THE ECOLOGY OF THE SALT-MARSH HARVEST MOUSE (*REITHRODONTOMYS RAVIVENTRIS*) IN A DIKED SALT MARSH

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ABSTRACT.—The salt-marsh harvest mouse (*Reithrodontomys raviventris*) was a fugitive species in this diked marsh. These mice were able to use more open and saltier pickleweed (*Salicornia virginica*) when numbers of meadow mice (*Microtus californicus*) were high and they moved into deeper and less salty pickleweed as the population of meadow mice declined. In this first extensive study of a diked marsh, salt-marsh harvest mice were shown to swim and run across larger open areas than they had been thought to cross previously.

The salt-marsh harvest mouse (*Reithrodontomys raviventris*) endemic to the marshes of San Francisco Bay (Fisler, 1965), has become endangered primarily because of destruction and modification of its habitat. Approximately 80% of the historic tidal marshes have been destroyed and most of those that remain support few to no mice because of backfilling, subsidence, or vegetation changes (Shellhammer, 1982). Approximately 30% of the historic tidal marshes of San Francisco Bay remain as diked marshes. Eighty percent of the diked marshes are located in Suisun Bay, the northeasterly component of the San Francisco Bay system. The habitat is primarily managed for waterfowl use; mouse populations are small and separated by large areas of inappropriate habitat. Approximately 13 km^2 of diked marshes remain in the South San Francisco Bay and constitute potential refuges for the more endangered of the two harvest mouse subspecies, *R. r. raviventris*, within a ring of large cities and extensive bayland development. Little, however, is known of the biology of the mouse in diked marshes subject to great changes in moisture and salinity throughout the year. Some are flooded periodically by rain waters or by bay water after breaks in outboard levees. Most surface water evaporates each summer.

This study was conducted to ascertain mouse numbers, distribution, and interactions with other species during the summer when moisture is low and salinities are high; the microhabitat requirements of these mice in diked marshes; and how barriers such as sloughs and open areas affect movements of the mice.

We expected a low population of harvest mice because Shellhammer et al. (in press) found that the mice persist in low numbers in marginal, diked areas as long as some halophytic vegetation persists. However, they become more numerous from time to time in such diked marshes. We sampled one such area in a diked marsh in the South San Francisco Bay.

MATERIALS AND METHODS

This study was conducted in a 2.7-ha portion of the New Chicago Marsh, a part of San Francisco Bay National Wildlife Refuge, approximately 2.5 km N Alviso, California. The study site, in the northwest corner of the 90-ha marsh, was bounded by a deep, 7-m-wide slough on three sides and a dike on the fourth. It was divided into two parts by a slough; the two portions were connected by a small isthmus of vegetation (Fig. 1). The dominant plant cover was common pickleweed (*Salicornia virginica*), however the middle of each portion of the site was interrupted by barren salt pans flooded in winter and dry in the summer (Fig. 1). Other species present included *Atriplex patula*, *A. semibaccata*, *Distichlis spicata*, and annual grasses.

The vegetated areas were overlaid with a grid of 173 trap sites placed 10 m apart; 15 trap sites were established along the base of the dike. Salt pans were not sampled until near the end of the study because they were still lightly flooded at the beginning of the study. Traps were operated at each of the trap sites for 30 nights on a rotating basis with 94 live traps between 18 May and 2 September 1986 for a total of

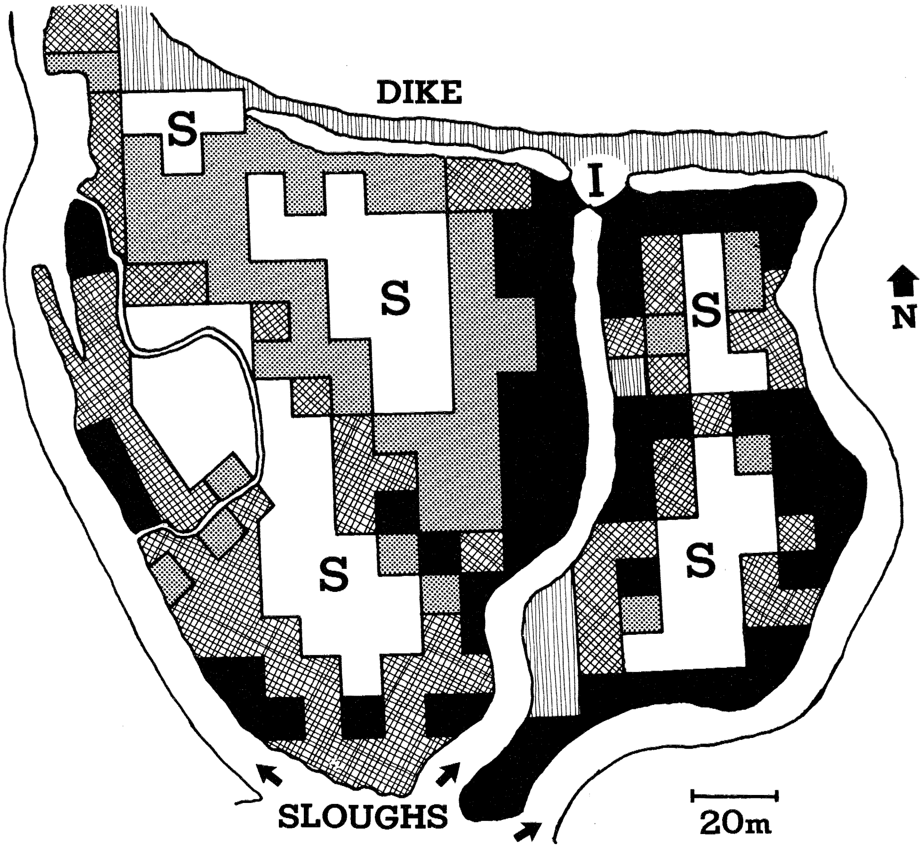

FIG. 1.—Study area in the New Chicago Marsh showing the distribution of vegetation: S, barren salt pans; vertical lines, grass-dominated, dry areas; stipple, highly saline open pickleweed; cross-hatch, pickleweed with 100% cover and ≤50 cm in height; and dark areas, pickleweed with 100% cover and >50 cm in height; I, narrow isthmus of land separating western and eastern portions of the study area.

2,820 trap nights. Two traps were placed at every fourth trap site for the first 16 days; subsequently one trap was placed at alternate trap sites. Three bare salt pans were sampled at the end of the study when 10 traps were placed in each approximately 500-m^2 salt pan for 3 nights. Data recorded for all small mammals included distinguishing characters (Fisler, 1965; Shellhammer, 1984), species, sex, sexual condition, mass, and trap site. Salt-marsh harvest mice were marked with numbered ear tags; all other species were marked by toe clipping.

Age classes were reduced from six used by Fisler (1971) to three because animals could not be sacrificed. Adults were identified as animals with adult pelage, tails >60 mm, and body mass >9.6 g; subadults had adult pelage, tail >60 mm and body mass <9.6 g; juveniles had juvenile pelage, tails <60 mm and were sexually immature. Density was measured as the minimum number known to be alive (Krebs, 1966).

The vegetation was measured within 1 m^2 of each trapsite; species, percent cover, and height of the tallest vegetation were recorded. Pickleweed was assessed for color and amount of dry parts present. Vegetation at various trap sites was arranged into five categories of increasing quality: bare salt pan; grasses and halophytes dominant, pickleweed much <100% cover; sparse pickleweed <100% cover and <40 cm in height; 100% cover of pickleweed <50 cm in height; and 100% cover of pickleweed >50 cm in height.

The salinity of the water of the larger sloughs was measured weekly by personnel of the San Francisco Bay Natural Wildlife Refuge. The senior author measured the salinities of the juices of pickleweed, squeezed from the tips of their stems by a garlic press, and the urine of 19 mice of various species with a Goldman refractometer (Behrens, 1965).

RESULTS

Density and population dynamics.—Sixty-five *Reithrodontomys raviventris* were captured 360 times during the study; also captured were 58 *Microtus californicus* (369 captures), 29 *Mus musculus* (139 captures), 6 *R. megalotis* (15 captures), and 21 *Sorex vagrans halicoetes*. Twenty-three salt-marsh harvest mice were adults, 34 were subadults, and 8 were juveniles when first captured. The overall sex ratio was 1.4:1 in favor of males. The sex ratio was not significantly different from 1:1 for adults or juveniles; however, subadult males were significantly more numerous than subadult females (25 to nine, $\chi^2 = 6.81$, $d.f. = 1$, $P < 0.001$). Eight of 29 males and four of 13 juvenile and subadult females recaptured during the period of the study attained adulthood.

Population dynamics differed among the three species of rodents present during the study (Fig. 2). The rise in numbers of salt-marsh harvest mice through June and July was related to high levels of reproduction and recruitment of young animals. Meadow mice ceased to reproduce in late May. Body mass declined for all individuals captured, and vole numbers declined throughout the summer. House mice were absent in the marsh portion of the study site through early June, although a few individuals were captured on the dike. *Mus* gradually increased in numbers from June through August but remained relatively low in number.

All adult salt-marsh harvest mice were reproductively active between 10 June and 2 September. Eighty percent of females ($n = 10$) captured in June, 42% ($n = 12$) in July, and 100% ($n = 10$) in August were lactating. During the same three months 80%, 100%, and 100% of males ($n =$ 10, 12, and 6), respectively, had descended testes. Some subadult males weighing only 7 g had scrotal testes.

Microhabitat use.—The use of pickleweed of lesser quality by salt-marsh harvest mice was most obvious during the first trapping period (16 May–4 July) when the number of meadow mice was still relatively high. Most salt-marsh harvest mice were captured in the sparse, highly saline pickleweed near the salt pans or in the second-best quality patches, (100% pickleweed < 50 cm in height). Most meadow mice were captured in the highest quality pickleweed (Table 1). The difference in habitat use by the two species was highly significant ($G = 45.66$, $d.f. = 2$, $P < 0.001$). The average height of pickleweed at the trap stations where meadow mice were captured was 48 cm; those where salt-marsh harvest mice were captured was 42 cm. The difference in height of pickleweeed was statistically significant ($t = 8.21$, $d.f. = 427$, $P < 0.01$). House mice were relatively rare in the marsh. They were captured in drier, grassier areas at the edge of the site and on the dike. All three species tended to avoid each other. The correlation coefficients for species avoidance, all of which had P values < 0.01, were salt-marsh harvest mice-meadow mice, $r = -0.51$; meadow mice-house mice, $r = -0.60$; and salt-marsh harvest mice-house mice, $r = -0.63$.

The second trapping period was 11 nights (15 July–2 September). Most salt-marsh harvest mice were captured in the two tallest vegetation categories of pickleweed, but more meadow mice were captured in poorer habitats including those dominated by dry grasses. The difference in habitat use was not statistically significant ($G = 4.47$, $d.f. = 2$, $P = 0.105$) but use of the best quality habitat was greater by salt-marsh harvest mice whereas that habitat had been dominated by meadow mice in the first trapping period (Table 1). The mean height of plants at stations at which meadow mice were captured changed little (48 to 49 cm) whereas that for salt-marsh harvest mice increased from 42 to 44 cm ($t = 2.33$, $d.f. = 341$, $P < 0.05$). House mice were trapped at more sites during the second trapping period (55 opposed to 35 trap stations) and were captured more often in the marsh than on the drier dike (75 opposed to 46%). Individual house mice stayed in the marsh rather than returning to the dike. The negative association among the three species did not change (salt-marsh harvest mice-meadow mice, $r = -0.53$; meadow mice-house mice, $r = -0.58$; and salt-marsh harvest mice-house mice, $r = -0.64$; all P values < 0.01).

Salinity measurements.—The salinity of the adjacent slough increased from 50‰ (parts/thousand) in late May to 160‰ in late August. During the latter period, the average salinity of

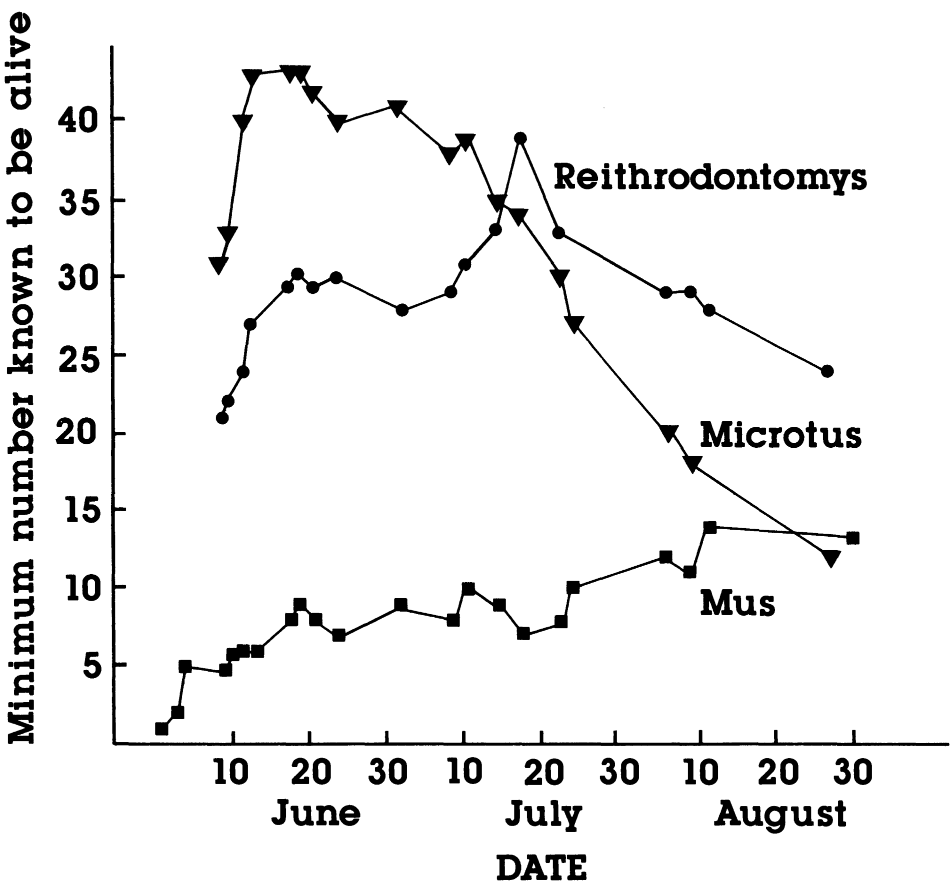

FIG. 2.—Estimated population sizes of the major species of rodents in the study area calculated by the minimum-known-to-be-alive method (Krebs, 1966).

the juices of 60 pickleweed plants sampled at 30 trap sites was 118‰ (97–139‰). There was a strong negative relationship between the height of pickleweed and the salinity of its juices ($r = -0.69$, $P < 0.01$) such that plants 60 cm tall had an average salinity of approximately 94‰, those 50 cm approximately 112‰, and those 40 cm approximately 130‰ salinity.

Degraded pickleweed, i.e. relatively short (30–40 cm) with <100% cover adjacent to salt pans, had the highest salinities (120–139‰) whereas that growing farther away from the pans was

TABLE 1.—*Captures of salt-marsh harvest mice and California meadow mice in various habitats in the New Chicago Marsh, San Francisco Bay, California, during two trapping periods, 16 May–14 July and 15 July–2 September, 1986.*

	Salt-marsh harvest mice alone or in majority[a]		Meadow mice alone or in majority[a]		Number trap sites in each type of vegetation
Vegetation type	First period[b]	Second period[c]	First period[b]	Second period[c]	
Grass dominated	2		1	8	21
Sparse, highly saline pickleweed, ≤40 cm high	27	21	3	4	46
100% pickleweed ≤50 cm high	21	28	20	12	62
100% pickleweed >50 cm high	2	22	36	15	59

[a] Animals captured alone in 76.2% of captures; majority ≥60%.
[b] $G = 45.66$ (*d.f.* = 2, $P < 0.001$) between species for total set excluding grass category.
[c] $G = 4.47$ (*d.f.* = 2, $P = 0.105$) between species for total set excluding grass category.

thicker, taller, and more robust, and had lower salinities (94–120‰). Six samples of urine of three salt-marsh harvest mice collected during late July to late August had an average salinity of 186‰ (139–237‰) with a *SD* of 35‰; samples of 13 meadow mice had 116‰ (94–158‰) with a *SD* of 18‰; and those of three house mice were 198‰ (149–220‰) with a *SD* of 43‰.

Home range and movement patterns of R. raviventris.—Home ranges were estimated for the 12 salt-marsh harvest mice captured 10 times or more each by the technique of Manville (1949). Average home-range for four adult males was 1,550 m^2 (range, 1,100–2,000 m^2), 1,300 m^2 (1,100–1,500 m^2) for four adult females, 667 m^2 (600–700 m^2) for three subadult males, and 600 m^2 for a single subadult female. The difference in home-range sizes between adult, and subadult and juvenile animals combined, was significant ($t = 4.91$, $d.f. = 10$, $P = <0.001$).

The average distance moved between captures for salt-marsh harvest mice was 23.8 m (maximum, 131.5 m). Adult males (30.8 m) moved farther than adult females (20.3 m), subadult males (22.7 m), or subadult females (21.7 m), but these differences were not statistically significant. Adult females generally stayed within a 600-m^2 portion of their home ranges for several weeks, then moved to another portion, whereas males moved throughout their home ranges. Long-distance movements of 85 m or more occurred for some adult males and were followed by return movements. The longest dispersals were made by subadult animals and adult females that stayed in their new areas.

Seventy-one percent of subadult and juvenile salt-marsh harvest mice left the area of their initial capture or died and were not found within 1 month of capture. Of these, 49% (20 males and six females) disappeared after 1 month whereas 22% (five males and four females) moved distances of 85 m or more and apparently stayed in their new areas.

Mice swam a 1.5-m wide slough in the western portion of the site at least nine times before it dried; it is assumed they walked across the dry slough bed later in the summer. Five long-distance movements were accomplished either by using the narrow (2-m wide) isthmus between the two parts of the site or swimming across the 7-m wide slough.

No animals were captured in two salt-pan sites but three animals were captured in a third salt pan that had approximately 20% cover of pickleweed and was crossed with narrow, dry, slough channels. The animals in the latter area were captured as far as 1.9 m from the nearest vegetation.

Discussion

Several investigators have demonstrated that *Microtus californicus* is a superior competitor to *Reithrodontomys megalotis* (Blaustein, 1980, 1981; Heske and Repp, 1986; Heske et al., 1984) and to *Mus musculus* (Blaustein, 1980, 1981; DeLong, 1966; Lidicker, 1966) but that *Reithrodontomys* and *Mus* compete more equally (Catlett and Shellhammer, 1962). Heske et al. (1984) found that reproductive behavior was seasonally complimentary in *Microtus* and *Reithrodontomys* in California grasslands where populations of *Reithrodontomys* declined to low numbers or became locally extirpated during irruptions of voles. During such periods, *Reithrodontomys* had negative spatial relationships with *Microtus*.

Heske and Repp (1986) found that western harvest mice avoided traps bearing the odor of meadow mice in the field and did not use pine shavings scented with their odor in the laboratory. The response was strongest when harvest mice were in breeding condition. Meadow mice, in contrast, were indifferent to odors of western harvest mice.

Blaustein (1980, 1981) found that western harvest mice and house mice were forced into suboptimal habitats when densities of meadow mice were high. The former species left their refugia, used better habitat, were more active, and had greater reproductive success when the populations of meadow mice crashed. DeLong (1966) found that the population of house mice declined by 50% when meadow mice were present, a phenomenon he attributed to a lower recruitment of young *Mus* and the killing of *Mus* nestlings by meadow mice.

Blaustein (1980) postulated that western harvest mice and house mice act as "fugitive" species as described by Hutchinson (1951) in his model of nonequilibrium coexistence and by Horn and

Mac Arthur (1972). Such fugitive species generally are inferior competitors that occupy poorer patches in a patchy environment and may be extirpated locally but that persist by balancing dispersal, and competitive and escape abilities. The salt-marsh harvest mouse also appears to be a "fugitive" species. It used poorer quality pickleweed when *Microtus* was numerous and moved into better quality vegetation when the meadow mouse population crashed. Its numbers and those of *Mus* appear to be regulated in diked pickleweed marshes to some degree by the size of meadow-mouse populations, that in turn appear to be influenced greatly by water availability and salinity.

Winters in marshes such as the New Chicago Marsh involve frequent precipitation that stimulates plant growth and creates standing ponds with lower salinities than in summer. The salinities of pickleweed, a major food source for these rodents (Fisler, 1965), also must have a lower salinity as the older, saltier portions are shed. Cockburn and Lidicker (1983) showed that breeding of *Microtus californicus* was highly seasonal and associated closely with the availability of green vegetation in grasslands in fall, winter, and spring. In their study, *Microtus* began to breed after the first rains and in 4 of 5 years declined abruptly at onset of summer. The same was true for this study.

The breeding cycle of *Microtus* seems to have strong effects on other species in diked salt marshes. Greater densities of *Microtus* seem to force salt-marsh harvest mice and house mice into marginal habitats or to become extirpated locally. In addition, we hypothesize that breeding in salt-marsh harvest mice is suppressed longer into the spring when *Microtus* numbers are high.

The situation can change dramatically during summer as we observed in the New Chicago Marsh. The salinities of both water in ponds and juices of pickleweed rose to high levels. During this period, we hypothesize that salt-marsh harvest mice gain a competitive advantage as they have been shown to survive on salinities near or at levels of sea water for long periods (Fisler, 1963; Haines, 1964). Coulombe (1970) studied the ability of various salt-marsh rodents, including *Microtus californicus*, to survive high salinities in their diet and drinking water. He showed that *Microtus californicus* is able to survive on pickleweed, but evaluated salt marshes as only marginal habitats for the meadow mouse. Fisler (1968) did not find *Microtus* in lower parts of tidal marshes where salt-marsh harvest mice still occurred, but concluded that *Microtus* is considerably less adapted than the salt-marsh harvest mouse to salt marshes. In the present study, urine concentrations of salt-marsh harvest mice were higher than the juices of the pickleweed; those of meadow mice were similar to those of the plant juices.

Coulombe (1970) and Zetterquist (1978) showed that pickleweed growing in highly saline areas has a greater concentration of salt in its sap than in less-saline areas. Coulombe (1970) found that pickleweed growing around salt pans had higher salinities than in higher parts of the marsh. He concluded that rainwater accumulates above the denser salt-water table like a "bubble" in high parts of the marsh. Zetterquist (1978), who studied salt-marsh harvest mouse populations in different and far more marginal, diked marshes during summer, noted that the greatest numbers of salt-marsh harvest mice were captured in areas where salinities were extremely high. Similarly, one of us (HS) has often observed fewer overall captures of small rodents of all species in highly saline, diked marshes but proportionally more salt-marsh harvest mice. We conclude that salt-marsh harvest mice are competitively superior to meadow mice in the most saline environments or in the most saline periods during the yearly cycle of the average diked marsh.

Before this study, there was little to indicate that the salt-marsh harvest mouse could be characterized as a fugitive species. Fisler (1965), Shellhammer et al. (1982), and Wondolleck et al. (1976) concluded that the optimal habitat is thick cover of *Salicornia virginica* mixed with minor amounts of various other halophytes. This species is dependent on thick cover in tidal marshes (Fisler, 1965; Shellhammer, 1977, 1982) and movements between marshes, such as crossing roads or bare areas, was considered to be highly infrequent and improbable.

This study concentrated on a diked marsh where conditions differ from tidal marshes. These mice appear to be less dependent on cover than in tidal marshes because they were caught several times in trap sites without cover. Similar captures are reported in diked, spoils ponds in the San Pablo Bay by S. D. Kovach (pers. comm.). Young animals in this study were shown to disperse considerable distances and in some cases to swim or run across moderately large (2-m wide or greater) open areas. Young salt-marsh harvest mice probably used the narrow isthmus of vegetation between the two areas (Fig. 1) during five long-distance dispersals between the two portions of the study area but it is possible that the animals swam the 7-m wide slough dividing the two portions. Rice (1974) demonstrated long-distance dispersals in a nearby, highly compressed tidal marsh but only through areas of thick cover.

Hence, it seems that in diked marshes salt-marsh harvest mice are mobile and their ability to utilize food with high salinities increases their competitive advantage as the salinity of the marsh increases. They, like the western harvest mouse, quickly colonize disturbed areas such as those subject to flooding (Blaustein, 1981). Their climbing and swimming abilities (Fisler, 1965) help them survive tidal flooding or seasonal flooding in diked marshes. The New Chicago Marsh and a large portion of the Alviso area was inundated completely by a major flood for 10 days in 1983. The present population of the marsh has to be descended from individuals that survived on the few dike tops not covered during that time. They quickly colonized areas vacated by potential competitors and probably rapidly increased as those competitors decreased as Blaustein (1981) showed in western harvest mice. They can use dew effectively and may enter daily torpor in response to osmotic stress, water deprivation, or low temperature (Coulombe, 1970; Fisler, 1965). Shellhammer et al. (in press) found that they persist in small numbers in many marginal, diked marshes in the South San Francisco Bay Area and that under certain circumstances, such as those at the study site, they may become abundant locally.

Managed, diked marshes appear to be the key to the survival of the southern subspecies, *R. r. raviventris*, of which we had little knowledge. Future management prescriptions may include the possibility of a more patchy environment with some areas of high salinities plus the acceptance of some open areas (narrow strips of water or denuded or lightly covered soil) within managed areas.

Trapping by Shellhammer et al. (in press) indicated that salt-marsh harvest mice used grasses to a greater extent in diked than in tidal marshes. That finding and those of this study suggest that salt-marsh harvest mice exhibit considerable plasticity in their behavior and that they expand their niche when subjected to the conditions found in diked marshes.

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