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Author(s): Laura E. Ellison and Charles van Riper, III

Source: *Journal of Mammalogy*, Vol. 79, No. 3 (Aug., 1998), pp. 972-985

Published by: American Society of Mammalogists

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# A COMPARISON OF SMALL-MAMMAL COMMUNITIES IN A DESERT RIPARIAN FLOODPLAIN

Laura E. Ellison and Charles Van Riper III

*Department of Biological Sciences and United States Geological Survey,  
Biological Resources Division, Colorado Plateau Research Station, P.O. Box 5614,  
Northern Arizona University, Flagstaff, AZ 86011*

*Present address of LEE: United States Geological Survey, Biological Resources Division,  
Midcontinent Ecological Science Center, 4512 McMurry Avenue, Fort Collins, CO 80525*

We compared small-mammal communities between inactive floodplain and actively flooded terraces of riparian habitat in the Verde Valley of central Arizona. We used species diversity, abundance, weight of adult males, number of juveniles, number of reproductively active individuals, longevity, residency status, and patterns of microhabitat use to compare the two communities. Although abundances of small mammals tended to be higher in the active floodplain, species diversity was greater in the inactive floodplain. Results were inconsistent with our initial prediction that actively flooded riparian habitat acts as a species source, whereas inactive floodplain acts as a sink or dispersal site for small mammals. Within each habitat type, we found evidence of significant microhabitat separation among the three most abundant small-mammal species (*Peromyscus boylii*, *P. eremicus*, and *Neotoma albigula*). Percent cover by annual and perennial grasses and shrubs, substrate, and frequency of shrubs, trees, and debris were significant determinants of small-mammal distribution within a habitat type. We found that the three most abundant species selected a nonrandom subset of available habitat. Nonrandom use of habitat and microhabitat separation were the two most important mechanisms structuring small-mammal communities in riparian habitat of central Arizona.

**Key words:** small-mammal communities, riparian floodplains, inactive floodplains, source-sink dynamics, habitat selection, Arizona

Riparian communities of the southwestern United States are distinguished by hydric, mesic, and xeric vegetative associations along ephemeral, intermittent, and perennial streams (Mitsch and Gosselink, 1993). In many areas of Arizona, a unique feature of the riparian community is mesquite-bosque habitat found on elevated de-watered soils, or soils that have been altered anthropogenically by a reduction in groundwater (Stromberg, 1993). Although riparian habitats are relatively limited in the arid Southwest, they contribute substantial biotic diversity to the region because of greater vegetative diversity and more complex habitat structure than adjacent upland habitats (Szaro, 1989).

Although a considerable amount of sci-

entific information exists on composition of small-mammal communities throughout desert ecosystems (Bowers, 1988; Brown, 1989; Morton et al., 1994; Price and Brown, 1983), much of that work has focused on granivorous rodents in stable xeric habitats because they provide excellent systems for assessing effects of food limitation, microhabitat use, and interspecific competition on a group of similar species (Brown and Munger, 1985). The importance of riparian habitat to small-mammal communities, however, is not as well documented. Most work in riparian areas on small mammals has found high species diversity, abundance, and reproductive activity in riparian corridors compared with adjacent upland habitats (Doyle, 1990; Olson

and Knopf, 1988; Stamp and Ohmart, 1979). But, little information exists on small-mammal communities in riparian habitat of southwestern streams, and how riparian vegetation contributes to overall mammalian species diversity.

Our purpose was to examine small-mammal communities in a riparian corridor in central Arizona, specifically examining differences between two distinct components: 1) the actively flooded riparian channel and floodplain, and 2) the adjacent upper terrace of mesquite bosque. The mesquite bosque historically was subjected to periodic flooding but is now elevated 2–4 m above the lower terrace and is not subject to inundation during flooding. Hereafter, the active riparian channel and floodplain will be designated “lower terrace” and the mesquite bosque designated “upper terrace.”

Our first objective was to test the hypothesis that the lower terrace was a source (i.e., superior habitat), whereas the adjacent upper terrace acts as a dispersal sink for small-mammal species. To investigate that hypothesis, we evaluated differences between two components of riparian habitat using the following eight criteria: abundance, species diversity, weight of adult males, number of captured subadults, number of reproductive adults captured, longevity, residency, and dispersal between habitat types. Assuming the lower terrace was a source habitat, we predicted that diversity and abundance would be higher in this area, individual adult males would weigh more, number of reproductive individuals would be significantly greater, and survival of individuals would be higher. We also predicted that number of subadults would be relatively higher in the upper terrace (as a result of dispersal because of competitive exclusion from the more optimal lower terrace habitat) and there would be a higher proportion of transient animals, lower male weights, lower reproduction, and lower survival.

Our second objective was to determine if patterns of microhabitat use by potentially

competing species differed between lower and upper terraces. We examined if microhabitat separation among species and non-random use of habitat were occurring and if these mechanisms were more useful than source-sink dynamics in explaining differences in structure of small-mammal communities between the two riparian habitats.

## MATERIALS AND METHODS

*Study area.*—Our study was conducted during 1993–1994 in Montezuma Castle National Monument located in the Verde Valley, Yavapai Co., ca. 48 km from Cottonwood in central Arizona. The 344-ha monument was located in a transitional life zone of desert scrubland near the base of the Mogollon Rim, the escarpment delimiting the southern edge of the Colorado Plateau. Wet Beaver Creek flowed through the Monument and eventually drained into the Verde River (Fig. 1).

Vegetation of the lower terrace in the Monument was dominated by *Chilopsis linearis* (desert willow), *Fraxinus pennsylvanica* (velvet ash), *Platanus wrightii* (Arizona sycamore), *Prosopis velutina* (velvet mesquite), and interspersed upland species such as *Acacia greggii* (catclaw acacia), *Berberis haematocarpa* (red barberry or mahonia), and *Juniperus monosperma* (one-seeded juniper). The floodplain had a rocky substrate, a well-defined channel morphology, and a periodic flood regime. The lower terrace was flooded in spring 1993 and did not flood again until spring 1995.

The upper terrace of mesquite habitat was located on a riparian terrace 2–4 m higher than the lower terrace. Vegetation of the mesquite zone was dominated by *Prosopis velutina*, *Acacia greggii*, *Gutierrezia sarothrae* (broom snakeweed), *Berberis haematocarpa*, and several annual and perennial grasses. Substrate of the upper terrace was a sandy-loam interspersed with patches of rock and gravel. Farther from the creek and at higher elevations, associations of *Larrea divaricata* (creosote) and *Canotia holocantha* (crucifixion-thorn) occurred.

*Habitat assessment.*—We sampled habitat structure during July–August 1994 when foliage cover was maximal by using a circular plot with a 2.5-m radius centered at each trapping station ( $n = 400$ ). A 5-m line transect, as suggested by Mueller-Dombois and Ellenberg (1974), was oriented randomly across the plot and centered on each trap

## Montezuma Castle National Monument, Arizona

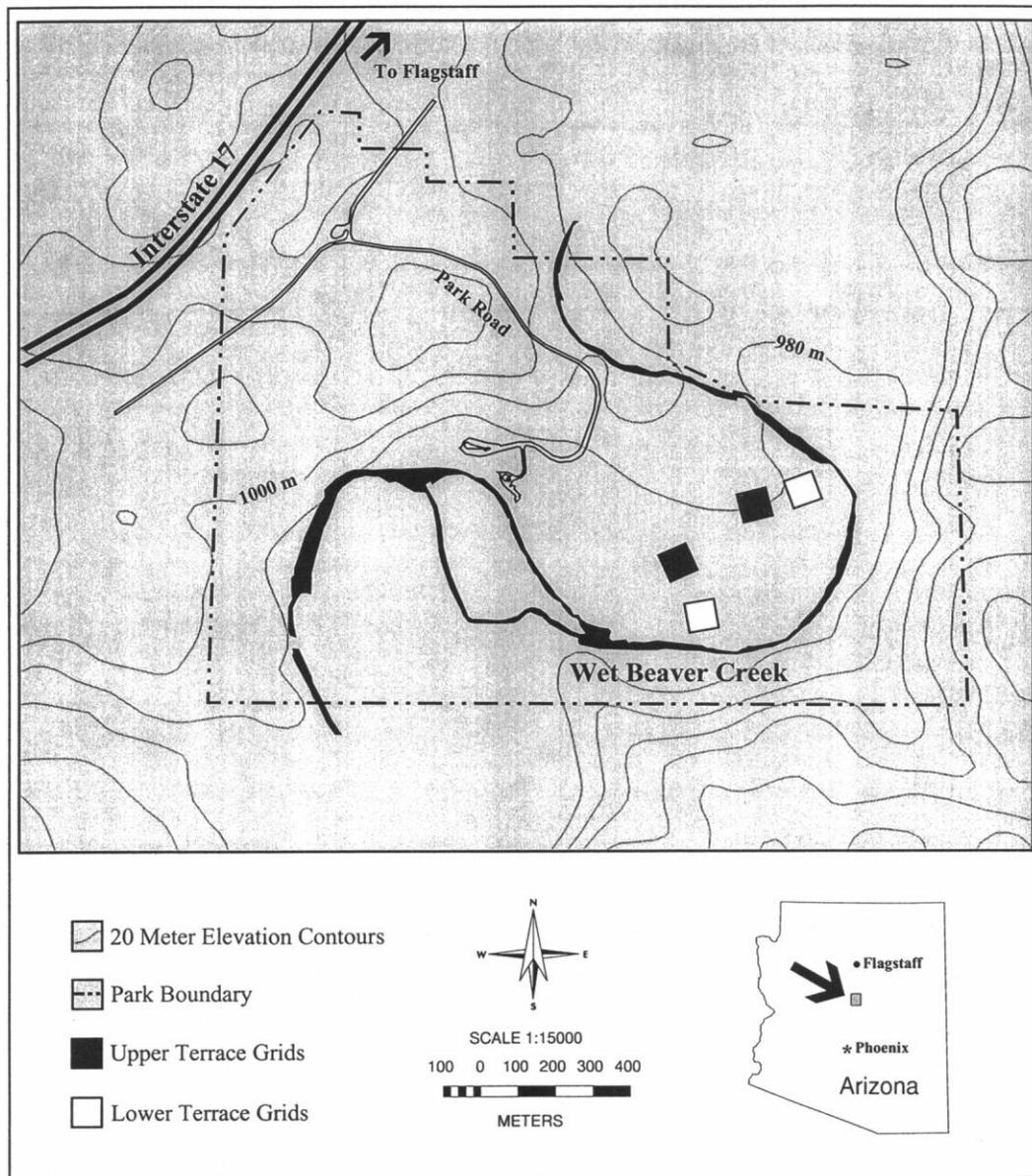


FIG. 1.—Montezuma Castle National Monument and the location of trapping grids on the upper and lower terrace in relation to Wet Beaver Creek, Verde Valley, Arizona. Each live-trapping grid was 0.81 ha.

position. We recorded length (cm) of the line intercepted by vertical projections of living plants by species and rocks, gravel, sand, bare soil, and litter. Mean percent cover for each plant species and substrate were calculated for each grid. To simplify

interpretation and reduce intercorrelation among habitat variables, we combined the percent cover of species with the same morphology to form five vegetative strata (annual grasses, perennial grasses, forbs, shrubs, and trees).

Physical habitat characteristics important to small mammals also were recorded in the 2.5-m radius circular plot: number of woody debris piles (debris piles were defined as woody ground structures >10 cm in depth and width and distinct from the surrounding ground litter), and numbers of trees and shrubs by species. Dead wood <3 cm in diameter was classified as litter cover; larger pieces were considered debris piles.

*Live trapping methodology.*—Using aerial photographs from 1992, we randomly selected two locations in the available riparian habitat to establish live-trapping grids. Each location had a lower-terrace grid that was situated adjacent to Wet Beaver Creek, with rows of traps running parallel and columns at right angles to the creek bank. The upper-terrace grid was placed 50 m above and parallel to the lower grid (Fig. 1). Each grid was confined to a distinct habitat and contained 100 trap stations spaced at 10-m intervals (90 by 90 m or 0.81 ha). We used that study design because of the linear nature of the riparian habitat and to facilitate detection of movement of small mammals between habitats.

A trapping session consisted of 4–8 consecutive nights of sampling (White et al., 1982). Four-night trapping sessions were conducted when the recapture rates exceeded 75% (when <25% of the animals captured were unmarked). Each location was sampled seasonally. A lower- and upper-terrace grid were trapped simultaneously at each location to uniformly distribute environmental variables across habitats, which also minimized confounding factors associated with time. Two trapping configurations were used; we set 50 traps using only every other column of the grid for the first half of the session and then moved those traps to alternate columns during the second half of the session. Sherman live traps (8 by 9 by 23 cm) were baited with whole oats at each station before sunset and checked at sunrise the following morning.

Information recorded at time of capture included trap station, species, body mass (g), sex, age, reproductive condition, and individual identification. *Peromyscus*, *Perognathus intermedius*, and *Reithrodontomys megalotis* were marked by toe-clipping, and *Neotoma* and *Dipodomys ordii* were marked with Monel ear-tags (Korn, 1987; Kumar, 1979). All field techniques followed guidelines of the *ad hoc* Committee on

Acceptable Field Methods in Mammalogy (1987).

*Abundance.*—We used the program CAPTURE (White et al., 1982) to screen for uniform trap responses, or heterogeneity in capture probabilities, and mean maximum distance moved (MMDM) by animals captured two or more times for the three most abundant species: *Peromyscus boylii* (brush mouse), *P. eremicus* (cactus mouse), and *Neotoma albigula* (white-throated woodrat). We used this information to estimate the effective trapping area for the three species by adding a boundary strip to the actual grid that was equal to one-half of the MMDM. That boundary strip compensated for an edge effect when we estimated the effective trapping grid area (Wilson and Anderson, 1985).

Because our data did not meet criteria suggested for using CAPTURE to estimate population size, we used Chapman's unbiased version of the Lincoln-Petersen estimator to determine the size of the small-mammal population and its associated variance (Krebs, 1989; Menkens and Anderson, 1988). We condensed data matrices for each trapping session ( $n = 4$  or 8) into two periods because the Lincoln-Petersen estimator used data from only two trap periods. We constructed 95% CI around population estimates for each trapping session using the Poisson approximation to the Binomial Interval, because the total number of individuals captured in the second period was <50 (Krebs, 1989).

*Species diversity.*—We calculated species diversities for upper and lower terraces by jackknifing the Shannon index (Krebs, 1989). We used the Shannon index because it reflected species richness, is moderately sensitive to sample size, and is better at discriminating between samples than other diversity indices (Magurran, 1988). Numbers of individuals of each species captured for each of the eight trapping sessions were used in the jackknife procedure to produce eight pseudo-values. We then constructed 95% CI using the average of these eight pseudo-values (Adams and McCune, 1979).

*Body mass, age class, and reproductive condition.*—We compared mean mass of adult males within a habitat type using independent *t*-tests (Zar, 1984:126–131). Body masses of adult females were excluded to eliminate bias from undetected pregnancies. We recorded the age class of each animal as adult, subadult, or juvenile. Criteria used for aging included body

mass and pelage color. Numbers of individuals in each age class and habitat type were determined, and proportions compared within a breeding season (April–July) using the *G*-test, a log likelihood ratio chi-square test for homogeneity of proportions (Sokal and Rohlf, 1981: 695–698).

Females were considered reproductive if they were pregnant or lactating, or if they had enlarged nipples; males were considered reproductive if they exhibited scrotal testes or an obvious epididymal bulge. We tallied number of individuals that were reproductively active during the breeding season (April–July in both years) for each habitat and each species and compared those values between habitats using *G*-tests.

*Longevity and residency.*—To investigate if animals persisted longer in the lower terrace than upper terrace and if there was a higher proportion of transients in the latter, we classified animals captured only once within a habitat as “transient.” We compared proportions of individuals captured in more than one trapping session with proportions of transients in each habitat type using *G*-tests (Lebreton et al., 1992).

*Microhabitat use.*—Vegetative and structural characteristics (vegetative cover by strata, substrate cover, and number of woody debris piles) were compared between lower and upper terrace habitats using the Wilcoxon two-sample test (Conover, 1980:280–283). Species richness of plants was estimated for each habitat using plot data (Magurran, 1988).

Canonical correspondence analysis (CCA) was used to explore patterns of microhabitat distribution among the three most abundant small-mammal species (*P. boylii*, *P. eremicus*, *N. albigula*). The CCA was a multivariate-direct-gradient analysis that related community composition to known variation in the environment (Ter Braak, 1986). We used number of unique individuals captured at each trap station by species and related that to habitat variables at the station. Habitat variables included eight structural characteristics (frequency of debris piles, trees, shrubs, and five substrate variables) and percent cover by the five vegetative strata. The program CANOCO (Canonical Community Ordination, version 3.1) was used to supply: 1) scores of species of small mammals on the ordination axis, 2) biplot scores of environmental variables and centroids for nominal environmental variables for the ordination diagram, 3) eigenvalues,

4) species-environment correlations, and 5) cumulative percent variance species data and for species-environment relation (Ter Braak, 1986). We constructed ordination diagrams (species-environment biplots) as a graphical summary of the weighted averages of the three species with respect to the 13 environmental variables. To investigate if observed differences in microhabitat use by the three species could be accounted for by chance, we used a Monte Carlo permutation test of the trap stations with the first eigenvalue as the test statistic. The permutation compared randomly calculated eigenvalues to the eigenvalue calculated from our data and tested for significance of the first canonical ordination axis distributions of species (Ter Braak, 1987–1992).

Canonical correspondence analysis explored patterns of microhabitat use at trap stations where animals were captured. We also were interested in exploring patterns of habitat use versus availability. A one-way multivariate analysis of variance (1-way MANOVA—Johnson and Wichern, 1992:246–248) was used to distinguish between microhabitats where animals were captured and were not captured. For each species, we compared habitat variables at traps where animals were captured (used habitat) with a random sample of traps where animals were not captured (Block and Brennan, 1993). Habitat variables included the eight structural characteristics and percent cover by the five vegetative strata also used in the CCA. For the 1-way MANOVA, presence or absence of an animal was considered the level encountered, and the 13 habitat variables were independent variables. We then ran univariate *F*-tests to determine which habitat variables were significantly different between used and available habitat (Snedecor and Cochran, 1989:223–224). Frequencies of debris piles, shrubs, and trees also were compared with *G*-tests for each species between used and available habitat. These analyses were conducted both between habitats (400 trap stations) and within a habitat (200 trap stations). A significance level of 0.05 was used for all analyses.

## RESULTS

*Habitat assessment.*—We found a significantly greater percent cover of trees, perennial grasses, and litter in the upper terrace than lower terrace (Table 1). Frequency of debris piles was higher in the lower ter-

TABLE 1.—Mean ( $\pm$ SE) percentages of cover of vegetative strata and ground cover between lower and upper terraces of riparian floodplain ( $n = 200$  for each terrace) at Montezuma Castle National Monument, Yavapai Co., Arizona.

Vegetative strata	Mean percent cover			
	Lower terrace		Upper terrace	
	$\bar{X}$	SE	$\bar{X}$	SE
Trees	28.0	3.4	43.4	2.6*
Shrubs	32.8	2.3	29.6	2.0
Forbs	4.0	0.9	0.03	0.02*
Perennial grasses	1.8	0.6	6.5	0.9*
Annual grasses	7.5	1.3	8.5	1.2
Ground cover				
Bare soil	12.4	1.4	19.7	1.4*
Gravel	5.0	0.9	3.8	0.7
Rock	20.9	2.2	3.7	0.3*
Litter	48.8	2.4	75.8	2.0*

\* Percent cover by strata were analyzed with a Wilcoxon signed-ranks test;  $P < 0.05$ .

race with 182 piles in the lower and 45 in the upper ( $G = 110.7$ ,  $d.f. = 1$ ,  $P < 0.05$ ). Percent cover of forbs was also higher in the lower terrace than the upper terrace. Because lower grids encompassed parts of active stream channels, we found a greater percentage of rock substrate in them, but percentage of exposed soil was higher on the upper terrace.

Species richness of plants was higher in the lower terrace, with a total of 29 species compared with 21 in the upper terrace. The most frequent shrubs in the lower terrace were *Chilopsis linearis*, *Gutierrezia sarothrae*, *Acacia greggii*, *Berberis haematocarpa*, and *Brickellia californica* (pachaba); dominant trees were *Platanus wrightii*, *Juniperus monosperma*, *Prosopis velutina*, *Fraxinus pennsylvanica*, and *Juglans major* (Arizona walnut). Four species of perennial grasses, several species of annual grasses, six species of forbs, and nine different shrub species were found in the lower terrace. In the upper terrace, predominant shrubs were *A. greggii*, *G. sarothrae*, *Atriplex canescens*, *Marrubium vulgare* (common horehound), and *B. haematocarpa*;

tree species were *J. monosperma* and *P. velutina*. Three species of perennial grasses, several species of annual grasses, two species of herbs, and 12 different shrub species were recorded in this habitat.

*Live trapping results.*—A total of 4,290 trapnights, equally divided between the upper and lower terraces, was recorded. An adjustment was made to trap-nights for traps found closed but empty. We captured 231 individuals 520 times. Recapture rates during each session averaged 72.0%, suggesting that each grid location was sampled adequately.

We captured 10 species, representing three rodent families; seven species were captured in the lower terrace and 9 species in the upper terrace. Three cricetine species were captured most frequently in both upper and lower terraces: *P. boylii* (66 individuals, 181 total captures), *P. eremicus* (65 individuals, 145 total captures), and *N. albigula* (55 individuals, 118 total captures). The effective trapping area was 1.06 ha for *P. boylii*, 0.99 for *P. eremicus*, and 1.02 for *N. albigula*.

*Species diversity.*—Species diversity was significantly greater in the upper terrace; Shannon diversity indices averaged  $1.30 \pm 0.05$  SE (95% CI = 1.18–1.41) for lower terrace habitat and  $1.78 \pm 0.15$  SE (95% CI = 1.43–2.14) for the upper terrace. This did not follow our initial prediction of greater mammal diversity in the lower terrace.

*Abundance.*—We restricted our remaining analyses to three cricetine species because other species generally had insufficient captures for demographic comparisons. For the majority of species and trapping occasions, CAPTURE indicated constant capture probabilities and no evidence of heterogeneous trap responses (i.e., no trap-shy or trap-happy individuals). To adequately estimate population size for an area with CAPTURE when  $n < 100$ , average probability of capture ( $p$ ) must be ca. 0.5. We used the Lincoln-Petersen estimator to calculate population size for all trapping occasions because most estimates of cap-

TABLE 2.—Number of unique animals captured ( $M_{t+1}$ ) and estimated capture probabilities ( $p$ -hats) with the model (M) chosen by program CAPTURE (White et al., 1982) and Lincoln-Peterson estimates of population size (N) with 95% CI for the three most abundant small mammals at Montezuma Castle National Monument, Yavapai Co., Arizona, 1993–1994. Missing values indicate that sample sizes were insufficient to calculate reliable Lincoln-Petersen estimates.

Species	Session <sup>a</sup>	Lower terrace			Upper terrace		
		$M_{t+1}$	$p$ -hat (Model) <sup>b</sup>	N (CI)	$M_{t+1}$	$p$ -hat (Model)	N (CI)
<i>Peromyscus boylii</i>	1	5	0.29 ( $M_{bb}$ )	8.1 (3.0–13.3)	0		
	2	7	0.38 ( $M_{bb}$ )	11.5 (5.3–17.6)	0		
	3	9	0.40 ( $M_0$ )	6.6 (2.0–11.2)	1		
	4	7	0.22 ( $M_0$ )	8.1 (3.0–13.3)	0		
	5	13	0.43 ( $M_{th}$ )	8.52 (3.37–13.8)	6	0.47 ( $M_0$ )	7.7 (2.6–12.8)
	6	15	0.36 ( $M_0$ )	13.52 (6.69–10.34)	0		
	7	1			4	0.16 ( $M_t$ )	5.5 (1.4–9.6)
<i>Peromyscus eremicus</i>	1	6	0.44 ( $M_0$ )	7.7 (2.6–12.8)	2		3.5 (0.4–6.7)
	2	0			6	0.27 ( $M_0$ )	8.5 (3.3–13.7)
	3	4	0.25 ( $M_0$ )	7.7 (2.6–12.8)	4	0.23 ( $M_0$ )	5.5 (3.3–14.9)
	4	6	0.29 ( $M_{00}$ )	7.7 (2.6–12.8)	6	0.31 ( $M_0$ )	6.6 (2.0–11.2)
	5	3	0.44 ( $M_{th}$ )	4.5 (0.8–8.1)	4	0.25 ( $M_t$ )	4.5 (0.8–8.1)
	6	9	0.38 ( $M_0$ )	10.6 (4.5–16.8)	6	0.16 ( $M_0$ )	7.7 (2.6–12.8)
	7	8	0.30 ( $M_b$ )	9.1 (3.3–15.0)	3	0.21 ( $M_0$ )	4.5 (0.8–8.1)
<i>Neotoma albigula</i>	1	1			3	0.20 ( $M_0$ )	4.5 (0.8–8.1)
	2	0			1		
	3	8	0.28 ( $M_0$ )	10.6 (4.5–16.8)	9	0.24 ( $M_0$ )	9.1 (3.3–15.0)
	4	1			0		
	5	6	0.31 ( $M_{th}$ )	6.6 (2.0–11.2)	1		
	6	5	0.30 ( $M_0$ )	6.6 (2.0–11.2)	2		
	7	9	0.29 ( $M_0$ )	11.5 (5.3–17.6)	6	0.14 ( $M_0$ )	7.7 (2.6–12.8)

<sup>a</sup> Trapping sessions 1–7 were conducted on 9–11, 23–25 April, 1–9 June, 6–14 July 1993, and 8–12 January, 8–10, 12–14 April, 17–25 May, and 17–25 July 1994, respectively.

<sup>b</sup>  $M_0$ , capture probabilities are constant;  $M_b$ , capture probabilities vary due to behavioral response;  $M_{th}$ , capture probabilities vary by time individual animal;  $M_{bb}$ , capture probabilities vary due to behavioral response and differences between individual animals;  $M_{00}$ , capture probabilities vary due to time, behavioral response, and differences between individual animals.

ture probabilities ( $p$ -hats) from our study were  $<0.3$ .

Abundances of small mammals differed between lower and upper terraces (Table 2). Abundances were generally greater in the lower terrace but not significantly so except for *P. boylii*. Abundances of *P. eremicus* were generally greater in the lower terrace except during April 1993 when all individuals were captured in the upper terrace. *Neotoma albigula* also was more abundant in the lower terrace.

**Body mass, age class, and reproductive condition.**—Mean weights of adult males differed significantly between habitat types only for *N. albigula*. Adult male *N. albigula* weighed  $191.2 \text{ g} \pm 7.7 \text{ SE}$  in the upper ter-

race habitats but only  $168.5 \text{ g} \pm 9.9$  in the lower terrace habitat ( $t = 1.83$ ,  $d.f. = 40$ ,  $P < 0.05$ ), counter to our prediction that larger-sized males would be found in the lower terrace.

We combined juveniles and subadults during the breeding season (April–June) into one age class to increase sample sizes for the  $G$ -test. We also analyzed age-class proportions without combining juveniles and subadults to make sure that we were not obscuring patterns. There was no significant difference between results of those two tests. The proportion of adults in the population during the breeding season was equal in the two habitats for all species except *N. albigula*. Eight juveniles were cap-

tered in the lower terrace and none in the upper terrace ( $G = 10.46$ ,  $d.f. = 1$ ,  $P < 0.05$ ), counter to our prediction that juveniles would be competitively excluded from the lower terrace.

A significantly larger proportion of adults of *P. eremicus* was reproductively active in the upper terrace habitat than in the lower terrace. Eight of 26 individuals were non-reproductive in the lower terrace, but only one of 19 individuals was nonreproductive in the upper terrace ( $G = 5.104$ ,  $d.f. = 1$ ,  $P < 0.05$ ). There was no significant difference in breeding activity of *P. boylii* or *N. albigula* between upper and lower terraces.

*Longevity, residency, and dispersal.*—We predicted that individuals would live longer in the lower terrace, if this area was indeed a source habitat, but the proportions of animals surviving between trapping occasions did not differ significantly between habitat types for any species. We also expected that the upper terrace would have a higher proportion of transient animals, but that was true only for *P. boylii* ( $G = 4.837$ ,  $d.f. = 1$ ,  $P < 0.05$ ). We observed few instances of inter-habitat movement by animals over the 2 years of this study. Only three of 231 animals, all *P. boylii*, moved between riparian terraces in 1994; one adult male and one female moved from the upper terrace to the lower terrace and one adult female moved from the lower terrace to the upper terrace—a net movement of only one animal.

*Microhabitat use.*—The CCA indicated that proportions of perennial grass cover, forb cover, tree cover, and frequency of trees were the strongest correlates with small-mammal distributions in the lower terrace (Fig. 2). Species points in CCA diagrams were weighted mean scores that indicated the center of a species' distribution along an environmental gradient. Distances between species points indicated separation of microhabitats. The position of the endpoint of lines of environmental variables depended on eigenvalues of axes and intraset correlations of environmental variables

with axes. Important environmental variables tended to be represented by longer arrows than less important environmental variables. We projected a perpendicular line from *P. eremicus* to the perennial grass axis in Fig. 2; endpoints of that line indicated the relative value of the weighted average of the species with regard to occurrence of perennial grasses. Therefore, *P. boylii* had the lowest weighted average with respect to perennial grass cover (this species occurred in areas with both high percent cover of litter and annual grass cover), *N. albigula* had the second lowest value, and *P. eremicus* had the highest weighted average. It also can be inferred that *P. eremicus* was captured mainly in areas where substrates were fairly rocky (Fig. 2). *Peromyscus boylii* was captured mainly in areas with high percent cover of forbs and annual grasses, high percent cover of litter, and where substrate was mostly exposed soil. *Neotoma albigula*, displayed in the lower left quadrant of Fig. 2, occurred in areas with high percent cover of litter and high frequency of trees. In the lower terrace, 100% of the cumulative variance of the species-environment relationship and 18.1% of the variation in the species data were accounted for by the first two axes (Table 3). Small percentages of explained variation (18.1%) are common in CCA and do not diminish the biological significance of the species-environment correlations (Ter Braak, 1987–1992).

Microhabitat separation among the three cricetines in the lower terrace was significant. The sum of all canonical eigenvalues was 1.07. The 99 random data sets generated by the Monte Carlo permutations of trap stations yielded a lower eigenvalue ( $\lambda = 0.13$ ,  $F = 14.68$  and  $P < 0.05$ ). Therefore, differences in vegetative strata and habitat structure found at a trap station in the lower terrace were important determinants of species occurrence.

We found that *P. eremicus* also occurred in areas with high percentages of perennial grasses in the upper terrace (Fig. 3) and was associated negatively with tree cover, tree

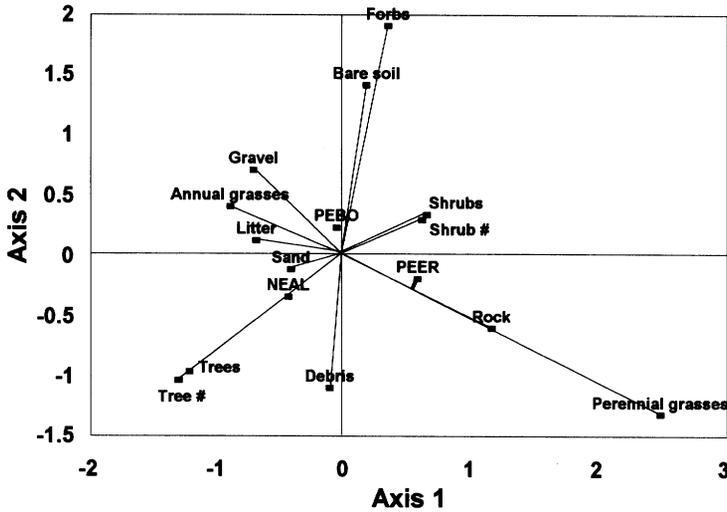


FIG. 2.—Ordination diagram from canonical correspondence analysis of three species of small mammals (clockwise from left top quadrant—PEBO = *Peromyscus boylii*, PEER = *P. eremicus*, and NEAL = *Neotoma albigula*) in the lower terrace of riparian floodplain habitat at Montezuma Castle National Monument, Yavapai Co., Arizona; species represented as points and environmental variables as lines ending in points. The projection of the small-mammal point labeled PEER onto the trajectory of the line of perennial grasses is shown in the lower right quadrant; the endpoint of this projection indicates the approximate weighting of the centers of distributions of *P. eremicus* along the variable perennial grasses. Environmental variables are: litter = percentage of substrate covered by litter, annual grasses = percent cover of annual grasses, gravel = percentage of substrate covered by gravel, bare soil = percentage of substrate covered by bare soil, forbs = percent cover of herbaceous vegetation, shrubs = percent cover of shrub species, shrub # = density of shrubs, rock = percentage of substrate covered by rock, perennial grasses = percent cover of perennial grasses, debris = frequency of debris piles, trees = percent cover by trees, tree # = density of trees, and sand = percentage of substrate covered by sand.

frequency, litter cover, and debris piles. *Neotoma albigula* occurred most often with debris piles, high percent tree cover, tree density, and high percent litter cover. *Peromyscus boylii* occurred in areas with high

percentage of annual grasses and where substrate was mostly rocky (Fig. 3). In the upper terrace, 100% of the cumulative variance of the species-environment relation also was explained by the first two axes

TABLE 3.—Summary of canonical correspondence analysis (CCA) in the lower terrace and upper terrace of riparian floodplain habitat at Montezuma Castle National Monument, Yavapai Co., Arizona. Results are from a CCA of three cricetines and 13 environmental variables shown in the ordinations of Figs. 2 and 3.

Axes	Lower terrace axes				Upper terrace axes			
	1	2	3	4	1	2	3	4
Eigenvalues	0.13	0.06	0.52	0.35	0.24	0.15	0.48	0.42
Species-environment correlations	0.52	0.33	0.00	0.00	0.59	0.49	0.00	0.00
Cumulative percentage variance of species data	12.2	18.1	67.0	100.0	18.4	29.8	66.9	100.0
Cumulative percentage variance of species-environment relation	67.1	100.0	0.00	0.00	62.0	100.0	0.00	0.00

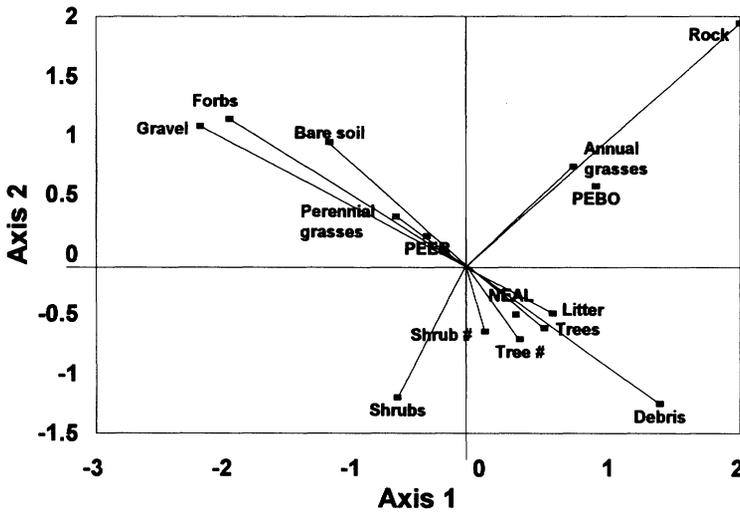


FIG. 3.—Ordination diagram from canonical correspondence analysis of three species of small mammals (clockwise from left top quadrant—PEER = *Peromyscus eremicus*, PEBO = *P. boylii*, and NEAL = *N. albigula*) in the upper terrace of riparian floodplain habitat at Montezuma Castle National Monument, Yavapai Co., Arizona; species as points and environmental variables as lines ending in points. Environmental variables are defined in the legend of Fig. 2.

(Table 3). The sum of all canonical eigenvalues was 1.28 and the Monte Carlo permutation of trap stations yielded a lower eigenvalue for the first canonical axis than for all other axes ( $\lambda = 0.24$ ,  $F = 12.67$ ,  $P = 0.02$ ), suggesting significant microhabitat segregation among species in the upper terrace.

Microhabitats where the three cricetines were caught and were never caught differed (*P. boylii*— $F = 5.98$ ,  $d.f. = 10$ ,  $199$ ,  $P < 0.05$ ; *P. eremicus*— $F = 2.09$ ,  $d.f. = 10$ ,  $185$ ,  $P < 0.05$ ; *N. albigula*— $F = 3.55$ ,  $d.f. = 10$ ,  $113$ ,  $P < 0.05$ ). The univariate  $F$ -tests showed that *P. boylii* was captured at trap stations with higher percent cover of shrubs ( $F = 11.14$ ,  $d.f. = 1$ ,  $P < 0.05$ ), frequency of debris piles ( $G = 66.34$ ,  $d.f. = 1$ ,  $P < 0.05$ ), and percent rocky ( $F = 26.49$ ,  $d.f. = 1$ ,  $P < 0.05$ ) and sandy ( $F = 13.18$ ,  $d.f. = 1$ ,  $P < 0.05$ ) substrates than randomly available. *Peromyscus boylii* also was captured at stations with less annual-grass cover ( $F = 5.91$ ,  $d.f. = 1$ ,  $P < 0.05$ ), percent cover by litter ( $F = 20.82$ ,  $d.f. = 1$ ,  $P < 0.05$ ), and frequency of trees ( $G = 9.86$ ,  $d.f. = 1$ ,  $P < 0.05$ ). *Peromyscus er-*

*emicus* was captured at trap stations with higher percent shrub cover ( $F = 8.64$ ,  $d.f. = 1$ ,  $P < 0.05$ ), higher frequency of shrubs ( $G = 3.80$ ,  $d.f. = 1$ ,  $P < 0.05$ ), rockier substrate ( $F = 4.91$ ,  $d.f. = 1$ ,  $P < 0.05$ ), and less exposed soil ( $F = 4.92$ ,  $d.f. = 1$ ,  $P < 0.05$ ). *Neotoma albigula* was captured in areas with higher tree cover ( $F = 6.38$ ,  $d.f. = 1$ ,  $P < 0.05$ ), frequency of debris piles ( $G = 28.81$ ,  $d.f. = 1$ ,  $P < 0.05$ ), and frequency of trees ( $G = 7.29$ ,  $d.f. = 1$ ,  $P < 0.05$ ). That species also was captured in areas with less exposed soil ( $F = 15.52$ ,  $d.f. = 1$ ,  $P < 0.05$ ) and cover of perennial grasses ( $F = 8.66$ ,  $d.f. = 1$ ,  $P < 0.05$ ).

#### DISCUSSION

Differences in habitat quality in a heterogeneous landscape can result in a source-sink population structure (Pulliam, 1988; Pulliam and Danielson, 1991). Source-sink populations manifest differences in performance and reproductive success of individuals because sources (high-quality habitats) are those areas that afford conditions necessary for relatively successful survival and reproduction, while marginal habitats

(sinks) support individuals but their rates of survival and reproduction are lower than in high-quality habitats (Kawecki, 1995; Morrison et al., 1992). Source and sink dynamics within a population have been documented in a variety of mammalian taxa (*Peromyscus maniculatus*—Van Horne, 1982; *Rangifer tarandus*—Bergerud, 1988; *Tamias townsendii*, *Glaucomys sabrinus*, *Zapus trinotatus*—Doyle, 1990; *Spermophilus undulatus*—Carl, 1971). These studies demonstrate that source-sink phenomena are widespread and can be determined when differential demographic success between marginal and prime habitats is shown to exist and active juvenile dispersal is observed (Andersen, 1994; Pulliam, 1996).

Riparian floodplains generally are considered to be more productive than adjacent ecosystems because of their hydrologic conditions (Mitsch and Gosselink, 1993), and this differential productivity is particularly apparent in the arid Southwest (Johnson, 1979). Thus, we predicted that the lower terrace would be the source for several small-mammal species, but our data did not support that prediction. We also predicted a more diverse small-mammal community in the lower terrace habitat but found species diversity greater in the upper terrace. For instance, we captured *Dipodomys ordii* (Ord's kangaroo rat) only in the upper terrace where the substrate included a greater amount of sandy, gravelly, and friable soil. The lower terraces also contained friable soil, but occurrence of this substrate was patchy due to fragmentation by stream channels. In addition, *Reithrodontomys megalotis* (western harvest mouse) was captured only in upper terrace habitats.

Although abundances of *P. boylii* were greater in the lower terrace, adult males were not significantly larger, reproductive activity was not greater, nor was there an increase in number of juveniles and subadults compared with the upper terrace. *P. boylii* did not appear to persist significantly longer in lower versus upper terraces, and we found no significant movement between

habitats. Population size of *P. eremicus* also tended to be larger in the lower terrace, but results from other criteria were inconclusive. Like the previous two species, population size of *Neotoma albigula* generally was greater in the lower terrace, but males were larger in the upper terrace and more juveniles and subadults were captured in the lower terrace. That suggested that the upper terrace was a higher quality habitat for *N. albigula* than the lower terrace.

We could not conclude that the lower terrace along Wet Beaver Creek acted as a source habitat and that the upper terrace acted as a dispersal sink for any small-mammal species. The fact that our data do not support source-sink dynamics may suggest that small mammals partition riparian habitat so that little movement occurs between habitat types. Although spatial and temporal scales of our study were relatively small, we still expected consistent patterns of abundance, residency, age structure, reproductive parameters, and particularly dispersal over the 2-year period if source-sink dynamics were operating.

Distribution of individuals among habitats may be determined largely by habitat selection (Pulliam and Danielson, 1991). Results from the 1-way MANOVA suggested that *P. boylii*, *P. eremicus*, and *N. albigula* were restricted to certain habitats within randomly available habitat, but the CCA suggested that within those used habitats, there was microhabitat separation among the three cricetines. Lack of significant responses by species to the eight demographic variables measured to test the source-sink hypothesis suggested that habitat selection and separation were probably more important mechanisms than source-sink dynamics in structuring small-mammal communities in this study.

*Peromyscus boylii* is a large-sized *Peromyscus* and frequently climbs in and through trees with ease (Hoffmeister, 1986). We found *P. boylii* to be more abundant in the lower terrace where it used microhabitats with more debris, sandy soils, and a

rocky substrate than in the upper terrace. In the Huachuca Mountains of Arizona, Hoffmeister and Goodpaster (1954) also found *P. boylii* to be the most common mammal in tree-covered areas with rocky substrate and heavy undergrowth and in riparian or wash habitat along streams. Goodwin and Hungerford (1979) found *P. boylii* in high densities along rocky slopes and brush-rock slopes. Association of *P. boylii* with floodplain habitats also may relate to the amount of herbaceous vegetation in floodplains. *P. boylii* has a flexible diet, but the main component is herbaceous vegetation (Goodwin and Hungerford, 1979). We found that percent cover of herbaceous vegetation was significantly higher in the lower terrace than in the upper terrace.

*Peromyscus eremicus* is common and widespread in the desert Southwest and is associated with cacti, creosote, woodpiles, rocks and rocky slopes, chaparral, and sandy flats. This species often uses abandoned burrows of other mammals or parts of woodrat piles (Hoffmeister, 1986). At Montezuma Castle, we found *P. eremicus* to be more abundant in the lower terrace, where it used microhabitats with more shrub cover, higher density of shrubs, and a rockier substrate than available in random microhabitats (Fig. 2).

*Neotoma albigula*, common in a variety of habitats throughout Arizona, builds large nests near cacti, shrubs (such as mesquite or acacia), or rock piles. We found that *N. albigula* used microhabitats with greater tree cover, increased tree density, and greater amounts of debris than in random microhabitats. This follows habitat-use patterns reported by Macedo and Mares (1988), who found *N. albigula* in areas with large quantities of debris and dead trees. Because large quantities of debris provide sufficient cover for house construction, Olsen (1973) hypothesized that shelter-site selection by this species is based on quantity of ground-level vegetation and debris available for cover.

In addition to demonstrating that small

mammals used certain habitat characteristics nonrandomly, we also found evidence of significant microhabitat separation among species. The CCA described how the three cricetines were related to environmental variables found at sites where they were captured. In the lower terrace, *N. albigula* was associated with trees and tree cover, *P. eremicus* with rocky substrates and cover of perennial grasses, and *P. boylii* was highly associated with herbaceous vegetation, exposed soil substrate, and cover by annual grasses. In the upper terrace, *P. boylii* was associated with annual grass cover and rocky substrate, *P. eremicus* was associated cover of perennial grass, herbaceous vegetation, and gravel soils, and *N. albigula* was associated with trees and tree cover. *Neotoma albigula* also was associated significantly with debris and litter.

Coexistence of small-mammal species within the same area is often facilitated by microhabitat separation (Dueser and Shugart, 1978; Price, 1978), and this segregation of resource use is a prominent feature of community structure in the Southwest (Holbrook, 1979; Rosenzweig and Winakur, 1969). However, this study is the first demonstration that small mammals exhibit microhabitat separation within a southwestern riparian zone. Nonrandom use of the habitat and microhabitat separation appear to be the most influential mechanisms in defining structure and composition of small-mammal communities within terraces of a riparian corridor.

#### ACKNOWLEDGMENTS

We are indebted to G. Henderson and S. Sandell of Montezuma Castle National Monument for their overall support of this project. We also thank G. Bateman, W. Block, and P. Price for their useful comments on the experimental design of this study and D. C. Andersen and T. J. O'Shea for their comments on a previous draft of this paper. Invaluable assistance with the vegetation sampling and habitat analyses was provided by P. Rowlands. This research was funded by the National Park Service Natural Resources Preservation Program Inventory and Monitoring

Program and the United States Geological Survey Biological Resources Division. This is contribution #96-11 of the Colorado Plateau Research Station.

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Submitted 9 May 1997. Accepted 13 October 1997.

Associate Editor was Robert K. Rose.