Research Article

Habitat Selection of the Salt Marsh Harvest Mouse and Sympatric Rodent Species

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Abstract

*We evaluated interspecific habitat use within a salt marsh small mammal assemblage on Mare Island, Solano County, California, USA, from 1989 to 1992, with emphasis on the endangered salt marsh harvest mice (*Reithrodontomys raviventris*). We livetrapped small mammals during 125 trap sessions at 20 different areas throughout Mare Island for a total of 55,189 trap-nights. We captured the salt marsh harvest mouse 4,147 times; the house mouse (*Mus musculus*), 1,936 times; the California vole (*Microtus californicus*), 372 times; and the shrew (*Sorex *spp.*), 117 times, among 12,927 captures. We captured fewer than 10 rats (*Rattus *spp.*), and we did not capture any western harvest mice (*Reithrodontomys megalotis*) or deer mice (*Peromyscus maniculatus*). We sampled vegetation characteristics at each trap location during 79 of 125 trap sessions for a total of 5,523 trap locations. During the summer, breeding, and fall seasons, habitats characterized by increased cover of forbs, particularly fat hen (*Atriplex patula*), were used to a greater extent by male than female salt marsh harvest mice. Both sexes of salt marsh harvest mice used areas with less cover of forbs, particularly fat hen and pickleweed (*Salicornia virginica*), during the winter, spring, postbreeding, and prebreeding seasons. House mice used habitats that were more patchily distributed or fragmented than salt marsh harvest mice. Habitat characteristics that were positively associated with salt marsh harvest mice tended to be negatively associated with house mice. Voles used habitats characterized by positive associations with shrub, pickleweed, litter, and woody debris cover, foliage height densities (0 to >40 cm), and mean vegetation height. Vole habitat use was negatively associated with water cover and depth. We suggest that reducing habitat patchiness throughout tidal marshes may reduce salt marsh harvest mouse competition with house mice, and restoring tidal action may reduce habitat competition with voles.* (JOURNAL OF WILDLIFE MANAGEMENT 70(3):732–742; 2006)

Key words

habitat use, Reithrodontomys raviventris*, rodents, salt marsh, salt marsh harvest mouse, small mammal assemblage.*

The salt marsh harvest mouse (*Reithrodontomys raviventris*) is endemic to the salt-marsh areas surrounding San Francisco Bay and its tributaries (Shellhammer 1982, 1989). This species was listed as endangered in 1970 by the U.S. Department of the Interior and in 1971 by the California Department of Fish and Game (Shellhammer 1982). Two subspecies of the mouse are recognized: *R. raviventris raviventris* occurs in the southern San Francisco Bay region, and *R. raviventris halicoetes* (under investigation in our study) occurs in the northern region of the bay (Shellhammer 1982). The principal reason for listing the salt marsh harvest mouse was habitat loss (U.S. Fish and Wildlife Service 1984). Shellhammer et al. (1982) described the primary habitat for salt marsh harvest mice as pickleweed-dominated areas with escape cover from inundation during high tides.

About 80% of the originally estimated 474 km^2 of historical tidal marshes in the San Francisco Bay area have been developed (Goals Project 1999). Most diked marshes occur in the Suisun Bay marshes, where a number of small, distinct populations of the northern subspecies exist (Harvey and Stanley Associates 1980). Habitat fragmentation, or increased isolation and decreased size of resource patches (an area that has more or less homogeneous environmental conditions), is one aspect that affects the persistence of breeding individuals or populations (Morrison et al. 1998). For example, the breeding cycle of California voles (*Microtus californicus*) seems to affect other species in and adjacent to salt marshes (Geissel et al. 1988). Greater densities of voles seem to force salt marsh harvest mice and house mice (*Mus musculus*) into marginal habitats or to become locally extirpated (Geissel et al. 1988).

Little is known of the life history of the salt marsh harvest mouse, especially in San Pablo Bay (U.S. Fish and Wildlife Service 1984). Fiser (1965) reported an apparent movement of salt marsh harvest mice to higher marshes in winter and proposed that this was a reaction to extremely high tides in December and January. Shellhammer (1982) concurred with the Fisler (1965) observations and reported the importance of an upper zone of nonsubmerged plants that can act as refugia for salt marsh harvest mice during the highest tides (see also Hulst et al. 2001). Using radiotelemetry, Bias and Morrison (1999) showed that salt marsh harvest mice move across levees and other structures and occupy habitats of varying quality (see also Zetterquist 1977, Hulst et al. 2001). Thus, the future of the salt marsh harvest mouse will depend on management programs for all tidal salt marsh zones (Shellhammer 1982). For successful recovery and management of the salt marsh harvest mouse, habitat use, reproductive requirements, and interspecific effects, especially in areas of varying habitat quality, must be determined throughout a year and across successive years (U.S. Fish and Wildlife Service 1984).

Our objectives were to improve understanding of salt marsh harvest mouse ecology by describing seasonal and sex-specific habitat use and to evaluate the potential impacts of interspecific habitat use. We use our results to develop recommendations for managing salt marsh harvest mouse habitat.

Study Area

Our study occurred at Mare Island, located at the eastern end of San Pablo Bay and west of the city of Vallejo, Solano County,

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California, USA, which occupied about 2,270 ha. The rectangular island was bordered by the San Pablo Unit of the San Francisco Bay National Wildlife Refuge to the north, the San Pablo Bay to the west and south, and the Napa River to the east. Except for a large hill at the southern end of the island (elevation 87 m), the island was flat, with typical elevations <6 m. Land use was largely industrial and residential along the northern and eastern portions of the island; little salt marsh occurred at these areas. The western portion of the island was composed of the least-disturbed, tidal salt-marsh area and encompassed about 160 ha. The salt-marsh area has been increasing because of sediment accretion since the construction of a jetty into San Pablo Bay in 1908. The predominant vegetation within this area was pickleweed (*Salicornia virginica*), with scattered patches of dodder (*Cuscuta salina*). Most of the flat, level land on the island was composed of diked salt marshes used as dredge-disposal ponds. The predominant plant species within the ponds was pickleweed. Other plant species within the ponds were fat hen (*Atriplex patula*), Australian saltbush (*Atriplex semibaccata*), thistles (*Cirsium* spp.), prickly lettuce (*Lactuca serriola*), curly dock (*Rumex crispus*), sweet fennel (*Foeniculum vulgare*), and coyote bush (*Baccharis pilularis*). Also abundant within the ponds were various grasses: ripgut brome (*Bromus diandrus*), soft brome (*B. mollis*), barleys (*Hordeum* spp.), annual ryegrass (*Lolium multiflorum*), creeping wildrye (*Elymus triticoides*), rabbitfoot grass (*Polypogon monspeliensis*), oats (*Avena* spp.), and saltgrass (*Distichlis spicata*).

The diked, dredge-disposal ponds ranged in size from 1.9 to 18.2 ha (Fig. 1). Ponds were numbered following a scheme developed by the U.S. Navy (until 1994, Mare Island was operated as a naval shipyard). Areas 14, 15, 16, 17, and 18; and 22, 22E, 23, and 24 occurred in 2 separate groupings, with each area adjacent to the other and separated only by a dike. The remaining ponds were more isolated from each other. Ponds 2 and 26 were immediately adjacent to tide-marsh areas. The Navy restored areas 22, 22E, 23, and 24 (existing ponds were graded and reintroduced to tidal action via channels) during the summers of 1990 and 1991. This area was separated from the tidal marsh by a dike and a 2-lane asphalt road. Only ponds 3 and 25 were used as active dredge-disposal ponds during our study (Fig. 1). Pond 3 was usually kept devoid of vegetation by disking. Pond 25 was routinely filled with dredge spoils. The remaining ponds and the tidal areas remained unaltered during our study.

Methods

Live Trapping

We livetrapped salt marsh harvest mice and other small mammals among permanently established trap grids within the ponds and other areas to assess patterns of habitat use. During 1989, the first year of the study, we livetrapped at 19 different areas (13 ponds, 4 tidal-marsh areas, and 2 upland areas), which we selected based on a vegetation successional continuum from salt marsh to upland vegetation types. During 1990 and 1991, we livetrapped 12 ponds and 2 tidal areas. During 1992, we livetrapped 8 ponds and 2 tidal areas. We sampled restored ponds and ponds scheduled for restoration work that represented special interest to the Navy and the U.S. Fish and Wildlife Service (i.e., 22, 23, 22E, 24, and 26) during all years.

The size and shape of the pond dictated trap grid dimensions, which were 8×8 with 15-m trap spacing among the tidal marsh grids, 10×10 or 8×8 with 10-m trap spacing among most of the ponds, 5×15 with 10-m spacing at ponds 22 and 23, and 2×10 with 10-m spacing at ponds 22E and 24.

During 1989, we sampled most areas, with a trapping effort of 4 consecutive nights. However, during 1989 we conducted some trapping sessions to 10 nights and showed that $\geq$5 consecutive nights were needed to obtain recapture rates of $\geq$60% for any species captured. Further, during 1989, we showed that $\geq$6 consecutive nights were needed to detect all species present for areas with low densities of some small mammal species. Therefore, after 1989, we livetrapped each area for a maximum of 9 nights or until daily recapture rates for salt marsh harvest mice were $\geq$90% for 2 consecutive nights.

We used collapsible Sherman small-mammal traps ($7.7 \times 9.0 \times 23.0$ cm, H. B. Sherman, Tallahassee, Florida) baited with ground English walnuts and birdseed at a 50:50 mixture by volume (Shellhammer et al. 1982). We covered all traps with rectangular closed-cell foam tubes and used polyester fiber for bedding material. We set all traps in late afternoon and began checking them within 1 hour of sunrise. Traps remained closed during the day.

We marked all small mammals captured using standard toe-clip methods and released them at the point of capture. We determined that toe-clipping did not negatively impact the study animals (Bias et al. 1992). For all captures, we recorded species, mass (weighed to the nearest 0.5 g using a Pesola scale; Pesola Company, Baar, Switzerland), body length, tail length, hind foot length, and ear notch length (all measured to the nearest 1.0 mm using a ruler). We also recorded age, sex, reproductive status, and presence of ectoparasites for each animal captured.

Because of the difficulty in distinguishing between western harvest mouse (*Reithrodontomys megalotis*) and salt marsh harvest mice, we also measured the distinguishing characteristics for salt marsh harvest mice described by Fisler (1965) as modified by Shellhammer (1984). These characteristics were tail diameter 20 mm from the base (measured to the nearest 0.05 mm using vernier calipers); blunt, intermediate, or pointed tail tip; amount of white hairs (many, few, none) on the ventral side of the tail; distinct, intermediate, or indistinct tail bicoloration; color pattern of venter (all white, pectoral spot, pectoral band, pectoral and ventral band, half white, trace of white, or no white); and the animal's behavior (active, intermediate, or docile). The primary criteria that we used to identify salt marsh harvest mice from western harvest mice were a tail–body ratio $\geq$105% and a tail diameter $\geq$2.00 mm. The other criteria that we used to distinguish salt marsh harvest mice were a blunt-to-intermediate tail tip or unicolor tail (Shellhammer 1984). We identified shrews (*Sorex* spp.) only to genus because identification to species in the field could not be done with reasonable accuracy.

Vegetation Sampling

We sampled vegetation characteristics (Appendix 1) at all trap stations at least once per year for all areas trapped. We measured vegetation characteristics at each trap station along one randomly

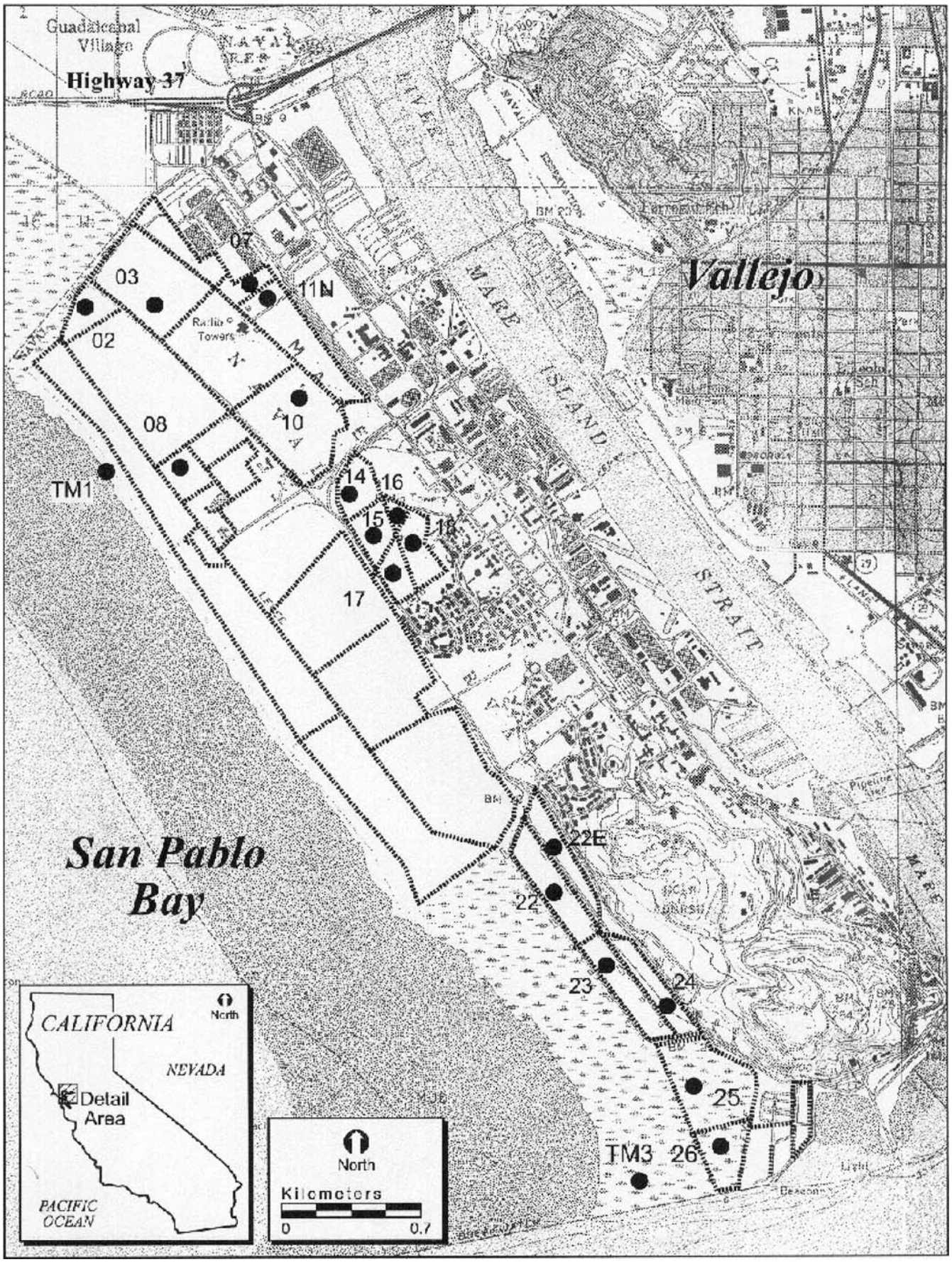

Figure 1. Mare Island Study Area, Vallejo, Solano County, Calif., USA. Heavy dotted lines are levee and dike boundaries; numbers refer to designated ponds and areas trapped during 1989–1992.

placed, 4-m transect, with 8 point intercepts, spaced at 0.5-m intervals.

For each vegetation sample plot, we visually estimated the percentage cover of soil, litter, water, grasses, forbs, shrubs, and individual plant species. At each point intercept, we measured vegetation height, litter depth, and water depth using a meter stick. We estimated vegetative height density at 9 5-cm intervals (0–5, 6–10, 11–15, 16–20, 21–25, 26–30, 31–35, 36–40, and >41). We also recorded the vigor class (dead or dormant, zero; 25% live, 1; 50% live, 2; 75% live, 3; 100% live, 4; flowering, 5; or seeding, 6) of the tallest plant at each point intercept. We calculated mean vegetation height, mean litter depth, and mean water depth (to the nearest cm) for each vegetation sample plot.

As an index to habitat heterogeneity, we visually estimated distance (m) from the plot center to the nearest microhabitat change, and we visually estimated the 3 most-dominant plant species within that microhabitat. We defined microhabitat change as a transition from that of the vegetation sample plot to an area with any difference in the structure or floristics of vegetation ≥4 m at its widest point.

Vegetation Analyses and Habitat Use

We used principal components analysis (PCA; Norusis 1992*a*:54–94) to describe important vegetation characteristics of all grids sampled. We calculated correlation matrices for all trap station characteristics for each grid sampled, and we omitted variables correlated <0.30, with ≤3 other variables from the PCA (Norusis 1992*a*:56). Following PCA, we used multivariate analysis of variance (MANOVA; Norusis 1992*b*:55–121) to test for differences of vegetation characteristics among the grids sampled. We only used variables that loaded relatively heavily in the PCA for each small mammal species in the MANOVA (see below; Stevens 1986:188).

To facilitate presentation and interpretation of the results from MANOVA, we calculated factor scores for each grid, by season, and we plotted them along the first 2 principal components (Collins 1983, Norusis 1992*a*:80–82). We based seasons on a calendar year: winter (Jan through Mar); spring (Apr through Jun); summer (Jul through Sep); and fall (Oct through Dec). Means of standardized values of the original variables were multiplied by the factor score coefficients of the first 2 principal components and added to calculate factor-score values for each case (Norusis 1992*a*:80–82).

We used 3 different multivariate methods to assess habitat use within, and separateness among, salt marsh harvest mice, house mice, and California voles. We used vegetation characteristics at each trap station where we captured an individual the first time during a trapping session for habitat-use analyses. Sample sizes for habitat-use characteristics were equal to the number of different individuals captured. We used PCA (Norusis 1992*a*:54–94) to describe vegetation characteristics of salt marsh harvest mouse, house mouse, and California vole habitat use. We also used PCA to reduce the number of dependant variables before any MANOVAs (Stevens 1986:365). Correlation matrices for all trap station characteristics for each species were calculated, and variables correlated <0.30 with ≤3 other variables were omitted from the PCA (Norusis 1992*a*:56).

Sample size requirements for PCA and MANOVA were based on those suggested by Stevens (1986). Sample sizes needed to obtain reliable components in a PCA should be ≥100 with at least 5 subjects per variable (Stevens 1986:365). Group sizes in MANOVA should be about equal, with the difference between largest to smallest <1.5 (Stevens 1986:199).

Two-factor MANOVA (Norusis 1992*b*:55–121) was used to test for differences within species habitat use by sex and season for salt marsh harvest mice, house mice, and California voles. Only variables that loaded relatively heavily in the PCA, for each species, were used in the MANOVAs (Stevens 1986:188). As with the vegetation analysis on grids, seasons were based on a calendar year. Additionally, 2-factor MANOVA was used to test for differences in salt marsh harvest mouse habitat use by sex and breeding season. Factor scores for each sex, by season and breeding season, were calculated and plotted along the first 2 principal components (Collins 1983, Norusis 1992*a*:80–82).

We used MANOVA (Norusis 1992*b*:55–121) and discriminant analysis (DA) with direct inclusion of variables (Norusis 1992*a*:3–52) to assess habitat use differences among species. A correlation matrix for all trap-station characteristics for all species was calculated. For highly correlated variables ($r \geq 0.65$), we omitted 1 from the pair, retaining the variables that had the greatest among-group variation or were ecologically interpretable (Whitmore 1981). We used a Box's *M*-test to test for heterogeneity between covariance matrices, and if significant, we used the individual group covariance matrices for classification analyses (Klecka 1980, Norusis 1992*a*:41). However, when sample sizes of the groups are large (i.e., >100), the significance probability of this test may be small, even if group covariance matrices are not too dissimilar (Norusis 1992*a*:41). Further, different sample sizes between groups can substantially influence results of classification analysis (Morrison et al. 1998). Therefore, we randomly subsampled enough cases from each group to meet sample size requirements of about 20 subjects per variable (Stevens 1986:259). The remaining, unselected cases from each group were classified based on the discriminant function derived from the subsampled cases.

We only tested habitat-use differences between salt marsh harvest mice and house mice using MANOVA because sample sizes for California voles ($n = 106$) and shrews ($n = 31$) were too few. Group sizes between salt marsh harvest mice and house mice were not approximately equal (largest/smallest = 2,150/1,025). Further, a Box's *M*-test revealed that significant heterogeneity existed between the variance–covariance matrices (Box's $M = 3317.27$, $F = 9.36$, $P < 0.01$). However, when large variances are associated with the smaller group, the test statistic is liberal (Stevens 1986:227). Salt marsh harvest mouse group size was 2,150 with the log of the variance–covariance matrix being 128.06, and house mouse group size was 1,025 with the log of the variance–covariance matrix being 129.85. Therefore, habitat-use differences between salt marsh harvest mice and house mice were tested at a more conservative α level of 0.01 (Stevens 1986:221). Further, Pillai's trace *V* is a robust test statistic; that is, significance levels based on it are reasonably correct, even when assumptions are violated (Norusis 1992*b*:84).

Results

From 1989 to 1992, we livetrapped small mammals during 125 trap sessions at 20 different areas throughout Mare Island for a total of 55,189 trap-nights. We captured the salt marsh harvest mouse 4,147

Table 1. Variable factor loadings on the principal components after a varimax rotation for all trap sites for all grids sampled at Mare Island, Vallejo, Solano County, Calif., USA, from 1990 to 1992.

Variable[a]	PC1	PC2	PC3	PC4	PC5
MHT	0.8953	−0.0407	0.1828	0.1871	0.0541
FHD7	0.8654	−0.0383	0.0927	0.0070	−0.0176
FHD6	0.8574	−0.0289	0.0817	−0.0393	0.1114
FHD8	0.8452	−0.0397	0.1028	0.0620	−0.1411
FHD5	0.8263	−0.0184	0.0901	−0.0993	0.2376
FHD9	0.7756	−0.0816	0.1459	0.2453	−0.2542
FHD4	0.7721	0.0071	0.1395	−0.1127	0.3442
FHD3	0.6853	0.0816	0.2390	−0.1199	0.4249
SHRB	0.6489	−0.5164	0.0833	−0.3639	0.1279
FHD2	0.5523	0.1608	0.3754	−0.0649	0.5023
GRAS	−0.0489	0.8984	0.1204	0.1029	0.1547
GL	−0.1102	0.8570	0.1859	0.1130	0.1248
BD	0.0724	0.8039	0.0679	0.0846	0.1224
WA	−0.0986	−0.0616	−0.9224	−0.1459	0.1064
MWA	−0.1221	−0.0402	−0.9005	−0.1243	0.0661
FHD1	0.3738	0.2460	0.6945	−0.0511	0.3921
MLT	0.2460	0.3220	0.6163	−0.0523	0.3314
DA	0.4041	−0.4601	0.5040	−0.3039	0.2482
AP	0.0428	0.0435	0.0135	0.8985	−0.0441
FORB	−0.0522	0.1465	0.1208	0.7909	0.2563
VIG6	0.0615	0.1327	0.0425	0.7412	−0.0455
DHAB	−0.0511	−0.1961	0.0165	−0.1245	−0.7323

[a] Variable names in Appendix 1.

times; house mouse, 1,936 times; California vole, 372 times; and shrew, 117 times, among 12,927 captures. We captured fewer than 10 rats (*Rattus* spp.), and we captured no western harvest mice or deer mice (*Peromyscus maniculatus*; Bias 1994:appendices B1–B15).

Vegetation Sampling

We sampled vegetation characteristics at each of 5,523 trap stations during 79 of 125 trap sessions (Bias 1994:appendices C1–C4). The greatest estimates for percentage cover of pickleweed, typically, occurred at the tidal marsh areas (TM1 and TM3). Ponds 2, 10, 11, 14, 17, and 26 were the most vegetatively diverse, typically, having >10% cover for grasses, forbs, and shrubs (Bias 1994:appendices C1–C4).

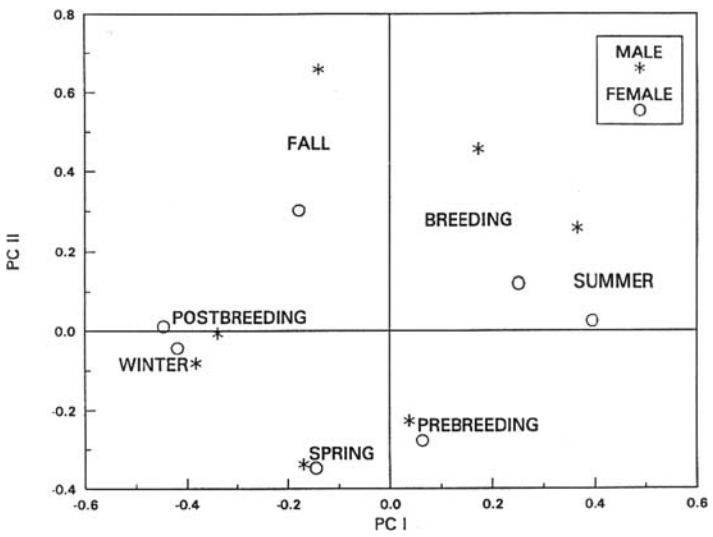

Figure 2. Factor scores plotted along the first 2 principal component axes generated from a principal component analysis of habitat variables for first-time capture sites of male and female salt marsh harvest mice (*Reithrodontomys raviventris*) by season from 1990–1992, Mare Island Study Area, Vallejo, Solano County, Calif., USA. Winter: Jan through Mar; spring: Apr through Jun; summer: Jul through Aug; fall: Sep through Nov; prebreeding: Apr through Jul; primary breeding: Aug through Nov; and postbreeding: Dec through Mar.

Of the all the areas that we sampled, 76.8% of the variation in vegetation characteristics was explained by 5 principal components (Table 1). Mean vegetation height, foliage height densities ≥5 cm, shrub cover, and pickleweed cover characterized principal component 1 (PC1). Grass cover, especially *Bromus diandrus*, and grass litter characterized PC2. Other ground cover, particularly foliage height density <5 cm, mean litter depth, and woody debris <1 cm in diameter were positively associated with PC3. Water cover and depth were negatively associated with PC3 (Table 1).

Vegetation characteristics were significantly different among all areas sampled (Pillai's trace $V = 6.38$; approx $F = 26.11$; df = 1,472; 100,108; $P < 0.01$). Ponds 26, 10, and 17 consistently had a greater grass component (PC2) than trapping areas 2, 8, 15, 22, 23, TM1, and TM3 (see Bias 1994:figs. 3–5). Areas 22 and 23 consistently had the least shrub (PC1) and grass (PC2) components of all areas sampled (see Bias 1994:figs. 3–5).

Within-Species Habitat Use

We used vegetation characteristics from 2,150 salt marsh harvest mouse captures, 1,025 house mouse captures, 106 California vole captures, and 31 shrew captures from 1990 to 1992 to assess species habitat use (Table 2). Of these species, salt marsh harvest mice used areas that averaged 26.8 m from the nearest habitat change. Shrews typically used areas that were furthest from the nearest habitat change ($\bar{x} = 35.8$ m), whereas house mice used areas that were closest to the nearest habitat change ($\bar{x} = 16.5$ m). Salt marsh harvest mice occurred in areas with the lowest mean vegetation height ($\bar{x} = 27.3$ cm), whereas shrews occurred in areas with the greatest mean vegetation height ($\bar{x} = 31.5$ cm). All species occurred in areas dominated by shrubs, primarily pickleweed. Salt marsh harvest mice occurred in areas with the greatest cover of water ($\bar{x} = 9.2\%$). House mice occurred in areas with the greatest grass cover ($\bar{x} = 13.7\%$), whereas California voles occurred in areas with the least grass coverage ($\bar{x} = 2.0\%$).

The first 3 principal components of vegetation characteristics associated with salt marsh harvest mouse captures ($n = 2{,}150$) accounted for 53.7% of the total variance (Table 3). Pickleweed cover with foliage height densities between 6 and 30 cm characterized PC1. Fat hen, forb, leaf litter, soil cover, and seeding vegetation (vigor class 6) characterized PC2. Grass cover, primarily *Bromus diandrus*, and grass litter were positively associated with PC3, and shrub cover was negatively associated with PC3.

The first 3 principal components of vegetation characteristics associated with house mouse captures ($n = 1{,}025$) accounted for 53.6% of the total variance (Table 4). Increasing litter depth, cover of <1-cm-diameter woody debris, pickleweed cover, foliage height densities ≤5 cm, and dead vegetation cover (vigor class zero) were positively associated with PC1. Seeding vegetation (vigor class 6), fat hen cover, and bare ground cover were negatively associated with PC1. Increasing vegetation height and foliage height densities ≥26 cm were positively associated with

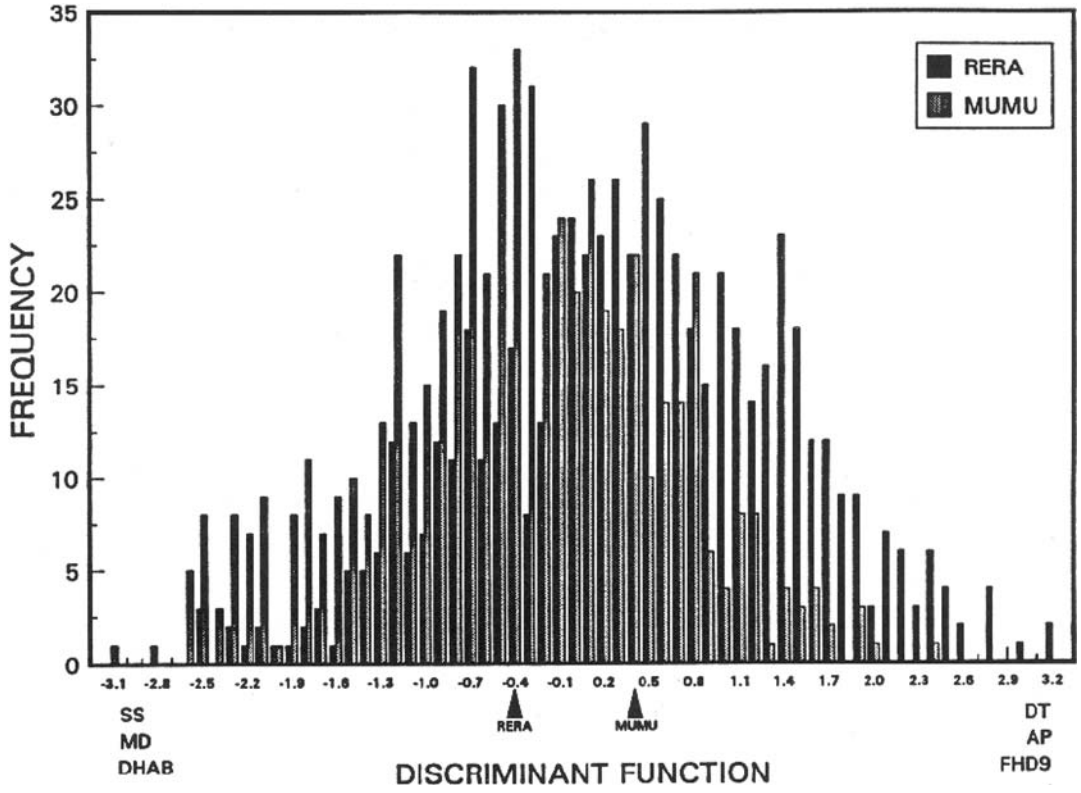

Figure 3. Frequencies of discriminant function scores for habitat variables sampled at 600 randomly sampled, first-time capture sites of salt marsh harvest mice (*Reithrodontomys raviventris*, RERA) and house mice (*Mus musculus*, MUMU), Mare Island Study Area, Vallejo, Solano County, Calif., USA. Arrows indicate group centroids for each species. Variable acronyms correspond to Appendix 1.

PC2. Grass cover and grass litter cover were positively associated with PC3, and shrub cover was negatively associated with PC3.

The first 3 principal components of vegetation characteristics associated with California vole captures ($n = 106$) accounted for 54.8% of the total variance (Table 5). Shrub and pickleweed cover and foliage height densities between 6 and 30 cm were positively associated with PC1. Fat hen cover was negatively associated with PC1. Increasing litter depth, cover of <1-cm-diameter woody debris, and foliage height densities ≤5 cm were positively associated with PC2. Water depth and cover were negatively associated with PC2. Foliage height densities >30 cm and mean vegetation height were positively associated with PC3.

We found no significant sex-by-season interactions in habitat use for salt marsh harvest mice (Pillai's trace $V = 0.05$; approx $F = 1.24$; df = 96, 6,351; $P = 0.07$). Therefore, we tested the main effects (Norusis 1992*b*:89). Habitat use of salt marsh harvest mice between sexes was not significantly different (Pillai's trace $V = 0.02$; approx $F = 1.46$; df = 27, 2,115; $P = 0.06$). However, habitat use of salt marsh harvest mice was significantly different among seasons (Pillai's trace $V = 0.84$; approx $F = 30.49$; df = 81, 6,351; $P < 0.01$).

Although there were no significant sex-by-calendar-season interactions, there were significant interactions of sex by reproductive season in habitat use for salt marsh harvest mice (Pillai's trace $V = 0.03$; approx $F = 1.37$; df = 54, 4,236; $P = 0.04$). Therefore, we did not test the main effects (Norusis 1992*b*:89). However, univariate F-tests (df = 2, 2,143) showed that ground cover by forbs ($F = 4.15$, $P = 0.02$), fat hen ($F = 5.89$, $P < 0.01$), water ($F = 4.80$, $P = 0.01$), bare ground ($F = 13.66$, $P < 0.01$), leaf litter ($F = 3.82$, $P = 0.02$), unknown grasses ($F = 3.26$, $P = 0.04$), and mean water depth ($F = 6.68$, $P < 0.01$) contributed significantly to the interactions.

Although sex-by-season interactions in habitat use for salt marsh harvest mice were not significant ($P = 0.07$), while sex-by-reproductive-season interactions was ($P = 0.04$), both values were close to the α level of $P = 0.05$. Therefore, to aid in interpretation of these results, we calculated sex-by-season and by-reproductive-season factor scores and plotted them along the first 2 principal components (Fig. 2). Recall that pickleweed cover with foliage height densities between 6 and 30 cm characterized PC1 (Table 3). Also, fat hen, forb, leaf litter, soil cover, and seeding vegetation (vigor class 6) characterized PC2 (Table 3). Further, variables that contributed to the significant interactions of sex-by-breeding-season habitat use (i.e., ground cover by forbs, fat hen, bare ground, and leaf litter) loaded most heavily on PC2. Differences in habitat use between sexes were greater along PC2 during summer, fall, and primary breeding than during winter, spring, postbreeding, or prebreeding (Fig. 2), whereas differences in habitat use between sexes along PC1 were similar for all seasons except postbreeding (Fig. 2). The months used to estimate reproductive seasons did not coincide with calendar seasons. That is, prebreeding occurred between spring and summer, primary breeding occurred between summer and fall, and postbreeding overlapped fall and winter. Therefore, significant sex-by-breeding-season interactions in habitat use may have been an artifact of which months were used to estimate reproductive seasons.

Table 2. Means of the vegetation variables for all *Reithrodontomys raviventris* (RERA), *Mus musculus* (MUMU), *Microtus californicus* (MICA), and Sorex spp. (SOSP) first-time capture sites from 1990 to 1992 at Mare Island, Vallejo, Solano County, Calif., USA from 1990 to 1992. Only variables that were ≥5% for at least 1 species are presented.

Variable[a]	RERA (n = 2,150)	MUMU (n = 1,025)	MICA (n = 106)	SOSP (n = 31)
DHAB	26.76	16.53	19.53	35.77
FHD1	81.13	80.90	89.03	89.11
FHD2	56.66	53.82	66.04	50.40
FHD3	52.70	47.35	63.80	45.16
FHD4	45.91	43.78	58.96	42.34
FHD5	42.20	39.38	51.53	42.34
FHD6	35.85	34.33	48.94	34.27
FHD7	30.97	30.83	39.15	25.81
FHD8	24.60	26.66	32.67	19.76
FHD9	27.87	36.74	34.08	43.55
VIG0	35.07	33.11	18.99	56.45
VIG1	5.15	3.22	5.54	4.03
VIG2	5.05	4.07	6.37	4.03
VIG3	5.85	5.84	8.84	3.63
VIG4	19.20	15.93	36.56	10.08
VIG5	4.39	3.99	6.01	1.61
VIG6	6.73	16.20	4.36	3.23
MHT	27.29	30.64	30.20	31.45
MLT	1.19	1.28	1.36	1.18
MWA	0.74	0.41	0.83	0.00
GRAS	8.16	13.74	2.00	4.03
FORB	7.81	14.28	3.89	10.89
SHRB	71.39	65.74	83.61	76.21
AP	6.74	16.41	2.00	5.24
BD	5.16	6.85	1.18	1.61
SS	68.76	56.96	83.25	75.81
WA	9.23	2.63	6.72	0.00
DA	60.79	55.15	76.30	71.37
DT	13.84	30.15	6.25	15.73
GL	9.15	15.05	3.89	9.27
LL	2.58	5.40	0.94	4.84
MD	21.51	10.27	39.27	2.02

[a] Variable names correspond to Appendix 1.

Table 3. Variable factor loadings on the principal components after a varimax rotation for all *Reithrodontomys raviventris* first-time capture sites from 1990 to 1992 (n = 2,150) and the percentage of the total variance (%VAR) attributable to each component, Mare Island, Vallejo, Solano County, Calif., USA.

Variable[a]	PC1	PC2	PC3
FHD3	0.83374	−0.05146	0.02075
FHD4	0.78303	−0.09555	−0.01569
FHD2	0.76203	0.01038	0.10897
FHD5	0.69228	−0.08411	−0.07142
FHD6	0.58914	−0.05938	−0.01533
SS	0.54600	−0.51759	−0.42429
AP	−0.19651	0.82263	0.08118
FORB	0.14560	0.77466	0.26177
VIG6	−0.15746	0.77215	−0.06050
LL	0.14615	0.76875	0.19954
DT	−0.16586	0.59459	0.11524
GRAS	0.03571	0.13069	0.92845
GL	−0.03643	0.16870	0.86611
BD	0.11231	0.18398	0.83958
UG	−0.05374	0.00342	0.60818
SHRB	0.42513	−0.38885	−0.49923
WA	0.03361	−0.14960	−0.05115
MWA	−0.03002	−0.14192	−0.03540
FHD1	0.33721	−0.09809	0.21001
MLT	0.18907	0.00185	0.18764
DA	0.26988	−0.28650	−0.33734
FHD9	0.01888	0.16090	−0.03421
MHT	0.30663	0.15154	−0.01669
FHD8	0.28332	−0.00723	−0.02919
FHD7	0.44822	−0.02475	−0.04522
VIG0	0.05548	−0.20043	0.07837
VIG4	0.31654	−0.16351	0.15105
%VAR	25.5	17.9	10.3

[a] Variable names correspond to Appendix 1.

There were no significant sex-by-season interactions in habitat use for house mice (Pillai's trace $V = 0.08$; approx $F = 0.94$; df = 84, 2,976; $P = 0.64$). Therefore, we tested the main effects (Norusis 1992*b*:89). Habitat use of house mice between sexes was not significantly different (Pillai's trace $V = 0.02$; approx $F = 0.86$; df = 28, 990; $P = 0.68$). However, as with salt marsh harvest mice, habitat use of house mice among seasons was significantly different (Pillai's trace $V = 1.05$; approx $F = 19.07$; df = 84, 2,976; $P < 0.01$).

We did not conduct a 2-factor MANOVA of sex by season in habitat use for California voles because group sizes were not approximately equal (largest/smallest = 79/8; Stevens 1986:199). Therefore, we conducted MANOVA only to test for differences in habitat use between sexes of California voles, which was not significantly different (Pillai's trace $V = 0.30$; approx $F = 1.33$; df = 26, 79; $P = 0.17$).

Among-Species Habitat Use

Habitat use between salt marsh harvest mice and house mice was significantly different (Pillai's trace $V = 0.12$; approx $F = 16.43$; df = 26, 3,148; $P < 0.001$). We randomly subsampled 600 cases from first-time capture sites of salt marsh harvest mice and house mice. Habitat use between salt marsh harvest mice (group centroid = 0.42) and house mice (group centroid = −0.42) separated significantly along the discriminant function (Wilks' $\lambda = 0.85$, $\chi^2 = 193.29$, df = 26, $P < 0.001$; Fig. 3). Cover of pickleweed and mud and distance to the nearest habitat change were positively associated with the discriminant function (Table 6). Bare ground and fat hen cover and foliage height densities ≥40 cm were negatively associated with the discriminant function (Table 6). A Box's M-test revealed that group covariance matrices were significantly heterogeneous (Box's $M = 1{,}738.4$, approx $F = 4.84$, $P < 0.001$). Therefore, we used the individual group covariance matrices for classification analyses (Klecka 1980, Norusis 1992*a*:41). Of the unselected first-time capture sites, 60.8% of salt marsh harvest mice ($n = 1{,}550$) were correctly classified, and 68.5% of house mice ($n = 425$) were correctly classified. Overall, 62.4% of the unselected first-time capture sites were correctly classified by the discriminant function.

Discussion

Our multivariate analyses of salt marsh harvest mouse habitat use supported previous findings and quantitatively detailed important habitat components. Our vegetation analyses of live trap data of salt marsh harvest mice showed that foliage densities from 6 to 30 cm, and pickleweed cover, were primarily associated with mouse locations (PC1, Table 3). Although alkali heath did not occur on any trap grid on Mare Island, other variables associated with

Table 4. Variable factor loadings on the principal components after a varimax rotation for all *Mus musculus* first-time capture sites from 1990 to 1992 (n = 1,025) and the percentage of the total variance (%VAR) attributable to each component, Mare Island, Vallejo, Solano County, Calif., USA.

Variable[a]	PC1	PC2	PC3
FHD1	0.75525	0.17980	0.29612
DA	0.71593	0.17464	−0.33718
VIG6	−0.71373	0.14004	0.02982
AP	−0.68537	0.29922	0.05236
MLT	0.67686	0.13038	0.33528
DT	−0.64634	−0.04006	0.14007
VIGO	0.62593	0.18510	0.13039
SS	0.59929	0.17350	−0.33788
MHT	−0.02623	0.90900	−0.08470
FHD9	−0.08193	0.85980	−0.10685
FHD8	0.04308	0.78510	−0.00537
FHD7	0.13892	0.71054	0.01013
FHD6	0.17043	0.62813	0.03666
GRAS	−0.00053	−0.07037	0.88242
GL	0.05636	−0.03548	0.87561
UG	0.02844	0.01699	0.72961
BD	−0.07267	−0.00384	0.71402
SHRB	0.17387	0.35500	−0.53865
FHD3	0.23841	0.27849	0.08985
FHD4	0.17751	0.45195	0.04287
FHD2	0.33435	0.17959	0.25623
FHD5	0.20365	0.55412	0.05049
VIG4	−0.02328	−0.12042	0.01697
LL	−0.13391	0.04702	0.18317
FORB	−0.10071	0.00322	0.31644
AT	−0.03280	−0.17204	0.09668
VIG2	0.18422	0.10986	−0.16310
DHAB	−0.27826	−0.00625	−0.32354
%VAR	25.6	18.3	12.4

[a] Variable names correspond to Appendix 1.

Table 5. Variable factor loadings on the principal components after a varimax rotation for all *Microtus californicus* first-time capture sites from 1990 to 1992 (n = 106) and the percentage of the total variance (%VAR) attributable to each component, Mare Island, Vallejo, Solano County, Calif., USA.

Variable[a]	PC1	PC2	PC3
FHD3	0.83783	0.14009	0.02630
FHD4	0.77302	0.07180	0.36465
FHD5	0.70506	0.03376	0.32979
FHD2	0.69492	0.29241	−0.00668
AP	−0.69378	0.14851	0.09753
SS	0.63582	0.33624	0.25444
SHRB	0.57444	0.32873	0.28998
FHD6	0.54120	0.06398	0.50186
WA	−0.04822	−0.86033	−0.25605
MWA	−0.10732	−0.84169	−0.19370
DA	0.14385	0.80164	0.12096
FHD1	0.15675	0.74894	0.12954
MLT	−0.00337	0.67200	0.06828
FHD9	−0.13315	0.13732	0.86068
FHD8	0.16294	0.19405	0.83868
MHT	0.25341	0.26919	0.75578
FHD7	0.39970	0.14142	0.73753
GRAS	−0.20720	0.01615	0.00313
BD	0.04537	0.00527	−0.01910
GL	−0.22767	0.04036	−0.08633
DT	−0.08269	−0.07025	−0.02905
FORB	−0.27790	0.13656	−0.17654
VIG6	−0.00601	0.13431	−0.00601
VIG4	0.30057	0.15459	0.28812
MD	0.24131	0.10242	0.10272
DHAB	0.31029	0.02103	0.12229
%VAR	31.9	14.0	8.9

[a] Variable names correspond to Appendix 1.

harvest mouse occurrence were fat hen and forb cover (PC2), and grass and grass litter cover (PC3).

Fisler (1965) and Shellhammer et al. (1982) showed that salt marsh harvest mice were dependant on thick plant cover. Fisler (1965) also suggested that harvest mice would be found within grasslands only when there was adequate cover, primarily from April to August. Zetterquist (1977), Shellhammer et al. (1982), and Geissel et al. (1988) began to quantify important habitat components of salt marsh harvest mice, and Shellhammer et al. (1982) described the primary habitat of the salt marsh harvest mouse as pickleweed with escape cover from inundation during high tides. Shellhammer et al. (1982) further described that the value of pickleweed increased with height, density, and the degree of intermixing with fat hen and alkali heath (*Frankenia grandifolia*).

To date there have been no studies that examined salt marsh harvest mouse habitat use differences either between sexes or among seasons. Our results showed that male and female salt marsh harvest mice used different habitats during the summer (breeding) and fall seasons (i.e., Jul through Dec) but tended to use similar habitats during the winter, spring, postbreeding, and prebreeding seasons (i.e., Dec through Jul). Structurally complex habitats may reduce the risk of predation on small mammals (Dice 1947, Lay 1974, Price and Brown 1983), thus offering an inducement for females to occupy such habitats (Seagle 1985), especially during the primary breeding season. Reduced predation, reduced intraspecific competition (Seagle 1985), and habitat variability (Belk et al. 1988) are factors proposed for observed differential habitat use by sexes. Seagle (1985) proposed that exact mechanisms for differential habitat use by sexes could only be postulated. Differential habitat use by sexes has been reported for several small mammals including *Peromyscus maniculatus* (Bowers and Smith 1979, Belk et al. 1988) and *P. leucopus* (Seagle 1985), *Zapus princeps*, *Clethrionomys gapperi*, and *Microtus montanus* (Belk et al. 1988). These patterns seem to represent a differential response to the structural environment by the sexes (Belk et al. 1988).

Several researchers (Fisler 1965, Shellhammer 1982, Shellhammer et al. 1982, Shellhammer 1989, Hulst et al. 2001) suggested the importance of upper-zone marshes and marginal habitats because of the importance as refugia during the highest tides. Geissel et al. (1988) suggested the importance of diked marshes for similar reasons. Further, Shellhammer (1989) suggested that management of diked marshes will play an important role in the future conservation of the salt marsh harvest mouse because of ultimate factors, such as rising sea levels and tectonic changes, which threaten tidal marshes by submergence.

However, management of tidal marsh zones should consider potential effects from exotic (i.e., house mouse) or native (i.e., California voles) competitors. Our multivariate analyses revealed significant differences in habitat use between salt marsh harvest mice and house mice. Distance to the nearest habitat change was a characteristic discriminating between habitat use of salt marsh

Table 6. Pooled within-groups correlations between the discriminate functions and the variables entered into the discriminate analysis between *Reithrodontomys raviventris* and *Mus musculus* first-time capture sites at Mare Island, Vallejo, Solano County, Calif., USA, from 1990 to 1992.

Variable[a]	Function 1
DT	−0.5627
AP	−0.5086
SS	0.4624
MD	0.4535
FHD9	−0.4477
DHAB	0.3581
WA	0.3388
FORB	−0.2966
UG	−0.2814
DE	−0.2679
GRAS	−0.2627
VIG1	0.2279
DA	0.2082
MPM	−0.2004
VIG2	0.1821
VIG4	0.1801
FHD8	−0.1667
VIG0	0.1415
AT	−0.1301
FHD2	0.1281
FHD6	0.0981
FHD4	0.0863
VIG5	0.0661
VIG3	−0.0329
FHD7	0.0144
FHD1	0.0008

[a] Variable means correspond to Appendix 1.

harvest mice and house mice (Table 6, Fig. 3). This suggested that house mice were using habitats that were more patchily distributed, or fragmented, than salt marsh harvest mice. Habitat use characteristics that were positively associated with salt marsh harvest mice tended to be negatively associated with house mice.

Geissel et al. (1988) found that most salt marsh harvest mice were captured at areas with 100% pickleweed cover $\leq$50 cm tall, whereas most voles were captured at areas with 100% pickleweed cover >50 cm tall. Mean pickleweed height was significantly different between salt marsh harvest mouse and vole capture sites (Geissel et al. 1988). Although our sample sizes were too few for multivariate comparisons between habitat use of salt marsh harvest mice and voles, vole habitat use was characterized by positive associations for shrub, pickleweed, litter, and $\leq$1-cm-diameter woody debris cover, all foliage height densities (0 to >40 cm), and mean vegetation height (Table 5). Vole habitat use was negatively associated with water cover and depth (Table 5).

Blaustein (1980, 1981) suggested that *Reithrodontomys* behaved as a fugitive species that was excluded from high-quality habitat by behaviorally dominant voles during peaks of vole abundance and that *Reithrodontomys* recolonized these areas following vole population crashes. Geissel et al. (1988) suggested that salt marsh harvest mice appear to be fugitive species as well; however, they concluded that salt marsh harvest mice were competitively superior to voles in high-saline environments. Catlett and Shellhammer (1962) suggested that a high degree of compatibility exists between salt marsh harvest mice and house mice.

Several studies (Dueser and Shugart 1978, Kincaid et al. 1983, Adler 1985, Scott and Dueser 1992) have suggested that intraspecific competition was a greater factor in determining habitat-use patterns than interspecific interactions and that habitat use was an important factor in the structure of small mammal communities. Therefore, we suggest that differential habitat use allows salt marsh harvest mice to coexist (Catlett and Shellhammer 1962) and explains why salt marsh harvest mice may behave as fugitive species in the presence of California voles (Geissell et al. 1988).

Management Implications

We showed that house mice occur in areas of greater habitat patchiness, or fragmentation, than salt marsh harvest mice. Reducing habitat patchiness within salt marsh harvest mouse habitats may reduce competition from house mice. Further, we showed that vole habitat use was negatively associated with water cover and depth. Therefore, restoring tidal action to areas may reduce habitat competition with voles. Because of the number of diked marshes already at Mare Island, we recommend that proper management of these areas will be of paramount importance to the conservation of the salt marsh harvest mouse. These management practices need to restore and reconnect isolated habitats, whether optimal or marginal (Zetterquist 1977).

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Appendix 1. Mnemonics and habitat variables measured at trap sites on Mare Island, Solano County, Calif., USA, from 1989 to 1992.

Variable		
Code	**Scientific name**	**Common name**
DHAB		Distance to nearest habitat change
MHT		Mean height of vegetation
MLT		Mean litter depth
MWA		Mean water depth
Grasses (GRAS)		
AS	*Avena* spp.	Wild oats
BD	*Bromus diandrus*	Ripgut grass
BM	*Bromus mollis*	Soft chess
DS	*Distichlis spicata*	Saltgrass
ES	*Elymus triticoides*	Wild Rye
EG	*Elymus glauca*	Wild Rye
FM	*Festuca megalura*	Foxtail fescue
HS	*Hordeum* spp.	Barleys
LM	*Lolium multiflorum*	Annual ryegrass
PM	*Polypogon monspeliensis*	Rabbitfoot grass
UG		Unknown Grass
Forbs (FORB)		
AP	*Atriplex patula*	Fat hen
AT	*Atriplex semibaccata*	Australian saltbush
BS	*Brassica* spp.	Mustard
CC	*Cotula coronopifolia*	Brass buttons
CS	*Cirsium* spp.	Thistles
CU	*Cuscuta salina*	Dodder
EP	*Epilobium paniculatum*	Parched fireweed
FG	*Frankenia grandifolia*	Alkali heath
GS	*Geranium* spp.	Geranium
HP	*Hemizonia pungens*	Common spikeweed
LS	*Lactuca serriola*	Prickly lettuce
PE	*Picris echioides*	Bristly oxtongue
RC	*Rumex crispus*	Curly dock
RS	*Rumex* spp.	Dock, sorrel
SM	*Spergularia macrotheca*	Sticky sandspurry
SO	*Sonchus oleraceus*	Common sow thistle
SR	*Scirpus robustus*	Alkali bulrush
VS	*Vicia sativa*	Spring vetch
UF		Unknown forb
Shrubs (SHRB)		
BP	*Baccharis pilularis*	Coyote brush
FV	*Foeniculum vulgare*	Sweet fennel
SS	*Salicornia* spp.	Pickleweed
US		Unknown Shrub
Other		
MO		Mosses
SH		Feces
WA		Water
DA		Dead woody debris (<1 cm diam)
DB		Dead woody debris (1–10 cm diam)
DC		Dead woody debris (>10 cm diam)
DE		Desiccation crack
DT		Dirt, bare ground
GL		Grass litter
LL		Leaf litter
MD		Mud