecological, genetic, and behavioral techniques will be needed before the ecophenotypic, taxonomic and systematic relationships of the clapper rail complex can be fully understood. Notwithstanding qualitative differences in their size, body measurements and color patterns, the recognition of five distinct subspecies of *Rallus longirostris* from the coast of the eastern United States does not appear to be supported by available information on their ecology, reproductive behavior, or food habits.

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