



Research Article

Waterfowl Management and Diet of the Salt Marsh Harvest Mouse

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ABSTRACT The salt marsh harvest mouse (*Reithrodontomys raviventris*) is an endangered species, endemic to the marshes of the San Francisco Bay, California, USA. This species is thought to feed primarily on pickleweed (*Salicornia pacifica*), although its diet is poorly understood, and a large proportion of remaining habitat for salt marsh harvest mice is managed for non-pickleweed vegetation to provide habitat for waterfowl. Using 2 sets of cafeteria trials, we tested food preferences of the salt marsh harvest mouse when offered a variety of plants and invertebrates from the Suisun Marsh, Solano County, California. In a set repeated menu, and unique seasonal menus, salt marsh harvest mice showed strong preferences for food types commonly grown for waterfowl, and also for non-native plants; in contrast, pickleweed was the most preferred during only some of the set and some of the seasonal trials. These results suggest that salt marsh harvest mice have a more flexible diet than previously thought, and will allow land managers in areas such as the Suisun Marsh to promote the growth of plants that provide foods that are preferred by both waterfowl and salt marsh harvest mice. © 2019 The Authors. The *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS cafeteria trial, diet, *Reithrodontomys raviventris*, salt marsh harvest mouse, San Francisco Estuary, Suisun Marsh, waterfowl management, wetlands.

The San Francisco Estuary (SFE; Fig. 1), California, USA, is biologically valuable and is one of the most threatened estuaries in the world. Twenty of the approximately 500 animal species found there are endangered (Goals Project 1999), and <20% of historical tidal marsh remains (Goals Project 2015). In addition to these ecological concerns, protecting this ecosystem has tremendous economic value. The economy of the greater San Francisco Bay Area (~\$535 billion in 2010) is the nineteenth largest in the world (Bay Area Council Economic Institute 2012). Recreational activities associated with wetlands in the San Francisco Bay engage tens of thousands of outdoor enthusiasts and bring in more than a billion dollars in local revenue annually (Goals Project 1999). Anthropogenic development and associated activities in the SFE have led to the introduction of dozens of non-native species, which have had diverse effects on the ecological and cultural value of wetlands, and recreation has contributed in part

to these introductions (Lampert et al. 2014, Moyle et al. 2014). Whereas most introductions fail (Mack et al. 2000), introduced species that become established can be harmful to the ecosystem (Cohen and Carlton 1998, Millennium Ecosystem Assessment 2005), though a proportion have provided cultural and economic benefits; for example, intentionally introduced striped bass (*Morone saxatilis*) support a lucrative recreational fishery (up to \$45 million/yr in the late 20th century; Cohen and Carlton 1998) in the SFE and Sacramento-San Joaquin Delta. Some introductions have even benefitted native, endangered species. As 1 example, non-native cordgrasses (*Spartina* spp.), intentionally introduced to the SFE, hybridize with native species and produce larger patches of vegetation than the pure native taxon (Zedler and Kercher 2004). Endangered Ridgway's rail (*Rallus obsoletus*) heavily colonize hybrid patches and populations increase; when managers remove hybrid patches, rail populations decrease (Lampert et al. 2014). As a result of dynamics such as these, the SFE has become a model system for managing and studying complex interactions between introduced and endangered native species (Lampert et al. 2014).

One SFE endemic species that is affected by introduced species is the salt marsh harvest mouse (*Reithrodontomys raviventris*; Fig. 2A; U.S. Fish and Wildlife Service [USFWS] 2010). The salt marsh harvest mouse was listed as endangered by the federal government in 1970 and by

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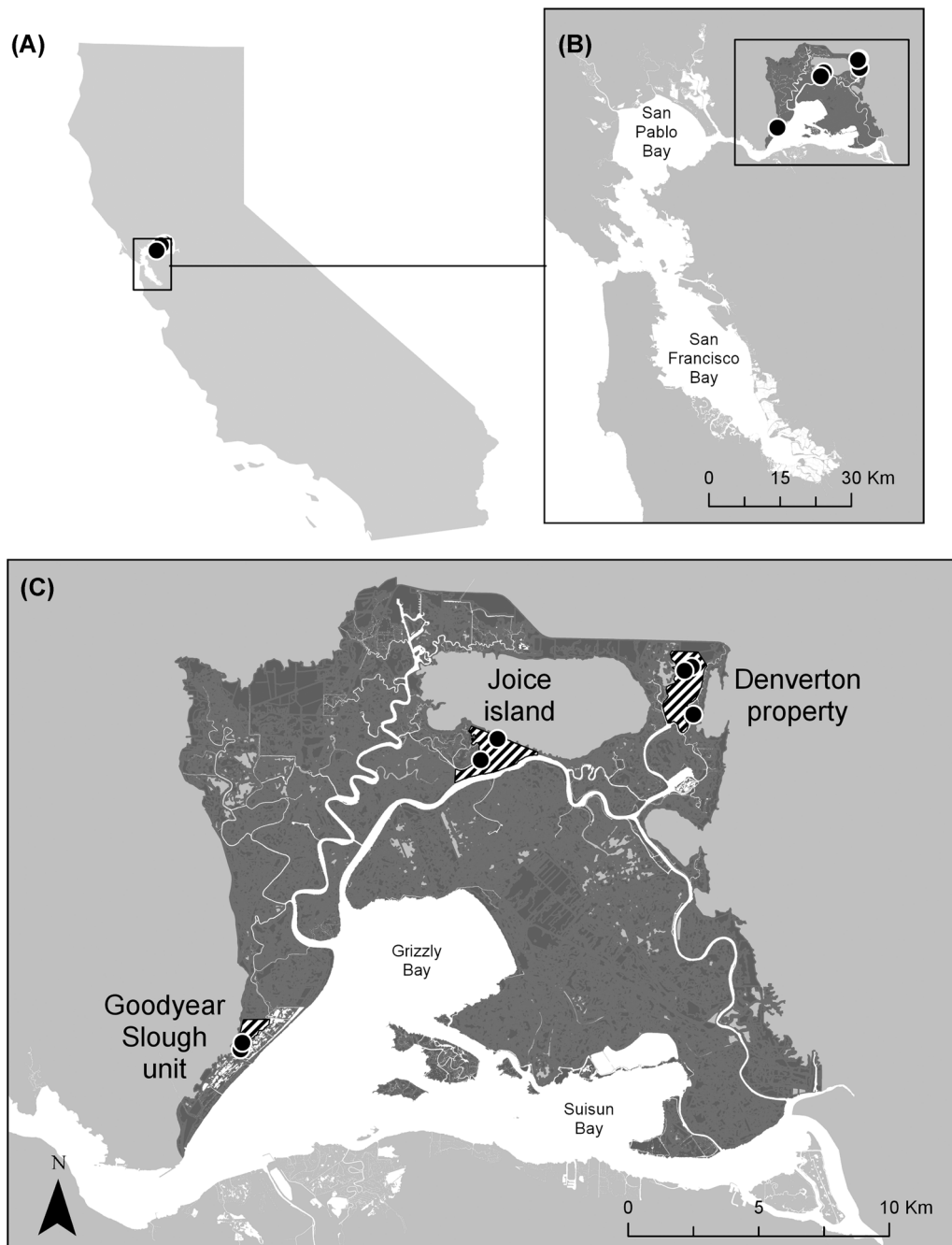


Figure 1. (A) The state of California, USA, with the San Francisco Estuary (B) enlarged in the upper inset, and the Suisun Marsh (C) enlarged in the lower inset. Study blocks used for a salt marsh harvest mouse diet preference study between September 2013 and August 2016 are marked by hatched polygons, and locations of trap grids are indicated by the black circles.

the State of California in 1971, primarily because of habitat loss (USFWS 1984). The salt marsh harvest mouse is a marsh obligate that is highly adapted for life in a physiologically (e.g., drinking saline water) and behaviorally (e.g., routinely avoiding tidal flux) stressful environments (Fisler 1965, Shellhammer et al. 2010, Smith et al. 2014), and is the only mammal species worldwide that is entirely restricted to coastal marshes (Greenberg and Maldonado 2006). Much early research on salt marsh harvest mice was primarily performed in the South San Francisco Bay where pickleweed (*Salicornia*

pacifica; Fig. 2B) is more dominant than in other areas of the SFE. These foundational efforts on the southern subspecies likely contributed to the management of salt marsh harvest mice overall as a relatively strict habitat specialist, relying heavily on tidal wetlands dominated by pickleweed (Fisler 1961, Shellhammer et al. 1982). Consequently, the effects of non-native species, especially plants, have been a conservation concern for salt marsh harvest mice for decades (USFWS 1984, 2013). The thought that salt marsh harvest mice require tidal wetlands dominated by pickleweed has persisted

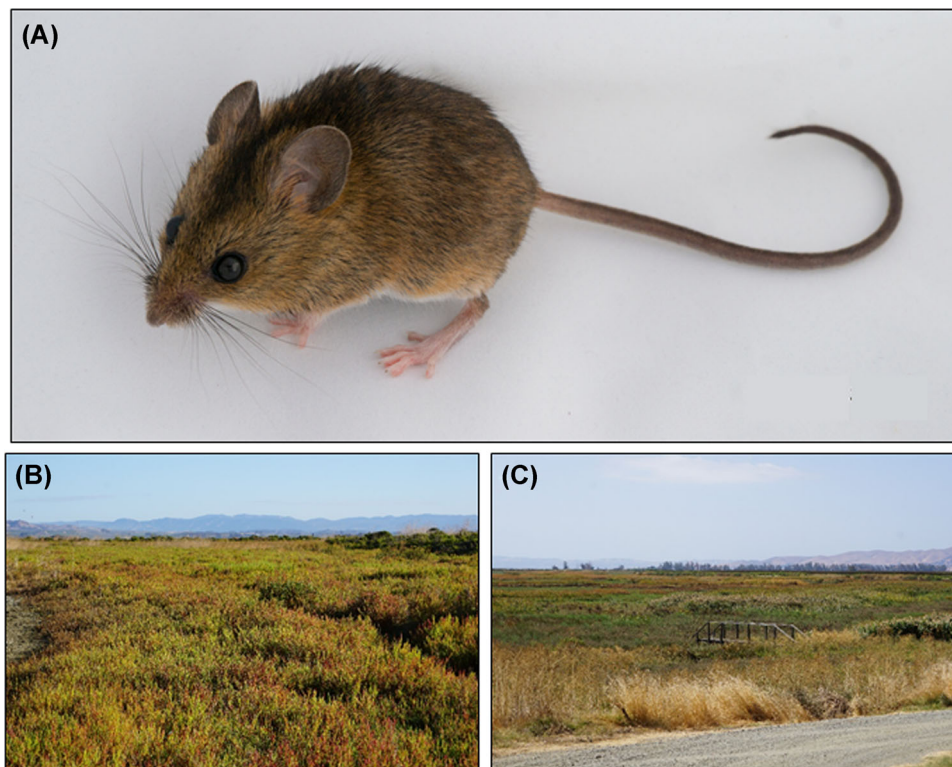


Figure 2. (A) A salt marsh harvest mouse. (B) A tidal wetland in the Suisun Marsh, Solano County, California, USA, dominated by pickleweed. This vegetation cover was considered necessary for persistence of salt marsh harvest mice. (C) A diked managed wetland in the Suisun Marsh, Solano County, California, USA, with a variety of vegetation types present. This land cover was thought to be detrimental to salt marsh harvest mice, but is now known to support healthy populations of this species. We used these wetland types for study on the diet preferences of salt marsh harvest mice between September 2013 and August 2016.

somewhat, despite the fact that researchers have increasingly reported that salt marsh harvest mice use non-tidal land cover types, and areas not dominated by pickleweed throughout the species' range (Fig. 2C; Zetterquist 1977; Botti et al. 1986; Shellhammer et al. 1988, 2010; Sustaita et al. 2011; Smith et al. 2014), though these areas were frequently considered marginal when compared to tidal wetlands dominated by pickleweed (Zetterquist 1977, Botti et al. 1986, Shellhammer et al. 1988). Additionally, to some unknown extent, some of our understanding, or misunderstanding, of habitat preferences by salt marsh harvest mice may reflect substantial challenges in field identification of sympatric harvest mice (Statham et al. 2016, Sustaita et al. 2018).

Use of non-tidal land cover types by salt marsh harvest mice has been studied in the Suisun Marsh (Fig. 1; Sustaita et al. 2011, Smith et al. 2014), which lies in the eastern SFE, composes a large proportion of remaining salt marsh harvest mouse habitat, and supports some of the largest remaining populations of the northern subspecies (*R. r. raviventris*). Suisun Marsh is maintained primarily as non-tidal wetlands (Sustaita et al. 2011), with tens of thousands of hectares managed by >150 private waterfowl hunting clubs, the California Department of Fish and Wildlife (CDFW), and others, to provide food and habitat for resident and migratory waterfowl and shorebirds. Managers promote growth of many non-native plant species, and favor vegetation assemblages that differ from

those found in the historical tidal wetlands in the SFE, a practice that provides wildlife habitat, and cultural and economic value through waterfowl hunting.

Resource agencies have assumed that pickleweed is the preferred and most important food source of salt marsh harvest mice, primarily based on the fact that salt marsh harvest mice are commonly trapped in pickleweed-dominated areas (USFWS 2010). The importance of pickleweed as a food source for salt marsh harvest mice, however, has never been directly investigated. Fisler (1965), making opportunistic observations, found that salt marsh harvest mouse gut contents were dominated by plant fibers but included few seed coats and insect remains. During dry months, stomach contents were brown and black, whereas during the wet months, when young grass was available, stomach contents were bright green. Fisler (1965) also reported that salt marsh harvest mice did not eat insects when these were offered in a laboratory setting. Unfortunately, there have been no studies directly investigating the diet or feeding ecology of salt marsh harvest mice in any capacity in the 5 decades since Fisler made these observations (Smith et al. 2018b), although several other species in the same genus have been reported to have flexible, omnivorous diets (Kincaid and Cameron 1982, Sealander and Heidt 1990, Clark et al. 2005). As a result, biologists and managers are unable to provide guidance to landowners on how to enhance food for this endangered species; this has raised concerns that wetlands managed for

waterfowl might not provide adequate food to sustain salt marsh harvest mouse populations. Researchers recently postulated that higher densities of salt marsh harvest mice in wetlands with a diverse mix of halophytic vegetation (as are commonly found in Suisun Marsh), as opposed to wetlands dominated by pickleweed, may be attributed to a greater diversity of food resources and indicate a flexible diet (Sustaita et al. 2011).

In contrast, the diets of waterfowl in Suisun have been better characterized, and biologists and wetland managers have developed methods of managing disturbance, hydrology, and water and soil salinity to encourage the growth of important waterfowl food types in managed wetlands (Ackerman et al. 2014). A study suggesting that large populations of rodents in the Suisun Marsh are correlated with higher nest success of waterfowl (Ackerman 2002), presumably by providing an alternative prey resource that relieves predation pressure on waterfowl nests, raises the possibility that promoting salt marsh harvest mouse populations may provide benefits to waterfowl managers. Hence, identifying preferred food types of salt marsh harvest mice, and overlaps in waterfowl and salt marsh harvest mouse diet, may lead to management recommendations that will provide an effective strategy for multispecies management.

We performed cafeteria trials on salt marsh harvest mice in the Suisun Marsh to identify important food sources for this species and to evaluate the extent of overlap with waterfowl food sources. We addressed the following questions: What plant and invertebrate species in the Suisun Marsh do salt marsh harvest mice prefer to consume, and are native species more strongly preferred? To what extent do the diet preferences of salt marsh harvest mouse overlap with those of waterfowl within the Suisun Marsh, and do mice in wetlands managed for waterfowl have preferences that differ from those occurring in tidal wetlands? We hypothesized that wetland type does not affect food preferences of salt marsh harvest mice, and predicted that they would consume a variety of foods, including non-native plants that are typically grown for waterfowl, but that they would more strongly prefer native plants.

STUDY AREA

We conducted this research between September 2013 and August 2016, on 3 blocks within the Suisun Marsh in Solano County, California (Fig. 1). We performed the study once per season (fall: Sep–Nov; winter: Dec–Feb; spring: Mar–May; summer: Jun–Aug) at each block, each year. Each block consisted of paired live-trapping grids (~1 ha), 1 in a tidal wetland and 1 in an adjacent (<1 km) managed wetland. One block (Denverton property) was owned and managed by the California Waterfowl Association, whereas the other 2 (Goodyear Slough and Joice Island) were units of the Grizzly Island Wildlife Area, owned and managed by CDFW.

The Suisun Marsh is a flat, low elevation (<3 m), wetland complex on the border of the San Francisco Bay Estuary and the Sacramento-San Joaquin Delta. The area is subject to a Mediterranean climate, with dry hot summers (\bar{x} high ~30°C); cool, wet falls and winters (\bar{x} high ~14°C); and warm, sometimes moist springs (\bar{x} high ~21°C). Dominant

flora within the marsh was characterized by emergent and high marsh vegetation in wetland areas, and annual grass and agriculture in upland areas. Land in the Suisun Marsh was managed for hunting (primarily for waterfowl) and fishing, outdoor recreation, and agriculture.

Dominant fauna of the Suisun Marsh consisted of wetland-associated species and generalists, including abundant waterfowl, shorebirds, passerines, mesocarnivores, and snakes, and the fish and invertebrates that inhabit aquatic features. Larger fauna were relatively rare but included black-tailed deer (*Odocoileus hemionus*), which were never observed at the study blocks, and feral hogs (*Sus scrofa*), which occurred commonly at Joice Island. Tule elk (*Cervus canadensis nannodes*) can occur at high densities in some areas of the Suisun Marsh but are largely restricted to the more isolated interior, distant from the study blocks. The small-mammal community was relatively depauperate, and included the salt marsh harvest mouse, western harvest mouse (*Reithrodontomys megalotis*), house mouse (*Mus musculus*), California vole (*Microtus californicus*), rats (*Rattus* spp.), and, at much lower densities, deer mice (*Peromyscus maniculatus*), shrews (*Sorex* spp.), and moles (*Scapanus* spp.).

METHODS

Diet Trials

We performed cafeteria trials once per season in each block, from fall (Sep) 2013 through summer (Aug) 2016 (hence, each of 4 seasons over 3 years). Within each block, we trapped 1 tidal area and 1 managed area simultaneously using Sherman live traps (Model LFA; H.B. Sherman Traps, Tallahassee, FL, USA) in grid arrangement. Trapping grids were large (1 ha, 60 traps [6 × 10] at 15-m spacing) and spanned a variety of plant assemblages in both wetland types. As part of a larger ecological study, we surveyed each block over 3 nights on a monthly (project yr 1) or bimonthly (project yrs 2 and 3) basis. We baited traps with birdseed and ground walnut, and provisioned them with cotton batting for warmth. We measured and individually marked animals with serially numbered ear tags (model 1005-1; National Band and Tag, Newport, KY, USA). During regular surveys we set traps shortly before sunset and checked them at sunrise (Smith 2018); on nights that we performed the diet study, we began checking traps several hours after they were deployed to obtain mice for cafeteria trials, which we conducted on site during the nocturnal active period of salt marsh harvest mice. We collected and tested up to 8 mice/wetland type/night (depending on capture success) and endeavored to balance sexes. Because of time constraints, we used the first 8 animals captured in the trials, unless sexes were extremely skewed and we deemed it prudent to wait for additional individuals to be captured. We captured few juveniles throughout the study, but we included them when possible.

We measured vegetation metrics (e.g., dominant species, height, percent cover of individual species) at each trap location within all grids on the seasonal basis, concurrent with trapping. We then summarized measurements at

individual traps to calculate grid-scale characteristics (e.g., average pickleweed cover at each grid). Tidal grids received natural tidal inundation, and managed trapping grids were subject to a variety of land management practices associated with waterfowl hunting (e.g., flooding, mowing, discing).

Because we baited live traps with a relatively large amount of high-fat bait, captured salt marsh harvest mice were capable of feeding to satiation before we retrieved them for use in cafeteria trials. To ensure that salt marsh harvest mice were hungry, we withheld food for 2 hours (~25% of their potential foraging time on the shortest summer nights) after capture. After fasting, we placed 1 mouse in each of 1–8 feeding arenas constructed from 19-L buckets. Each bucket contained 7 glass containers (tea light candle holders) filled (by volume) with different food types (see below) and arranged in a circle. For insulation we placed a handful of cotton batting at the center of the arena (Fig. 3A). We covered each bucket with a lid that was fitted with a video camera (Swann SWDVR-16150H; Swann Communications, Port Melbourne, Victoria, Australia; Fig. 3B), and we recorded all activities for 2 hours. We then removed mice and returned them to their point of capture. We tested up to 8 mice simultaneously, and the logistics of checking traps in a timely manner dictated that these all came from 1 randomly selected trapping grid (e.g., either tidal or managed wetland). While the first round of mice were completing the trial, we collected up to 8 more mice from the other wetland type. We tested these animals after the first trial and the second fasting period were completed. We ran only 2 sets of trials in a given night, which required about 8 hours. Because summer nights last about 9 hours at our site, this protocol allowed us to maximize the number of trials performed.

We presented salt marsh harvest mice with 1 of 2 menus: set and seasonal. We developed the set menu in consultation with a representative from California Waterfowl Association and it included 4 plant species (food types) known to be eaten commonly by waterfowl in the Suisun Marsh (alkali bulrush [*Bolboschoenus maritimus*], fat-hen [*Atriplex prostrata*], rabbitsfoot grass [*Polypogon monspeliensis*], and watergrass [*Echinochloa crus-galli*]), and 3 plant species that are strongly associated with salt marsh harvest mouse captures during live trapping in Suisun Marsh (pickleweed, saltgrass [*Distichlis spicata*], tricorner bulrush [*Schoenoplectus americanus*]; Fig. 3C). The set menu consisted of the dehydrated seed-containing portions of these plants (e.g., seed heads, dried succulent stems) collected from all study blocks and combined by food type.

There were 2 limitations of the set menu. First, we collected seeds at peak ripeness, dried them, and offered them throughout all 3 years of the study. Thus, during all seasons, we offered mice ripe seeds, even though these were not available from all plant species in each season in each wetland type. Second, watergrass was not naturally available throughout the duration of the study because of an extended drought. To compensate to some extent for these constraints, and to test seasonally relevant foods, we developed the seasonal menu. The seasonal menu consisted of the 7 most abundant plant or invertebrate species at each wetland during the focal season (based on vegetation metrics recorded as part of the live-trapping study). Consequently, the seasonal menu varied somewhat across wetlands and seasons. The food types offered in the seasonal menu included seeds, leaves and blades, flowers, fruits, and roots in various stages of development, and live beetles and amphipods (see Appendix B, available online in Supporting Information).



Figure 3. (A) A salt marsh harvest mouse inside the feeding arena provisioned with a sample seasonal menu used for a diet preference study in the Suisun Marsh, Solano County, California, USA, September 2016 to August 2018. (B) We fitted video cameras into holes in the top of the bucket lids to record feeding behaviors while keeping mice sheltered. (C) The plants of the set menu. From left to right: rabbitsfoot grass, fat-hen, pickleweed, watergrass, alkali bulrush, tricorner bulrush, and salt grass.

Following the trials, trained technicians coded and analyzed videos; they recorded the duration of time a mouse smelled, physically inspected without eating, or ate any of the food types. We then spot-checked the data, verifying each of the 3 longest feeding events (uninterrupted period feeding on 1 food type) and resolving instances in which video technicians were unsure about potential feeding behaviors or food type.

If an individual mouse did not investigate (smell, inspect, eat) ≥ 3 different food types during a trial, or spend ≥ 30 seconds eating during the trial (suggesting that it was not hungry), or if technical malfunctions led to missing videos or portions of videos, we omitted that individual's trial from analysis ($n = 39$ individual trials from the set menu and 31 individual trials from the seasonal menu). Five mice were offered the set menu over multiple seasons; for these animals, we retained only the trial from the more under-represented season to help balance sample sizes. In preparation for analysis, we summed the time each mouse spent eating each food type during a given trial.

Despite fasting for 2 hours before the cafeteria trials, there were substantial differences in the apparent hunger levels of individual mice when exposed to foods in the cafeteria trials; some individuals spent more than an hour eating (max. 73 min) and others did not eat at all during their trial. We presume that these differences indicate variation in baseline metabolic needs over which we had no control, but this variation should add noise to the data and not bias results in any direction. Nonetheless, to account for this we also transformed the time each individual spent eating each food type during set menu trials into a proportion of time spent eating overall (all food types) during their trial.

This study followed American Society of Mammalogists guidelines (Sikes 2016). It was approved by the University of California at Davis Animal Care and Use Committee (19323), and was conducted under a Cooperative Agreement between CDFW and the USFWS.

Data Analysis

Set and seasonal menus.—Because our data included a large number of zero values (for animals that spent no time eating a given food type), it proved impossible to transform these for parametric analyses. Consequently, to determine overall effects on the amount of time salt marsh harvest mice spent eating, we performed a semiparametric repeated measures multivariate analysis of variance (MANOVA; function RM in package MANOVA.RM in program R; R Development Core Team 2016, Friedrich et al. 2018). This package allows for a permutational approach (Friedrich et al. 2017), and provides a Wald-type statistic, which is interpreted as a traditional F -statistic. We ran 10,000 iterations on the time each mouse spent eating. Main factors included food type, wetland type, season, block, percent cover of food type within trapping grid, project year, and sex. Additionally, to evaluate whether food preferences varied across other factors, we included the interaction of food type with all other factors. Because of constraints of the analysis (insufficient factor-level combinations), the model could not accommodate all main

effects, and we approached this analysis in 2 *a priori* phases. In the first phase, we assessed which main factors (block, percent cover of food type, sex, wetland type, season, project year, and food type) significantly influenced time spent eating and food type choice in the set menu. These analyses indicated that block, percent cover of food type, and sex did not significantly affect mouse foraging in the set menu; thus, we omitted these from subsequent analysis. Hence, our second (final) phase modeled time \sim wetland type \times season \times project year \times food type (e.g., testing the remaining 4 factors and all 2-, 3-, and 4-way interactions), where food type was the repeated measure and individual mice were the subjects. We performed the same analysis with proportion of time spent eating the various food types to account for different hunger levels. Results for these analyses (e.g., actual vs. proportional time) were qualitatively similar, so we report only the time data.

These analyses were not parametric, so traditional *post hoc* tests (e.g., Scheffé, Tukey) were not available. Consequently, we made *post hoc* comparisons using medians and quartiles. We identified differences between time spent eating food types by evaluating overlap of median values with median values and quartiles (25% lower and 75% upper) of the same food type in the other wetland type (e.g., pickleweed in managed vs. tidal wetlands), and with the medians and quartiles of the other food types in both wetland types (e.g., pickleweed in managed wetlands vs. fathen in managed wetlands). If quartiles overlapped with both medians, we considered there to be no difference between them. If quartiles overlapped, but ≥ 1 median was outside of the quartiles being compared, then we concluded that it was likely that there was a difference between the 2 groups. If there was no overlap between medians and quartiles, then we considered the 2 groups to be different.

As noted above, we developed seasonal menus to compensate for limitations with the set menu. These also presented analytical constraints, however, because menus varied (e.g., site to site, season to season). As such, food types were not balanced across sites, seasons, or years, precluding a MANOVA-style analysis. Instead, we calculated the time each mouse spent eating each food type during its trial, pooled all individuals by season and wetland type (e.g., across sites and years; hence, 4 seasons \times 2 wetland types = 8 sets of data) and calculated the mean time spent eating the food types offered. We also applied a linear model (function lm in package stats in program R; R Development Core Team 2016) to test for a correlation between the mean time spent eating each of the food types offered during a session (trial corresponding to 1 wetland type within a site, season, and yr; $\alpha = 0.05$) and the only correlate for which sufficient data exist, the percent cover of the food type at the wetland during that session (time spent eating food type \sim percent cover of food type corresponding to that wetland type at that site within that season and year). We developed separate models for each season and wetland type combination, and because these 8 analyses are not entirely independent, any results should be interpreted cautiously; we provide Bonferroni-adjusted critical values for comparison (assuming replicate tests within seasons

may not be fully independent, $P_{\text{crit(adj)}} = 0.05/2 = 0.025$). More conservative adjustments could be made (e.g., $P_{\text{crit(adj)}} = 0.05/8 = 0.00625$), but this would not influence interpretation.

Comparing diets of salt marsh harvest mouse and waterfowl.—Mall (1969) and Burns (2003) studied waterfowl diet in Suisun Marsh, and both found that waterfowl selected strongly for alkali bulrush and watergrass (Appendix A, available online in Supporting Information). Waterfowl commonly consumed, but did not necessarily select for, pickleweed, annual grasses (including rabbitsfoot grass), saltgrass, and tricorner bulrush. Notably, waterfowl strongly selected for fat-hen in Mall’s study (1969) but not in Burns’ study (2003). In the context of these studies, we examined potential overlap between waterfowl and salt marsh harvest mouse diet preferences by calculating the proportion of the top 1, 2, and 3 most favored foods (per individual) in the set menu that were waterfowl foods (i.e., alkali bulrush, fat-hen, rabbitsfoot grass, watergrass) versus mouse foods (i.e., pickleweed, saltgrass, tricorner bulrush). For example, if 2 of the top 3 foods an individual mouse spent the most time eating were duck foods, then 66.66% of its top choices were duck foods. We then calculated the mean proportions of the top 1, 2, and 3 most favored foods, across all set menu trials, that were waterfowl foods. For further comparison we extracted data on waterfowl diet preferences from Mall (1969) and Burns (2003), who presented 4 metrics of diet: a use index (frequency of occurrence in diet \times percent volume of plant species in waterfowl diet), a selection index (the use index \div the relative abundance of plant species), percent occurrence in individuals, and percent dry esophageal content. To determine if salt marsh harvest mice and waterfowl in Suisun Marsh have similar patterns of preference, we compared the ranking of the set menu food types with the rankings of the top food types in the waterfowl diet studies with a Kendall rank

correlation (function `cor.test` in package `stats` in program R; R Development Core Team 2016).

RESULTS

Set and Seasonal Menus

We presented the set menu on 59 occasions (managed wetlands, $n = 32$; tidal wetlands, $n = 27$). This included 293 salt marsh harvest mice that were offered the set menu 303 times, yielding 12,571 smelling, investigating, and feeding events. Food type, wetland type, and season significantly influenced the total time individual salt marsh harvest mice spent eating (Table 1). Moreover, the MANOVA revealed 3 pairwise interactions and 1 3-way interaction, all involving food type, were significant (Table 1; Fig. 4). Based on means and confidence intervals calculated in the MANOVA, mice in managed wetlands spent more time eating than mice in tidal wetlands ($\bar{x} = 308.20$ [CI = 272.04, 344.36] seconds, $n = 155$, vs. 232.91 [198.77, 267.05] seconds, $n = 102$; Table 1). This pattern appears to be attributable to the time spent eating rabbitsfoot grass in managed wetlands (Fig. 5); if rabbitsfoot grass is omitted, there is no difference in time spent eating between wetland types (206.68 [178.66, 234.69] seconds in managed vs. 216.46 [181.37, 251.55] seconds in tidal wetlands). Mice spent more time eating in the fall (345.83 [269.96, 421.71] seconds, $n = 50$) than in the spring (265.22 [224.78, 305.67] seconds, $n = 78$) and summer (230.43 [178.06, 282.80] seconds, $n = 59$), and more time in winter (285.05 [240.28, 329.82] seconds, $n = 70$) than summer. As expected, project year did not affect the mean time spent eating overall.

All pairwise interactions with food type tested in the MANOVA were significant, indicating that food type preferences differed between wetland types, across seasons, and across project years. Overall, salt marsh harvest mouse mean food preferences declined in the following order: rabbitsfoot grass > fat-hen > pickleweed > watergrass > alkali

Table 1. Test statistics, including the Wald-type statistic (WTS), degrees of freedom, P -values, and resampling-based P -values, resulting from the 10,000-iteration repeated measures multivariate analysis of variance for a set menu cafeteria trial for salt marsh harvest mice in a diet preference study in the Suisun Marsh, Solano County, California, USA, September 2016 to August 2018.

	WTS	df	P	Resampled P
Food type	370.51	6	<0.001***	<0.001***
Wetland type	13.10	1	<0.001***	<0.001***
Season	13.67	3	0.003**	0.022*
Project year	4.42	2	0.298	0.331
Wetland type \times food type	45.18	6	<0.001***	<0.001***
Season type \times food type	71.59	18	<0.001***	0.006**
Project year \times food type	50.02	12	<0.001***	0.002**
Wetland type \times season	2.42	3	0.595	0.639
Wetland type \times project year	1.91	2	0.385	0.409
Season \times project year	16.12	6	0.013*	0.061
Wetland type \times season \times food type	33.84	18	0.013*	0.162
Wetland type \times project year \times food type	11.55	12	0.482	0.675
Season \times project year \times food type	141.13	36	<0.001***	0.020*
Wetland type \times season \times project year	10.33	6	0.111	0.206
Wetland type \times season \times project year \times food type	70.02	36	0.001**	0.299

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

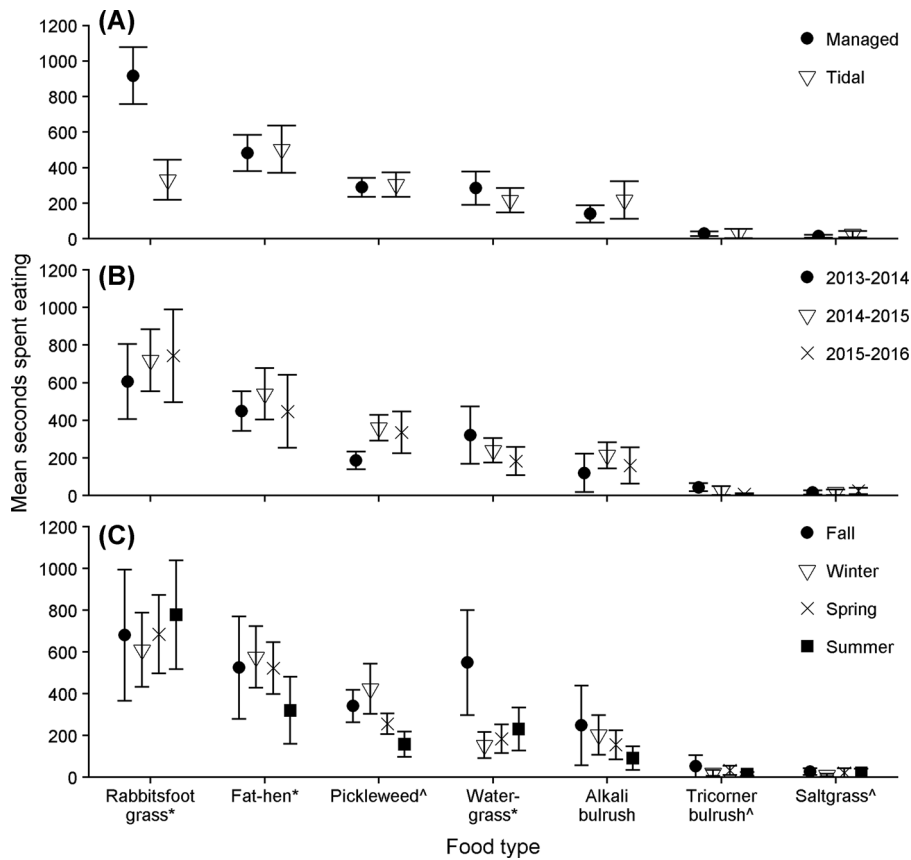


Figure 4. Plots for interactions between the main effects in the cafeteria trial set menu for salt marsh harvest mice in a diet preference study in the Suisun Marsh, Solano County, California, USA, September 2016 to August 2018. We present relationships by food type between mean time spent feeding (seconds) and wetland type (A), project year (B), and season (C). Non-native plants are marked with an asterisk (*). Plants that were chosen because of their association with salt marsh harvest mice, but are not typical waterfowl foods, are marked with a caret (^).

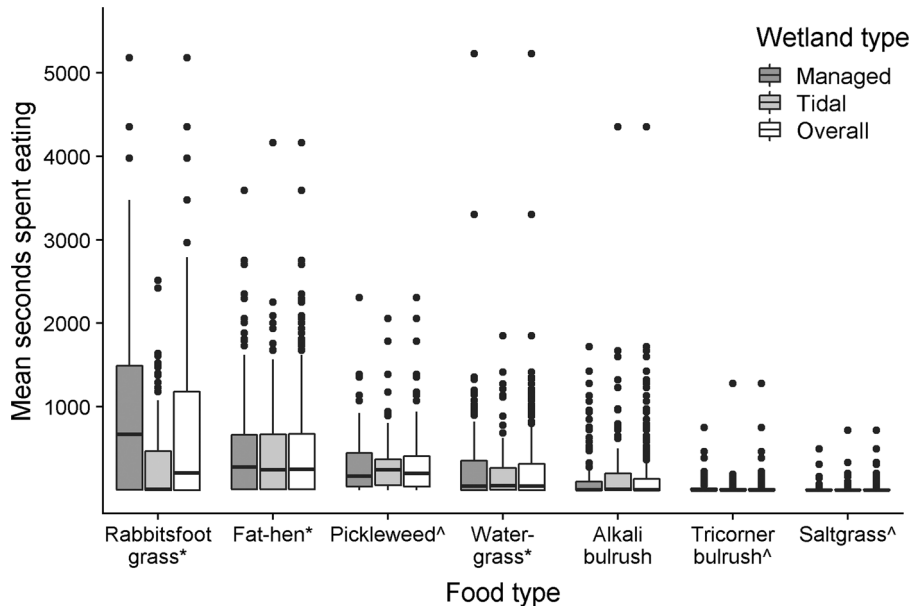


Figure 5. Time salt marsh harvest mice spent eating set menu foods by wetland type, and overall medians (combined managed and tidal values) in a diet preference study in the Suisun Marsh, Solano County, California, USA, September 2016 to August 2018. Non-native plants are marked with an asterisk (*). Plants that were chosen because of their association with salt marsh harvest mice, but are not typical waterfowl foods, are marked with a caret (^).

Table 2. Median time, in seconds, salt marsh harvest mice in a diet preference study in the Suisun Marsh, Solano County, California, USA, September 2016 to August 2018, spent eating foods in the set menu with 25% lower quartile (Q1) and 75% upper quartile (Q3) values. Differences in time spent eating different food types are indicated by superscripted letters in the median columns; foods with different letters received significantly different levels of attention from mice.

	Overall				Managed wetlands				Tidal wetlands			
	<i>n</i>	Median	Q1	Q3	<i>n</i>	Median	Q1	Q3	<i>n</i>	Median	Q1	Q3
Rabbitsfoot grass	257	99.00	0.00	1164.00	155	703.00	7.50	1518.50	102	5.00	0.00	446.00
Fat-hen	257	177.00	0.00	630.00	155	178.50	0.00	625.75	102	176.00	3.50	638.00
Pickleweed	257	158.00 ^A	18.00	365.00	155	146.00 ^A	28.25	415.25	102	182.00 ^A	12.00	335.50
Watergrass	257	37.00	0.00	256.00	155	40.50	0.00	291.00	102	32.00	0.00	183.00
Alkali bulrush	257	0.00	0.00	107.00	155	0.00	0.00	96.00	102	0.00	0.00	136.00
Tricorner bulrush	257	0.00 ^B	0.00	16.00	155	0.00 ^B	0.00	19.00	102	0.00 ^B	0.00	9.50
Saltgrass	257	0.00 ^B	0.00	8.00	155	0.00 ^B	0.00	8.00	102	0.00 ^B	0.00	8.00

bulrush > tricorner bulrush > saltgrass, and all paired means differed except between pickleweed and watergrass, and between watergrass and alkali bulrush. When contrasted by medians and 25% (Q1) and 75% (Q3) quartiles, many of the significant differences dropped out and the ranking changed slightly: pickleweed > fat-hen > rabbitsfoot grass > watergrass > alkali bulrush > tricorner bulrush > saltgrass (Table 2; Fig. 5). There were still a large number of less than significant but potentially biologically relevant differences (e.g., when quartiles overlapped, but medians fell outside contrasting quartiles). Based on this measure, all 4 of the top ranked food types were eaten for more time than the lowest 2 ranked foods (tricorner bulrush, saltgrass), except in the case of rabbitsfoot grass in tidal wetlands. As noted previously, salt marsh harvest mice spent more time eating rabbitsfoot grass in managed than in tidal wetlands (median = 703.00 [Q1 = 7.500, Q3 = 1518.50] seconds vs. 5.00 [0, 446.00] seconds respectively; Fig. 5), although no other food types elicited responses across wetland type.

The MANOVA indicated interannual variation in consumption of 2 food types, spending significantly more time eating pickleweed in the second than the first year of the project (\bar{x} = 360.19 [CI = 291.26, 429.11] seconds and 187.02 [139.64, 234.41] seconds, respectively), whereas the time spent eating during the third year was intermediate but much closer to the second year time than the first (336.04 [224.06, 448.02] seconds; Fig. 4B). Mean time eating tricorner bulrush decreased steadily throughout the study, from year 1 (44.39 [22.57, 66.22] seconds) to year 2 (26.53 [3.87, 49.27] seconds) and year 3 (7.78 [3.11, 12.45] seconds), with the first year being significantly higher than the last (Fig. 4B). Finally, salt marsh harvest mice exhibited seasonal preferences for only 2 food types. They spent significantly more time eating watergrass in the fall (549.04 [297.07, 801.00] seconds, n = 50) than either spring (184.51 [115.45, 253.58] seconds, n = 78) or winter (153.50 [90.82, 216.18] seconds, n = 70) but not summer (230.81 [127.12, 334.51] seconds, n = 59; Fig. 4C), and more time eating pickleweed in winter (423.29 [303.71, 542.86] seconds, n = 70) than spring (255.77 [206.64, 304.90] seconds, n = 78) or summer (158.20 [97.22, 219.19] seconds, n = 59) but not fall (340.70 [262.21, 419.19] seconds, n = 50; Fig. 4C).

Of the 5 mice that were offered the set menu more than once, only 1 individual favored different foods in different seasons; in fall 2013 it spent the greatest amount of time eating alkali bulrush, and in winter 2014, it spent most of its

time eating fat-hen. Two individuals spent the most time eating fat-hen in both spring and summer 2014, and a third spent most of its time eating rabbitsfoot grass during spring and summer. One individual tested in the winter, spring, and summer of 2015 spent most of its time eating rabbitsfoot grass during all 3 seasons.

We offered salt marsh harvest mice (n = 251) the seasonal menu on 45 occasions (managed wetlands, n = 25; tidal wetlands, n = 20), and recorded 12,583 smelling, investigating, and feeding events. Overall, the seasonal menu included 39 different plants and invertebrates, all of which were eaten by salt marsh harvest mice at least once (Appendix B, available online in Supporting Information). Pickleweed was the only food type that occurred in every seasonal menu (e.g., 25 different seasonal menus in managed wetlands, 20 different seasonal menus in tidal wetlands). The next most common types were fat-hen (19 managed, 9 tidal), common reed (*Phragmites australis*; 19 managed, 4 tidal), saltgrass (13 managed, 7 tidal), hardstem bulrush (*Schoenoplectus* spp.; 8 managed, 9 tidal), and pepperweed (*Lepidium latifolia*; 7 managed, 10 tidal). In managed wetlands, food types that were ranked in relative preference (e.g., top 5 species) during ≥ 2 seasons included the 3 top food types from the set menu (rabbitsfoot grass, fat-hen, and pickleweed), annual grasses, hardstem bulrush, sea purslane (*Sesuvium verrucosum*), and saltgrass (Table 3), the latter of which ranked lowest in the set menu (Table 2). In tidal wetlands, food types that were highly ranked in ≥ 2 seasons included 2 of the top 3 food types from the set menu (fat-hen and pickleweed), cattail (*Typha* spp.), Baltic rush (*Juncus balticus*), hardstem bulrush, and marsh arrowgrass (*Triglochin maritima*; Table 3). Finally, most of the 8 linear models (4 seasons \times 2 wetland types) we evaluated yielded very poor correlations between time spent eating seasonal menu food types and their associated seasonal percent covers in each wetland type (all $P \geq 0.25$, all $R_{adj}^2 \leq 0.088$).

Salt Marsh Harvest Mice and Waterfowl

A very high proportion of mice in the set menu trials spent most of their time eating waterfowl foods (e.g., alkali bulrush, fat-hen, rabbitsfoot grass, watergrass). Indeed, almost 90% of mice in managed wetlands and >80% of individuals in tidal wetlands ranked a waterfowl food highest (managed wetlands, 88.39 ± 2.58 [SE] %, n = 155; tidal wetlands, $81.37 \pm 3.87\%$,

Table 3. The top 5 seasonal food choices of salt marsh harvest mice in managed and tidal wetlands, in a diet preference study in the Suisun Marsh, Solano County, California, USA, September 2016 to August 2018. Preferences were pooled by season and wetland type. Number of menus pooled is denoted by *n*, and mean and standard deviation are presented. Superscripts denote non-native species (¹) and species with non-native genotypes, or groups with some non-native species present (²).

Managed wetlands				Tidal wetlands			
	<i>n</i>	\bar{x}	SD		<i>n</i>	\bar{x}	SD
Fall				Fall			
Pickleweed	21	0.46	0.32	Fat-hen ¹	18	0.39	0.25
Fat-hen ¹	21	0.27	0.25	Cattail ²	19	0.29	0.36
Sea purslane	5	0.15	0.2	Pickleweed	24	0.27	0.26
Hardstem bulrush	7	0.1	0.22	Baltic rush	6	0.13	0.16
California rose	13	0.1	0.27	Hardstem bulrush	17	0.09	0.14
Winter				Winter			
Pickleweed	34	0.47	0.36	Fat-hen ¹	9	0.6	0.23
Fat-hen ¹	23	0.33	0.25	Pickleweed	20	0.23	0.23
Young annual grass ²	12	0.22	0.29	Cattail ²	16	0.21	0.21
Rabbitsfoot grass ¹	17	0.14	0.24	Baltic rush	11	0.11	0.19
Saltgrass	14	0.08	0.16	Alkali heath	8	0.11	0.04
Spring				Spring			
Rabbitsfoot grass ¹	20	0.34	0.3	Baltic rush	17	0.49	0.35
Annual grass ²	10	0.26	0.14	Marsh arrowgrass	17	0.31	0.26
Hardstem bulrush	16	0.23	0.24	Tricorner bulrush	10	0.13	0.18
Fat-hen ¹	16	0.17	0.25	Invertebrates	11	0.05	0.08
Saltgrass	20	0.14	0.17	Pickleweed	17	0.04	0.08
Summer				Summer			
Rabbitsfoot grass ¹	34	0.41	0.37	Marsh arrowgrass	13	0.59	0.28
Knotweed ²	8	0.34	0.26	Common reed ²	16	0.38	0.36
Common reed ²	29	0.22	0.33	Hardstem bulrush	18	0.24	0.3
Dock spp.	6	0.21	0.24	Cattail ²	16	0.22	0.28
Sea purslane	26	0.17	0.22	Dodder	8	0.11	0.03

n = 102). When we included the top 2 and top 3 ranked foods, the percentages remained high ($77.42 \pm 2.16\%$ and $70.54 \pm 1.52\%$ for the top 2 and 3 in managed wetlands, respectively, and $70.59 \pm 2.64\%$ and $63.07 \pm 1.85\%$ for the top 2 and 3 in tidal wetlands, respectively). These patterns of preference suggest that there may be common preferences between salt marsh harvest mice and waterfowl.

Integrating our set menu (Fig. 5) with results of Mall (1969) and Burns (2003), both salt marsh harvest mice and waterfowl ranked fat-hen, pickleweed, rabbitsfoot grass, and watergrass high, whereas they ranked saltgrass and tricorn bulrush low (Fig. 6). In contrast, alkali bulrush was the top choice in both waterfowl studies but ranked relatively low in the set menu (but notably higher than saltgrass and tricorn bulrush; Fig. 6). Despite these qualitative similarities, a rank correlation revealed that none of the pairwise comparisons, including a comparison of the 2 waterfowl diet studies, were significantly correlated (all Kendall's tau ≤ 0.43 , and all $P \geq 0.23$).

DISCUSSION

We designed our cafeteria trials to characterize the seasonal diet preferences of salt marsh harvest mice, to test salt marsh harvest mouse preferences for native plants versus non-native, and to determine if salt marsh harvest mice and waterfowl have similar diet preferences. Across both menus, at least one salt marsh harvest mouse consumed at least some of each of the 39 different plants and animals offered to them, but overall showed preferences (e.g., >10% of their time eating) for only about half of the food types. When offered the set menu, salt marsh harvest mice spent the

greatest amount of time eating non-native plants (rabbitsfoot grass and fat-hen). Further, even though the majority of foods in the seasonal menu were native food types (>85%), 37.50% of the highest-ranked food types each season were non-native foods.

There was no evidence that time spent eating different food types was proportional to their availability in wetlands. Rabbitsfoot grass ranked high in the set menu in both wetland types, despite being relatively rare in tidal wetlands, and watergrass ranked high in both wetland types, despite not being present at any of the study blocks. Further, in the seasonal menu, salt marsh harvest mice spent considerable time eating some plant species that are rare in both wetland types. For example, marsh arrowgrass, which occurred at <50 seeding stems/study wetland (and seeds only for a very short time during the summer), was allocated a large amount of time by salt marsh harvest mice in all seasonal menus where it was presented (Table 3). Hence, salt marsh harvest mice have a flexible diet, with no apparent preference for allocating time to eating native over non-natives plants or common over rare plants, which could indicate that they may preferentially forage on non-native and or rare foods *in situ*.

Salt marsh harvest mice spent a large proportion of their time eating foods favored by waterfowl (Fig. 6; Tables 2, 3). Waterfowl foods ranked in the top 2 in managed (rabbitsfoot grass, highest) and tidal wetlands (fat-hen, second highest behind pickleweed) in the set menu. In contrast, pickleweed (generally assumed to be the most preferred food) ranked behind the non-native fat-hen in the set menu overall (Table 2) and was highly selected only about half of the time in the seasonal menu (Table 3).

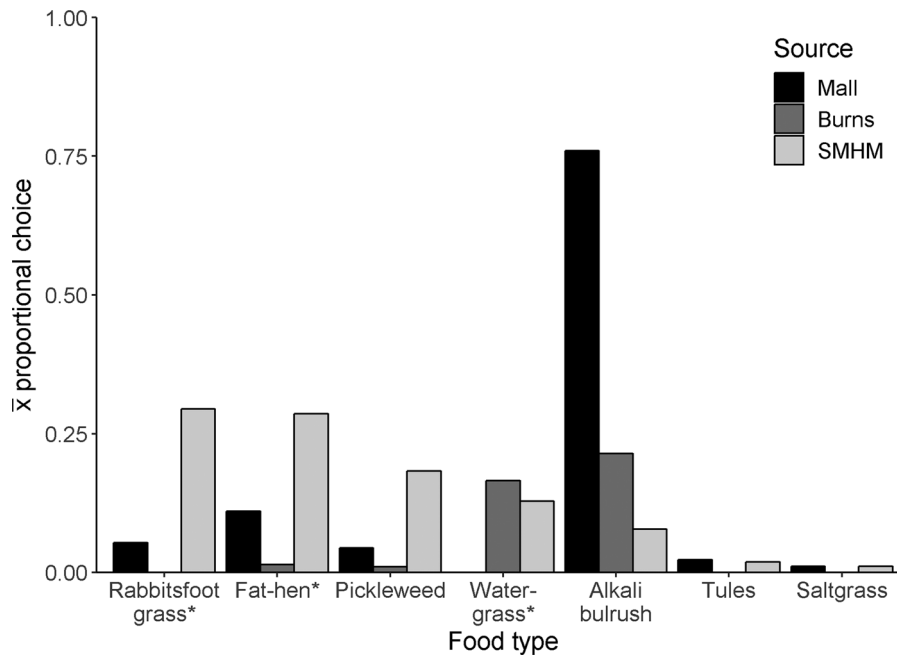


Figure 6. Mean proportional preferences of waterfowl from Mall (1969) and Burns (2003) compared with those of the salt marsh harvest mouse (SMHM) in the set menu in a diet preference study in the Suisun Marsh, Solano County, California, USA, September 2016 to August 2018. Bulrushes of the genus *Schoenoplectus* (tricornet bulrush and hardstem bulrush or tule) are combined as tules.

Salt marsh harvest mice in our cafeteria trials consumed 39 different foods, including beetles and amphipods, in opposition to Fisler (1965). Further, during field efforts we saw salt marsh harvest mice eating insects and consuming a variety of plant species (K. R. Smith, University of California, Davis, personal observation). Only 7 of the 23 species of harvest mice have been subjected to dietary studies, but they generally exhibit omnivorous and seasonally flexible diets (e.g., eastern harvest mouse [*R. humulis*], Sealander and Heidt 1990; fulvous harvest mouse [*R. fulvescens*], Kincaid and Cameron 1982; western harvest mouse, Webster and Jones 1982; plains harvest mouse [*R. montanus*], the closest relative of the salt marsh harvest mouse, Clark et al. 2005).

Additionally, rodent species of other genera that occur in the SFE exhibit flexible diet habits. The diet of California voles in the SFE is composed primarily of grass leaves and stems (~88%) and forb leaves (9.3%) during the wet season but shifts to specialize on grass seeds (72.6%) and forb leaves (15.4%) during the dry season (Batzli and Pitelka 1971). Further, these preferences held even when individuals originally from the SFE were bred several generations in captivity (Gill 1977).

We recognize that cafeteria trials have limitations, but the more direct approach of stomach content analysis is not an option for endangered species, and microhistological analysis of feces suffers from bias associated with differential digestibility of foods (Vavra and Holechek 1980). Chief concerns with our approach are that animals are differentially allocating time to a limited subset of potential foods, and that we interpret differential time allocated to different foods as preference; other factors could influence the time spent on a given food item, such as handling time,

processing time, novelty, or familiarity. All foods used in our study occur in the Suisun Marsh and therefore should be relatively familiar to salt marsh harvest mice. Moreover, time allocated to food types was similar across menus, sites, seasons, and years (and thus generations of salt marsh harvest mice, which typically live less than 1 year according to Fisler [1965]), suggesting that results presented here reflect biologically relevant preferences. Hence, although directly comparing salt marsh harvest mouse diet based on cafeteria trials against waterfowl diets based on esophageal content is not ideal, we think that any associated bias is conservative and that our results (i.e., that foods planted for waterfowl are readily consumed by salt marsh harvest mice) are robust to any methodological concerns. Nonetheless, we recommend that the diet of salt marsh harvest mouse continue to be investigated, preferably using modern genetic techniques (Valentini et al. 2009), and throughout the SFE.

This study illustrates an unrecognized positive influence of waterfowl management on salt marsh harvest mice (e.g., providing food), suggesting that simultaneous management of waterfowl and endangered salt marsh harvest mice may be more practical than previously thought. Finally, climate change and sea level rise are projected to lead to large-scale shifts in vegetation communities in the SFE (Takekawa et al. 2013), and understanding how salt marsh harvest mice will respond to these changes is a high priority research need (Smith et al. 2018a). Whether the flexible diet of salt marsh harvest mice, and their ability to use non-native plants as food, will provide them with some resilience to these changes remains an important research priority (e.g., Cudworth and Koprowski 2013, Juškaitis and Baltrūnaitė 2013). Regardless, this work suggests that even habitats that have been considered marginal for salt marsh harvest mice

(e.g., weedy levees, grass-dominated uplands) may provide a valuable food base for this species. It also presents further evidence of the complex, but at least partially positive, relationships between non-native species and native, endangered species in the SFE.

MANAGEMENT IMPLICATIONS

The results of this study have important implications for salt marsh harvest mouse conservation, and for habitat management in general in the SFE. Two points stand out in particular. First, the general classification of non-native plants as a threat to salt marsh harvest mice warrants reevaluation; some non-native plant species may provide substantial food value for salt marsh harvest mice and still have overall negative effects on habitat structure. Indeed, some of the non-native plants that were strongly selected in cafeteria trials, such as perennial pepperweed, are considered to pose potential conservation threats to salt marsh harvest mice (USFWS 2013). Further work on the diet of salt marsh harvest mice under natural conditions is needed in light of these observations because non-native plants may be important food sources in the modern marshes of the SFE. The second major implication of this study is that waterfowl management, which has at times been considered harmful to salt marsh harvest mice (Shellhammer 1982), appears to promote the production of plants that salt marsh harvest mice readily consume. This suggests that holistic management for waterfowl and salt marsh harvest mice is feasible and may be readily accomplished. Waterfowl management also reintroduces successional processes that have been arrested by various habitat management practices throughout the state (i.e., regulating reservoir releases and normalizing Delta outflows, fire suppression). Although unmanaged tidal wetlands frequently are characterized by large monotypic vegetation stands (Goals Project 1999), management at waterfowl clubs encourages a more diverse plant community, which may provide a more stable food supply throughout the year (Sustaita et al. 2011). The importance of this temporally diverse food base has likely been underestimated because of the very strong association between salt marsh harvest mice and pickleweed.

Finally, this study supports an emerging consensus that salt marsh harvest mice are much more flexible in their habitat use (and diet) than previously thought (Trombley and Smith 2017, Smith et al. 2018b). This suggests that a reconciliation approach to salt marsh harvest mouse recovery may be preferable (Rosenzweig 2003); it may be possible to relax conservation actions that specifically target habitats dominated by pickleweed and still achieve conservation objectives for salt marsh harvest mice, which would increase efficiency of habitat management and conserve resources.

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