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Demography of the salt marsh harvest mouse (*Reithrodontomys raviventris halicoetes*) and associated rodents in tidal and managed wetlands

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Suisun Marsh (Solano County, California) is the largest contiguous marsh remaining on the West Coast of the United States, and makes up approximately 10% of the wetlands remaining in the San Francisco Estuary. Suisun Marsh has been safeguarded from development through the operation of over 100 privately owned waterfowl hunting clubs, which manage for diked waterfowl habitat. However, this management—and the subsequent loss of tidal influence—has been considered harmful for some species, including the endangered salt marsh harvest mouse (SMHM; *Reithrodontomys raviventris*). To determine the value of tidal wetlands relative to those managed for waterfowl, we performed periodic surveys for rodents in managed and tidal wetlands over 5 years, and used capture-mark-recapture analyses to estimate demographic parameters and abundance for the three most common rodents—the northern SMHM (*R. r. halicoetes*), the western harvest mouse (a sympatric native species; *R. megalotis*, WHM), and the house mouse (a sympatric invasive species; *Mus musculus*). Wetland type had no effect on detection, temporary emigration, or survival for any of these species. However, fecundity and population growth for all three species were affected by an interaction of season and wetland type, although none of these parameters was consistently superior in either habitat type. Estimated abundance of SMHM and *Mus* was similar in both wetland types, whereas WHM were more abundant in managed wetlands. Salt marsh harvest mice also showed no affinity for any microhabitat characteristics associated with tidal wetlands. Managed wetlands in Suisun Marsh support SMHM and *Mus* equally, and abundances of WHM were greater than in tidal wetlands, suggesting managed wetlands may be superior in terms of supporting native rodents. As climate change and sea level rise are predicted to threaten coastal marshes, these results suggest the recovery strategy for SMHM could incorporate managed wetlands.

Key words: endangered species, habitat management, *Mus*, *Reithrodontomys*, RMark, robust design, San Francisco Estuary, Suisun Marsh, waterfowl management, western harvest mouse

Coastal wetlands and the species they support are imperiled worldwide. A recent meta-analysis of 189 reports indicated that more than 50%—and up to 87%—of global wetlands have been lost to anthropogenic activities (Davidson 2014). Losses in the San Francisco Estuary (SFE) have been even more extreme: it is estimated that < 10% of historic tidal wetlands remain (Goals Project 2015). However, this loss has not affected wildlife uniformly throughout the SFE. Many tidal wetlands in the South San Francisco Bay were converted to salt ponds, which provide habitat only for a very select group of wildlife (e.g., shorebirds and waterfowl—Warnock et al. 2002), whereas the wetlands managed for waterfowl that dominate the northern portion of the estuary support much of the remaining wildlife community, including the salt marsh harvest mouse

(*Reithrodontomys raviventris*, SMHM hereafter—Sustaita et al. 2011; Smith et al. 2014).

The SMHM (Fig. 1A) is an endangered species endemic to the SFE (USFWS 2013). It is the only mammal species restricted entirely to coastal marshes (Greenberg et al. 2006), and exhibits numerous morphological and physiological adaptations for life in this challenging environment (Fisler 1965). They can subsist on salt water, climb well in emergent vegetation, and swim better than their upland counterparts (Fisler 1965). This apparent specialization for tidal wetlands, along with a legacy of regional research, led managers and researchers to conclude that SMHM are dependent on tidal wetlands dominated by pickleweed (*Salicornia pacifica*) and, by inference, that management of wetlands in a nontidal state would be harmful to the species (Shellhammer et al. 1982). However, subsequent surveys in managed wetlands confirmed that these habitats supported substantial SMHM populations (Shellhammer et al. 2010; Sustaita et al. 2011), although with almost no data regarding the demographic value of tidal and managed wetlands, managers have been unable to properly evaluate the value of this novel habitat type for SMHM.

Demographic parameters in rodents (e.g., population density, survival, fecundity) may vary across managed and unmanaged areas of otherwise similar habitat (e.g., in production forests where downed woody debris are removed versus left behind—Homyack et al. 2014; see also Fritts et al. 2017; Larsen et al. 2018), and some small mammals may perform better in, or adjacent to, managed areas (Hadley and Wilson 2004a, 2004b; Converse et al. 2006; Sustaita et al. 2011). Understanding which habitat features favor native species, and disfavor invasive species, is critical for the recovery of species, such as SMHM, facing severe habitat loss. As such, determining environmental and biotic variables that affect interactions between SMHM and sympatric small mammals was listed as an objective in the recovery plan for the species (USFWS 2013).

We investigated the relative value of tidal and managed wetlands for rodent species in Suisun Marsh, Solano County, California, with a focus on the three most abundant species.

Fig. 1.—(A) Northern salt marsh harvest mouse (*Reithrodontomys raviventris halicoetes*), (B) western harvest mouse (*R. megalotis*), and (C) house mouse (*Mus musculus*).

These were the northern SMHM (*R. raviventris halicoetes*), a sympatric native congener (the western harvest mouse, *R. megalotis*; Fig. 1B; WHM hereafter), and a sympatric invasive species (the house mouse, *Mus musculus*; Fig. 1C; *Mus* hereafter). We addressed three specific objectives. First, do tidal and managed wetlands differ in their demographic value (e.g., survival, fecundity, population growth rate) for these rodents? Managed wetlands experience greater daily habitat stability than do tidal wetlands; nests in the latter habitat are vulnerable to flooding and adults must avoid irregular twice daily tidal inundation. Based on previous work in the system (Sustaita et al. 2011), and tidally induced differences in habitat stability, we predicted that survival, fecundity, and population growth of these rodents would be equal to or greater in managed wetlands than in tidal wetlands. Our second objective follows directly from the first: we ask if abundances of these three species differ in tidal and managed wetlands. Because management of the latter emphasizes high food production for waterfowl, and as we expected small mammals there to have greater survival, fecundity, and population growth, we also expected managed wetlands to support higher densities of all three rodent species. Finally, our third objective was to determine whether a series of microhabitat and other environmental characteristics (e.g., high plant species and structural diversity, mean temperatures, and rainfall) influence estimated abundance of small mammals.

Different small mammal species are likely to favor different habitat characteristics, which in turn vary across wetland types. As SMHM are more likely to occur deep in wetland habitat, as opposed to the transitional and upland margins of wetlands (Bias and Morrison 2006; Sustaita et al. 2011), we expected this species to be associated with microhabitat characteristics that provide refuge—both to adults and their nests—from water fluctuations as well as predators. These were predicted to include dense vegetation with high structural complexity, high pickleweed cover (Bias and Morrison 2006), and greater distances from anthropogenic influences, which can subsidize native and invasive predators. In the SFE, WHM are found in marsh habitat, but are more frequently associated with lower diversity grasslands adjacent to marshes, which is consistent with general habitat associations of the species (Webster and Jones 1982). Therefore, we expected WHM to be associated with low plant species and structural diversity, and high grass cover, which provides abundant grass seed, the most common food of the species in the SFE (Fisler 1965). Finally, *Mus* is an extreme habitat generalist that has invaded diverse habitats across the globe (Long 2003); we thus expected no strong associations with any particular microhabitat characteristics. We did, however, expect *Mus* to be most abundant at sites nearer to roads and other anthropogenic developments, and areas with higher patch fragmentation (Bias and Morrison 2006). Because they frequently are human commensals, dispersal from developed areas into wetlands may supplement local *Mus* populations.

Materials and Methods

Study area.—Suisun Marsh (38°08′11.8″N, 121°57′27.6″W) is the largest remaining contiguous marsh on the West Coast of North America and comprises approximately 10% of wetlands remaining in California (Moyle et al. 2014). It also contains more than half of remaining SMHM habitat, and supports some of the highest recorded densities of the species (USFWS 2010). Suisun Marsh is situated between the SFE and the Sacramento-San Joaquin Delta. Due to a large influx of fresh water from the Sacramento and San Joaquin rivers, waters here are more brackish than in other parts of the species' range. This area was largely protected from filling, development, and industrial use, because it provided excellent waterfowl habitat. Abundant waterfowl hunting opportunities in the mid-1800s to early 1900s led to the development of numerous waterfowl hunting clubs throughout Suisun Marsh and, as of 2013, over 150 private and public landowners maintain the majority of the acreage in the marsh as wildlife habitat (Moyle et al. 2014). Most of this habitat is maintained as diked, managed wetlands through an extensive network of levees and ditches. Vegetation is subject to discing, burning, mowing, herbicides, and other activities meant to increase heterogeneity and provide food and cover for waterfowl (Coates et al. 2012). Managed wetlands generally are flooded in September or October, held as circulated ponds until February or March, and then flushed with fresher water during March and April, before draining in June. After leaching and draining, managed wetlands persist as moist to dry fields with a mix of wetland and upland plant species, and small shallow ponds that may persist until the autumn when ponds are again flooded to attract waterfowl.

Our research took place in three blocks within Suisun Marsh (Fig. 2). Joice Island Wildlife Area (38°11′14.5″N, 121°59′47.4″W; Joice hereafter) and the Goodyear Slough Unit (38°05′14.9″N, 122°06′12.2″W; Goodyear hereafter) are part of the Grizzly Island Wildlife Area, operated by the California Department of Fish and Wildlife (CDFW). Each was represented by one trapping grid in tidal wetland and one in a managed wetland. Denverton Property (38°12′41.6″N, 121°54′50.2″W; Denverton hereafter) is a private property owned by the California Waterfowl Association. This site was sampled with one trapping grid in a tidal wetland and two in managed wetlands. All managed wetlands were subject to standard flooding and leach cycles associated with waterfowl management (Moyle et al. 2014). One of the managed wetlands at Denverton was under heavy management during the project; the trapping grid area was almost completely disced directly before the project began. The other three managed grids were subject to moderate management activity, which included discing adjacent to the second managed grid at Denverton, mowing adjacent to the managed grid at Goodyear, and burning near (~200 m) the managed grid at Joice. However, no vegetation control or ground disturbance occurred within these three trapping grids.

Livetrapping.—Within the three blocks previously outlined, we monitored small mammals at seven trapping grids from autumn 2013 through winter 2017–2018. Sampling varied somewhat over the course of this study. During the first year (September 2013 through August 2014) we sampled Denverton and Joice every month. During years 2 and 3

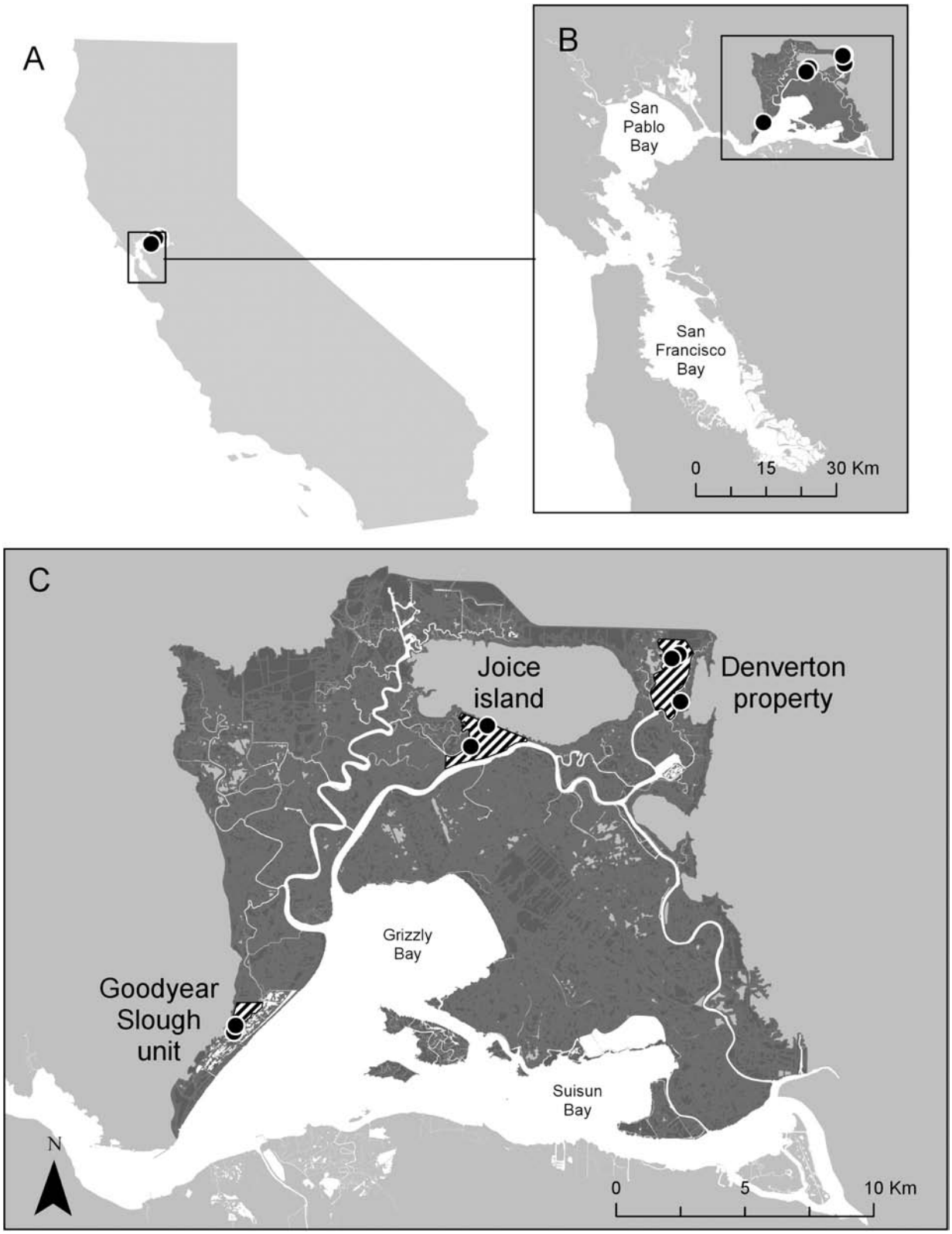

Fig. 2.—Study blocks were located in California (A), in the San Francisco Estuary (B), within the Suisun Marsh (C). Study blocks used to investigate demographics and abundances of salt marsh harvest mice (*Reithrodontomys raviventris halicoetes*), western harvest mice (*R. megalotis*), and house mice (*Mus musculus*) at Suisun Marsh (38°08′11.8″N, 121°57′27.6″W), Solano County, California, September 2013 through February 2018. Blocks included two California Department of Fish and Wildlife properties (Goodyear Slough Unit and Joice Island Wildlife Area), and one property owned and managed by the California Waterfowl Association (Denverton Property).

(September 2014 through August 2016) we added Goodyear and sampled all sites bimonthly. During the last 1.5 years of the study (September 2016 through February 2018) we sampled only Goodyear and Joice, and did so quarterly. This study followed ASM guidelines (Sikes et al. 2016), was approved by the University of California at Davis Institutional Animal Care and Use Committee, and was conducted under a Cooperative Agreement between CDFW and the USFWS.

Small mammals at all sites were surveyed using Sherman live traps (Model LFA; H.B. Sherman Traps, Tallahassee, Florida) arrayed in 6 × 10 grids (15-m spacing; ca. 1 ha total area). Trapping occurred simultaneously in managed and tidal wetlands within blocks. Trapping grids were placed to sample representative vegetation and microhabitat types. Traps were set in the evening and examined and closed in the morning for three consecutive nights, except during waterfowl hunting season when a 1-day gap was necessary to safely accommodate hunt days.

All captured rodents were identified to species and individually marked with uniquely numbered ear tags (Monel self-piercing tags, Model 1005-1, National Band & Tag Co., Newport, Kentucky). We recorded standard characteristics and measurements, including sex, reproductive condition, and mass measured to the nearest 0.25 g using a spring scale. We assessed all captured rodents for reproductive condition based on the condition of the testes in males (abdominal or scrotal), and of the fur around the nipples (haired, developed, or worn), pregnancy, or copulatory plugs in females (Adler and Wilson 1987; Skupski 1995).

Because SMHM may be difficult to distinguish from WHM, we applied a multiple logistic regression model developed by Sustaita et al. (2011, 2018) to improve our identification accuracy. We recorded additional standard measurements, including: total length, tail length (Hall 1962; Nagorsen and Peterson 1980), body length (by subtracting tail from total length), and tail diameter 2 cm from the base (SMHM have thicker tails than do WHM—Shellhammer 1982). Total length was measured by draping the animals across the end of a ruler and letting them grasp the edge with their paws. Field technicians then used one hand to line up the tip of the mouse's nose with the edge of the ruler by placing a finger behind the animal's skull, and with the other hand, smoothed the tail out to its full length. We recognize that some readers may question the accuracy and consistency of this measurement, but it was enabled by the docility of SMHM, which allowed them to be manipulated with limited resistance. Moreover, measurements were consistent across multiple captures and different technicians (e.g., mean body length 150.29 mm, SD = 1.83 mm, which is 1.22% of mean body length [range 0–6.42%], n = 4,725 captures of 2,018 individuals; mean tail length 84.07 mm, SD = 1.08 mm, which is 1.29% of mean tail length [range 0–8.73%], n = 4,737 captures of 2,018 individuals; mean tail diameter 2.14 mm, SD = 0.07 mm, which is 3.03% of mean tail diameter [range 0–36.11%], n = 4,689 captures of 2,012 individuals).

We also noted that total length as recorded here was not comparable to that recorded from standard museum specimens (e.g., Hall 1962; Nagorsen and Peterson 1980). Because SMHM tend to have much blunter tails than WHM (Sustaita et al. 2018), we characterized the tail tip as blunt, intermediate, or pointed. SMHM also tend to be redder in coloration than WHM, often with reddish on the venter and orange ear tufts, whereas WHM are much more gray (Sustaita et al. 2018). Consequently, we recorded the color of both dorsal and ventral pelage, that of tail hairs, and the presence of orange ear tufts. Finally, reflecting the docility referred to above, we recorded observations of behavior, as docile or active.

Field technicians recorded provisional identification of harvest mice in the field, based on measurements, appearance, and behavior while the mouse was in hand. In addition, many mice were photographed, and many individuals identified with genetic markers. We made final species identification based on a combination of field identifications, photographs, genetics, and the multiple logistic regression of Sustaita et al. (2018). Supporting our approach, animals identified as SMHM in the field by experienced crew members matched the final species determination about 98% of the time, and fewer than 1% of animals identified in the field as probable SMHM were subsequently identified as WHM using these methods. Further, genetic testing was performed preferentially on the most ambiguous individuals (n = 213), 56 (35.67%) of which were juveniles or subadults. Of the 462 provisional field identifications recorded for these more ambiguous individuals, genetic tests confirmed that 434 were correct (93.55%). We concluded that even without secondary tools (genetics, multiple logistic regression), experienced technicians were highly successful at correctly identifying the species of even the most difficult to distinguish harvest mice while they were in hand.

Microhabitat characteristics.—We measured habitat characteristics each season. We recorded the species, percent cover (ocular estimation), and approximate mean height (rounded to the nearest 10 cm) of the three most dominant plant species or species assemblages within a 5-m radius of each trap location. We also noted other species that, while not dominant, are likely important to managers concerned with SMHM recovery (e.g., invasive plant subject to active control). We defined the grid-level species richness as the number of plant species recorded within the trapping grid. To characterize grid-level vegetative structural diversity, we calculated the difference in vegetative height at every trap location relative to each of the eight most proximal traps (hence, the mean of eight pairwise comparisons); the mean of these values across all trap locations within the grid was our metric of grid-level structural diversity. Weather data, including total rainfall and mean daily (24-h) temperature during the 14 days preceding a given trapping period, were obtained from the Rush Ranch weather station, which is maintained by the National Estuarine Research Reserve System (station code SFBRRMET; located < 3 km from Joice, < 10 km from Denverton, and < 15 km from Goodyear). These habitat characteristics were used in all capture-mark-recapture RMark models to test for their effects on the parameters.

Parameter and abundance estimates and statistical analyses.—Prior to this effort, the longest study of SMHM demography spanned 2 years and sampled only three seasons (spring, summer, autumn) each year (Sustaita et al. 2011). The current study incorporates monthly to quarterly sampling that encompasses all seasons over 5 years, including both drought and typical rain years. In addition, whereas Sustaita et al. (2011) sampled two managed and two tidal sites, we have increased replication both within and across wetland types. Consequently, we were able to incorporate many parameters in our analyses (e.g., annual variation within season) not previously applied to SMHM demography. Because so little is known about SMHM demography, and because managers and researchers have a wide variety of data needs, we included a relatively large suite of factors and covariates to test a number of potential models. These included trap night, trap session, month, season, year, wetland type, pickleweed cover, vegetative species richness, vegetative structural diversity, recent mean daily temperature, recent rainfall, and preliminary estimated abundances of SMHM, WHM, and *Mus*. These were used in analysis of capture-mark-recapture (CMR) models to estimate survival, fecundity, population growth, and other parameters for each species. Subsequently they were used, along with final estimated abundances of SMHM, WHM, and *Mus*, in a generalized linear model (GLM) to evaluate potential effects of these factors and covariates on the final abundance estimates for each of the three focal species.

Capture-mark-recapture modeling.—A goodness-of-fit test in program MARK (White and Burnham 1999) through extension RELEASE (Burnham et al. 1987) indicated good fit of CMR data (TEST 2 + TEST 3: $P > 0.90$ for all species). We used a median ĉ adjustment and a quasi-likelihood Akaike's Information Criterion (QAIC) for selection of competitive models (e.g., ΔQAIC < 2.0). We applied Pradel's robust design with a Huggins full likelihood closed-capture estimator (RMark model RDHFHet—Pollock et al. 1990; Huggins 1991) in RMark (Laake 2019) to estimate abundance (N) and both capture (p) and recapture (c) probabilities during each trapping period, and survival (S) and temporary emigration (γ'' = the probability of temporarily moving out of the study area, and γ' = the probability of remaining outside the study area) between trapping periods ("survival models"; Table 1; Supplementary Data SD1). We used Pradel's robust design with a Huggins closed-capture estimator (Huggins 1991; Pradel 1996) to estimate fecundity (f; RMark model RDPdfHugFullHet; "fecundity models") and population growth rates (λ; RMark model RDPdLHugFullHet; "population growth models"). Candidate CMR models were specified a priori (e.g., random movement, Markovian movement, etc.), and models were designed by first addressing fitted detection parameters (p, c), then fitted temporary emigration parameters (γ', γ''), and finally fitted demographic parameters (S, f, and λ; see Supplementary Data SD1 for parameter descriptions). We calculated all CMR parameters as monthly rates. To accommodate the large number of factors we wished to evaluate, we tested a suite of structures for each parameter (e.g., fixed, random, and by covariate), and accepted as informative those structures for which QAIC < 2.0 (sensu Reeves et al. 2016). These parameter structures then were compared in the final CMR models to determine the most competitive survival, fecundity, and population growth, models (e.g., QAIC < 2.0). Model selection was based on Akaike's weights

Table 1.—Final survival, fecundity, and population growth models analyzed for salt marsh harvest mice (SMHM; *Reithrodontomys raviventris halicoetes*), western harvest mice (WHM; *R. megalotis*), and house mice (*Mus musculus*) captured at Suisun Marsh (38°08′11.8″N, 121°57′27.6″W), Solano County, California, September 2013 through February 2018.

Species	Model type	Final models
SMHM	Survival	1.p(period), c(period), γ'(sex), γ''(sex), S(season * sex)
		2.p(period), c(period), γ'(sex) = γ''(sex), S(season * sex)
	Fecundity	1.p(period), c(period), Phi(rain * season), f(season * wetland)
	Population growth	1.p(period), c(period), Phi(rain * season), λ(season * wetland)
WHM	Survival	1.p(night), c(temp), γ'(WHM), γ''(WHM), S(season * rain)
		2.p(night), c(temp), γ'(WHM), γ''(WHM), S(season)
		3.p(night), c(temp), γ'(WHM) = γ''(WHM), S(season * rain)
		4.p(night), c(temp), γ'(WHM) = γ''(WHM), S(season)
	Fecundity	1.p(night), c(temp), S(season * rain), f(season * wetland)
		2.p(night), c(temp), S(season), f(season * wetland)
	Population growth	1.p(night), c(temp), S(season * rain), λ(season * wetland)
		2.p(night), c(temp), S(season), λ(season * wetland)
Mus	Survival	1.p(night), c(SMHM + WHM + HM), γ'(season), γ''(season), S(season)
		2.p(night), c(temp), γ'(season), γ''(season), S(season)
		3.p(night), c(rain), γ'(season), γ''(season), S(season)
		4.p(night), c(SMHM + WHM + HM), γ'(season) = γ''(season), S(season)
		5.p(night), c(temp), γ'(season) = γ''(season), S(season)
		6.p(night), c(rain), γ'(season) = γ''(season), S(season)
	Fecundity	1.p(night), c(SMHM + WHM + HM), S(season * rain), f(season * wetland)
		2.p(night), c(temp), S(season), f(season * wetland)
		3.p(night), c(rain), S(season), f(season * wetland)
	Population growth	1.p(night), c(SMHM + WHM + HM), S(season * rain), λ(season * wetland)
		2.p(night), c(temp), S(season), λ(season * wetland)
		3.p(night), c(rain), S(season), λ(season * wetland)

(w_i) when more than one competitive model with identical structures for the parameter was available. After running the final models, we calculated the means of all estimated demographic parameters and derived abundance estimates ($\hat{N}$) based on Akaike's weights for each model (model-averaging). We considered factors to be biologically informative if a model with a given factor performed substantially better than a similar model lacking that factor (based on QAIC). After model-averaging within each of the three CMR model types, an unweighted mean was calculated for values of $\hat{N}$ across the survival, fecundity, and population growth models.

Generalized linear model.—As estimated abundance ($\hat{N}$) is derived from initial capture probability (White and Burnham 1999), the effects that factors included in these CMR models may have on $\hat{N}$ could not be tested directly within the CMR models. Demographic parameters that have strong effects on abundance (e.g., survival, fecundity, and population growth) are tested within the CMR models, however, and can be logically correlated with estimate abundance. To test for effects of these factors on abundance estimates, we used a post hoc GLM with a Poisson distribution and Type III sum of squares to determine whether the factors determined to affect S, f, and λ, also had an effect on derived abundance estimates (R Development Core Team 2016). All means are reported ± *SE*.

Results

Across 73 primary trapping occasions totaling almost 30,000 trap nights we captured 2,028 SMHM, 583 WHM, and 1,213 *Mus*. We were unable to identify to species level 209 harvest mice, most of which were juveniles; these were classified as "unknown harvest mice" and excluded from full analyses. Captures of other rodent species totaled 118 individuals and were omitted from all analyses; these included 55 California voles (*Microtus californicus*), 43 rats (*Rattus* sp.), and 20 deer mice (*Peromyscus maniculatus*).

Demographic Parameters

Salt marsh harvest mice.—Most CMR model parameters for SMHM were best modeled with a single structure (e.g., only one variable, or one interaction if two variables were competitive; Supplementary Data SD2A); the single exception was temporary emigration (γ' and γ''), which presented two competitive structures (structure 1: $\gamma'(\text{sex}) = \gamma''(\text{sex})$; structure 2: $\gamma'(\text{sex}) \neq \gamma''(\text{sex})$). This resulted in two final CMR models for survival (which uses temporary emigration), and one each for the fecundity and population growth models (which do not use temporary emigration; Table 1). This species exhibited no behavioral response to trapping; that is, none of the factors tested affected capture probabilities, and neither capture (p) nor recapture (c) probabilities varied across trap nights within primary trapping periods. However, both probabilities did vary across primary trapping periods, and capture and recapture probabilities differed within primary trapping periods (p(period) ≠ c(period)), indicating a random response to trapping by SMHM. Temporary emigration was affected by sex, and both a constant random ($\gamma'(\text{sex}) = \gamma''(\text{sex})$) and a Markovian temporary ($\gamma'(\text{sex}) \neq \gamma''(\text{sex})$) model were competitive, and indicated that temporary immigration was occurring.

Monthly survival was influenced by an interaction between season and sex (Fig. 3A; Supplementary Data SD2A). Survival was highest in autumn, intermediate in winter and summer, and lowest in spring, and differed between males and females in the winter and summer (based on *SE*). Both fecundity and population growth rates for SMHM were driven by an interaction of wetland type with season, although interaction plots show that seasonal changes in these parameters were much more important than wetland type (Figs. 4 and 5). For both wetland types, fecundity and population growth rates

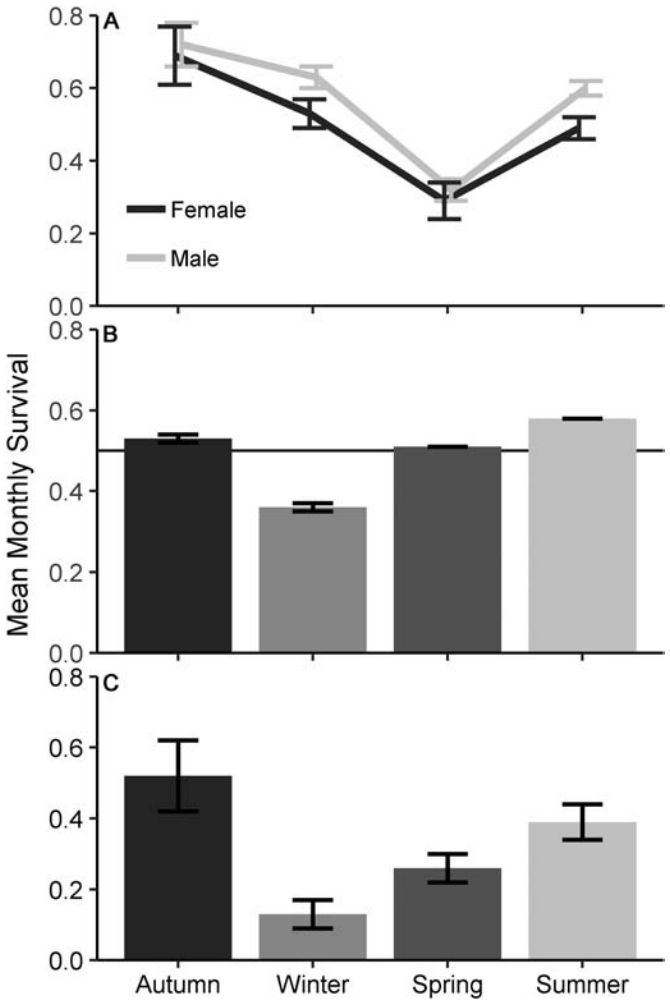

Fig. 3.—Monthly survival (± *SE*) for three species of rodents at Suisun Marsh (38°08′11.8″N, 121°57′27.6″W), Solano County, California, September 2013 through February 2018. (A) Survival for salt marsh harvest mice (*Reithrodontomys raviventris halicoetes*), depicted in an interaction plot, was best explained by an interaction between season and sex; (B) for western harvest mouse (*R. megalotis*), survival was explained both by rain and by a season × rain interaction; presented here are monthly estimates from the season × rain interaction indicated by bars, and an overall estimate for the rain-only model indicated by the horizontal line; (C) survival of house mice (*Mus musculus*) was best modeled by season, indicated here by bars.

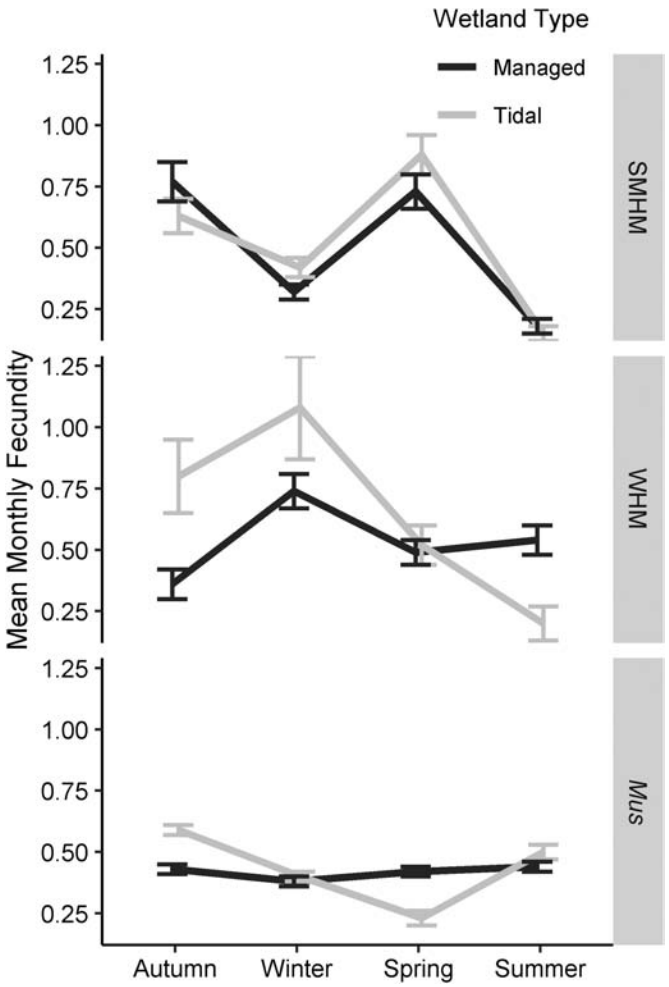

Fig. 4.—Monthly fecundity (± *SE*) for salt marsh harvest mice (*Reithrodontomys raviventris halicoetes*), western harvest mice (*R. megalotis*), and house mice (*Mus musculus*) at Suisun Marsh (38°08′11.8″N, 121°57′27.6″W), Solano County, California, September 2013 through February 2018, grouped by season and wetland type.

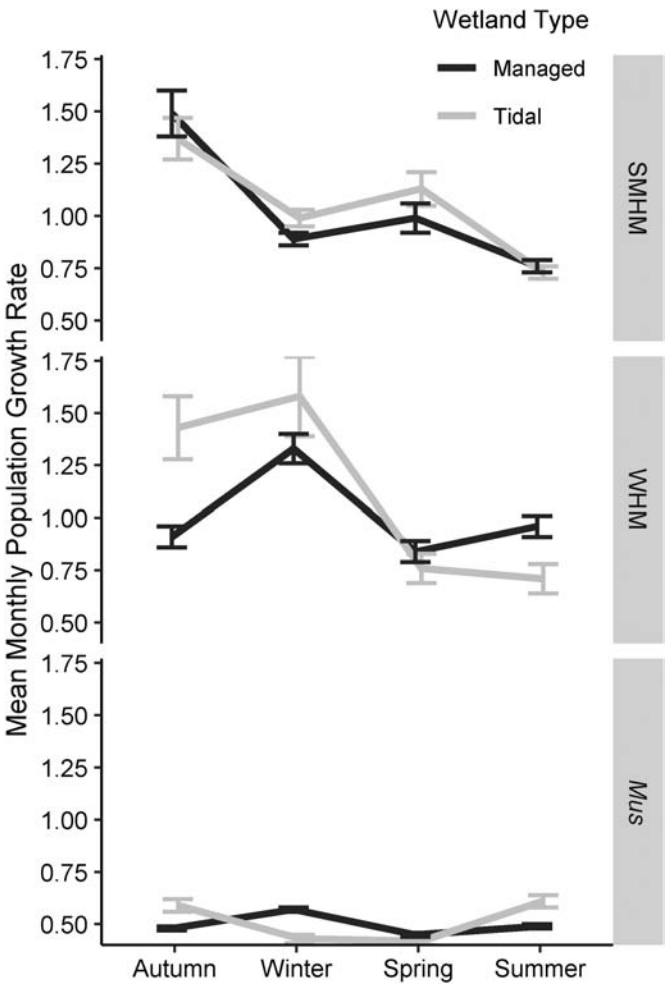

Fig. 5.—Monthly population growth rate (± *SE*) for salt marsh harvest mice (*Reithrodontomys raviventris halicoetes*), western harvest mice (*R. megalotis*), and house mice (*Mus musculus*) captured at Suisun Marsh (38°08′11.8″N, 121°57′27.6″W), Solano County, California, September 2013 through February 2018, grouped by season and wetland type.

followed a bimodal annual cycle, being high in the fall, low in the winter, high in the spring, and low in the summer (Figs. 4 and 5; Supplementary Data SD2A). While there was no single seasonal peak in fecundity, population growth rates in both wetland types were substantially higher in autumn than in other seasons (managed: 1.49 ± 0.11; tidal: 1.37 ± 0.10). In both wetland types, fecundity and population growth rates were lowest in the summer (fecundity—managed: 0.18 ± 0.03; tidal: 0.15 ± 0.03; population growth rate—managed: 0.76 ± 0.03; tidal: 0.73 ± 0.03).

Western harvest mice.—Temporary emigration and survival were influenced by more than one factor for WHM (Supplementary Data SD2B), resulting in four competitive models for survival (which uses temporary emigration and survival), and two for both fecundity and population growth (both of which use survival; Table 1). The probability of initial capture of WHM was strongly influenced by trap night, with capture probability increasing substantially with each successive night (night 1: 0.25 ± 0.03; night 2: 0.39 ± 0.06; night 3: 0.43 ± 0.10) and an overall mean of 0.36 ± 0.06. Temperature positively influenced recapture probability for WHM, albeit weakly (β = 0.05 ± 0.02). The overall mean recapture rate (0.35 ± 0.01) was very similar to the overall mean for initial capture. Temporary emigration was dependent on the estimated abundance of WHM, and both random (γ'(WHM) = γ''(WHM)) and Markovian (γ'(WHM) ≠ γ''(WHM)) models were competitive, indicating that temporary immigration was occurring.

Monthly survival of WHM was influenced by recent rainfall (over the previous 14 days), and by an interaction of season and recent rainfall (Fig. 3B; Supplementary Data SD2B). Beta values indicated seasonal influence of rain was driven largely by a strong positive effect of rainfall during summer months. Survival was highest in the summer ($0.58 \pm 0.11 \times 10^{-2}$), lowest in the winter (0.36 ± 0.01), and overall mean rates were 0.49 ± 0.02 (for the S(rain) model) and $0.50 \pm 0.15 \times 10^{-2}$ (for the S(season × rain) model). As with SMHM, both fecundity and population growth rates for WHM were influenced by an interaction of season and wetland type (Figs. 4 and 5). Fecundity

and population growth rates were highest in the winter in both wetland types (fecundity—managed: 0.74 ± 0.07, tidal: 1.08 ± 0.21; population growth rate—managed: 1.33 ± 0.07, tidal: 1.58 ± 0.19). While there was no seasonal low for fecundity or population growth rates in managed wetlands, in tidal wetlands rates were substantially lower in the spring, and lowest in summer (fecundity: 0.20 ± 0.07; population growth rate: 0.71 ± 0.07). Fecundity and population growth rates generally were more stable across seasons in managed wetlands than tidal (e.g., seasonal means differed less in managed wetlands, and *SE*s were smaller).

Mus.—Recapture probability and temporary emigration were influenced by more than one factor for *Mus* (Supplementary Data SD2C), resulting in a total of six models for survival, and three each for fecundity and population growth (Table 1). *Mus* capture probabilities were strongly influenced by trap night, with capture probability more than doubling between the first and third trap night (night 1: 0.19 ± 0.03; night 2: 0.32 ± 0.07; night 3: 0.43 ± 0.15), and an overall mean of 0.31 (± 0.08). The probability of recapture was influenced by abundance of rodents in the trapping area (SMHM + WHM + *Mus*; positively by SMHM, negatively by WHM and *Mus*) as well as temperature and rain. Beta values indicated that density of SMHM had a minimal positive effect on *Mus* captures, WHM had a minor negative effect, and *Mus* had a moderate negative effect. Temperature had a slightly positive effect on recapture probability, whereas rain had a slightly negative effect. Recapture values across the six models ranged from 0.30 (± 0.04) to 0.44 (± 0.03), and the mean for the highest ranked model was 0.40 (± 0.03). Temporary emigration for *Mus* was affected by season, and competitive models included those where this was both constant and random (γ'(season) = γ''(season)), and Markovian (γ'(season) ≠ γ''(season)), though the Markovian model had a very low AIC weight. Cumulatively, these values indicated that temporary immigration was occurring, and was largely constant and random.

Monthly survival of *Mus* varied only by season, and other than autumn, survival was lower than that observed for either harvest mouse species (Fig. 3C). Survival was lowest in the winter (0.13 ± 0.04), and increased seasonally until it reached its highest point in the autumn (0.52 ± 0.10; Fig. 3C). As for both harvest mouse species, fecundity and population growth rates for *Mus* were influenced by an interaction of season and wetland type. For *Mus*, monthly fecundity declined from autumn (0.59 ± 0.02) to spring (0.23 ± 0.03) in tidal wetlands, but exhibited no seasonal pattern in managed wetlands (Fig. 4). Population growth was low in all seasons, exhibiting modest seasonal variation (Fig. 5). Rates in managed wetlands were slightly higher in winter (0.57 ± 0.01) than other seasons, and those in tidal wetlands were greater in summer (0.61 ± 0.03) and autumn (0.59 ± 0.03).

Abundance Estimates and Microhabitat Associations

Both SMHM and WHM displayed clear and dominant influences of seasonality in terms of survival, fecundity, and population growth rates; for *Mus*, only survival was notably influenced by season (Figs. 3–5). Parameters were secondarily influenced by sex (on survival in SMHM), rainfall (survival in WHM), or wetland type (fecundity and growth rate in all three species). Notably, microhabitat factors did not emerge in any of the competitive models for survival, fecundity, or population growth rates. For each species, only season (SMHM), wetland type (WHM), or their interaction (*Mus*) significantly influenced abundance estimates (Table 2).

Overall, SMHM was the most abundant species, and WHM least abundant (Table 3; Supplementary Data SD3A). Abundances of SMHM were significantly affected by season but not by wetland type, and there was no significant interaction between these factors (Table 2A). Abundance estimates were highest in winter (managed: 24.80 ± 1.65; tidal: 38.50 ± 1.68) and lowest in summer (managed: 9.49 ± 0.49; tidal: 12.81 ± 0.81). In contrast to SMHM, WHM abundance was significantly affected by wetland type (managed: 6.10 ± 0.43; tidal: 3.20 ± 0.63) but neither by season nor the interaction effect (Table 2A). Finally, *Mus* abundances were not influenced by season or wetland type, but the interaction between these was significant (Table 2C). This appears to reflect a strongly modal pattern in tidal wetlands (high abundance in autumn [10.19 ± 10.38] and winter [11.40 ± 13.42]; low abundance in spring [4.10 ± 4.19] and summer [4.81 ± 3.74]) but relatively constant numbers across seasons in managed wetlands (Supplementary Data SD3B).

Of the 209 harvest mice we were unable to identify to species level, 131 occurred in managed wetlands, whereas 78 occurred in tidal sites. In the unlikely situation where all of the unknown harvest mice were actually SMHM, population

Table 2.—Results of a post hoc generalized linear model with a Poisson distribution and Type III sum of squares, testing whether the factors determined to affect survival, fecundity, and population growth rate in the capture-mark-recapture analyses also had an effect on derived abundance estimates for salt marsh harvest mice (SMHM; *Reithrodontomys raviventris halicoetes*), western harvest mice (WHM; *R. megalotis*), and house mice (*Mus musculus*) captured at Suisun Marsh, Solano County (38°08′11.8” N, 121°57′27.6” W), California, September 2013 through February 2018. * indicates significant at alpha = 0.05.

	d.f.	Deviance	*F*-value	Pr(>*F*)
(A) SMHM				
Intercept	NA	840.82	NA	NA
Season	3	1,031.98	11.67	< 0.001*
Wetland Type	1	840.85	0.01	0.94
Season * Wetland Type	3	865.95	1.53	0.21
(B) WHM				
Intercept	NA	213.97	NA	NA
Season	3	217.05	0.59	0.61
Wetland Type	1	225.43	6.64	0.01*
Rain	1	214.40	0.25	0.62
Season * Wetland Type	3	220.77	1.31	0.27
Season * Rain	3	216.61	0.51	0.68
(C) *Mus*				
Intercept	NA	766.51	NA	NA
Season	3	771.12	0.27	0.85
Wetland Type	1	766.93	0.07	0.79
Season * Wetland Type	3	843.16	4.50	< 0.01*

Table 3.—Mean seasonal abundance estimates for salt marsh harvest mice (SMHM; *Reithrodontomys raviventris halicoetes*), western harvest mice (WHM; *R. megalotis*), and house mice (*Mus musculus*) captured at Suisun Marsh (38°08′11.8″N, 121°57′27.6″W), Solano County, California, September 2013 through February 2018.

Species	Autumn				Winter				Spring				Summer			
	Managed		Tidal		Managed		Tidal		Managed		Tidal		Managed		Tidal	
	$\hat{N}$	*SE*	$\hat{N}$	*SE*	$\hat{N}$	*SE*	$\hat{N}$	*SE*	$\hat{N}$	*SE*	$\hat{N}$	*SE*	$\hat{N}$	*SE*	$\hat{N}$	*SE*
SMHM	19.86	1.36	19.59	1.16	24.80	1.65	38.50	1.68	14.87	0.89	19.01	1.28	9.49	0.49	12.81	0.81
WHM	6.88	0.44	4.00	0.24	5.74	0.32	4.43	0.52	5.06	0.26	1.64	0.04	6.71	0.44	2.73	0.43
Mus	10.44	0.94	10.19	1.21	9.88	1.21	11.40	1.51	8.16	0.79	4.10	0.51	10.21	0.74	4.81	0.53

estimates would have been similar to the analysis conducted without these unidentified harvest mice, and trends would be the same. In most seasons, the difference in abundance estimates between the analysis excluding and including the unknown harvest mice was fewer than 1.5 individuals; in winter, estimates differed by up to six individuals. Abundance estimates were still highest in winter, though lower than in the analysis that excluded unknown mice (managed = 20.44 ± 1.65; tidal = 32.58 ± 1.68), and lowest in summer, though higher than in the analysis that excluded unknown mice (managed = 10.59 ± 0.88; tidal = 13.03 ± 1.54). In contrast, if all unknown harvest mice were considered to be WHM, estimated seasonal abundances would increase by less than one individual in each wetland type, in all seasons. Mean abundance estimates per wetland type would have been consistent with the analysis without unknown mice included (managed = 6.16 ± 0.32; tidal = 3.27 ± 0.64). We conclude that the results of this study would not have differed significantly had the 209 unidentified harvest mice been either all SMHM or all WHM.

Discussion

Suisun Marsh comprises one of the most extensive remaining areas of suitable habitat for the endangered SMHM (Sustaita et al. 2011). We applied demographic analyses to the longest time series available for this species, as well as to WHM and *Mus*, the two numerically dominant potential competitors in that marsh. Our objectives were 3-fold. First, to determine whether tidal and managed wetlands differ in demographic value to the dominant rodent species. Second, to determine whether any such differences result in variation in abundance estimates between tidal and managed wetlands. Finally, we sought to determine what—if any—microhabitat characteristics were associated with the abundances of these species. Wetland type in Suisun Marsh had a significant influence on abundance estimates for only one species (WHM), although abundances of *Mus* were influenced by an interaction between season and wetland type. Abundance estimates of SMHM, in contrast, were most strongly influenced by season, although more so in tidal than managed wetlands.

Demography of SMHM, a presumed wetland obligate, was not strongly influenced by most of the factors we tested. Wetland type affected fecundity and population growth, but only seasonally (Supplementary Data SD2A). Temporary emigration rates for SMHM were low overall, but females were much more likely than males to move on or off the trapping area. This is unusual for rodents, a group for which males generally are more likely than females to disperse (e.g., Dobson 1982; Selonen and Wistbacka 2017; Kawamura et al. 2018). Monthly survival generally was quite low, and was affected by an interaction of sex and season. If low survival rates lead to frequently vacated territories, this could account for the limited dispersal (i.e., low temporary emigration rates). Survival varied greatly across seasons, being highest in the autumn, but declining by over 50% by spring. This could be due to density-dependent effects; the long breeding season (peaking from spring to autumn) results in the largest abundance estimates during the autumn and winter, which could reduce the per capita risk of predation. Alternatively, high survival during the autumn could reflect an abundance of food, as many of the common plant species that SMHM consume produce seed during this period (Smith and Kelt 2019). The bimodal pattern of reproductive parameters for SMHM (high fecundity and population growth in the autumn and spring) could be an artifact of the almost year-round breeding observed during this study (pregnant females were captured during every season). If peak breeding begins immediately in early spring, the summer lull could be a result of a recovery period for breeding individuals, after which breeding increases again during the autumn.

Trombley and Smith (2017) provided evidence that male SMHM may participate in parental care, suggesting that successfully raising young is challenging in this environment. Whether this reflects thermal constraints (e.g., one parent keeping young warm while the other is foraging) or nutritional limitations, however, is not certain. Winters are cold and wet, and summers warm and humid in Suisun Marsh, which could make reproduction more physiologically stressful. The winter peak in abundance estimates of SMHM likely reflects the culmination of almost continuous breeding from early spring to autumn. It is worth emphasizing that juvenile SMHM generally are too small to be trapped, so trapping efforts effectively sample only the adult population. Regardless of the mechanisms driving these patterns, results reported herein suggest that tidal and managed wetlands provide relatively similar demographic value for SMHM, although these parameters may exhibit greater seasonal variation in tidal wetlands.

As WHM is generally more of an upland generalist, we assume that it is competitively inferior in wetland habitat (Fisler 1965). Our data suggest that this species is somewhat more sensitive to environmental and competitive dynamics than SMHM (Supplementary Data SD2B). Nonetheless, results for

WHM are unremarkable and predictable. Survival was lowest in the winter and highest in the summer, an unsurprising trend for a species less adapted for wetland life (Fisler 1965) and one that has a strong preference for food sources common during the summer and uncommon during the winter (Smith and Kelt 2019). Because SMHM abundances are highest in winter, competition for food or nesting resources may also contribute to lower survival for WHM during that season. However, fecundity and population growth rates for WHM were highest in the winter in both wetland types, so there may be some nuanced drivers at play, such as high levels of emigration (a parameter we could not characterize here) being interpreted as low survival. Although reproductive parameters for WHM generally were lower in managed wetlands, abundance estimates still were significantly greater there. These contrasting observations could indicate that managed wetlands act as a demographic sink for this species. Further work to understand the spatial dynamics of these harvest mouse species would be constructive.

Similar to WHM, *Mus* showed some response to environmental and competitive influences, and while season was a driver in their demography, the magnitude of this influence (excluding survival) generally was minor, and was lower than in either SMHM or WHM (Figs. 4 and 5; Supplementary Data SD2C). Estimates for temporary emigration rates hovered near 0.50, suggesting that *Mus* moves relatively randomly across the landscape, consistent with the abilities of these extreme habitat generalists to exploit almost any habitat type (Long 2003; Macholán et al. 2012). Survival, fecundity, and population growth were driven by season (interacting with wetland type for fecundity and population growth models), and whereas the former of these parameters showed strong seasonality (Fig. 3) the latter two tended to be relatively constant across seasons, albeit differing slightly in each wetland type (Figs. 4 and 5). Overall, abundance estimates of *Mus* were similar in both wetland types (Table 3), suggesting that these two wetland types do not differ greatly in value for *Mus*. It is notable that seasonal variation was much greater in tidal than managed wetlands (Supplementary Data SD3).

We predicted that SMHM would be associated with microhabitat characteristics that provide good refuge. In particular, we expected SMHM to be associated with microhabitats providing dense vegetation with high structural complexity, high pickleweed cover, and greater distances from anthropogenic influence (which can subsidize native and invasive predators), as these microhabitats should provide refuge to adults and nests from standing and tidal water, as well as from predators. However, none of these predictions were borne out in this study, and no physical microhabitat characteristics (i.e., vegetation species richness, vegetation structure, pickleweed cover) were retained in any models, suggesting that these had relatively minor effects on the dynamics and abundance estimates of this species. In addition, none of these factors affected temporary emigration for SMHM, suggesting that SMHM may interact with the two wetland types similarly. Moreover, even though the interaction of wetland type and season affected demographic parameters for all species, there was no consistent trend to indicate the superiority of either wetland type for any of the species.

Capture success varied across trapping areas and did not appear to correlate with any microhabitat characteristic. To some extent, this variation directly counters prevailing understanding of SMHM biology, and assumptions that SMHM are strongly dependent on relatively pristine and undisturbed tidal marshes dominated by pickleweed (USFWS 2013). For example, the tidal wetland grid at Joice—which is directly adjacent to the relatively heavily utilized Grizzly Island Road and to a gravel parking area—had the highest monthly abundances of SMHM (overall mean 20.50 ± 5.58), whereas the tidal wetland grid at Denverton—which was the most spatially isolated from anthropogenic influence—had the lowest monthly abundance estimates (overall mean 7.90 ± 2.26), and was the only site (managed or tidal) where no SMHM were captured during at least 1 month. Note that all tidal wetlands in this study have had some degree of disturbance: there are no undisturbed habitats in the SFE (Smith et al. 2018a). Furthermore, trapping grids with the greatest pickleweed cover (~60% or more) did not have significantly greater monthly SMHM abundances (overall mean 11.66 ± 3.14) than grids with moderate (~30–60%) pickleweed cover (overall mean 17.30 ± 6.04).

These results contrast with relatively recent research at Mare Island, located about 15–35 km west of our study sites (Goodyear and Denverton sites, respectively), where Bias and Morrison (2006) reported SMHM captures to be positively correlated with pickleweed cover, although their study contrasted wetlands with upland areas and ponds that were not managed for wildlife habitat. They also reported that SMHM were captured in areas with shorter vegetation, while the sites with the shortest vegetation overall sampled in our study had some of the lowest abundance estimates. It is notable that Bias and Morrison (2006) reported capturing no WHM in their extensive sampling throughout Mare Island. This species is a common habitat generalist in grasslands, and one of us (KRS) has captured genetically confirmed WHM in the central part of Mare Island within the last year (K. R. Smith, pers. obs.). Given the known challenges in distinguishing these species (Sustaita 2011, 2018), some of the discrepancy between our results and those of Bias and Morrison (2006) may reflect misidentification of WHM. Regardless of these differences, however, it appears that for SMHM, as with most species, we cannot simplify "ideal SMHM habitat" to a singular wetland type with one dominant vegetation type.

We predicted that WHM abundance estimates would be greater in managed than tidal wetlands, as the former more closely mimic grassy upland habitat where this species is commonly found, and that they would be associated with microhabitats with low plant species and structural diversity. In this we were partially correct; populations of WHM were indeed larger in managed wetlands, although they exhibited no association with plant species diversity or structural diversity.

Finally, we expected *Mus* populations to be greater in managed than tidal wetlands, and greatest at sites in close proximity to roads and other anthropogenic development, as they

are highly associated with disturbance. Neither of these predictions were supported. Wetland type had no effect on population size for *Mus* (although they were more stable across seasons in managed than tidal wetlands; Supplementary Data SD3), and they were no more common at sites near disturbance than at isolated sites. This also contrasts with Bias and Morrison (2006) who found *Mus* to be positively associated with pickleweed cover and habitat patchiness at Mare Island, although differences in associations between the two studies could be attributed to differences in the scale of our efforts and in the types of habitats studied.

Management implications.—Overall, the results presented herein indicate that relative value of tidal and managed wetlands is not markedly different in terms of demography and population estimates for either native or invasive rodents in Suisun Marsh. Whereas the former wetlands are subject to natural diel fluctuations in water levels, the latter are managed in a relatively static state for production of food for waterfowl, which also are highly preferred by SMHM (Smith and Kelt 2019). Where wetland type did affect demographic parameters of this species, these effects were manifested as general shifts in timing rather than absolute differences in quality; one wetland type supported high reproduction during one season, whereas reproductive activity was shifted, either earlier or later, in the other wetland type. We infer from such patterns that SMHM, which move freely between these habitat types when they are adjacent (Smith 2012), may perceive seasonal differences in microhabitat characteristics (e.g., cues such as seed set); it also suggests, however, that neither is implicitly superior to the other. Thus, seasonally differential use of the two wetland types for supporting life history events could buffer sensitive species such as SMHM from stochastic influences such as the catastrophic weather events projected to become more common as a result of climate change (Thorne et al. 2018).

Population estimates for the upland-associated WHM differed by wetland type, while differences in SMHM demography varied across wetland types only in a seasonal context. This could indicate that while SMHM may perceive seasonal differences in microhabitat characteristics between wetland types, they may not perceive a difference in overall quality, contrary to long-held beliefs by resource managers (Smith et al. 2018a). Why WHM differ across these habitats is not clear without experimentation, but presumably they either are less adapted for tidal marshes or, they simply fare more poorly in competition with SMHM, which is better adapted to this habitat. One of the managed trapping areas we studied was fully disced directly before trapping began (autumn 2013), and in several of the managed wetlands, about 5% of the trapping area was occupied by gravel levee roads. Therefore, these sites presented lower acreage of usable habitat in the managed than tidal trapping areas in this study; it is possible that without these factors, SMHM populations in managed wetlands could exceed those in tidal wetlands.

Results presented herein suggest that waterfowl management is not inherently harmful to SMHM; indeed, the efforts of recreational waterfowl hunters over the last century have resulted in the protection of the largest remaining tract of SMHM habitat, indirectly benefiting SMHM. Because the relationship between the brackish tidal marshes and managed marshes in our study area may differ in other parts of SMHM range, where salinities are higher and vegetation less diverse, we recommend that this study be replicated in the marshes of San Pablo and south San Francisco bays (Smith et al. 2018b). Overall, however, for the purposes of supporting SMHM and its associated species, our data suggest that managed wetlands are at least as valuable as tidal wetlands, and in some respects (e.g., supporting populations of other native rodents) may be superior.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Notation and definitions of parameters used in capture-mark-recapture analyses (survival, fecundity, and population growth models) for the salt marsh harvest mouse (*Reithrodontomys raviventris halicoetes*), western harvest mouse (*R. megalotis*), and house mouse (*Mus musculus*) at Suisun Marsh (38°08′11.8″N, 121°57′27.6″W), Solano County, California, September 2013 through February 2018.

Supplementary Data SD2.—Parameters, parameter structure, weights, beta values (± *SE*) for the highest ranked model containing that parameter, and mean (± *SE*; model averaged when appropriate, range in parentheses if applicable) of monthly estimates for final survival,[1] fecundity,[2] and population growth[3] models for the salt marsh harvest mouse (A; *Reithrodontomys raviventris halicoetes*), western harvest mouse (B; *R. megalotis*), and house mouse (C; *Mus musculus*) at Suisun Marsh (38°08′11.8″N, 121°57′27.6″W), Solano

County, California, September 2013 through February 2018. Superscripts indicate which model type(s) the parameters were utilized in.

Supplementary Data SD3.—(A) Mean abundance estimates (± *SE*) grouped by wetland type for the salt marsh harvest mouse (SMHM; *Reithrodontomys raviventris halicoetes*), western harvest mouse (WHM; *R. megalotis*), and house mouse (*Mus musculus*) captured at Suisun Marsh, Solano County, California, September 2013 through February 2018, across all study seasons. Note the different scales for each species. (B) Mean abundance estimates (± *SE*) for the salt marsh harvest mouse (SMHM; *Reithrodontomys raviventris halicoetes*), western harvest mouse (WHM; *R. megalotis*), and house mouse (*Mus musculus*) captured at Suisun Marsh (38°08′11.8″N, 121°57′27.6″W), Solano County, California, September 2013 through February 2018, grouped by season, year, and wetland type. Note the different scales for each species.

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