The Journal of Wildlife Management 75(6):1498–1507; 2011; DOI: 10.1002/jwmg.187

Research Article

Salt Marsh Harvest Mouse Demography and Habitat Use in the Suisun Marsh, California

DIEGO SUSTAITA,[1,2] *California Department of Fish and Game, Bay Delta Region, 7329 Silverado Trail, Napa, CA 94558, USA*
PATTY FINFROCK QUICKERT, *California Department of Water Resources, FloodSAFE Environmental Stewardship and Statewide Resources Office, 1416 Ninth Street Room 1623, Sacramento, CA 95814, USA*
LAURA PATTERSON, *California Department of Water Resources, Division of Environmental Services, 3500 Industrial Boulevard, West Sacramento, CA 95691, USA*
LAUREEN BARTHMAN-THOMPSON, *California Department of Fish and Game, Bay Delta Region, 7329 Silverado Trail, Napa, CA 94558, USA*
SARAH ESTRELLA, *California Department of Fish and Game, Bay Delta Region, 7329 Silverado Trail, Napa, CA 94558, USA*

ABSTRACT We undertook a 2-year (2002–2004) mark–recapture study to investigate demographic performance and habitat use of salt marsh harvest mice (*Reithrodontomys raviventris halicoetes*) in the Suisun Marsh. We examined the effects of different wetland types and microhabitats on 3 demographic variables: density, reproductive potential, and persistence. Our results indicate that microhabitats dominated by mixed vegetation or pickleweed (*Salicornia* spp.) supported similar salt marsh harvest mouse densities, reproductive potential, and persistence throughout much of the year, whereas few salt marsh harvest mice inhabited upland grass-dominated microhabitats. We found that densities were higher in diked wetlands, whereas post-winter persistence was higher in tidal wetlands, and reproductive potential did not differ statistically between wetland types. Our results emphasize the importance of mixed vegetation for providing adequate salt marsh harvest mouse habitat and suggest that, despite their physiognomic and hydrological differences, both diked and tidal wetlands support salt marsh harvest mouse populations by promoting different demographic attributes. We recommend that habitat management, restoration, and enhancement efforts include areas containing mixed vegetation in addition to pickleweed in both diked and tidal wetlands.
© 2011 The Wildlife Society.

KEY WORDS density, diked, microhabitat, persistence, *Reithrodontomys raviventris halicoetes*, reproduction, salt marsh harvest mouse, Suisun Marsh, tidal, wetlands.

The salt marsh harvest mouse (*Reithrodontomys raviventris*) is endemic to the marshes of the San Francisco Bay Estuary in northern California. There are 2 subspecies: the southern (*R. r. raviventris*), which occurs in salt marshes around San Francisco Bay, and the northern (*R. r. halicoetes*), which occurs in brackish marshes around Suisun Bay and San Pablo Bay (Fisler 1965, Shellhammer 1982). The species' historical tidal marsh habitat has decreased by approximately 80% due to diking, draining, and filling for urban, industrial, and agricultural development (Goals Project 1999), leading to its listing as endangered by both the federal and state governments (Federal Register 50 CFR 17.11; U.S. Fish and Wildlife Service [USFWS] 1973; California Code of Regulations Title 14, Section 670.5[a][6][F]). Most published research on salt marsh harvest mouse ecology was conducted in salt marshes around the South San Francisco Bay. Based on those studies, optimal salt marsh harvest mouse habitat has commonly been described as tidal marsh dominated by pickleweed (*Salicornia* spp.; Shellhammer et al. 1982, Shellhammer 1989, USFWS 2009). However, ecological conditions vary considerably across the range of the species, so the attributes of preferred habitat in one geographic area may not apply universally (Fisler 1965, Shellhammer 1982, Goals Project 1999). Marshes in the San Francisco Bay have generally been more heavily impacted by development. Remaining salt marsh harvest mouse habitat in this area occurs as narrow bands of high tidal marsh with low-growing pickleweed and Pacific cordgrass (*Spartina foliosa*; Goals Project 1999) and little or no high marsh transition zone or bordering uplands to serve as refugia during high tides (Shellhammer 1977, Duke and Shellhammer 2006). In contrast to those in the San Francisco Bay, marshes in and around Suisun and San Pablo bays are generally larger in area and have significant transition zones and adjacent uplands. Tidal marshes in San Pablo Bay are vegetated primarily with pickleweed, whereas Suisun Marsh is more botanically diverse than other parts of the estuary (Goals Project 1999).

Received: 12 February 2010; Accepted: 22 December 2010;
Published: 18 July 2011

Additional Supporting Information may be found in the online version of this article.

[1] *E-mail: diego.sustaita@uconn.edu*

[2] *Present Address: Department of Ecology and Evolutionary Biology, University of Connecticut, 75 North Eagleville Road, Unit 3043, Storrs, CT 06269-3043, USA.*

Due to the diversity of vegetation in Suisun, pickleweed, which has traditionally epitomized prime salt marsh harvest mouse habitat, is more patchily distributed than in the range of the southern subspecies. Previous studies in the San Francisco Bay (Wondolleck et al. 1976, Zetterquist 1978, Geissel et al. 1988, Padgett-Flohr and Isakson 2003), in the San Pablo Bay (Bias 1994, Bias and Morrison 2006), and our own surveys in the Suisun Marsh (L. Barthman-Thompson, California Department of Fish and Game [CDFG]; L. Patterson, California Department of Water Resources [CDWR], unpublished data) have found salt marsh harvest mice in not only tidal wetlands dominated by pickleweed, but also in wetlands with little or no pickleweed, in diked wetlands, and in transition zones dominated by annual grasses. However, the extent to which salt marsh harvest mice depend upon these habitats has not been explicitly quantified.

Although several researchers have examined salt marsh harvest mouse abundance and habitat associations (e.g., Schaub 1971, Botti et al. 1986, Geissel et al. 1988, Padgett-Flohr and Isakson 2003, Bias and Morrison 2006), to our knowledge none have examined potential differences between diked and tidal wetlands. Furthermore, since Bias's (1994) comprehensive study on salt marsh harvest mice in the San Pablo Bay region, no studies have quantified additional demographic characteristics, such as reproduction and survival. Our objective, therefore, was to compare estimates of salt marsh harvest mouse density, reproductive output, and survival across pickleweed-dominated, mixed vegetation-dominated, and upland grass-dominated microhabitats and between diked and tidal wetlands.

STUDY AREA

We conducted our study in the Suisun Marsh, Solano County, California, located approximately 30 miles east of San Francisco (Fig. 1). As one of the largest contiguous brackish marshes remaining on the west coast of North America (17,000 ha), it has been considered an important part of the San Francisco Bay-Delta Estuary (CDWR 1984). Its geographical location at the confluence of fresh and saline waters has resulted in a wider range of salinity conditions than in other parts of the Estuary. Before levee construction began in the 1860s, the area was a complex of sloughs, ponds, and tidal marshes. Since then, the Suisun Marsh has become a mosaic of diked marshes managed for waterfowl and other wildlife, relatively unaltered tidal marshes, uplands, bays, sloughs, and other waterways (CDWR 2000).

Vegetation in the tidal marshes of Suisun grew in bands: typically with hardstem bulrush (*Schoenoplectus acutus*) in the low marsh near the sloughs, a diversity of halophytic plant species such as Baltic rush (*Juncus balticus*) and Olney's threesquare bulrush (*Schoenoplectus americanus*) in the mid marsh, and pickleweed (*Salicornia virginica* with some *Salicornia subterminalis*) and saltgrass (*Distichlis spicata*) in the high marsh that bordered uplands. Vegetation in the diked wetlands grew either more homogeneously or in patches rather than in bands like the tidal wetlands. Although the 2 wetland types shared many of the same plant species, particularly pickleweed, Baltic rush, saltgrass, fat hen (*Atriplex triangularis*), and Olney's threesquare bulrush, there was a greater diversity in the tidal wetlands because many of the mid-marsh species such as sea milkwort (*Glaux maritima*), marsh jaumea (*Jaumea carnosa*), and seaside arrowgrass (*Triglochin maritima*) rarely occurred in the diked wetlands.

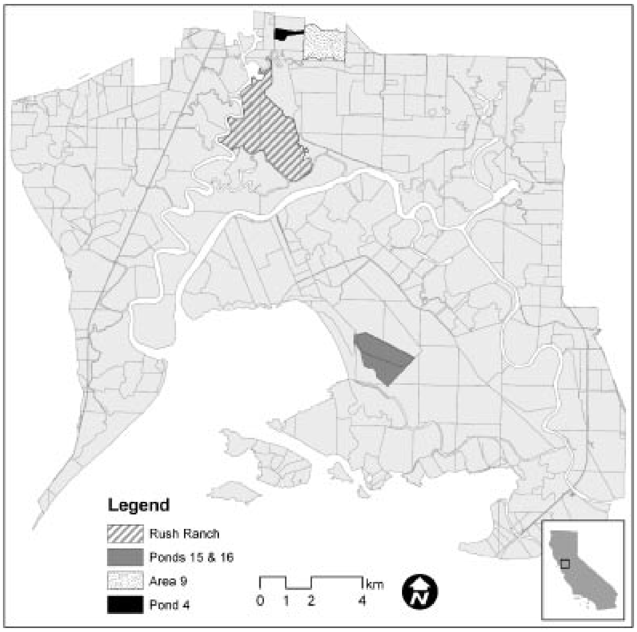

Figure 1. Detail of Suisun Marsh salt marsh harvest mouse study area, located in central California (lower right inset), 09 June 2002–25 May 2004. Diked marsh areas (solid symbols) include two salt marsh harvest mouse Conservation Areas, Ponds 15 and 16 (263.2 ha), and Pond 4 (70.6 ha). Tidal wetland areas (striped symbols) include Hill Slough Area 9 (180.3 ha; a salt marsh harvest mouse Conservation Area) and Rush Ranch (1,109.7 ha).

Over 1,000 ha of tidal and diked wetlands were set aside for salt marsh harvest mouse conservation in the Suisun Marsh. We surveyed 4 locations, 3 of which were salt marsh harvest mouse Conservation Areas. The fourth location (Rush Ranch), although not a Conservation Area, was the largest remaining tract of tidal marsh within Suisun Marsh (Fig. 1).

METHODS

Small-Mammal Trapping

To investigate the effect of wetland type on salt marsh harvest mouse demography, we chose 2 diked and 2 tidal locations (Fig. 1) based on their accessibility and their comparable assemblages of vegetation. To investigate the effect of microhabitat, we employed a stratified random study design (Skalski and Robson 1992) by dividing each of the 4 locations into 3 coarse-level vegetation strata common to both diked and tidal wetlands: 1) pickleweed-dominated (PW: living and dead), 2) mixed vegetation-dominated (MV: various native and non-native wetland species, other than pickleweed and upland grasses, such as fat hen, saltgrass, Baltic rush, and Olney's three-square bulrush), and 3) upland grass-dominated (UP: all upland grasses, such as Italian ryegrass [*Lolium multiflorum*] and bromes [*Bromus* spp.]). We subsequently verified these strata by quantitative sampling and analysis of key vegetation characteristics (see Supplemental Material available online at www.onlinelibrary.wiley.com).

We used maps generated by the Suisun Marsh Vegetation Survey (Keeler-Wolf 2000) to delineate the boundaries of each microhabitat a priori using a Geographic Information System, upon which we superimposed a network of approximately 0.31-ha cells. We randomly selected 2 cells in each microhabitat in each of the 4 locations, for a total of 24 cells (hereafter grids). To ensure spatial independence, we discarded grids that fell within 50 m of another grid. We obtained the coordinates for centers of the randomly selected grids and located them on the ground using a Global Positioning System. This study design resulted in replication at the lowest (grids within microhabitats) and highest (locations within wetland types) levels of the analyses.

Each grid consisted of 48–49 Sherman live traps (H.B. Sherman Traps, Tallahassee, FL) spaced 8 m apart. We used a square 7 × 7 trap configuration for most sites; however, we altered the grid dimensions (6 × 8, 4 × 12) to best fit the shape of the microhabitat while maintaining a consistent area of coverage. We baited traps with bird seed and ground walnuts, set traps at dusk, and checked them at dawn for 4 consecutive nights during each trapping period. We trapped each grid once during each of 3 trapping periods per year: summer (15 Jun–23 Jul), fall (14 Sep–29 Oct), and spring (22 Mar–14 May) from summer 2002 to spring 2004. We did not trap during winter due to the increased risk of mortality to captured rodents from flooding and hypothermia. Within each of the 4 locations, we trapped all 6 grids simultaneously; however, we only sampled 1 location at a time, with an average of 13 days separating surveys among locations within a given trapping period. We conducted salt marsh harvest mouse trapping under a CDFG Memorandum of Understanding with CDWR, a recovery permit between CDWR and USFWS (no. TE835365-2), and a Cooperative Agreement between CDFG and USFWS.

We identified all captured rodents to species, determined sex, visually assessed reproductive condition (males noted as non-scrotal, semi-scrotal, or scrotal; females noted as non-reproductive, lactating, pregnant, or vaginal plug), marked, and released them at the site of capture. We measured salt marsh harvest mice and congeneric western harvest mice (*R. megalotis*) for their total and tail lengths (to the nearest mm with a metric ruler), tail diameter (measured at 20 mm from the base of the tail to the nearest 0.05 mm with calipers; after Shellhammer 1984), and weight (to the nearest 0.25 g with a 30-g Pesola spring scale; Pesola AG, Baar, Switzerland). We individually marked all harvest mice using aluminum coded ear tags (size 0.1,018 M National Band and Tag Co., Newport, KY) and batch-marked house mice (*Mus musculus*) and California voles (*Microtus californicus*) by clipping fur along different regions of the body for each night (Wilson et al. 1996).

Salt marsh harvest mice and western harvest mice are similar morphologically (Fisler 1965, Shellhammer 1984), and identification in the field was not always possible. For the most part, we distinguished the 2 species based on the characteristics described by Shellhammer (1984) but relied most heavily upon tail length and tail length to body length ratio (>79 mm and >123%, respectively, for salt marsh harvest mice), adapted specifically for the Suisun Marsh populations under study (after Brown 2003). We used multiple logistic regression analysis to assign 163 ambiguous individuals to the most probable species. This model was based on a subset of individuals from earlier studies for which species identity had been determined genetically ($n = 256$; Brown 2003, F. Villablanca, California Polytechnic State University, unpublished data) using tail length, body length, tail diameter, sex, and reproductive condition (D. Sustaita, CDFG, unpublished data). We excluded 47 cases that we could not adequately classify (e.g., individuals lacking data and neonates) from demographic analyses.

We determined juvenile and adult salt marsh harvest mouse age classes by examining relative frequency distributions of the number of individuals in reproductive condition within 8 body-length class-intervals (Sullivan and Krebs 1981, Mayfield et al. 2000). The lower boundary of the smallest size class in which ≥50% of the individuals were in reproductive condition determined the length above which we considered individuals adults (≥68 mm for females; ≥64 mm for males), and we considered those which fell below juveniles.

Demographic Variables

To estimate abundance we employed several closed-capture models using Program CAPTURE (White et al. 1978) as implemented in Program MARK (Version 4.3, http://warnercnr.colostate.edu/~gwhite/mark/mark.htm, accessed 09 Feb 2006), in addition to the condensed Lincoln–Peterson estimator (Menkens and Anderson 1988). The CAPTURE models we evaluated consisted of the 2 most appropriate models for the data based on the relative weightings produced by Program CAPTURE's internal model selection procedure (Otis et al. 1978, White et al. 1982) as well as the model suggested by Manning et al. (1995) for the [estimated] population size and observed variation in capture probabilities. When we captured ≤10 individuals in a grid during a given trapping period, sample size was too small to use the above-described models, so we used the number of unique individuals captured (M_{t+1}) to approximate abundance (after Andersen 1994, Moses and Boutin 2001). When sample sizes were >10, we evaluated the 4 abundance estimates and selected the one that best satisfied the following criteria: 1) narrowest 95% confidence limits, 2) lowest standard error (SE), 3) lowest coefficient of variation, and 4) M_{t+1} at or below the lower 95% confidence limit (Otis et al. 1978, White et al. 1982, Menkens and Anderson 1988, Pollock et al. 1990).

We derived estimates of density by dividing the estimate of abundance for each grid by its effective trapping area (in hectares). We approximated the effective trapping area (sensu Stafford and Stout 1983, Andersen 1994) by adding a boundary strip of half the average maximum distance salt marsh harvest mice moved within a grid between successive captures during a given trapping period for each location and season (after Adler and Tamarin 1984; Wilson and Anderson 1985*a*, *b*; Williams et al. 2002). We computed density estimates of coexisting species based on the effective trapping areas of salt marsh harvest mice as we were unable to track the other species' individual movements.

We examined reproductive potential in 2 ways: the proportion of females in reproductive condition (Adler and Wilson 1987, Smith and Nichols 2004) and the proportion of juveniles (Craig et al. 2006) during a given trapping period at each location. We used both of these metrics because each imparts slightly different information regarding potential reproductive output in a given place and time. We only examined reproductive potential in PW and MV microhabitats because low capture success in the UP grids prevented analysis of this microhabitat.

Our low cross-season recapture rates precluded the use of probabilistic models for deriving survival estimates, so we used the proportion of cross-season recaptures as an index for survival. We calculated the proportion of cross-season recaptures by dividing the number of individuals recaptured during a particular trapping period by the total number of individuals captured during the previous trapping period (after Mayfield et al. 2000, Moses and Boutin 2001, Smith and Nichols 2004). This metric is similar to persistence used by Agrell et al. (1992) and Getz et al. (2005) in that it is intended to reflect the relative longevities of individual mice throughout the study area over time (but see Sullivan and Krebs 1981, Mayfield et al. 2000 for statistical caveats). To minimize the effects of temporal autocorrelation, we compiled cross-season recapture data into 2 blocks for each year: pre-winter (summer to fall) and post-winter (fall to spring). As with reproductive potential, we excluded UP grids from analysis due to the low capture success in this microhabitat.

Statistical Analyses

We analyzed each demographic variable separately because the ratio of the number of cases to the number of variables precluded the use of multivariate procedures. We used a partly nested repeated-measures analyses of variance (RMANOVA; after Morris 1996, Quinn and Keough 2002, Smith and Nichols 2004) for salt marsh harvest mouse density. We treated wetland type (2 levels: diked and tidal) and microhabitat (3 levels: PW, MV, and UP) as fixed, between-subjects factors, with location as an additional random factor nested within wetland type to account for any variation in wetland effects due to potential geographic differences. We treated each trapping grid as a subject, and the within-subjects factor comprised 6 seasonal trapping periods. We employed a similar, but unreplicated, partly nested RMANOVA design for the proportions of reproductive females and juveniles because we pooled numbers of individuals from replicate grids within each microhabitat to obtain more meaningful proportions.

We analyzed persistence data (based on numbers of captures and cross-season recaptures pooled over replicate grids and locations) using separate logit–loglinear analyses (Agresti 1996, Quinn and Keough 2002) for each pre- ($n = 356$ captures, 38 recaptures) and post-winter ($n = 313$ captures, 19 recaptures) period to examine how persistence varied among wetland types, microhabitats, and years. These logit–loglinear models treated persistence as a dependent variable by crossing it with each term and including the interaction among wetland type, microhabitat, and year in every model. We tested terms in a hierarchical fashion based on deviances of −2log-likelihood (G^2) values and degrees of freedom between full and reduced models to examine the significance of 3- and 2-way interactions (Quinn and Keough 2002).

Because high densities may adversely affect population growth rates and individual fitness through intra- and interspecific competition (Van Horne 1983, Adler and Wilson 1987, Arcese and Smith 1988, Geissel et al. 1988, Ostfeld and Canham 1995), we examined whether salt marsh harvest mouse density affected reproductive potential or persistence and whether the densities of coexisting rodent species affected salt marsh harvest mouse densities. We ran separate linear mixed models for the proportions of reproductive females and juveniles (pooled over replicate grids; $n = 12$ for each trapping period) and cross-season recaptures (pooled over replicate grids, excluding UP microhabitats; $n = 8$ for each trapping period), on salt marsh harvest mouse density. Because these relationships are likely to vary seasonally, we included season as a repeated-measures effect fit to a first-order factor analytic covariance matrix (based on lowest Akaike Information Criterion [AIC] value). We examined the relationship between coexisting species and salt marsh harvest mouse densities in a similar manner, except using all grids ($n = 24$) and fit to an unstructured covariance matrix. For these analyses, we took significantly negative parameter estimates (β) for the effects of coexisting species and salt marsh harvest mouse densities to indicate a potential adverse impact on salt marsh harvest mouse density and other demographic variables, respectively.

We transformed data prior to analyses to improve normality and ensure homoscedasticity, which we evaluated by graphing normal probability plots of residuals from initial runs of each analysis (below) and checking Levene's test of equality of error variances. We square root- and $\log_{10}$-transformed densities of salt marsh harvest mice and coexisting species, respectively; arcsine-square root-(+0.05)-transformed the proportions of reproductive females and juveniles (after Zar 1999); and analyzed persistence data as raw frequencies. We used the PASW (PASW Statistics GradPack 18.0 for Windows, Somers, NY) GLM command to run RMANOVAs, the GENLOG command to run logit–loglinear analyses, and the MIXED command to run linear mixed models. We used Excel (version 2003, Microsoft Corporation, Redmond, WA) to compute *F*-ratios and *P*-values of hierarchically nested terms from mean square values from RMANOVA outputs and to compute deviances (and their significance) in likelihood ratios from the logit–loglinear outputs.

RESULTS

We captured 1,191 individual salt marsh harvest mice in 28,104 trap-nights. Mean ± SE salt marsh harvest mouse density estimates were 32.3 ± 3.4 mice/ha in diked and 18.9 ± 2.5 mice/ha in tidal wetlands ($n = 72$ across grids, locations, microhabitats, and seasons); and 43.5 ± 4.5 mice/ha in MV, 27.2 ± 2.5 mice/ha in PW, and 6.1 ± 1.5 mice/ha in UP microhabitats ($n = 48$ across grids, locations, wetland types, and seasons). Between-subjects interaction and nested terms were not significant (Table 1), and salt marsh harvest mouse densities were higher, overall, in diked than in tidal wetlands after accounting for variation among microhabitats ($P = 0.013$; wetland effect size, $\eta^2_{\text{partial}} = 0.27$; Table 1; Fig. 2A). There was also an effect of microhabitat after accounting for variation between wetland types ($P < 0.001$; microhabitat effect size, $\eta^2_{\text{partial}} = 0.70$). However, densities did not differ between MV and PW microhabitats (Tukey HSD test, mean difference = 1.21, $P = 0.165$) but were higher in each of these than in the UP microhabitat (mean difference between MV and UP = 4.19, $P < 0.001$; mean difference between PW and UP = 2.98, $P < 0.001$). Overall, densities were affected by season ($P < 0.001$), reflecting significant and non-significant peaks during both spring trapping periods (within-subjects difference contrasts, $F_{1,18} = 14.64$, $P = 0.001$ and $F_{1,18} = 5.44$, $P = 0.064$, for 2003 and 2004, respectively).

We captured females in reproductive condition during each trapping event, from March to October, and although proportions varied significantly across seasons (within-subjects effect of season, $P = 0.022$; Fig. 2B; Table 1), they were greatest in fall. Mean ± SE proportions of salt marsh harvest mouse females in reproductive condition were 0.18 ± 0.03 in diked and 0.23 ± 0.02 in tidal wetlands ($n = 24$ across microhabitats, locations, and seasons), and 0.21 ± 0.02 in MV and 0.20 ± 0.03 in PW microhabitats ($n = 24$ across locations, wetland types, and seasons). However, neither the effect of wetland ($P = 0.155$; wetland effect size, $\eta^2_{\text{partial}} = 0.36$) nor microhabitat ($P = 0.531$; microhabitat effect size, $\eta^2_{\text{partial}} = 0.08$; Table 1) was significant after adjusting for variation among wetland types, microhabitats, and seasons. The proportion of juveniles also varied seasonally ($P = 0.049$) but was greater, overall, in diked (0.37 ± 0.02) than in tidal (0.27 ± 0.03) wetlands after accounting for variation between microhabitats ($P = 0.035$; wetland effect size, $\eta^2_{\text{partial}} = 0.62$; Fig. 2C; Table 1). However, there was no difference between microhabitats (0.31 ± 0.03 in MV and 0.33 ± 0.02 in PW) after accounting for variation between wetland types ($P = 0.572$; microhabitat effect size, $\eta^2_{\text{partial}} = 0.07$).

Mean ± SE percentages of pre-winter salt marsh harvest mouse cross-season recaptures (summer to fall) were 11.1 ± 3.4% in diked and 8.4 ± 2.3% in tidal wetlands ($n = 4$ across microhabitats and years) and 10.1 ± 2.8% in MV and 9.5 ± 3.2% in PW microhabitats ($n = 4$ across wetland types and years; Table 2). When considered collectively, there were no effects of wetland type ($P = 0.823$), microhabitat ($P = 0.804$), or their interaction ($P = 0.052$), on pre-winter persistence (Table 3). Post-winter salt marsh harvest mouse cross-season recaptures (fall to spring) were 1.8 ± 1.1% in diked and 12.4 ± 3.1% in tidal wetlands, and 8.0 ± 2.6% in MV and 6.3 ± 4.7% in PW microhabitats (Table 2). The 3-way interaction among persistence, wetland type, and microhabitat was not significant (goodness of fit test, $P = 0.053$; Table 3). Post-winter persistence was roughly seven-fold greater in the tidal than in the diked wetlands (analysis of deviances, $P = 0.001$; Tables 2 and 3),

Table 1. Results of repeated-measures analyses of variance testing for the effects of wetland type (Wetl), microhabitat (Micro), location (Loc), and season (Seas) on salt marsh harvest mouse density estimates (no./ha) and proportions (of total no. of individuals captured per grid per season) of reproductive females and juveniles in the Suisun Marsh, California, from 09 June 2002–25 May 2004.

	Estimated density				Proportion reproductive females				Proportion juveniles			
Source	Df	MS	*F*	*P*	Df	MS	*F*	*P*	Df	MS	*F*	*P*
Between-subjects factors												
Wetl[a]	1	71.69	3.11	0.220	1	0.05	4.45	0.169	1	0.17	4.34	0.173
Micro	2	222.75	16.21	0.004	1	0.01	0.37	0.587	1	0.01	0.958	0.400
Loc(Wetl)	2	23.02	1.68	0.264	2	0.01	0.53	0.634	2	0.04	5.07	0.109
Micro × Loc(Wetl)	6	13.74	2.51	0.082								
Error	12	5.47			3	0.02			3	0.01		
Pooled nested and/or interaction[b]												
Wetl	1	71.69	7.39	0.013	1	0.05	2.81	0.155	1	0.17	8.27	0.035
Micro	2	222.75	22.95	<0.001	1	0.01	0.45	0.531	1	0.01	0.37	0.572
Error	20	9.71			5	0.02			5	0.02		
Within-subjects factors												
Seas	5	10.42	7.39	<0.001	5	0.06	3.69	0.022	5	0.03	2.92	0.049
Seas × Wetl	5	3.00	2.13	0.075	5	0.01	0.54	0.746	5	0.01	0.78	0.580
Seas × Micro	10	2.35	1.66	0.111	5	0.04	2.40	0.087	5	0.02	1.56	0.232
Seas × Loc (Wetl)	10	4.30	3.05	0.003								
Seas × Micro × Loc(Wetl)	30	1.96	1.39	0.138								
Error	60	1.41			15	0.02			15	0.01		

[a] We tested the mean squares (MS) of Wetland over that of Location (Wetland type), and we tested MS of Microhabitat and Loc(Wetl) over MS of Micro × Loc(Wet) (adapted from Zar 1999, Quinn and Keough 2002).

[b] We pooled non-significant ($P > 0.05$) nested and interaction terms to maximize degrees of freedom for subsequent analyses of main effects (adapted from Sokal and Rohlf 1995, Quinn and Keough 2002). When the effect of microhabitat was significant, we performed post hoc pairwise comparisons using Tukey HSD tests (Quinn and Keough 2002; see text for results).

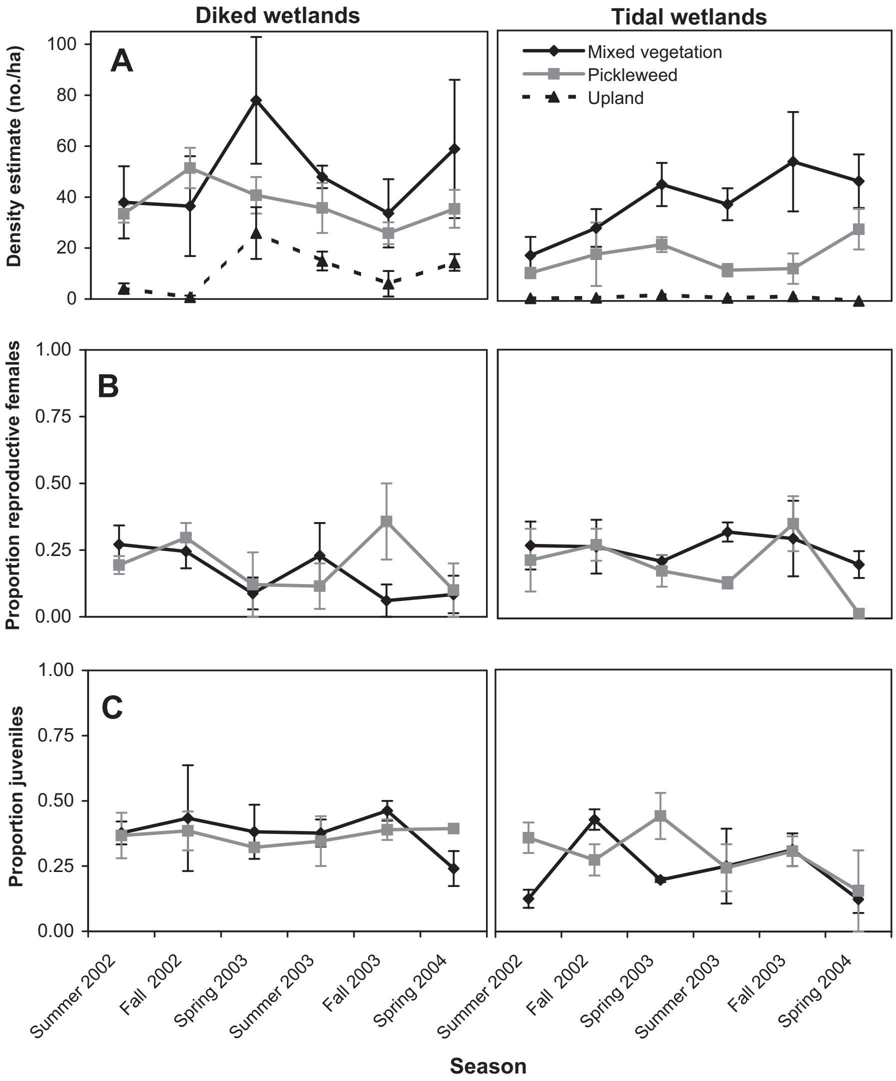

Figure 2. (A) Seasonal salt marsh harvest mouse density estimates (no./ha) and proportions (of total no. of individuals captured per grid per season) of females in reproductive condition (B) and juveniles (C), for each microhabitat in Suisun Marsh, California, from 09 June 2002–25 May 2004. Diked and tidal wetlands are represented in left- and right-hand panels, respectively, and means (± SE) are based on $n = 4$ trapping grids.

Table 2. Pre- and post-winter persistence, computed as the number of cross-seasonal salt marsh harvest mouse recaptures relative to the total number of individuals caught in the preceding season, in pickleweed (PW) and mixed vegetation (MV) microhabitats (combined over replicate grids and locations) in the Suisun Marsh, California, from 09 June 2002–25 May 2004.

	Pre-winter			**Post-winter**		
Wetland Microhabitat	**Captures**	**Recaptures**	**%**	**Captures**	**Recaptures**	**%**
		2002			2003	
Diked						
MV	53	1	1.9	46	2	4.3
PW	47	5	10.6	66	0	0.0
Tidal						
MV	36	5	13.9	48	6	12.5
PW	22	1	4.5	20	1	5.0
		2003			2004	
Diked						
MV	65	9	13.8	35	1	2.9
PW	55	10	18.2	34	0	0.0
Tidal						
MV	56	6	10.7	49	6	12.2
PW	22	1	4.6	15	3	20.0

Table 3. Results of logit–loglinear analyses testing the effects of wetland type (wetl) and microhabitat (micro), and their interaction, on pre- (top) and post-winter (bottom) persistence (pers; no. captured during one season vs. the no. recaptured during the subsequent season, pooled over replicate grids and locations) of salt marsh harvest mice in the Suisun Marsh, California, from 09 June 2002–25 May 2004. The goodness-of-model-fit statistics represent the difference between null and residual models; we tested the significance of main effects by analysis of deviances (i.e., difference between full and reduced models; Quinn and Keough 2002).

	Goodness-of-fit			Analysis of deviances			
Model[a]	G^2	Df	P	Model term	G^2	Df	P
Pre-winter persistence							
Constant + pers + pers × micro + pers × wetl + wetl × micro	3.43	1	0.067				
Constant + pers + pers × micro + wetl × micro	3.52	2	0.172	pers × wetl	0.175	1	0.676
Constant + pers + pers × wetl + wetl × micro	3.48	2	0.176	pers × micro	0.134	1	0.714
Post-winter persistence							
Constant + pers + pers × micro + pers × wetl + wetl × micro	3.75	1	0.053				
Constant + pers + pers × micro + wetl × micro	14.45	2	0.001	pers × wetl	10.70	1	0.001
Constant + pers + pers × wetl + wetl × micro	4.78	2	0.092	pers × micro	1.03	1	0.309

[a] The effect of year (2003 vs. 2004) and its interactions with micro and wetl were originally included among the set of models compared, but because they performed inferiorly compared to those without year effects (based on Akaike's Information Criterion), and did not contribute significantly to model fit (based on analysis of deviances), for brevity they are not shown.

but there was no effect of microhabitat ($P = 0.309$). Furthermore, in both sets of analyses the effect of year did not contribute significantly to model fit (all models including the year term, and interactions of year with other terms, were >2 ΔAIC units [Burnham and Anderson 2002] from those without it) and was not significant in any of the tests of deviances ($G_1^2 \leq 3.05$, $P \geq 0.081$ for all).

The proportion of reproductive females was independent of salt marsh harvest mouse density ($\beta = 0.015 \pm 0.009$ [SE], $t_{38.6} = 1.59$, $P = 0.120$). Although the proportion of juveniles was significantly dependent upon salt marsh harvest mouse density, the relationship was positive ($\beta = 0.035 \pm 0.008$, $t_{58.1} = 4.35$, $P < 0.001$), suggesting that juveniles comprise a greater proportion of the total density at higher densities. The proportion of cross-season recaptures was independent of salt marsh harvest mouse density ($\beta = 0.008 \pm 0.011$, $t_{23.7} = 0.375$, $P = 0.451$). Salt marsh harvest mouse densities were positively related to those of California voles ($\beta = 0.113 \pm 0.053$, $t_{21.0} = 2.13$, $P = 0.046$; Table 4) but not significantly related to those of house mice ($\beta = 0.0003 \pm 0.031$, $t_{20.0} = 0.010$, $P = 0.992$) or western harvest mice ($\beta = -0.065 \pm 0.051$, $t_{20.8} = -1.27$, $P = 0.217$).

DISCUSSION

Salt Marsh Harvest Mouse Demographic Performance

Although we cannot formally attribute differential use of habitats to salt marsh harvest mouse preference (Garshelis 2000), we have demonstrated how 3 demographic parameters (density, reproductive potential, and persistence) are affected by wetland types and microhabitats. None of the demographic variables we evaluated appeared to differ between PW and MV microhabitats, suggesting that both constitute suitable salt marsh harvest mouse habitat. This is not surprising, as others have noted that the value of pickleweed to salt marsh harvest mice increases when other halophytes such as fat hen or alkali heath (*Frankenia salina*) are intermixed (Geissel et al. 1988, Shellhammer et al. 1988). We found clearer differences in salt marsh harvest mouse demographic variables between diked and tidal wetlands. Studies of other animals have also indicated that managed wetlands can harbor higher densities than their natural counterparts (Weber and Haig 1996, and references therein). High densities may be useful performance indicators for salt marsh harvest mouse Conservation Areas, although

Table 4. Mean ($\bar{x}$) and SE density estimates (no./ha) of salt marsh harvest mice and coexisting rodent species ($n = 2$ grids × 6 seasons = 12) for each wetland type (MV = mixed vegetation, PW = pickleweed, UP = upland), location, and microhabitat in the Suisun Marsh, California, from 09 June 2002–25 May 2004.

Wetland type and location	Microhabitat	Salt marsh harvest mouse		Western harvest mouse		California vole		House mouse	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Diked wetlands									
P1516	MV	25.0	5.6	0.0	0.0	54.6	23.7	48.5	15.3
	PW	35.3	4.3	0.4	0.3	49.3	22.6	53.9	21.0
	UP	12.4	4.2	0.2	0.2	10.5	5.9	44.4	25.1
HSP4	MV	72.7	10.2	24.2	11.9	4.8	1.7	43.3	16.7
	PW	38.9	4.4	3.2	1.2	8.1	4.8	82.2	21.1
	UP	9.6	3.0	1.7	0.9	0.4	0.3	14.6	5.9
Tidal wetlands									
HSA9	MV	47.2	7.3	7.3	2.8	6.4	2.1	3.9	1.6
	PW	22.3	4.6	10.7	5.7	0.7	0.5	11.0	6.9
	UP	2.1	0.7	7.9	2.6	0.2	0.2	4.6	2.1
RRanch	MV	29.2	4.7	0.7	0.4	8.6	2.6	4.1	1.5
	PW	12.1	2.2	2.1	0.9	1.4	0.4	4.7	2.4
	UP	0.4	0.3	3.9	1.5	0.8	0.5	6.8	2.9

we acknowledge that those densities could mislead assessments of habitat quality (Van Horne 1983, Winker et al. 1995), which is why we also examined differences in reproductive potential and persistence.

Although proportions of reproductive females were similar between wetlands, proportions of juveniles were greater in diked wetlands. Post-winter persistence, however, was significantly higher in tidal wetlands. There was no indication that increased salt marsh harvest mouse densities negatively affected these demographic variables. Lower proportions of juveniles in tidal wetlands may indicate lower reproductive success from the previous fall-winter season (Skupski 1995) or may be the result of greater longevity, which is what higher long-term (i.e., post-winter) persistence in the tidal wetlands seems to suggest. However, the implications of these long-term persistence rates are not entirely clear. Most small-mammal survival indices are computed on the scale of a few weeks to a few months (e.g., Krebs 1966, Adler and Wilson 1987, Getz et al. 2005). Post-winter persistence here spanned a period of roughly 200 days (approx. 6.6 months), which is quite long relative to the approximately 12-month life span typical of harvest mice (Fisler 1971). Thus, we cannot exclude the possibility that these indices might reflect the persistence of older individuals of questionable fitness (Tkadlec and Krejčová 2001). Furthermore, there are various other factors than those we measured (e.g., differences in predator densities) that may ultimately account for differences in persistence rates.

Bias et al. (1992) discussed how tag-loss and tag-retention time could affect estimates of salt marsh harvest mouse abundance and survival. We recorded 31 salt marsh harvest mice with torn ears, amounting to 2.6% of total captures over the 2-year study. We treated these mice as new captures, which could theoretically inflate abundance estimates and underestimate persistence rates. However, these mice were distributed roughly in proportion to the overall numbers of captures within each wetland type and microhabitat. Thus, we believe our results were not biased by these potential lost marks.

Salt Marsh Harvest Mouse Habitat in Suisun Marsh

Our quantitative analyses of vegetation cover supported our initial PW, MV, and UP microhabitat designations and validated their distinctiveness (see Supplemental Material available online at www.onlinelibrary.wiley.com), suggesting that visual assessments of vegetation composition were useful for categorizing potential salt marsh harvest mouse habitats. The MV microhabitats were composed predominantly of various native halophytic (e.g., fat hen, alkali heath, saltgrass, Baltic rush, and Olney's threesquare bulrush) and non-native weedy species (prickly lettuce [*Lactuca serriola*] or sow thistle [*Sonchus* sp.]) in addition to pickleweed. Bias and Morrison (2006) found that salt marsh harvest mouse captures in San Pablo Bay were primarily associated not only with pickleweed cover, but also with that of fat hen, forbs, and grasses, to lesser extents. Although pickleweed constitutes an important component of salt marsh harvest mouse habitat in the Suisun Marsh, our analyses suggest areas with mixed vegetation not dominated by pickleweed can be equally productive. It is not clear specifically how mixed vegetation benefits salt marsh harvest mice, but perhaps a greater variety of food resources, associated with a greater diversity of plant species, can be exploited in these microhabitats. Aside from plant species diversity, the greater structural diversity of mixed vegetation (see Supplemental Material available online at www.onlinelibrary.wiley.com) may also play a role in supporting high densities of salt marsh harvest mice, for instance, by reducing risk of predation (Bias and Morrison 2006 and references therein).

Height may also play an important role in habitat use. Vegetation was taller in diked wetlands (see Supplemental Material available online at www.onlinelibrary.wiley.com), which also had higher salt marsh harvest mouse densities. Perhaps greater concealment from predators and refuge from flooding afforded by taller vegetation facilitate high salt marsh harvest mouse densities in these areas. Padgett-Flohr and Isakson (2003) suggested that salt marsh harvest mice may cue on pickleweed salinity, rather than plant height, based in part on the negative relationship Geissel et al. (1988) found between pickleweed height and salinity. However, we did not measure salinity, so we could not determine whether such a relationship also exists in Suisun Marsh or whether it translates to plant species other than pickleweed.

We found no cursory evidence of competitive exclusion as may be suggested by negative associations between salt marsh harvest mice and coexisting rodent species (e.g., Geissel et al. 1988). Whereas Padgett-Flohr and Isakson (2003) found no association between California voles and salt marsh harvest mice in a South Bay study, we found a positive relationship. Collectively, these results suggest that, although population densities of coexisting species may vary among wetland types and microhabitats, on a larger scale, densities of coexisting species appear not to influence salt marsh harvest mouse habitat use. Bias and Morrison (2006) found significant differences in habitat use between house mice and salt marsh harvest mice in the San Pablo Bay and that trap-station-level habitat characteristics positively associated with one species were negatively associated with the other. Our null and positive grid-level relationships suggest that perhaps these species cue on similar resources in the Suisun Marsh but likely coexist by partitioning them on a finer scale than we could detect from our analysis. Population-level patterns may mask individual-level interactions and vice versa, underscoring the importance of examining patterns of habitat selection across spatial scales (Morris 1987).

General Conclusions

Salt marsh harvest mouse demographic performance across the wetland types and microhabitats that we defined suggests a tendency for MV and PW microhabitats to support roughly similar densities, reproductive potential, and persistence. Furthermore, both diked and tidal wetlands appeared to support similar levels of reproductive potential and short-term (i.e., pre-winter) persistence. The main differences between wetland types were higher densities in diked wetlands and greater long-term (i.e., post-winter) persistence in tidal wetlands. Thus, both diked and tidal wetlands in Suisun Marsh were capable of sustaining salt marsh harvest mouse populations, but our results suggest that they may do so by promoting different demographic parameters. We caution that the 2 diked wetlands in our study were not heavily managed and therefore our results may not apply to other types of diked wetlands, such as those managed for waterfowl. Furthermore, our data represent only a 2-year snapshot, and despite the strength of our study design regarding unbiased sampling, spatial representation, and replication, our statistical power was restricted by both the total numbers of trapping grids and (re)captures relative to the number of factors, levels, and interactions we tested. Finally, how these demographic parameters may interact to affect long-term fitness and population viability remains unclear (Van Horne 1983, Adler and Wilson 1987). Nevertheless, our annual monitoring in the salt marsh harvest mouse Conservation Areas as well as other parts of Suisun Marsh before, during, and since this study has consistently located salt marsh harvest mice in both tidal and diked areas, indicating that both wetland types are supporting populations over the long term (L. Barthman-Thompson, L. Patterson, unpublished reports).

Our results demonstrate that there is a diversity of habitats throughout the Suisun Marsh that salt marsh harvest mice can inhabit, in some cases at high densities. For comparison, the capture efficiencies (i.e., number of individual salt marsh harvest mice/number of trap nights × 100) during our study averaged 4.2 (including the UP microhabitats where we captured few salt marsh harvest mice), whereas those from the San Francisco Bay rarely exceed 3.0 (San Francisco Estuary Institute 2009). In addition, Brown (2003) found that salt marsh harvest mice in the Suisun Marsh appeared to exhibit relatively high haplotype diversity (Brown 2003). These results taken together suggest a potential role for these habitats in metapopulation dynamics marsh-wide that warrants further study.

MANAGEMENT IMPLICATIONS

Previous assessments of the acreage of potential salt marsh harvest mouse habitat in Suisun Marsh were based solely on relative cover of pickleweed, and our study makes it clear that there is more suitable salt marsh harvest mouse habitat in the Suisun Marsh than previously expected. We suggest that habitat management, restoration, and enhancement efforts should be expanded to areas containing mixed vegetation in addition to pickleweed in both diked and tidal wetlands.

Shellhammer (1989) suggested that management of diked marshes will play an important role in future salt marsh harvest mouse conservation efforts, as a result of both natural and anthropogenic threats to tidal marshes. In recent years, Suisun Marsh agencies have moved from focusing on single-species benefits to multi-species restoration projects and enhancement of diked wetland operations, which are expected to provide benefits at the ecosystem level. Such benefits are difficult to measure, and we expect that monitoring of salt marsh harvest mice will be an integral part of enhancement and restoration projects in Suisun Marsh.

ACKNOWLEDGMENTS

Very special thanks to G. Van Klompenburg, L. Briden, J. Niceswanger, and P. Garrison for assistance and support. We are grateful to the Grizzly Island Wildlife Area and Solano Land Trust for access. We kindly thank F. Hertel, P. Wilson, and R. Mayfield for sharing their valuable insight with various components of this project. I. Castro-Arellano, C. Elphick, and H. Shellhammer commented on previous versions of this manuscript, and 2 anonymous reviewers considerably improved the final product. Funding was provided by CDWR and the United States Bureau of Reclamation.

LITERATURE CITED

Adler, G. H., and R. H. Tamarin. 1984. Demography and reproduction in island and mainland white-footed mice (*Peromyscus leucopus*) in southeastern Massachusetts. Canadian Journal of Zoology 62:58–64.

Adler, G. H., and M. L. Wilson. 1987. Demography of a habitat generalist, the white-footed mouse, in a heterogeneous environment. Ecology 68:1785–1796.

Agrell, J., S. Erlinge, and J. Nelson. 1992. Body weight and population dynamics: cyclic demography in a noncyclic population of the field vole (*Microtus agrestis*). Canadian Journal of Zoology 70:494–501.

Agresti, A. 1996. An introduction to categorical data analysis. Wiley, New York, New York, USA.

Andersen, D. C. 1994. Demographics of small mammals using anthropogenic desert riparian habitat in Arizona. Journal of Wildlife Management 58:445–454.

Arcese, P., and J. N. M. Smith. 1988. Effects of population density and supplemental food on reproduction in song sparrows. Journal of Animal Ecology 57:119–136.

Bias, M. A. 1994. Ecology of the salt marsh harvest mouse in San Pablo Bay. Dissertation, University of California–Berkeley, Berkeley, USA.

Bias, M. A., N. L. Breuner, and M. L. Morrison. 1992. House mice as indicators of marking effects on salt marsh harvest mice. Transactions of the Western Section of The Wildlife Society 28:34–37.

Bias, M. A., and M. L. Morrison. 2006. Habitat selection of the salt marsh harvest mouse and sympatric rodent species. Journal of Wildlife Management 70:732–742.

Botti, F., D. Warenycia, and D. Becker. 1986. Utilization by salt marsh harvest mice *Reithrodontomys raviventris halicoetes* of a non-pickleweed marsh. California Fish and Game 72:62–64.

Brown, S. K. 2003. Development of a molecular diagnostic technique to identify salt marsh harvest mice (*Reithrodontomys raviventris*) and western harvest mice (*Reithrodontomys megalotis*) in Suisun Marsh, California. Thesis, California Polytechnic University, San Luis Obispo, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.

California Department of Water Resources. 1984. Plan of protection for the Suisun Marsh including environmental impact report. California Department of Water Resources, Sacramento, USA.

California Department of Water Resources. 2000. Suisun Marsh monitoring program reference guide. The Environmental Services Office of the California, Department of Water Resources of The Resources Agency of the State of California, Sacramento, USA.

Craig, V. J., W. Klenner, M. C. Feller, and T. P. Sullivan. 2006. Relationships between deer mice and downed wood in managed forests of southern British Columbia. Canadian Journal of Forest Research 36:2189–2203.

Duke, R. R., and H. S. Shellhammer. 2006. Estimating relative numbers of salt marsh harvest mice, *Reithrodontomys raviventris*, in tidal marshes by trapping the high marsh zone. California Fish and Game 92:184–190.

Fisler, G. F. 1965. Adaptations and speciation in harvest mice of the San Francisco Bay. University of California Publication in Zoology 77:1–108.

Fisler, G. F. 1971. Age structure and sex ratio in populations of *Reithrodontomys*. Journal of Mammalogy 52:653–662.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–164 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology. Columbia University Press, New York, New York, USA.

Geissel, W., H. Shellhammer, and H. T. Harvey. 1988. The ecology of the salt marsh harvest mouse (*Reithrodontomys raviventris*) in a diked salt marsh. Journal of Mammalogy 69:696–703.

Getz, L. L., M. K. Oli, J. E. Hoffman, and B. McGuire. 2005. Habitat specific demography of sympatric vole populations over 25 years. Journal of Mammalogy 86:561–568.

Goals Project. 1999. Baylands ecosystem habitat goals. A report of habitat recommendations prepared by the San Francisco Bay Area Ecosystems Goals Project. U.S. Environmental Protection Agency, San Francisco, California, and San Francisco Bay Regional Water Quality Control Board, Oakland, California, USA.

Keeler-Wolf, T. 2000. Suisun Marsh vegetation mapping 1999 second edition with change detection 2000. California Department of Fish and Game, Wildlife Habitat, Data Analysis Branch, Sacramento, USA.

Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs 36:239–273.

Manning, T., W. D. Edge, and J. O. Wolff. 1995. Evaluating population-size estimators: an empirical approach. Journal of Mammalogy 76:1149–1158.

Mayfield, R. L., D. Van Vuren, and M. Johnson. 2000. Demography of an insular endemic rodent, *Peromyscus maniculatus santacruzae*, on Santa Cruz Island. Southwestern Naturalist 45:508–513.

Menkens, G. E. J., and S. H. Anderson. 1988. Estimation of small-mammal population size. Ecology 69:1952–1959.

Morris, D. W. 1987. Ecological scale and habitat use. Ecology 68:362–369.

Morris, D. W. 1996. Coexistence of specialist and generalist rodents via habitat selection. Ecology 77:2352–2364.

Moses, R. A., and S. Boutin. 2001. The influence of clear-cut logging and residual leave material on small mammal populations in aspen-dominated boreal mixed woods. Canadian Journal of Forest Research 31:483–495.

Ostfeld, R. S., and C. D. Canham. 1995. Density-dependent processes in meadow voles: an experimental approach. Ecology 76:521–532.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62.

Padgett-Flohr, G. E., and L. Isakson. 2003. A random sampling of salt marsh harvest mice in a muted tidal marsh. Journal of Wildlife Management 67:646–653.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs 107.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press: Cambridge, United Kingdom.

San Francisco Estuary Institute [SFEI]. 2009. Howard Shellhammer, H.T. Harvey and Associates. Salt marsh harvest mouse, *Reithrodontomys raviventris*, database and maps. <http://legacy.sfei.org/ecoatlas/smhm>. Accessed 6 Jul 2011.

Schaub, D. B. 1971. Salt marsh harvest mouse survey. California Department of Fish and Game: Sacramento, USA.

Shellhammer, H. S. 1977. Of mice and marshes. San Jose State University Studies 3:23–35.

Shellhammer, H. S. 1982. Reithrodontomys raviventris. Mammalian Species 169:1–3.

Shellhammer, H. S. 1984. Identification of salt marsh harvest mice, *Reithrodontomys raviventris*, in the field and with cranial characteristics. California Fish and Game 70:113–120.

Shellhammer, H. S. 1989. Salt marsh harvest mice, urban development, and rising sea levels. Conservation Biology 3:59–65.

Shellhammer, H. S., R. Duke, H. T. Harvey, V. Jennings, V. Johnson, and M. Newcomer. 1988. Salt marsh harvest mice in the diked marshes of southern San Francisco Bay. Wasmann Journal of Biology 46:89–103.

Shellhammer, H. S., R. Jackson, W. DaVilla, A. M. Gilroy, H. T. Harvey, and L. Simons. 1982. Habitat preference of salt marsh harvest mice (*Reithrodontomys raviventris*). Wasmann Journal of Biology 40:102–114.

Skalski, J. A., and D. S. Robson. 1992. Techniques for wildlife investigations: design and analysis of capture data. Academic Press, San Diego, California, USA.

Skupski, M. 1995. Population ecology of the western harvest mouse, *Reithrodontomys megalotis*: a long-term perspective. Journal of Mammalogy 76:358–367.

Smith, W. P., and J. V. Nichols. 2004. Demography of two endemic forest-floor mammals of southeastern Alaskan temperate rain forest. Journal of Mammalogy 85:540–551.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. W.H. Freeman and Company, New York, New York, USA.

Stafford, S. R., and I. J. Stout. 1983. Dispersal of the cotton rat, *Sigmodon hispidus*. Journal of Mammalogy 64:210–217.

Sullivan, T. P., and C. J. Krebs. 1981. *Microtus* population biology: demography of *M. oregoni* in southwestern British Columbia. Canadian Journal of Zoology 59:2092–2102.

Tkadlec, E., and P. Krejčová. 2001. Age-specific effect of parity on litter size in the common vole (*Microtus arvalis*). Journal of Mammalogy 82:545–550.

U.S. Fish and Wildlife Service. 2009. Draft recovery plan for Tidal Marsh ecosystems of Northern and Central California. Sacramento Fish and Wildlife Office of the U.S. Fish and, Wildlife Service, Sacramento, California, USA.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Weber, L. M., and S. M. Haig. 1996. Shorebird use of South Carolina managed and natural wetlands. Journal of Wildlife Management 60: 73–82.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. LA-8787-NERP, UC-11. Los Alamos National Laboratory, Los Alamos, New Mexico, USA.

White, G. C., K. P. Burnham, D. L. Otis, and D. R. Anderson. 1978. User's manual for Program CAPTURE. Utah State University Press, Logan, USA.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Wilson, K. R., and D. R. Anderson. 1985*a*. Evaluation of a nested grid approach for estimating density. Journal of Wildlife Management 49:675–678.

Wilson, K. R., and D. R. Anderson. 1985*b*. Evaluation of two density estimators of small mammal population size. Journal of Mammalogy 66:13–21.

Wilson D. E., F. R. Cole, J. D. Nichols, R. Rudran, and M. S. Foster, editors. 1996. Measuring and monitoring biological diversity: standard methods for mammals. Smithsonian Institution Press, Washington, D.C., USA.

Winker, K., J. H. Rappole, and M. A. Ramos. 1995. The use of movement data as an assay of habitat quality. Oecologia 101:211–216.

Wondolleck, J. T., W. Zolan, and L. Stevens. 1976. A population study of harvest mice in the Palo Alto Salt Marsh. Wasmann Journal of Biology 34:52–64.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zetterquist, D. K. 1978. The salt marsh harvest mouse (*Reithrodontomys raviventris raviventris*) in marginal habitats. Wasmann Journal of Biology 35:68–76.

Associate Editor: Amy J. Kuenzi.