

Small Mammals in Saltcedar (*Tamarix ramosissima*)—Invaded and Native Riparian Habitats of the Western Great Basin

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Invasive saltcedar species have replaced native riparian trees on numerous river systems throughout the western United States, raising concerns about how this habitat conversion may affect wildlife. For periods ranging from 2 to 11 yr, I used live-trapping to monitor small mammal populations in paired saltcedar and native riparian woodlands at four sites in western Nevada and eastern California. Heteromyid rodents, such as Merriam's and Ord's kangaroo rats, were more likely to occur in saltcedar habitats, but other rodent species, particularly the montane vole and western harvest mouse, occurred more often in native habitats, and this balanced species richness in habitat comparisons. The most common species at all sites, the deer mouse, did not show any consistent differences in abundance or in mean body mass between the two habitat types. However, the ratio of captured male to female deer mice was higher in saltcedar than native habitats at two sites. Deer mice as well as Ord's kangaroo rats also had higher rates of being recaptured following initial capture in native habitats, which may have been due to fewer transient individuals occurring in these habitats. By contrast, Merriam's kangaroo rats may have been more transient in native habitats because they were more likely to be recaptured in saltcedar. Individuals of two species, pinyon mouse and white-tailed antelope ground squirrel, had greater mean body mass in native habitats than they did in saltcedar, implying that they may have maintained superior condition in native habitats.

Nomenclature: Saltcedar, *Tamarix ramosissima* Ledeb.

Key words: Heteromyidae, native, nonnative, riparian woodlands, rodents.

In the arid, southwestern United States, riparian corridors occupy a small fraction of the landscape yet are tremendously important for the ecosystem services they provide. Additionally, riparian areas in desert environments support a disproportionately large number of wildlife species (Knopf et al. 1988; Stamp and Ohmart 1979; Szaro 1991). Woody species of the genus *Tamarix* (i.e., saltcedar or tamarisk), which range in growth form from large shrubs to small trees, have invaded many of these riparian systems, replacing native woody plants, such as cottonwood (*Populus* spp.) and willows (*Salix* spp.), and raising concerns about impacts on wildlife (Fleishman et al. 2003; Szaro 1991).

Although several studies have been published regarding the effects of saltcedar invasion on riparian birds (e.g., Anderson et al. 1977; Anderson and Ohmart 1984; Ellis 1995; Fleishman et al. 2003; Hink and Ohmart 1984; Hunter et al. 1988; Sogge et al. 2008; van Riper et al. 2008; Walker 2006), relatively little literature addresses

such impacts on other wildlife taxa. For example, despite the ease by which small mammal abundance and certain life history variables can be assessed using trapping, only a few studies have compared small mammal use of native riparian and saltcedar habitats, and those studies have been restricted to the Sonoran and Chihuahuan deserts of Arizona and New Mexico and to short-term monitoring along single river systems (Andersen and Nelson 1999; Anderson and Ohmart 1984; Ellis et al. 1997; Hink and Ohmart 1984) or single sites (Andersen 1994). Because habitat characteristics of small mammals, especially rodents, have been studied intensively (e.g., King 1968; Genoways and Brown 1993; Reichman and Brown 1983), it may be possible to understand how habitat modification by invasive plants facilitates potential changes in small mammal abundance or species composition. Furthermore, species that are found to be affected either positively or negatively by riparian habitat conversion may provide useful indicators of habitat quality in mixed native and saltcedar riparian woodlands, such as during intermediate stages of invasion.

Here, I report results of small mammal monitoring along three river systems and a wetland area in the Great

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Management Implications

Invasion of riverside and other riparian vegetation by saltcedar species changes the appearance and structure of riparian habitats in the arid western United States conspicuously. Because riparian environments occupy a small fraction of these arid lands yet support an inordinately high number of animal species, there is considerable concern regarding effects of saltcedar invasion on wildlife. Here, I present results of small mammal monitoring using annual live-trapping for up to 11 years at four sites in the western Great Basin in both saltcedar-invaded and native riparian habitats. Although the total number of species found during the entire monitoring period was equal or greater in native habitat than in saltcedar at all sites, the number of small mammal species sampled did not differ statistically between native and saltcedar habitats. A general effect of saltcedar invasion was an increase in rodents in the family Heteromyidae. This is consistent with well-known adaptations of heteromyid rodents to open, arid environments and conversion of riparian areas to more open, desert-like habitats at many sites invaded by saltcedar. By contrast, rodent species, such as montane voles and western harvest mice, which are typically associated with the greater cover and more mesic conditions provided by native riparian vegetation tended to be uncommon or absent in saltcedar-converted habitat. Such species may benefit at sites where native vegetation can be successfully restored following saltcedar removal.

Basin Desert of western Nevada and eastern California. These monitoring efforts have been conducted annually for up to 11 yr and involved identical live-trapping protocols in paired native-dominated and saltcedar (*Tamarix ramosissima* Ledeb.)-dominated riparian habitats (hereafter, referred to simply as *native* and *saltcedar*). I specifically focused on the following questions that can be addressed using mark–release–recapture trapping: (1) Does species richness differ between saltcedar and native habitats? (2) Does abundance of small mammal species differ between saltcedar and native habitats in a manner suggesting an affinity for one of these habitats and avoidance of the other? (3) Do recapture rates, which may reflect residence time or survival, differ between saltcedar and native habitats? (4) Does body mass vary systematically between saltcedar and native habitats? (5) Does an important metric of population structure, sex ratio, differ consistently between saltcedar and native habitats for the deer mouse (*Peromyscus maniculatus*), the most widespread and abundant species sampled in the study?

Materials and Methods

Study Sites and Trapping. Small-mammal trapping was conducted at four sites that permitted simultaneous sampling of native and saltcedar-invaded habitats. In 2001, I initiated trapping along transects in paired native and saltcedar habitats at sites on the Walker River Paiute Reservation (native habitat, approximately 6 km [3.73 mi] northwest of Schurz, NV: 39°01'44"N, 118°51'45"W;

saltcedar habitat, approximately 7 km south of Schurz, NV: 38°53'35"N, 118°46'56"W), on the Owens River (both habitats, approximately 13 km southeast of Big Pine, CA: 37°05'18"N, 118°13'42"W), and at Stillwater National Wildlife Refuge (both habitats ~22 km E of Fallon, NV: 39°31'29"N, 118°30'45"W). Annual trapping was continued at two of these sites through 2011 but was discontinued after 3 yr at the Owens site (i.e., 2001 to 2003). In 2010 and 2011, an additional site was trapped on the Pyramid Lake Paiute Reservation. The Pyramid site had adjacent, paired habitats on the south side of the Truckee River near its delta with Pyramid Lake (approximately 4 km northwest of Nixon, NV: 39°51'20"N, 119°24'52"W).

Saltcedar and native habitats were in close proximity (< 200 m [656 ft] apart) at most sites but were separated by approximately 7 km at Walker. At most sites, both habitats extended many kilometers beyond the ends of trapping transects, but at Stillwater the habitats occurred in smaller patches, and the transects extended the entire length of the saltcedar patch. As is typical of riparian habitats on arid western rangelands, riparian vegetation was usually limited to narrow bands along the water courses. Saltcedar extended up to 50 m from the water's edge at most sites, as did the native habitats at Walker and Pyramid. The native habitat at Owens was narrower, extending up to 20 m from the water's edge along trapping transects. Both native and saltcedar habitats followed narrow bands approximately 10 to 15 m wide at Stillwater.

Plant communities and soils at the Owens, Walker, and Pyramid sites were similar. The saltcedar habitats at these sites were typically sandy substrates and scattered, salt-tolerant Great Basin shrubs, such as shadscale [*Atriplex confertifolia* (Torr. & Frém) S. Wats.], fourwing saltbush [*Atriplex canescens* (Pursh) Nutt.], and greasewood [*Sarcobatus vermiculatus* (Hook.) Torr.] occurred among dense patches of saltcedar. The native habitats had distinct vegetation layers consisting of an herbaceous understory of native grasses and forbs, a lower tree canopy composed mainly of coyote willow (*Salix exigua* Nutt.) and an upper canopy composed mainly of Fremont cottonwood (*Populus fremontii* S. Wats.). Some relict patches of these native riparian species also remained scattered throughout the saltcedar habitat at Walker. At Stillwater, the soil was mixed clay and sand, and compared with the other sites, the saltcedar was more sparsely distributed, as were the cottonwoods in the native habitat, which ran along an irrigation canal lined with dense coyote willows.

Trapping was conducted using aluminum live traps (LFA folding traps, H. B. Sherman Traps, 3731 Peddie Drive, Tallahassee, FL 32303) measuring 7.6 by 8.9 by 22.9 cm (3 by 3.5 by 9 in). I used two transects of 25 trap stations each in both habitats with 10-m spacing between consecutive stations. A single trap was placed at each station. One transect in each habitat was directly adjacent

to the flowing river at Owens, Walker, and Pyramid and the second ran parallel to that at 15 to 25 m from the water. At Stillwater, the two native riparian transects were placed along either edge of an irrigation canal, and the two saltcedar transects were placed along roughly parallel, linear patches of saltcedar separated by approximately 25 m. Transects were linear at Stillwater and Pyramid, but followed the meandering path of the adjacent rivers at Owens and Walker.

Traps were baited with a mix composed mostly of wild-proso millet (*Panicum miliaceum* L.) and common sunflower (*Helianthus annuus* L.) seeds, activated in midafternoon or early evening, and checked for captures the following morning. Captured animals were identified by species and sex, weighed, and fitted with a uniquely numbered metal ear tag (1005-1 small animal ear tags, National Band and Tag Company, 721 York Street, P.O. Box 72430, Newport, KY 41072-0430) for subsequent assignment as recaptures. They were released at the location of capture, usually after < 2 min of handling. I focused on nighttime trapping because most small mammals are nocturnal, but traps were generally activated for a few hours of daylight to allow access to diurnal species. Trapping sessions ran for three consecutive nights, so each session involved 300 trap–nights (25 traps/transect times 4 transects times 3 nights) or 150 trap–nights per habitat. Each study site was sampled over one or two sessions annually. I ran the first trapping session during May or June each year and the second, when they occurred, during July or August. Two trapping sessions were conducted at Walker and Stillwater during 2001 to 2006; other sites and other years at these sites were limited to one session per year.

Data Analysis. Species richness and abundance data were analyzed with generalized estimating equations (GEEs) using PROC GENMOD (SAS 2009 statistical software, SAS Institute Inc., 100 SAS Campus Drive, Cary, NC 27513-2414). GEEs are particularly suited for count data that may be nonnormally distributed, including small mammal trapping data (Amacher et al. 2008). The specific GEE models applied were Poisson regressions with log-link functions, which were evaluated for fit by examining deviance and Pearson χ^2 statistics. Significance of terms in each model was evaluated with Wald χ^2 statistics.

I compared the number of small mammal species captured in a GEE model using *year*, *site*, *habitat*, and their interaction terms as independent class variables; *year* was specified as a repeated factor to account for potential autocorrelation between sampling periods. A species was counted if one or more individuals were captured during a session.

I used direct counts of number of individuals captured as an index of small mammal species abundances. Counts were combined for what may have been two different species of grasshopper mice (*Onychomys leucogaster* and

Onychomys torridus) and cottontail rabbits (*Sylvilagus nuttallii* and *Sylvilagus audubonii*). For each species captured at multiple sites, I ran a GEE model using the number of individuals captured per 100 trap–nights as the dependent variable, and *year*, *site*, *habitat*, and their interactions as independent variables, specifying *year* as a repeated factor. The number of sites used in analyses differed among species because only sites where a given species was captured in ≥ 1 trap session were included in each analysis. I also ran an analogous model to test effects of the same terms on total numbers of captures for all small mammal species combined. To test for potential habitat effects on recapture rates, I reran models substituting the proportion of captured individuals that were recaptured as the dependent variable (i.e., *number of individuals recaptured per trap session*/*total number captured*, or 0 on the infrequent occasions when none were recaptured); an arcsine transformation was applied to the proportions for these analyses (Sokal and Rohlf 1994).

To contrast sex ratios between native and saltcedar habitats for the most abundant, widespread rodent species sampled, *Peromyscus maniculatus*, I ran a GEE model using *year*, *site*, *habitat*, and their interactions as independent variables, again specifying *year* as a repeated factor, and the proportion of *P. maniculatus* individuals captured that were males (i.e., *males captured*/*[males + females captured]*) as the dependent variable. Proportions were arcsine-transformed for the analysis.

Finally, I tested whether the same variables affected body mass, but added a *sex* effect to the models because this often influences body mass. For each species with sufficient captures, I ran a GEE model using *year*, *site*, *habitat*, and *sex* as independent variables (with *year* as a repeated factor), and *body mass* of each animal as the dependent variable. Body mass analyses were the only GEE models that used data on individual animals rather than population-level data (i.e., counts or proportions of individuals).

Results

I captured at least 16 species of small mammals during trapping; more if either of the genera *Onychomys* or *Sylvilagus* included > 1 species (Table 1). Although more species were captured in native than in saltcedar habitats at three of four sites (Table 1), the mean number of species captured annually across all sites did not differ significantly between habitats ($\chi^2 = 0.73$, $df = 1$, $P = 0.397$; Table 2). Species richness differed among sites ($\chi^2 = 10.70$, $df = 3$, $P = 0.013$) because more species were captured at the two sites sampled for the entire 11 yr (Stillwater and Walker) than at the other sites (Table 1), but the site by habitat interaction was nonsignificant ($\chi^2 = 5.23$, $df = 3$, $P = 0.156$). The year effect was also nonsignificant ($\chi^2 = 10.51$, $df = 10$, $P = 0.397$), as were the year by habitat ($\chi^2 = 9.79$, $df = 10$, $P = 0.460$) and the year by site interactions ($\chi^2 = 11.00$, $df = 11$, $P = 0.443$).

Table 1. Number of individual animals captured for each small mammal species sampled at each of four study sites (total number of trap–nights at each site in parentheses). The total number of animals captured across all species (including recaptures) mean number captured per 100 trap–nights, and total number of species captured are also given. Paired habitats, one dominated by native riparian vegetation and the other by saltcedar, were trapped with equal effort at all sites.

Species	No. of animals captured per study site							
	Owens (900)		Pyramid (600)		Stillwater (5100)		Walker (5100)	
	Native	Saltcedar	Native	Saltcedar	Native	Saltcedar	Native	Saltcedar
<i>Ammospermophilus leucurus</i>	0	0	0	0	4	4	2	28
<i>Chaetodipus formosus</i>	0	0	0	0	0	0	3	0
<i>Dipodomys merriami</i>	1	68	4	5	1	2	45	196
<i>Dipodomys microps</i>	0	0	0	0	3	8	1	12
<i>Dipodomys ordii</i>	0	0	7	17	9	72	22	20
<i>Dipodomys panamintinus</i>	0	0	0	4	0	0	0	0
<i>Microtus montanus</i>	8	0	1	0	7	3	0	0
<i>Mus musculus</i>	0	0	2	0	1	0	0	0
<i>Neotoma lepida</i>	0	0	2	7	17	2	44	29
<i>Onychomys</i> spp.	0	1	1	0	0	0	0	4
<i>Perognathus longimembris</i>	0	0	0	0	0	0	5	33
<i>Perognathus parvus</i>	0	0	0	0	0	0	2	0
<i>Peromyscus maniculatus</i>	16	21	36	45	249	199	97	90
<i>Peromyscus truei</i>	5	5	0	0	5	1	30	40
<i>Reithrodontomys megalotis</i>	9	0	1	0	51	10	10	17
<i>Sylvilagus</i> spp.	1	0	0	0	1	0	2	0
Total No. animals captured	78	192	108	156	742	623	522	940
Mean No./100 trap–nights	17.3	42.7	36.0	52.0	29.1	24.4	20.5	36.9
Total No. species captured	5	5	8	5	11	9	12	10

Table 2. Number of small mammal species captured at each of four study sites. Paired riparian habitats, one dominated by native vegetation and the other by saltcedar, were trapped with equal effort at each site. Lines represent sites/habitats that were not sampled in that year.

Year	No. of species captured per study site							
	Owens		Pyramid		Stillwater		Walker	
	Native	Saltcedar	Native	Saltcedar	Native	Saltcedar	Native	Saltcedar
2001	3	3	—	—	4	5	4	7
2002	3	2	—	—	2	3	6	4
2003	4	3	—	—	5	3	6	6
2004	—	—	—	—	4	3	5	6
2005	—	—	—	—	2	2	5	7
2006	—	—	—	—	5	3	7	9
2007	—	—	—	—	5	2	3	6
2008	—	—	—	—	3	2	2	5
2009	—	—	—	—	5	6	3	5
2010	—	—	6	4	6	4	2	2
2011	—	—	5	5	5	6	3	5
Mean (± SD)	3.3 (0.58)	2.7 (0.58)	5.5 (0.71)	4.5 (0.71)	4.2 (1.33)	3.5 (1.51)	4.2 (1.72)	5.6 (1.80)

Table 3. Sex ratios ($No. of males / [No. of males + No. of females]$) of *Peromyscus maniculatus* trap captures in native riparian and saltcedar habitats at four paired-habitat study sites.

Site (No. of yr sampled)	Habitat	Mean sex ratio (\pm SD)
Owens (3)	Native	0.72 (0.24)
	Saltcedar	0.20 (0.20)
Pyramid (2)	Native	0.61 (0.04)
	Saltcedar	0.50 (0.16)
Stillwater (11)	Native	0.55 (0.13)
	Saltcedar	0.52 (0.12)
Walker (11)	Native	0.67 (0.31)
	Saltcedar	0.69 (0.29)

Sylvilagus spp. and five rodent species—long-tailed pocket mouse (*Chaetodipus formosus*), Panamint kangaroo rat (*Dipodomys panamintinus*), house mouse (*Mus musculus*), Pacific pocket mouse (*Perognathus longimembris*), Great Basin pocket mouse (*Perognathus parvus*)—that were either recorded at a single study site or were rarely captured were excluded from abundance analyses. GEE models for six of the remaining 10 species converged on solutions that yielded a strong fit to trapping data. Abundance of the most widespread and commonly trapped species, *P. maniculatus* (family Cricetidae), did not differ consistently as a function of habitat ($\chi^2 = 0.14$, $df = 1$, $P = 0.713$). However, there was a significant site by habitat interaction ($\chi^2 = 9.17$, $df = 3$, $P = 0.027$) because more *P. maniculatus* individuals were captured in native habitat at Stillwater, whereas capture frequencies were similar or greater in saltcedar habitats at the other sites (Table 1). The GEE model for the desert woodrat (*Neotoma lepida*), another cricetid rodent, also lacked evidence of differential capture frequency between habitats ($\chi^2 = 0.11$, $df = 1$, $P = 0.741$), and that was consistent among sites (site by habitat: $\chi^2 = 4.54$, $df = 2$, $P = 0.103$). By contrast, the habitat term was significant for two additional cricetid species, montane vole (*Microtus montanus*; $\chi^2 = 18.96$, $df = 1$, $P < 0.0001$) and western harvest mouse (*Reithrodontomys megalotis*; $\chi^2 = 12.37$, $df = 1$, $P = 0.0004$), resulting from more frequent captures in native habitats (Table 1). Significant site by habitat interactions indicated that this apparent affinity for native riparian vegetation varied among sites (*M. montanus*: $\chi^2 = 7.46$, $df = 1$, $P < 0.006$; *R. megalotis*: $\chi^2 = 35.56$, $df = 2$, $P < 0.0001$). Habitat terms were also significant for two species in the family Heteromyidae, Merriam's kangaroo rat (*Dipodomys merriami*; habitat: $\chi^2 = 39.58$, $df = 1$, $P < 0.0001$; site by habitat: $\chi^2 = 22.51$, $df = 2$, $P < 0.0001$) and Ord's kangaroo rat (*Dipodomys ordii*; habitat: $\chi^2 = 14.11$, $df = 1$, $P = 0.0002$; site by habitat: $\chi^2 = 16.42$, $df = 2$, $P = 0.0003$). However, unlike the latter two cricetid species, these heteromyids exhibited an apparent affinity for saltcedar (Table 1). Combining abundance data

for all species, both habitat ($\chi^2 = 19.15$, $df = 1$, $P < 0.0001$) and site by habitat ($\chi^2 = 38.97$, $df = 3$, $P < 0.0001$) had highly significant effects on numbers of captures. Overall capture frequency was greater in saltcedar than it was in native habitats at all sites, except Stillwater, where it was similar (Table 1).

GEE models fit data on recapture rates of four rodent species, and habitat or site by habitat interactions were significant for three of these species. *D. merriami* recapture frequencies were greater in saltcedar (61.9% of captured animals were recaptured) than they were in native habitats (38.8%), yielding a significant habitat effect ($\chi^2 = 10.72$, $df = 1$, $P = 0.001$); site by habitat was significant ($\chi^2 = 15.06$, $df = 2$, $P = 0.0005$) because the difference was bigger at the Owens site than it was elsewhere. The habitat term was also significant for *D. ordii* ($\chi^2 = 14.07$, $df = 1$, $P = 0.0002$), which showed a pattern opposite its congener, with more recaptures in native (75.6%) than in saltcedar habitats (46.5%). *P. maniculatus* was also recaptured significantly more often in native habitats (55.1%) than it was in saltcedar (44.3%; $\chi^2 = 4.37$, $df = 1$, $P = 0.037$). *R. megalotis* had similar habitat-specific recapture frequencies ($\chi^2 = 1.60$, $df = 1$, $P = 0.206$).

Analyses of body mass as a function of year, site, sex, and habitat yielded significant GEE models with strong fits to data for six rodent species. Year, sex and site effects and associated interactions affected body mass occasionally, but the habitat effect was significant in models for only two species, the white-tailed antelope squirrel (*Ammospermophilus leucurus*; $\chi^2 = 79.89$, $df = 1$, $P < 0.0001$) and the pinyon mouse (*Peromyscus truei*; $\chi^2 = 20.23$, $df = 1$, $P = 0.0001$). Individuals of both of these species had greater mean mass in native habitats than they did in saltcedar (mean mass \pm SD for *A. leucurus* = 96.7 ± 6.11 g [3.4 ± 0.22 oz] in native vs. 80.9 ± 13.51 g in saltcedar; *P. truei*: native = 21.3 ± 3.92 g, saltcedar = 20.3 ± 3.58 g). Between-site differences in the magnitude of this habitat effect led to a significant site by habitat interactions for both *A. leucurus* ($\chi^2 = 6.18$, $df = 1$, $P = 0.013$) and *P. truei* ($\chi^2 = 13.51$, $df = 1$, $P = 0.0002$).

All terms were significant in the GEE model on sex ratios of *P. maniculatus* ($P \leq 0.025$). Significance of the habitat effect ($\chi^2 = 10.60$, $df = 1$, $P = 0.001$) and site by habitat interaction ($\chi^2 = 9.59$, $df = 3$, $P < 0.022$) was due to a higher proportion of male *P. maniculatus* sampled in native habitats compared with saltcedar at three of the four sites (Table 3). Sex ratios were similar in saltcedar and native habitats at two sites with the most years of data, Stillwater and Walker (Table 3), raising concerns that results may have been driven by skewed sex ratio estimates at the less-sampled sites. When the analysis was restricted to data from Stillwater and Walker, habitat ($\chi^2 = 0.02$, $df = 1$, $P = 0.875$) and the site by habitat terms ($\chi^2 = 0.18$, $df = 1$, $P = 0.668$) were not significant.

Discussion

Species richness of small mammals was generally similar in native riparian and saltcedar-invaded riparian habitats based on annual sampling, although that may depend somewhat on the temporal scale under consideration because the cumulative number of species sampled was greater in native habitats than it was in saltcedar at three of four study sites and equal at the fourth site (Table 1). Although the effect of the conversion of native riparian habitat to saltcedar on species richness may, therefore, be arguable, overall capture frequencies of small mammals were greater in saltcedar than they were in native habitats. Of greater importance, however, are species-specific effects of habitat conversion on abundance.

Two species of heteromyid rodents (*D. merriami* and *D. ordii*), both kangaroo rats, were captured significantly more often in saltcedar than they were in native riparian habitats. Two additional kangaroo rat species (*D. microps* and *D. panamintinus*) and yet another heteromyid species (*Perognathus longimembris*) also showed clear trends in that direction (Table 1), but they either yielded GEE models that fit trapping data poorly or they were excluded from analyses because of being sampled at only one site. Although the two remaining heteromyid species sampled (*Perognathus parvus* and *C. formosus*) were captured exclusively in native habitats, they were represented by just two and three individuals, respectively, over 11 yr of trapping effort. The apparent affinity of most heteromyid species for saltcedar habitats is consistent with results of two trapping studies on the middle Rio Grande of New Mexico, both of which found that heteromyids tended to occur in the drier, more desert-like habitats that result when riparian vegetation is converted to saltcedar dominance (Ellis et al. 1997; Hink and Ohmart 1984). Heteromyid species, which are uniquely adapted to xeric desert environments (Genoways and Brown 1993), contributed to higher small mammal species richness in saltcedar-invaded riparian areas compared with native habitats in those studies. In the present study, however, a few species that were found more often in native riparian habitats tended to balance species numbers in the two habitat types. These included two species of cricetid rodents—an uncommon microtine species (*M. montanus*) and a relatively common species (*R. megalotis*).

Preferential use of native vegetation by *M. montanus* is consistent with known affinities of microtine species for riparian habitats with dense herbaceous undergrowth (Jannett 1999). *R. megalotis* also tends to occur most abundantly in such mesic habitats, especially where considerable herbaceous cover occurs, although this species has a wider ecological amplitude and can be found in diverse habitats, including deserts (Webster and Jones 1982). The generalized nature of habitat use by *R. megalotis* probably accounts for disparities in their relative abun-

dances in native vs. saltcedar habitats among different studies and, perhaps, even among sites within this study. For example, on the middle Rio Grande, Ellis et al. (1997) recorded *R. megalotis* exclusively in saltcedar habitats, whereas Hink and Ohmart (1984) found them most abundantly where cottonwoods occurred. On the lower Colorado River, *R. megalotis* abundance was nearly an order of magnitude greater in cottonwood/willow associations than it was in saltcedar (Anderson and Ohmart 1984). In the present study, more *R. megalotis* were trapped in native habitats than in saltcedar at three of four study areas, although only one individual was found at Pyramid.

Peromyscus maniculatus, another cricetid rodent, differed from the cricetids discussed above in two respects—it was the most abundant small mammal species captured at nearly all sites, and it was a habitat generalist. By contrast, *P. maniculatus* was both less common and less generalized in habitat use along river systems in the southern deserts. For example, Ellis et al. (1997) found *P. maniculatus* exclusively in saltcedar on the middle Rio Grande, but at only one of two study sites and in only 1 of 3 yr, whereas Hink and Ohmart (1984) found relatively more *P. maniculatus* in native cottonwoods than in saltcedar. On the lower Colorado River, Anderson and Nelson (1999) had high capture success for *P. maniculatus* at only one of three saltcedar sites, and it was entirely absent from a native site. In each of these southern desert studies, *P. maniculatus* was not the numerically dominant species as it was in this study; instead, a congeneric species—white-footed mouse (*Peromyscus leucopus*)—occurred more commonly in Ellis et al. (1997) and Hink and Ohmart (1984) and the cactus mouse (*Peromyscus eremicus*) in Anderson and Nelson (1999). Perhaps, these more abundant congeners, which tended to be habitat generalists like *P. maniculatus* in this study, had competitive effects on the distribution of *P. maniculatus*. *P. leucopus* may be behaviorally dominant to *P. maniculatus* (Kantak 1983) and can reduce or replace the latter species when they come into sympatry (Long 1996).

In addition to the lack of a habitat effect on *P. maniculatus* abundance, habitat had no consistent effect on the mean body mass of individuals of this species. Sex ratios did differ as a function of habitat with a higher proportion of male *P. maniculatus* being captured in native habitats, but this result may have been driven by small *P. maniculatus* sample sizes at the sites where skewed sex ratios occurred. Ellis et al. (1997) found that sex ratios of *P. leucopus* did not differ between native riparian and saltcedar habitats.

In contrast to *P. maniculatus*, I did find a difference in habitat-specific body masses of a congeneric species, *P. truei*, and a sciurid rodent species, *A. leucurus*. Individuals of these species were consistently heavier in native habitats. Although some literature suggests that the abundance of arthropods, which constitute prey for *P. truei* and *A. leucurus*, is reduced in saltcedar habitats relative to native vegetation (DeLay et

al. 1999; Nelson and Wydoski 2008), that may not generally be the case (Anderson et al. 2004; Durst et al. 2008; Ellis et al. 2000). Regardless of underlying causes, to the extent that body mass reflects condition, this result suggests that native vegetation supports higher-condition individuals than does saltcedar. This may occur either because native vegetation offers superior habitat for these species or because larger, dominant animals displace smaller subordinates from native habitats.

Recapture rates differed as a function of habitat type for *D. ordii* and *P. maniculatus*, which had higher recapture rates in native habitats, and for *D. merriami* individuals, which were recaptured more often in saltcedar. It is not clear why the two *Dipodomys* species showed such habitat differences in recaptures when initial capture frequencies were greater in saltcedar habitats for both species. A significant habitat effect on recaptures could occur because of either a higher rate of transience or reduced survival probabilities in the habitat with the lower recapture frequency. Habitat differences in transience offer a more probable explanation in this study because it is unlikely that mortality differentially affected survival over the short (3-d) duration of trapping sessions.

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