

Biological Control of Saltcedar (*Tamarix* spp.) by Saltcedar Leaf Beetles (*Diorhabda* spp.): Effects on Small Mammals

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BIOLOGICAL CONTROL OF SALTCEDAR (*TAMARIX* SPP.) BY SALTCEDAR LEAF BEETLES (*DIORHABDA* SPP.): EFFECTS ON SMALL MAMMALS

William S. Longland¹

ABSTRACT.—The spread of introduced salteedar (*Tamarix* spp.) throughout many riparian systems across the western United States motivated the introduction of salteedar leaf beetles (*Diorhabda carinulata*, *D. elongata*; Chrysomelidae) as a biological control agent specific to salteedar. I monitored small mammal populations for up to 12 years as salteedar defoliation progressed at 3 of the original salteedar beetle release sites and at an additional site where beetles established through dispersal. There was no evidence of any linear effect of increasing defoliation over time on small mammal species richness. Estimated population sizes of 4 small mammal species, based on mark-release-recapture trapping, showed linear responses to salteedar defoliation at particular sites, but all of these species were represented by only 3 years of data at those sites. Increases in the abundance of 2 species of desert-adapted heteromyid rodents, Merriam's kangaroo rat (*Dipodomys merriami*) and Panamint kangaroo rat (*D. panamintinus*), may have occurred due to increasing habitat desertification associated with salteedar biocontrol. Overall, however, results imply that salteedar biological control is likely to have negligible effects on resident small mammal populations.

RESUMEN.—La propagación de tamarisco (*Tamarix* spp.) introducido en muchos sistemas ribereños en todo el oeste de los Estados Unidos motivó la introducción de escarabajos de hojas de tamarisco (*Diorhabda carinulata, D. elongata;* Chrysomelidae) como agente de control biológico. Monitoreé pequeñas poblaciones de mamíferos durante casi 12 años mientras la defoliación de tamarisco progresaba en tres de los sitios originales en los que se liberaron escarabajos y un sitio adicional donde los escarabajos se establecieron por dispersión. No se encontró evidencia de ningún efecto lineal en el aumento de la defoliación en el tiempo, en la riqueza de especies de mamíferos pequeños. El tamaño aproximado de las poblaciones de cuatro especies de mamíferos pequeños basado en el método de marca y recaptura, mostró respuestas lineales a la defoliación de tamarisco en sitios particulares, pero estas especies de roedores heterómidos adaptados al desierto, la rata canguro de Merriam (*Dipodomys merriami*) y la rata canguro Panamint (*D. panamintinus*), puede deberse al incremento de la desertificación del hábitat asociada con el control biológico de tamarisco. En general, los resultados implican que el control biológico del tamarisco tiene efectos poco importantes en las poblaciones pequeñas de mamíferos resultados implican que el control biológico del tamarisco tiene efectos poco importantes en las poblaciones pequeñas de mamíferos resultados implican que el control biológico de tamarisco tiene efectos poco importantes en las poblaciones pequeñas de mamíferos resultados implican que el control biológico del tamarisco tiene efectos poco importantes en las poblaciones pequeñas de mamíferos resultados implican que el control biológico del tamarisco tiene efectos poco importantes en las poblaciones pequeñas de mamíferos resultados implican que el control biológico del tamarisco tiene efectos poco importantes en las poblaciones pequeñas de mamíferos resultados implican que el control biológico del tamarisco tiene efectos poco impor

Since their introduction to western North America from their native ranges in Eurasia and northern Africa, certain species in the genus *Tamarix* (aka tamarisk or saltcedar) have spread extensively and currently occur on hundreds of thousands of hectares (Shafroth et al. 2005, Sher 2013). These deciduous woody plants, which grow in both tree- and shrub-like forms, occupy riparian corridors, wetlands, and other mesic sites in high densities, often replacing native woody species, such as willows (Salix spp.) and cottonwoods (Populus spp.). Given the maintenance of water quality and wildlife habitat that riparian environments provide, the relative rarity of these environments in arid western North America has long raised concern regarding the effects of conversion of these habitats to Tamarix dominance (Knopf et al. 1988). Because of such concerns, a *Tamarix* biological control program was initiated, with the first open field release of saltcedar leaf beetles (*Diorhabda carinulata* and *D. elongata*; Chrysomelidae) collected from their native ranges in spring 2001 at 7 sites in 6 western states (Bean et al. 2013).

Numerous studies have investigated how conversion of riparian vegetation to *Tamarix* domination affects bird species (e.g., Anderson et al. 1977, Anderson and Ohmart 1984, Hink and Ohmart 1984, Hunter et al. 1988, Ellis 1995, Fleishman et al. 2003, Walker 2006, Sogge et al. 2008, van Riper et al. 2008). Although such studies differ in their conclusions regarding the degree to which saltcedar may benefit or harm specific bird populations, this is probably to be expected, since the

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effects would likely differ among bird species and sites, and due to other variables (Sogge et al. 2013). Similarly, though the number of studies comparing small mammal use of saltcedar and native riparian woodlands is considerably smaller than the number of studies involving birds, riparian conversion to saltcedar benefits certain small mammals, such as desert-adapted rodents in the family Heteromyidae, while reducing populations of select species (Anderson and Ohmart 1984, Hink and Ohmart 1984, Ellis et al. 1997, Bateman and Ostoja 2012, Longland 2012). Despite the rapid rate at which saltcedar leaf beetles have spread and defoliated large areas of saltcedar since the initial releases just over a decade ago, as well as the dramatic changes that this biocontrol program is expected to facilitate in affected riparian habitats, there have been virtually no published studies to date that test for effects of saltcedar biocontrol on wildlife populations.

Previously, I used an 11-year set of small mammal trapping data from paired saltcedar and native riparian woodland sites to document how saltcedar conversion affects small mammal populations and species richness (Longland 2012). Here, I consider potential time-series trends in species richness and abundance of small mammal species at 4 sites in western Nevada that have been affected by the saltcedar biocontrol program for up to 12 years.

Methods

Study Sites and Small Mammal Sampling

In 2001, I initiated trapping in *Tamarix* ramosissima habitats at sites on the Humboldt River (~ 10 km S of Lovelock, NV: 40.0° N, 118.5°W), the Walker River (Walker River Paiute Reservation, ~ 7 km S of Schurz, NV: 38.9° N, 118.8° W), and at Stillwater National Wildlife Refuge (~22 km E of Fallon, NV: 39.5°N, 118.5°W). Annual trapping continued through 2012 at Stillwater and Humboldt (excluding 2006, when the latter site was heavily flooded) but was discontinued after 2011 at Walker due to difficult access to the site. Beginning in 2010, an additional site was trapped along the Truckee River (Pyramid Lake Paiute Reservation, $\sim 4 \text{ km NW}$ of Nixon, NV: 39.8° N, 118.4° W). All trapping transects were placed within saltcedar-dominated habitat, which extended many kilometers beyond

trapping transects at all sites except Stillwater, where saltcedar occurred in smaller patches. These sites (excluding Pyramid) were locations of initial experimental releases of saltcedar leaf beetles in 2001 and/or 2002. The beetles established successfully at Humboldt and at Walker, where some defoliation of saltcedar was evident in the year they were released and extensive defoliation was observed by 2003 and 2004, respectively (Bean et al. 2013). Initial releases failed to establish at Stillwater, but beetles were found there and conspicuous defoliation had occurred by 2004 through natural dispersal from either Walker or Humboldt. Beetles had dispersed to the Pyramid site by 2009 and conspicuous defoliation was evident in 2010 (personal observation). In addition to saltcedar, plants occurring at Stillwater, Walker, and Pyramid were generally salt-tolerant desert shrubs, such as shadscale (Atriplex confertifolia), four-wing saltbush (A. canescens), and greasewood (Sarcobatus vermiculatus); the Humboldt site had an understory of native saltgrass (Distichlis spicata) and introduced herbaceous plants (Russian knapweed [Acroptilon repens], and perennial pepperweed [Lep*idium latifolium*) that became very dense as saltcedar defoliation progressed. The Humboldt and Stillwater sites had compacted clay soils, whereas Walker was sandy and Pyramid had clay mixed with coarse sand and gravel.

I conducted small mammal trapping using Sherman[®] live traps ("large, folding") with modified doors to prevent injury to animals' tails. Linear trapping transects of 25 trap stations were established at each site, with a single trap per station and 10-m spacing between consecutive trap stations. At the Humboldt site, I established 4 such transects separated by 25–100 m along a series of parallel irrigation canals running through dense *Tamarix*. Two parallel transects were established 25 m apart in saltcedar at the remaining sites, both within 100 m of the nearby river (Pyramid, Walker) or irrigation canal (Stillwater).

Traps were set in midafternoon or early evening, baited with wild birdseed mix, and checked for captures the following morning. Captured animals were identified by species, marked with uniquely numbered metal eartags for subsequent identification as recaptures, and released at the location of capture after a brief handling period. Overnight trapping was emphasized because most small mammal species that may have been sampled are nocturnal, but traps were open for a few hours during daylight to allow access to diurnal species, such as sciurid rodents. Trapping sessions ran for 3 consecutive nights, so each trapping session involved 300 trap-nights at Humboldt (25 traps per transect \times 4 transects \times 3 nights) or 150 trap-nights at the other sites. Two trapping sessions per year were conducted at Humboldt during 2001-2004 and at Walker and Stillwater during 2001–2006, but trapping at other sites and in other years at these sites was limited to one session per year. The first trapping session occurred during May or June each year and the second, when it occurred, during July or August.

Data Analysis

To estimate population sizes (N) for each combination of species, year, and site, I used full likelihood closed-population capturerecapture models in Program MARK and chose the N value from the specific modeling approach identified as most appropriate for each set of capture data (Lukacs 2014). These specific approaches differ in the manner in which capture probability is modeled—either as a constant or as varying with time, behavior, or heterogeneity effects. I chose to use a closed-population model because of the short duration of each trapping session (3 days) and because the frequency of recaptures from one session to the next was either zero or exceedingly low in most cases; thus, it was seldom possible to estimate between-session survival. For years with 2 trapping sessions (2001–2006), I used the mean of the 2 population estimates in cases with sufficient captures to obtain estimates for both sessions. There were 23 such cases, and the two Nestimates were within the 95% confidence limits of each other in all of these. The 2 estimates differed by <25% in 21 of 23 cases. There were 9 cases in which it was possible to estimate N for one trap session in a given year, but not for both. By using a single N estimate per year, equal weight was given to all years across species and sites in data analyses that follow.

Data were analyzed with generalized estimating equations (GEEs), specifically Poisson regressions with log link functions, using PROC GENMOD (SAS 2009). Models were evaluated for fit by examining the deviance value, and a scale term in each model was varied until the scaled deviance was 1.0 \pm 0.05. Significance of terms in each model was evaluated with Wald χ^2 statistics. Least-squares means were examined for significant terms with >2 levels to determine where differences occurred among specific levels.

To test for time series effects of biological control on small mammal species richness, I ran a GEE using the number of species trapped in a given year as the dependent variable, site as an independent class variable, and years since the inception of the biocontrol program (i.e., year 1 was 2010 for Pyramid and 2001 for remaining sites) as a continuous independent variable. A similar set of models was used to test for potential time series effects of biological control on abundances of each species. For each species with sufficient captures to yield N estimates for ≥ 3 years at a particular site, I used estimated N as a dependent variable, and specified site and years since inception of biocontrol as independent variables as described above. I ran another set of these analyses substituting arcsinetransformed proportion of captured individuals that were recaptured as the dependent variable. Although tests were conducted separately for different species, the number of species captured consistently over time for which the analysis was feasible was relatively small. To separate underlying causes of any significant site effects or site \times year interactions in these analyses, I also ran separate GEEs for each of these species at each site where they occurred, using the same variables but omitting the site term. Because there was a larger number of these individual species and site analyses that tested for time-series trends in both N estimates (15 total tests) and recapture rates (17), I used sequential Bonferroni adjustments (Rice 1989) to consider the significance of results.

Underlying variation in small mammal abundance unrelated to saltcedar biological control could either obscure potential population trends that are a result of biological control or suggest the existence of trends that are not due to biocontrol. I therefore conducted the same analyses as described above for reference areas that lacked biological control agents near the sites. Unfortunately, it was not possible to find saltcedar habitats lacking biological control agents, but I conducted small TABLE 1. Number of individuals captured for each small mammal species sampled at each of 4 study sites (total number of trap-nights at each site in parentheses) dominated by *Tamarix ramosissima*.

	Individuals captured by study site			
Species	Humboldt (4800)	Pyramid (450)	Stillwater (2700)	Walker (2700)
White-tailed antelope squirrel (Ammospermophilus leucurus)	0	0	2	10
Merriam's kangaroo rat (Dipodomys merriami)	14	17	1	180
Great Basin kangaroo rat (Dipodomys microps)	0	0	15	11
Ord's kangaroo rat (Dipodomys ordii)	321	16	70	10
Panamint kangaroo rat (Dipodomys panamintinus)	0	29	0	0
Montane vole (Microtus montanus)	0	0	1	0
House mouse (Mus musculus)	74	0	0	0
Desert woodrat (Neotoma lepida)	0	6	0	27
Grasshopper mouse (Onychomys spp.)	0	0	0	4
Little pocket mouse (Perognathus longimembris)	0	0	0	33
Deer mouse (Peromyscus maniculatus)	398	22	187	78
Piñon mouse (Peromyscus truei)	8	0	1	40
Western harvest mouse (Reithrodontomys megalotus)	18	0	12	19
Cottontail rabbit (Sylvilagus sp.)	1	0	0	0
Total number of individuals captured	834	90	289	412
Mean number of individuals per 100 trap-nights	17.4	12.0	10.7	15.3
Total number of species	7	5	8	10

mammal trapping in native riparian woodlands (see Longland 2012) at all of the sites except Humboldt, which did not have any extensive areas of native riparian vegetation nearby. Consequently, these reference areas do not represent true controls for effects of biological control agents, but they still represent a temporal reference for local variation in small mammal species abundances that is independent of potential effects of biological control agents.

RESULTS

I captured at least 14 species of small mammals over 12 years of trapping in saltcedar habitats, although 2 species were represented by only a single individual at one site (Table 1). Grasshopper mice (*Onychomys* spp.) were represented by only 4 individuals at one site, and these could have included either or both of 2 species (*O. leucogaster* or *O. torridus*), as the site is within the range of both species and they are difficult to distinguish (Riddle 1999). All captures were rodents except for a single cottontail rabbit (*Sylvilagus* sp.), which was the only lagomorph.

There were no effects of years since inception of biological control on species richness ($\chi^2 = 0.35$, df = 1, P = 0.552), nor was the interaction between year and site significant ($\chi^2 = 0.49$, df = 3, P = 0.920). However, the site effect was significant ($\chi^2 = 8.27$, df = 3, P = 0.041), as the mean number of species captured annually at Walker (5.6) was considerably greater than at the remaining sites (Table 2).

Captures in saltcedar habitats were sufficient to yield estimates of N for multiple years and sites for only 3 small mammal species: Merriam's kangaroo rat, Ord's kangaroo rat, and deer mouse. Estimates were possible at single sites for an additional 4 species: Panamint kangaroo rat, house mouse, desert woodrat, and piñon mouse (Table 3). The only significant term in multisite analyses of N estimates was the year \times site interaction for deer mice $(\chi^2 = 12.17, df = 3, P = 0.007)$. Individual site analyses showed that this result occurred due to a significant negative effect of years since inception of biological control for deer mice at the Pyramid site ($\chi^2 = 122.39$, df = 1, P < 0.0001) and small, nonsignificant positive effects at remaining sites (Table 3). The multisite analysis for Merriam's kangaroo rat yielded a marginally nonsignificant year \times site interaction ($\chi^2 = 5.49$, df = 2, *P* = 0.06) due to a significant positive effect of years on estimated N at the Pyramid site (Table 3). There was no significant main effect of years since inception of biological control in multisite analyses for any species. There was, however, a significant year term in estimated N analyses for both Panamint kangaroo rats 382

TABLE 2. Number of small mammal species captured in saltcedar habitats at each of 4 study sites. Dashes represent sites that were not sampled in that year. Each year of sampling is based on 300 trap-nights at the Humboldt site and 150 trap-nights at the other sites.

Year	Species captured by study site				
	Humboldt	Pyramid	Stillwater	Walker	
2001	3	_	5	7	
2002	4	_	3	4	
2003	3	_	3	6	
2004	4	_	3	6	
2005	2	_	2	7	
2006	_	_	3	9	
2007	4	_	2	6	
2008	4	_	2	5	
2009	4	_	6	5	
2010	3	4	4	2	
2011	4	4	6	5	
2012	3	5	4	—	
Mean (SD)	3.5(0.69)	4.3(0.58)	3.6(1.44)	5.6(1.80)	
Total number of species	7	5	8	10	

TABLE 3. Top row of each entry shows range of Program MARK annual estimates of population sizes (*N*) of small mammal species sampled at each of 4 study sites dominated by *Tamarix ramosissima* (years trapped in parentheses for sites in heading; number of years with sufficient captures to yield estimated *N* in parentheses for each species and site). Zeros indicate no captures of a given species. NE = no estimates (<3 years with sufficient captures to yield *N* estimates). Bottom row of each entry shows effect size in the Poisson regression of *N* estimates on years since inception of biological control (SE in parentheses); an asterisk (*) indicates a significant χ^2 value for regression (*P* < 0.01 in all cases).

Species	Estimated population size range (years)				
	Humboldt (2001–2005, 2007–2012)	Pyramid (2010–2012)	Stillwater (2001–2012)	Walker (2001–2011)	
Merriam's kangaroo rat (Dipodomys merriami)	NE	5–21 (3) 1.443 (0.442)*	NE	5–28 (11) 0.049 (0.052)	
Ord's kangaroo rat (Dipodomys ordii)	$\begin{array}{c} 6-56~(11)\\ 0.012~(0.047)\end{array}$	$\begin{array}{c} 9-28 \ (3) \\ 0.179 \ (0.625) \end{array}$	5–17 (6) 0.083 (0.050)	NE	
Panamint kangaroo rat (Dipodomys panamintinus)	0	$\begin{array}{c} 6-25 \ (3) \\ 1.579 \ (0.478) * \end{array}$	0	0	
House mouse (Mus musculus)	$\begin{array}{c} 18 - 336 \ (4) \\ - 0.029 \ (0.306) \end{array}$	0	0	0	
Desert woodrat (Neotoma lepida)	0	NE	0	$1016\ (3)\\-0.048\ (0.207)$	
Deer mouse (Peromyscus maniculatus)	$\begin{array}{c} 8-217\ (11)\\ 0.028\ (0.082)\end{array}$	30–122 (3) –0.728 (0.066)*	$\begin{array}{c} 5-59\ (11)\\ 0.086\ (0.074)\end{array}$	$\begin{array}{c} 4-24 \ (5) \\ 0.065 \ (0.093) \end{array}$	
Piñon mouse (Peromyscus truei)	NE	0	NE	$\begin{array}{c} 5-22 \ (3) \\ -0.542 \ (0.137)^* \end{array}$	

 $(\chi^2 = 10.93, df = 1, P < 0.0001)$ and piñon mice $(\chi^2 = 15.77, df = 1, P < 0.0001)$ at the single sites where estimates were possible for these species (Table 3). All significant terms in the analyses highlighted above which tested for time-series trends in estimated *N* remained significant (P < 0.05) following Bonferroni adjustment of *P* values.

Among species showing significant trends in the estimated N analyses for saltcedar habitats, there were sufficient captures to conduct individual site analyses in reference native woodland sites for only deer mice and piñon mice, but there were no significant effects involving years since inception of biocontrol in reference site analyses (P > 0.15in all cases). There were also no significant terms in the analyses of recapture rates for any of the small mammal species tested following Bonferroni adjustment of results.

DISCUSSION

Small mammal trapping in saltcedar habitats at 4 western Great Basin sites showed no evidence of increasing effects of saltcedar biological control on species richness and few effects on estimated abundances of species captured. Time series effects of years since inception of biological control occurred for individual species only at select study sites, and the direction of these effects varied among species (Table 3). Merriam's and Panamint kangaroo rats both showed strong positive effects of years since inception of biocontrol on estimated populations at the Pyramid site, whereas deer mice showed a moderate negative response over the same time period. Piñon mice, congeners of deer mice, similarly showed a moderate negative response at the Walker site (Table 3). Neither piñon mice or deer mice previously showed significant responses in comparisons of capture rates in saltcedar with capture rates in native riparian woodlands, but kangoroo rats often showed positive responses to saltcedar (Longland 2012).

In studies comparing small mammal fauna between saltcedar and native riparian woodlands, heteromyid rodents, represented in Table 1 by 4 species of kangaroo rats (Dipodomys merriami, D. microps, D. ordii, and D. panamintinus) and one species of pocket mouse (Perognathus longimembris), tend to occur more frequently in saltcedar habitats (Ellis et al. 1997, Hink and Ohmart 1984, Longland 2012). I argued that this higher frequency of occurrence is due to well-known adaptations of these animals to desert habitats and conditions and the desertification effects that often come with conversion of riparian woodland to saltcedar (Longland 2012). Saltcedar habitats have a very different appearance after infestation with and defoliation by saltcedar leaf beetles; they become more open and allow more light transmission to understory plants, and the habitat thus appears even more desert-like. At a Mojave Desert site, Bateman et al. (2013) documented significantly increased temperature, decreased relative humidity, and reduced green biomass concomitant with saltcedar defoliation by saltcedar leaf beetles. If the positive population trend for Merriam's and Panamint kangaroo rats at my Pyramid site is truly associated with biological control, this increase in desertification may be the underlying driver of this response.

It is noteworthy that all significant population responses to time since inception of biocontrol occurred at a site trapped for only 3 years (Pyramid) or at sites where the species for which a response was detected was only captured in 3 years of the study. Correlations based on just 3 years could be spurious. However, the absence of significant population responses over 11-12 year periods does not mean that trends did not exist during the early phases of biocontrol when expansion of defoliation was rapid. Bean et al. (2013) assessed mortality of saltcedar at several sites where saltcedar leaf beetles established and showed rapid increases in tree mortality over 3-year periods postestablishment, which is consistent with observations at my sites. A longer record at the only site included in my study for which they present mortality data (i.e., Humboldt) shows mortality leveling off after 6-7 years of defoliation (Bean et al. 2013). Interestingly, I reanalyzed estimated N values using the first 6 years of trapping data at the 3 sites monitored since 2001 and found additional significant positive effects of years since inception of biocontrol on abundance of heteromyd rodent species. These positive effects were not evident in the longer-term data (Ord's kangroo rat at Stillwater: $\chi^2 = 5.04$, df = 1, P = 0.025, effect size = 0.263; Merriam's kangoaroo rat at Walker: $\chi^2 = 27.09$, df = 1, *P* < 0.0001, effect size = 0.303). Although my analysis also vielded one negative effect (Ord's kangaroo rat at Humboldt: $\chi^2 = 5.62$, df = 1, P = 0.018, effect size = -0.216), it may be an exception that supports the generalization that desertification associated with saltcedar benefits heteromyid populations. The latter site has an understory of invasive herbaceous plants that has increased dramatically in density as saltcedar defoliation has progressed, and dense herbaceous vegetation makes poor kangaroo rat habitat, perhaps because it deters movement of these bipedal rodents (Rieder et al. 2010). At sites where kangaroo rat species showed increasing trends, the density of herbaceous understory plants decreased noticeably as defoliation of saltcedar progressed.

Small mammal species tend to exhibit high levels of annual variation in population densities, even in the absence of conspicuous changes in habitat (Fryxell et al. 1998, Dickman et al. 2010), making it difficult to attribute annual differences in population sizes to effects of saltcedar defoliation. Because I had no a priori expectation as to how defoliation of saltcedar might affect population trajectories of small mammal species, I simply considered potentially increasing effects of defoliation by testing for linear effects of time since inception of biological control on small mammal populations. For any given species affected by habitat perturbations, a negative effect on population size may be more easily detected than a positive effect, since a negative response should drive populations to low numbers or local extinction and keep them there. By contrast, even if a habitat perturbation, such as overstory defoliation, benefits a certain species and leads to an increasing population trend, the species' numbers would still be depressed in some years due to the inherent variability in small mammal population sizes. This variability could easily obscure any positive effects of habitat changes. Such considerations illustrate the utility of long-term monitoring of wildlife, especially as changes inevitably accrue to *Tamarix* habitats as control efforts progress.

My trapping efforts clearly do not include all of the small mammal species that inhabit saltcedar habitats in the western Great Basin. It is quite likely that species differ in detectability. Each site had at least one species that was sampled only at that particular site. Some of these unique species were represented by only a single animal (montane vole, cottontail rabbit) or a few individuals (grasshopper mouse), but others (house mouse, little pocket mouse, Panamint kangaroo rat) were represented by enough animals to suggest that the captures were not simply incidental (Table 1). These trapping results illustrate 2 points relevant to comparisons of species richness. First, the absence of a species in trapping data for a particular site does not indicate that it was absent at that site. For example, it would have been easy to miss either of the species represented by a single capture. Second, although most species sampled occurred at 2 or more sites, species-specific habitat affinities and habitat differences among sites may facilitate the presence of unique species at different sites. For example, the presence of Panamint kangaroo rats at the Pyramid site is likely due to their greater affinity for coarse soils (Best 1999) compared to the other kangaroo rat species sampled and due to the higher rock content in soils at Pyramid than at the other sites. Similarly, the unique occurrence of house mice at Humboldt is probably due to this site being on a ranch and thus substantially closer to human activity than other sites. Because local species pools have subtle differences at different sites, sampling additional sites would almost certainly have added to the species list.

The long-term results of introduction of biological control to saltcedar woodlands are yet to be realized. As is typical with biocontrol, saltcedar will persist in these riparian systems, but at lower densities (Bean et al. 2013). Responses to reduced saltcedar densities are likely to show at least some degree of site specificity and will continue to play out for some time. To date, however, monitoring of small mammal populations at my western Great Basin study areas suggests that biological control of saltcedar with saltcedar leaf beetles has not impacted species richness and has generally had negligible effects on estimated abundances of rodent species occurring in riparian woodlands that have been converted to saltcedar monocultures.

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