rarely feeds the female at the nest (pers. observ.). Perhaps if both sexes incubated or the male fed the female on the nest there would be less selective advantage to having thermally tolerant embryos; conversely, intolerant embryos may necessitate biparental incubation or male incubation feeding.

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FORAGING BEHAVIOR AND FOODS OF THE LIGHT-FOOTED CLAPPER RAIL[1]

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Key words: Clapper Rail; foods; foraging; Rallus longirostris levipes; *salt marsh.*

Several reports are available on the foods and foraging of subspecies of Clapper Rails, *Rallus longirostris* (Bent 1926, Orr 1939, Moffitt 1941, Sibley 1955, Ohmart and Tomlinson 1977, Heard 1982), but nothing has been published for the Light-footed Clapper Rail (*Rallus longirostris levipes*). Because, the Light-footed Clapper Rail is considered endangered, such information could be critical for effective management of the habitat and this bird's recovery (U.S. Fish and Wildlife Service 1985).

The Light-footed Clapper Rail occurs in California's coastal marshes from Santa Barbara County south to the Mexican border and in northwestern Baja California, Mexico (Bent 1926, AOU 1957). Annual censusing of the rails in California since 1980 revealed a high count of 277 pairs distributed in 19 marshes in 1984 (Zembal and Massey 1981, 1985a), followed by a crash to 142 pairs in 14 marshes in 1985. As of the spring of 1987, the state population had only poorly recovered.

We have been investigating the habits of this endangered race since 1979 (see Zembal and Massey 1983a, 1983b, 1985b, 1987; Massey et al. 1984; Zembal et al. 1985; Massey and Zembal 1987). Herein are presented our observations on the known foods and foraging strategies.

STUDY AREA AND METHODS

Foraging Clapper Rails were observed at Upper Newport Bay, an ecological reserve of the California Department of Fish and Game in Orange County. Upper Newport Bay is a largely unmodified embayment, subject to unconstrained tidal influence (tidal range of 2.6 m) and winter freshwater storm flows. The total area of the reserve is about 304 ha, including a 111-ha salt marsh (California Department of Fish and Game 1984).

Descriptions of foraging behavior, presented here, summarize approximately 180 hr of visual contact with feeding Clapper Rails during the period March 1979–August 1987. In addition, several hours of foraging were captured on video tape, mostly in January and February 1983. The tape of 11 foraging bouts by four rails, totaling 46.3 min of feeding, was detailed enough to allow excellent monitoring of all their activities. The motions and foraging success (swallowings) of these birds were quantified.

A total of 49.85 g of materials regurgitated by Light-footed Clapper Rails was collected in the spring of 1979 and of 1986. Of the total, 77% was collected at Upper Newport Bay, 15.2% from the Seal Beach National Wildlife Refuge in Orange County, 4% from the Kendall-Frost Reserve in Mission Bay, San Diego County, and 3.8% from the Tijuana Estuary National Wildlife Refuge on the Mexican border. The pellets and fragments were separated under a dissecting microscope and recognizable remains were identified.

RESULTS AND DISCUSSION

Over 90% of the time that Clapper Rails were observed foraging, they hunted in the marsh vegetation, executing numerous surface gleans and usually shallow probes. They appeared to be hunting by sight and erratically changed their direction of travel in response to cues, presumably movements by potential prey items. Consequently, this general foraging behavior involved a lot of abrupt turns and direction reversals, and the foraging birds often covered only very small areas.

The movements involved in 11 bouts of foraging revealed rates of foraging that varied nearly eightfold (Table 1). Higher intensity foraging was regularly observed during peak foraging hours in the late evening. Rates of 1,000–2,000 gleans and probes per hour appeared to be commonly sustained. Lower frequency of feeding motions with more travel by a rail was typical of "crabbing," or the exploration of burrows, particularly along creek banks, for crabs and other larger prey

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TABLE 1. Foraging movements and success of four Light-footed Clapper Rails.

Duration (sec)	Rail band number	Surface gleans n	Surface gleans /min	Success[1] n	Success[1] %	Steps by the rail	Direction reversals	Maximum distance moved (m)
121	439	67	33.2	28	41.8	3	0	0.2
238	—	17	4.3	9	52.9	148	6	8
314	—	55	10.5	18	32.7	113	5	10
433	439	76	10.5	32	42.1	177	8	10
280	439	38	8.1	15	39.5	162	9	10
414	440	114	16.5	43	37.7	121	9	5
48	439	17	21.3	6	35.3	14	0	1
134	440	14	6.3	4	28.6	70	4	2
266	440	33	7.4	6	18.2	103	6	5
240	439	30	7.5	12	40.0	105	6	5
287	439	60	12.6	16	26.7	43	4	3

[1] A successful foraging motion was followed by an obvious swallowing by the rail.

(see below). The average rate of foraging for the 11 bouts was about 675 gleans/hr.

The overall success (number of swallows) for all 11 bouts extrapolates to approximately 250 morsels of tiny prey in an hour. The lower success rates were associated with crabbing or casually foraging rails, and the higher rates were by birds that found food concentrations. Consequently, an average percent success varying from the high 20s to the low 40s appeared to be common for moderately to intensely active foragers.

Rails engaged in standard foraging behavior, gleaning and shallowly probing the marsh, often moved from one bonanza to the next. As illustrated by the first entry in Table 1, concentrations of food were often quite near one another, requiring little travel by a rail. Concentrations were often discovered at the bases of shrubs or under small bits of cover that the rail would toss aside. These concentrations were worked vigorously by a bird and appeared to be caches of small, very mobile organisms that scattered quickly when their cover was thrown or nudged away.

Clapper Rails observed foraging for periods of 1–3.5 hr would almost invariably crab for a few minutes during that time. After a rail had swallowed hundreds of tiny prey items, too small for us to identify from just 10 m away, it would walk into a tidal creek and hunt the bank. A bird would search burrows and probe several of them, often lunging into one neck-deep, and within minutes one or more crabs (*Pachygrapsus crassipes, Hemigrapsus oregonensis,* and *Uca crenulata*) would be eaten. Smaller crabs were swallowed whole; medium-sized crabs were dismembered by shaking and the parts swallowed. Larger crabs were dismembered, the appendages swallowed, but the body was broken open and only the flesh consumed.

Other less frequently observed foraging strategies included mudflat foraging, fishing, and scavenging. The Clapper Rails we observed were mostly within marsh vegetation or along its edge. The rails were warier and moved more quickly when away from cover but did venture onto the mudflats regularly. This was most apparent in the summer and fall, when family groups were observed on the mudflats and algal mats in the evenings. Crabbing was commonly observed of rails on the flats along the central drain creeks. A portion of the crabs and other foods taken by adults was fed to the youngsters. However, even very young rails foraged somewhat; snapping up dipterans seemed to be one of their first pursuits.

Chicks sometimes lurked along the edge of the vegetation until an adult found food but were observed as often in the close company of a foraging adult. Young birds, as old as about 6 weeks, were fed in part by adults. The behavior of one youngster of about this age and an adult indicates how some foraging strategies may be learned. The adult hunted along with the immature at its heels. When the adult froze with its head slightly above the substrate, ready to strike, the immature raced in and snapped up a spider from the spot concentrated upon by the adult.

One rail was observed taking two different longjaw mudsuckers (*Gillichthys mirabilis*) from the mudflat. The fish were too bulky to swallow at first, so they were jabbed, shaken, and tossed about until finally massaged to a shape that could be swallowed whole.

Three different rails were observed eating ribbed horse mussels (*Ischadium demissum*) on the mudflat. One bird pulled flesh from an open but intact mussel and swallowed six times before moving on. Two others walked along a dense algal mat over shallow water gleaning and probing. Both encountered mussels; one worked on three of them. The mussels were not visible initially on the surface; a rail, after probing around, would suddenly pull one up with vigorous head shaking and the bird would swallow something. In the process, the mussel was cast to the side, it released a squirt of water, and closed. The rail would return to the mussel, probe it for a short time, and then move on. This behavior was repeated on all three mussels, not one of which was successfully reopened and entirely consumed.

The abundance of this nonnative mussel in San Francisco Bay was considered a potential threat to California Clapper Rails (*R. l. obsoletus*) following observations of rails stuck in closed mussels (DeGroot 1927). We rescued an emaciated and easily captured rail with a mussel clamped tightly to one toe in Upper Newport Bay. We have also observed many rails with partly missing toes. Moffitt (1941), in contrast, analyzed the contents of 18 stomachs of California Clapper Rails and found the ribbed horse mussel to be the single most abundant food item. He specifically mentioned mussel shell fragments and apparently deduced that the flesh had been consumed as well. We have no evidence, so far, that the Light-footed Clapper Rail is capable of breaking the thick valves of this mussel. Perhaps small ones are swallowed whole.

Clapper Rails were observed fishing seven times. They paddled around vigorously, partially submerged in pursuit, and occasionally dove. One rail took four California killifish (*Fundulus parvipinnis*) in 17 min from a small pond. Another took six fish from the same pond in 30 min. A rail was also observed once wading through a very small pond feeding on tadpoles of the Pacific tree frog (*Hyla regila*). The bird took 19 tadpoles in 10 min. Fishing may be more common than our observations would indicate. Small pools left by receding tides often strand abundant and easy prey but most such locations were screened from our view by dense vegetation.

Scavenging was observed three times and involved rails feeding on dead mullet (*Mugil cephalis*). One of the birds fed for 40 min on the same carcass. These birds may have been eating insect larvae as well as decaying fish flesh.

The materials regurgitated by Clapper Rails and collected in 1979 included 18 intact pellets. The average size and weight of these were 1.30 cm × 1.05 cm and 0.52 g. Thus, all of the regurgitated materials we collected represented about 96 average-sized castings by weight.

The composition of the materials collected in 1986 was very similar to that of the 1979 samples. The 1979 materials, representing 75.7% of the total, were collected in 24 samples, mostly from different nests. Frequency of occurrence was determined for the recognizable components per sample whereas the 1986 materials were pooled by marsh. Crab remains were the most abundantly represented item; they were found in 19 of 24 samples. One pellet contained evidence of at least five crabs. *Pachygrapsus crassipes* and *Hemigrapsus oregonensis* were the two more common species. Although the sizes of dactyls from crab chelipeds found in the pellets ranged in length from 2.5 mm to 12 mm, most were 4 mm to 8 mm long, from mostly small to medium-sized crabs.

The next most abundant remains were of California horn snails (*Cerithidea californica*), found in 10 of 24 samples, and salt marsh snails (*Melampus olivaceous*), found in seven samples. One pellet contained the remains of 21 horn snails. Another held evidence of eight *Melampus*. A few of the larger individuals of both snail species were intact and undigested.

Other organisms represented in the samples included crayfish (*Procambarus* sp.) (in one sample), beetles (in one sample), isopods (in two samples), and decapods (in one sample).

About 22% of the 1986 samples were collected along a freshwater ditch at the upper edge of Upper Newport Bay. These materials, as in 1979, were composed mostly of the fragmented exoskeletons of crayfish. There were also 21 tiny cup-shaped items of unknown source but high calcium carbonate content (perhaps the white stones mentioned by Ohmart and Tomlinson 1977) and pieces of beetle elytra, as in 1979.

Two of the pellets collected at the ditch contained a total of 75 seeds, representing as many as 25 fruits of the elderberry (*Sambucus mexicana*). A small number of elderberry trees overhang the ditch. This latter observation was unusual. Plant remains were rare in the pellets and other than the elderberry, totalled three very small unidentified seeds and several cordgrass (*Spartina foliosa*) seeds. Only three Clapper Rails were ever observed with certainty feeding on plants. Two, while incubating on upper marsh nests, pulled off the tips of pickleweed (*Salicornia virginica*) stems and swallowed them. Another moved from one broken stem of cordgrass to the next, extracting and swallowing pith from the stems.

Clapper Rails may eat a wide variety of foods that we have been unable to identify specifically. Most of a rail's foraging is done in dense vegetation, often in cordgrass, and usually out of view. When a bird was finally in view, most of what was consumed during many hours of observation from just a few meters away was too small to identify. These tiny items are probably soft-bodied and totally digested, so that pellet analysis does not aid in the identification of what may be numerous species. Castings do occasionally yield an additional food item, however, that happens to be partly undigestible. In addition to the items already mentioned, other known foods included amphipods, garden snails (*Helix* sp.), crane flies (Tipulidae), grasshoppers or crickets (orthopterans, from foraging on upland slopes), and perhaps mice (*Microtus californica* and *Mus musculus*). We have seen mice being carried by several rails, mostly during high tides. Mice have also been found packed into nesting materials. A small enough mouse would most certainly be swallowed whole.

In summary, crabs are certainly important in the diet. Birds observed foraging take them regularly and they are an extremely large meal compared to the usual items seen swallowed. Snails may also be important; they are relatively large, abundant in the marsh, and well-represented in pellet samples, although it is unusual to observe one being eaten. There are also several very important dietary items that have not been identified specifically. They are quite small, some are quite mobile as well, and they are eaten by the hundreds during a long foraging bout. These tiny morsels are mostly surface-gleaned, often from the bases of plants and regularly from under dried pieces of algae or debris that the rail flips out of the way. Whether the small invertebrates of the salt marsh are consumed in direct proportion to their relative abundances is unknown.

Heard (1982) examined the contents of 187 stomachs of five subspecies of Clapper Rails from the east and gulf coasts of the United States. He concluded that the subspecies he studied ate basically the same kinds of foods: crabs; snails; and to a lesser extent, insects; polychaetes; bivalves; fishes; and limited plant materials. The contents of 16 stomachs of two other subspecies from western Mexico were analyzed by Ohmart and Tomlinson (1977); the major recognizable foods were crabs, snails, and insects. These latter authors also examined the contents of 16 stomachs of the Yuma Clapper Rail (*R. l. yumanensis*) and found crayfish, isopods, insects, and mollusks to be most abundant. These findings and Heard's (1982) view of the Clapper

Rail as an opportunistic omnivore that occupies a relatively broad feeding niche within marsh ecosystems, mesh well with our observations. It is doubtful that food is a limiting factor for the Light-footed Clapper Rail in marshes that have not been badly degraded.

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EGGSHELL DIFFERENCES BETWEEN PARASITIC AND NONPARASITIC ICTERIDAE[1]

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Key words: Eggshell thickness; eggshell mass; parasitic icterids; Icteridae.

In their recent report Spaw and Rohwer (1987) state that good comparative data on the relative eggshell thickness for both parasitic and nonparasitic species of the family Icteridae are largely lacking and present measurements of several parasitic *Molothrus* species which showed significantly greater shell thickness compared with 17 nonparasitic representatives. These authors suggest that the thicker eggshell may be an adaptation to parasitism, making eggs more resistant to damage by the host species. In this report we call attention to and review additional data from the tables

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