A Comparison of Small Mammal Communities at Montezuma Castle National Monument

Technical Report
NPS/NAUMOCA/NRTR-96/11

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ABSTRACT

We compared small mammal community patterns between riparian floodplain and mesquite habitats at Montezuma Castle National Monument, Yavapai County, Arizona. Species diversity, abundance, weight of adult males, number of juveniles, number of reproductively active individuals, longevity, residency status, and patterns of microhabitat selection were the combined criteria that we used to compare between communities. Although abundances of small mammals tended to be higher in floodplain habitats, species diversity was greater in the mesquite habitat. Results from the remaining demographic variables were inconsistent with source-sink predictions, and the data do not substantiate the hypothesis that riparian floodplain habitats act as species sources whereas mesquite upland areas act as sinks or dispersal sites for small mammals.

Percent cover of trees, perennial grasses, litter, and exposed soil were greater in the mesquite. The floodplain habitat had a rockier substrate and was structurally more heterogeneous with higher frequency of debris piles. Significant microhabitat separation among the three most abundant small mammal species (*Peromyscus boylii*, *P. eremicus*, and *Neotoma albigula*) was evident within both habitat types. 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. In addition, we found that habitat selectivity by the three most abundant species was significant, indicating that these species select a nonrandom subset of available habitat. Of the factors that we examined, habitat selection and microhabitat separation are contributing factors that determine small mammal community assemblages in riparian floodplain and mesquite habitats in the Verde Valley of central Arizona.

CHAPTER 1
INTRODUCTION

Riparian communities of the Southwest are distinguished by hydric, mesic, and xeric vegetation associations along ephemeral, intermittent, and perennial streams (Mitsch and Gosselink 1993). Although riparian habitats in the southwest are relatively limited in area, they contribute more biotic diversity to a region than adjacent upland vegetation communities due to a greater vegetational diversity, a perennial water source, and a more complex habitat structure (Szaro 1989; Szaro and Belfit 1987).

Many comprehensive studies of avian use of riparian habitats have been conducted in the western United States (Finch 1986, 1988, 1989; Hehnke and Stone 1978; Knopf 1985), while much of the research on riparian vertebrates in the southwestern deserts has focused on avian communities (Carothers et al. 1974; Johnson and Haight 1985; Stamp 1978; Stauffer and Best 1980; Stevens et al. 1977; Strong and Bock 1990; Szaro 1980). Hence, the importance of riparian habitat to birds, whether it is a hydro-, meso-, or xero-riparian habitat, is well documented. For instance, Johnson and Haight (1985) found that avian use of xeroriparian (dry, desert riparian including washes and arroyos) ecosystems in the Sonoran Desert was greater when compared with the adjacent upland ecosystems during all seasons. Avian species diversity and population densities were approximately five to ten times those of the surrounding uplands.

The importance of southwestern riparian habitat to small mammal communities, however, is not as well documented. Although a plethora of scientific literature exists on small mammals in a variety of desert ecosystems and on the mechanisms determining their community composition (Bowers 1982, 1988; Bowers and Brown 1982; Brown 1989; M'Closkey 1978, 1981; Morton et al. 1994; Munger et al. 1983; Murray et al. 1986; Price and Brown 1983; Thompson 1982), most of these studies have focused on granivorous rodents because the relatively stable, xeric habitats provide excellent systems for assessing the effects of food limitation, microhabitat utilization, and interspecific competition on a group of ecologically similar species (Brown and Munger 1985). Of existing studies focusing on small mammals in riparian habitat, most researchers have compared riparian small mammal communities to adjacent upland small mammal communities, and found an increase in species diversity, abundance, and reproductive activity in riparian versus upland areas (Cross 1985; Doyle 1990; Geier and Best 1980; Olson and Knopf 1988; Stamp and Ohmart 1979). Conversely, Boeer and Schmidly (1977) found that riparian communities in Big Bend National Park, Texas, had lower species richness and diversity indices of small mammals than the other major plant communities. Hence, no consistent generalization exists regarding small mammal assemblages and diversity in riparian versus adjacent habitats.

The purpose of this research effort was to examine small mammal community patterns between riparian floodplain habitat and the adjacent, transitional, mesquite habitat. Our first objective was to test the hypothesis that riparian floodplain at Montezuma Castle National Monument is a source or is superior habitat for most of the small mammal species, whereas the adjacent mesquite habitat is a dispersal sink for these species. To investigate this hypothesis, we evaluated the differences between these two habitats using the following criteria: species diversity and abundance, weight of adult males, number of captured juveniles and subadults, number of reproductive adults captured, then longevity, and residency. We also examined dispersal between habitats.

We made several predictions about how each of the above criteria would differ between the two habitats. Assuming the floodplain is a source habitat, we predicted that diversity and abundance would be higher in the floodplain, individual adult males would weigh more in the floodplain, and the number of postbreeding season juveniles would increase in the mesquite due to competitive exclusion from the more optimal floodplain habitat. Number of reproductive individuals would be significantly greater in the floodplain, and survival of individuals would be greatest in the floodplain. We also expected mesquite habitat to have a higher proportion of transient animals. Finally, significant dispersal from floodplain habitat (emigration) into mesquite habitat (immigration) should occur.

Our second objective involved testing the hypothesis that patterns of microhabitat use by small mammals do not differ between riparian floodplain and mesquite habitat types. We specifically examined whether microhabitat separation and selection were both occurring among small mammal species in the two habitats.

CHAPTER 2
METHODS

Study Site

The study site was within Montezuma Castle National Monument located in the Verde Valley, Yavapai County, approximately 48.3 km (30 miles) from Cottonwood, in central Arizona. This Monument is approximately 344 hectares in size, and located in a desert scrubland transitional life zone at the base of the Mogollon Rim, the escarpment representing the southern limit of the Colorado Plateau.

Vegetation of the riparian floodplain within the Monument is dominated by *Chilopsis linearis* (desert willow), *Fraxinus pennsylvanica* (velvet ash), *Platanus wrightii* (Arizona sycamore), *Prosopis velutina* (velvet mesquite), and interspersed characteristic "upland" species such as *Acacia greggii* (catclaw acacia), *Berberis haematocarpa* (red barberry or mahonia), and *Juniperus monosperma* (one-seeded juniper). This active floodplain has a rocky substrate, a well-developed channel morphology, and a regular flood regime (Figure 1).

The adjacent mesquite habitat is located on a higher riparian terrace distinct from the floodplain habitat. The vegetation of the mesquite zone is dominated by *Prosopis velutina*, *Acacia greggii*, *Gutierrezia sarothrae* (broom snakeweed), *Atriplex canescens* (four-wing saltbush), *Berberis haematocarpa*, and several species of annual and perennial grasses. The upland substrate is a sandy-loam soil interspersed with rock and gravel patches. Further distance from the creek and at higher elevations, *Larrea divaricata* (creosote) associations and *Canotia holocantha* (crucifixion-thorn) associations develop.

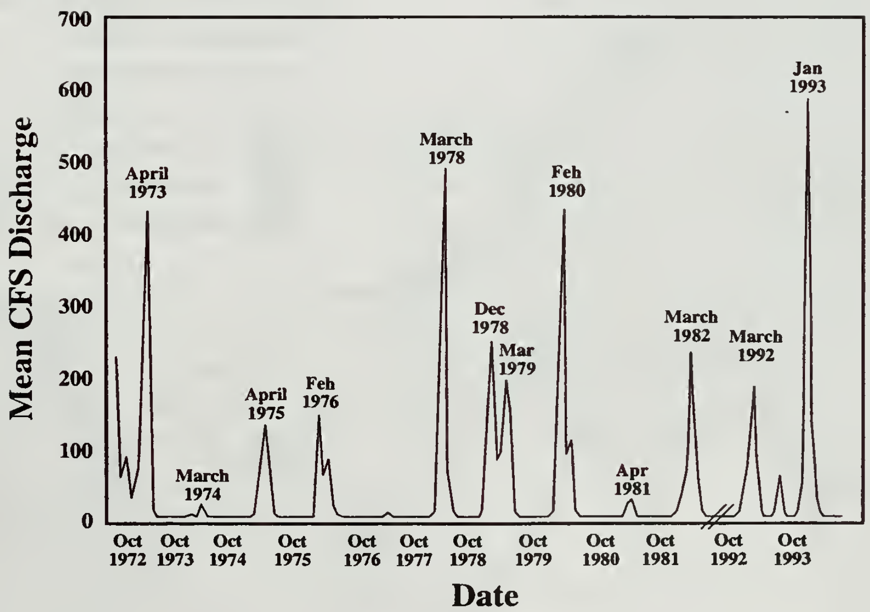

Figure 1. Time series of average Cubic Feet per Second (CFS) discharge data for Wet Beaver Creek from October 1972 throught September 1993. Data were not collected from the gauge during October 1982 through September 1991. Data were collected by United States Geological Survey steam gauge/ weather station above Montezuma Castle National Monument near Rimrock, Arizona.

Live Trapping Methodologies

We chose two locations within Montezuma Castle National Monument to establish live-trapping grids, randomly selecting two locations from available riparian floodplain strips with adjacent mesquite habitat using aerial photographs. The floodplain grids were situated adjacent to Wet Beaver Creek about 20-25 m from the stream bank with the rows running parallel and columns running at right angles to the bank. We placed mesquite grids 50 m above and parallel to the floodplain grids (Figure 2). Grids contained 100 trap stations spaced 10 m apart (90 by 90 meters or 0.81 hectares). Each grid encompassed a distinct habitat type. We employed this particular study design to determine if significant animal dispersal from one habitat to another was occurring between sampling periods.

We trapped both a floodplain and a mesquite grid simultaneously at each location in order to uniformly distribute environmental variables across habitats. This design would also potentially minimize the confounding factors associated with time. To accomplish this, we utilized two trapping configurations: 1) for the first half of the session, we set 50 traps in every other column; 2) then we moved these traps to alternate columns during the second half of the session. We set one Sherman live trap (8 by 9 by 23 cm) baited with whole oats at each station before sunset and checked traps at sunrise the following morning, sampling each location seasonally from 4 to 8 nights, or until adequate recaptures were attained. Up to 8 night sampling sessions were chosen following White et al.'s (1982) guidelines.

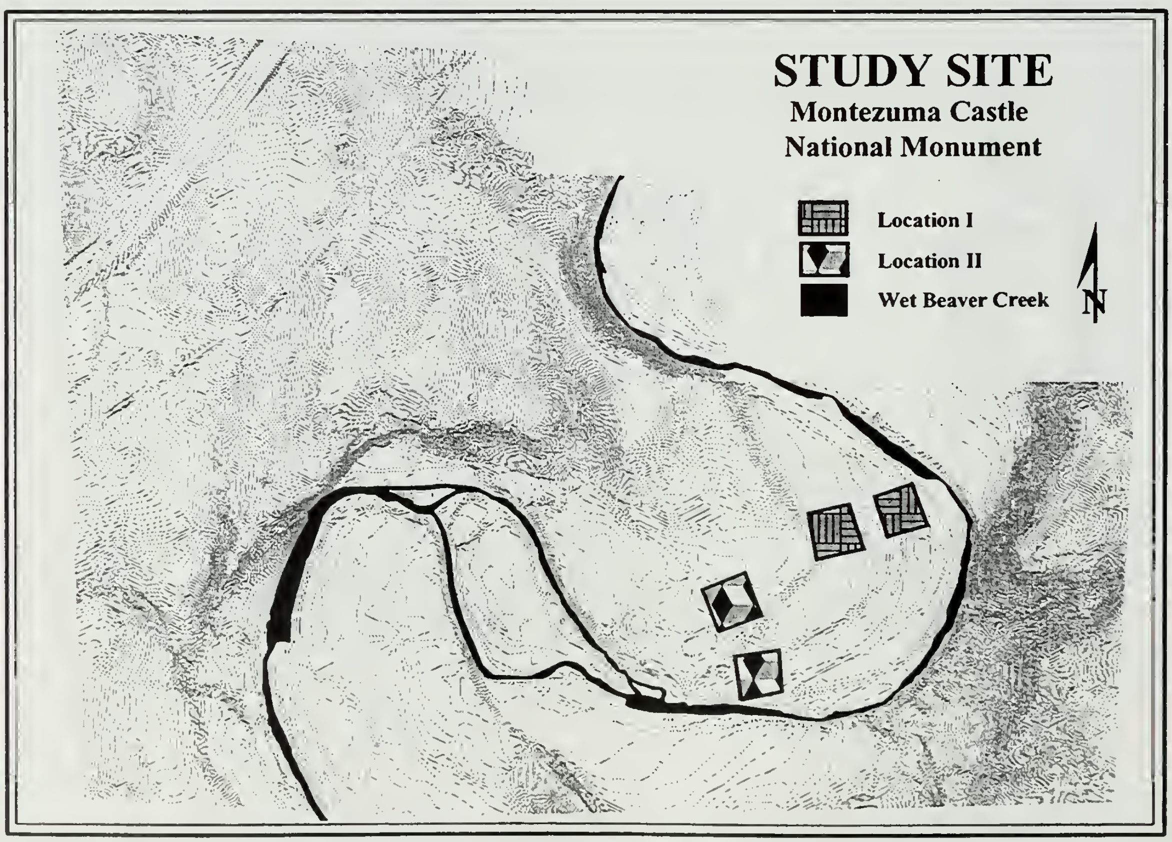

Figure 2. Montezuma Castle National Monument and the location of the two study locations in relation to Wet Beaver Creek. Each location contains a riparian floodplain and a mesquite live-trapping grid 0.81 hectares in size.

Information that we recorded at the time of capture included date, grid number, trap station, species, weight in grams, and an individual mark or number. We also assessed sex, age, and reproductive condition at time of capture. *Peromyscus spp.*, *Perognathus intermedius*, and *Reithrodontomys megalotis* were marked with toe-clips, whereas the larger *Neotoma spp.* and *Dipodomys ordii* were marked using Monel ear-tags (Korn 1987; Kumar 1979). All field techniques followed the American Society of Mammalogists (1987) recommendations for acceptable field methods in mammalogical research.

Species Diversity

We calculated species diversity for both floodplain and mesquite habitats by jackknifing the Shannon diversity index (Krebs 1989; Magurran 1988). Numbers of individuals of each species captured for each of the eight trapping occasions were used in the jackknife procedure to produce eight pseudo-values. We constructed 95% confidence intervals using the average of these eight pseudo-values (Adams and McCune 1979).

Abundances

We used the program CAPTURE to screen for uniform trap responses and/or heterogeneity in capture probabilities for the three most abundant species: *Peromyscus boylii* (brush mouse), *P. eremicus* (cactus mouse), and *Neotoma albigula* (white-throated woodrat) (White et al. 1982). The program CAPTURE also calculates the mean maximum distance moved (MMDM) by animals captured two or more times. We used this information to estimate the effective trapping area for the three species by adding a boundary strip to the actual grid area. The boundary strip was equal to the MMDM. This boundary strip compensates for "edge effect" in estimating the area of a trapping grid (Wilson and Anderson 1985).

We used Chapman's unbiased version of the Lincoln-Petersen estimator to determine small mammal population size and its associated variance (Krebs 1989; Menkens and Anderson 1988). Since the Lincoln-Petersen estimator uses data from only two trap periods, data matrices were condensed from four and eight trapping periods to two periods. The first half of the trapnights during a session was denoted n_1; the second half of the trapnights, n_2. The number of unique animals trapped in each of these periods, n_1 and n_2, and the number trapped in the second period previously caught and marked in the first period, m_2, were then computed. We constructed 95% confidence intervals around population estimates for each trapping session using the Poisson approximation to the Binomial Interval, since the total number of individuals captured in the second period was less than 50 (Krebs 1989).

Five indices were employed to evaluate habitat quality: 1) body weight of adult males; 2) age class; 3) reproductive condition; 4) longevity; and 5) residency.

Body Weights

We averaged body weights of adult males within a habitat type and compared the averages using independent *t*-tests (Zar 1984:126-131). Adult female body weights were excluded to eliminate bias from undetected pregnancies.

Age Classes

The age class of each animal was recorded into one of three categories: adult, subadult, and juvenile. The criteria that we used for aging included body size and color of pelage. Number of individuals within each age class and within each habitat type were determined and proportions compared within a breeding season (April - July) using the G-test, or the log likelihood ratio chi-square test for homogeneity of proportions (Sokal and Rohlf 1981:695-698).

Reproductive Conditions

Reproductive condition of each animal was determined as follows: females were considered reproductive if pregnant, lactating, or if they had enlarged nipples; males were considered reproductive if they exhibited scrotal testes or an obvious epididymal bulge. We calculated number of individuals reproductively active during the breeding season (April - July, both years) for each habitat and each species and compared between habitats using G-tests.

Longevity and Residency

We expected animals to survive longer in the source habitat. To investigate if animals survived longer in floodplain than in mesquite, and whether there was a higher proportion of transients in the mesquite, we considered animals as transients if captured only once within a habitat. As an indication of survival or longevity differences between habitat types, we compared proportions of individuals captured in more than one trapping occasion with proportion of transients, using G-tests (Lebreton et al. 1992). Proportion of residents (individuals recaptured within a trapping occasion and between occasions) were also compared to the proportion of transients using G-tests.

Habitat

We measured habitats during July and August 1994, a period in which foliage and cover was maximal, measuring habitat characteristics within a 2.5-meter radius plot centered at each trapping station on each grid (n=400). We used a 5-meter line intercept (diameter of the plot) as suggested by Rowlands (1994) and Mueller-Dombois and Ellenberg (1974). Each 5-meter line intercept was randomly oriented and centered on the Sherman live-trap position. We recorded length in cm of the line intercepted by each individual plant portion; we also recorded rocks, gravel, sand, bare soil, and litter. We calculated mean percent cover by species of plant and mean percent substrate for each grid. In order to simplify interpretation by reducing the data set and eliminating intercorrelation among habitat variables, we combined the percent cover values of species with the same morphology to form five vegetative strata used for all subsequent data analyses (annual grasses, perennial grasses, forbs, shrubs, and trees).

We also recorded physical habitat characteristics deemed important to small mammals within the 2.5-m radius circular plot; these included number of woody debris piles (debris piles are defined as woody ground structures exceeding 10 cm in depth and width and distinct from the surrounding ground litter), as well as the number and species of trees and shrubs. Dead wood smaller than 3 cm in diameter was classified as litter, while larger pieces were termed debris.

Vegetation and structural characteristics (vegetative cover by strata, substrate cover, and number of woody debris piles) were compared between floodplain and mesquite using the Wilcoxon two-sample test (Conover 1980:280-283). Species richness or the total number of plant species was calculated for each habitat (Magurran 1988).

We used canonical correspondence analysis (CCA) to compare patterns of microhabitat distribution among the three most abundant small mammal species (*P. boylii*, *P. eremicus*, *N. albigula*). The program CANOCO (Canonical Community Ordination) was used to supply:

1) scores of species of small mammals on the ordination axis;
2) biplot scores of the environmental variables and centroids for nominal environmental variables for the ordination diagram;
3) eigenvalues;
4) species-environment correlations; and,
5) cumulative percentage variance for species data and for species-environment relation (Ter Braak 1986).

To investigate whether the observed differences in microhabitat utilization by the three species shown in the resulting ordination diagram could be accounted for by pure chance, we used a Monte Carlo permutation test of the trap stations with the first eigenvalue as the test statistic. This permutation exercise compares randomly calculated eigenvalues to the eigenvalue calculated from the data and tests for significance of the first canonical ordination axis to the species distributions (Ter Braak 1988).

We utilized a one-way multivariate analysis of variance (1-way MANOVA, Johnson and Wichern 1992:246-248) to distinguish between microhabitats that were used by a species and microhabitats where animals were not captured. For each species, we compared habitat variables between traps where animals were captured (used habitat) to a random sample of traps where animals were not captured (available habitat) (Block and Brennan 1993). Habitat variables included the eight structural characteristics (frequency of debris piles, trees, shrubs, and five substrate variables) and percentage cover by the five vegetative strata also used in the canonical correspondence analysis. For the 1-way MANOVA, presence or absence of an animal were considered the levels 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). Frequency of debris piles, shrubs, and trees were also compared for each species between used and available habitat with G-tests. The above analyses were conducted both between habitats (400 trap stations) and within a habitat (200 trap stations). We used a significance level of 0.05 throughout all analyses.

CHAPTER 3
RESULTS

Live Trapping Results

A total of 4290 trap-nights, 2145 in riparian floodplain and 2145 in upland mesquite, were completed during the course of this study. After adjusting trap-nights for traps found closed, but empty, we captured a total of 231 individuals 520 times. Recapture rates averaged 72.0%, and for most trapping occasions, recapture rates exceeded 75%, suggesting that each grid location was sampled adequately (Table 1).

We captured 10 species representing three families of rodents (Table 2). A total of seven species were captured in the floodplains, and nine species in the mesquite habitats. We captured three cricetine species (Muridae: Cricetinae) most frequently in both floodplain and mesquite habitats: *P. boylii* (66 first-captures, 181 total captures), *P. eremicus* (65 first-captures, 145 total captures), and *N. albigula* (55 first-captures, 118 total captures). Because other species generally had insufficient

Table 1. Summary of live-trapping occasions, dates, adjusted effort (trap-nights adjusted for traps closed before entry), and recapture rate (calculated using all species combined) at Montezuma Castle National Monument from April 1993 - May 1994.

Grid Location	Dates	Adjusted Trap-nights (effort)	Recapture rate (total)
Floodplain I	April 9-11, 1993	100	50.0%
	April 23-25, 1993	99	100.0%
Mesquite I	April 9-11, 1993	100	100.0%
	April 23-25, 1993	93	80.0%
Floodplain II	June 1-9, 1993	399	52.4%
Mesquite II	June 1-9, 1993	399	64.7%
Floodplain I	July 6-14, 1993	392	88.6%
Mesquite I	July 6-14, 1993	385	80.0%
Floodplain II	January 8-12, 1994	192	54.5%
Mesquite II	January 8-12, 1994	195	66.7%
Floodplain I	April 8-10, 1994	94	75.0%
	April 12-14, 1994	96	72.0%
Mesquite I	April 8-10, 1994	95	75.0%
	April 12-14, 1994	93	55.6%
Floodplain II	May 17-25, 1994	387	80.0%
Mesquite II	May 17-25, 1994	396	50.0%
Floodplain I	June 17-25, 1994	386	80.0%
Mesquite I	June 17-25, 1994	389	71.4%
Total adjusted trap-nights		4290	
Average recapture rate			72.0%

Table 2. Numbers of small mammal captures by species and habitat type at Montezuma Castle National Monument from April 1993 through June 1994. Numbers in parentheses are first captures within a trapping occasion.

Species	Number of Individuals	
	Floodplain	Mesquite
Thomomys bottae (Botta's pocket gopher)	0 (0)	2 (2)
Dipodomys ordii (Ord's kangaroo rat)	0 (0)	15 (7)
Perognathus intermedius (Rock pocket mouse)	2 (2)	0 (0)
Reithrodontomys megalotis (Western harvest mouse)	1 (1)	8 (6)
Peromyscus eremicus (Cactus mouse)	76 (34)	69 (31)
Peromyscus maniculatus (Deer mouse)	0 (0)	9 (3)
Peromyscus spp. (juveniles)	17 (9)	9 (8)
Peromyscus boylii (Brush mouse)	159 (54)	22 (12)
Neotoma albigula (White-throated woodrat)	71 (31)	47 (24)
Neotoma stephensi (Stephen's woodrat)	0 (0)	2 (2)
Neotoma mexicana (Mexican woodrat)	11 (5)	(0)
Totals	337 (136)	183 (95)

captures for quantitative comparisons, except for calculations of species diversity, we restricted the remaining analyses to these three species. Effective trapping area for *P. boylii* was 1.06 hectares, 0.99 for *P. eremicus*, and 1.02 for *N. albigula*.

Species Diversity

Species diversity was significantly greatest in the mesquite habitat (Figure 3). Shannon diversity indices averaged 1.30 (±0.05 in standard error) for floodplain habitat and 1.78 (±0.15 in standard error) for mesquite. This did not follow our initial prediction of greater diversity in the floodplain.

Abundances

For most species and most trapping occasions, CAPTURE chose the model M_o, constant capture probabilities and no evidence of heterogeneous trap responses, or trap shy or trap happy animals (Appendix A). Capture probabilities (p-hats) were calculated by CAPTURE depending on the model chosen. If the model was M_h, or there was evidence of a heterogeneous trap response, then p-hat was calculated by averaging capture probabilities. In order to adequately estimate population size for an area when N<100 using the program CAPTURE, the average probability of capture (p) must be in the neighborhood of 0.5. Since most p-hats were less than 0.30, the Lincoln-Petersen estimator was used to calculate population size for all trapping occasions.

Abundance of small mammals differed between floodplain and mesquite habitats (Figure 4). Abundance for each species was generally greater in floodplain, but not significantly so except for *P. boylii*. *Peromyscus eremicus* abundance was generally greater in floodplain except during June 1993 where 6 individuals were captured in the mesquite, and none in the floodplain. *Neotoma albigula* were also more abundant in the floodplain. Values miss-

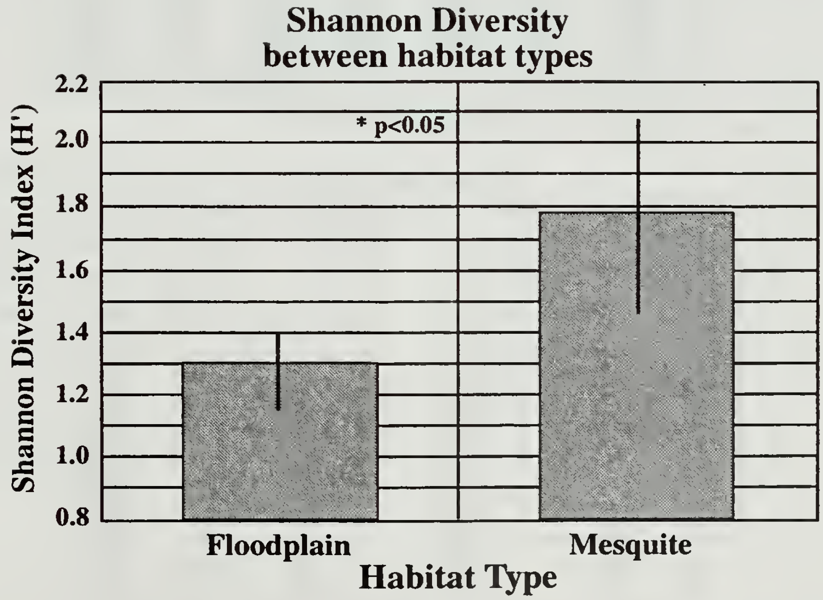

Figure 3. Comparison of small mammal diversities in riparian floodplain and mesquite habitats at Montezuma Castle National Monument from April 1993 - June 1994. Bar values are the averages of all pseudovalues from jackknifing the Shannon diversity index. Lines on bars are 95% confidence intervals.

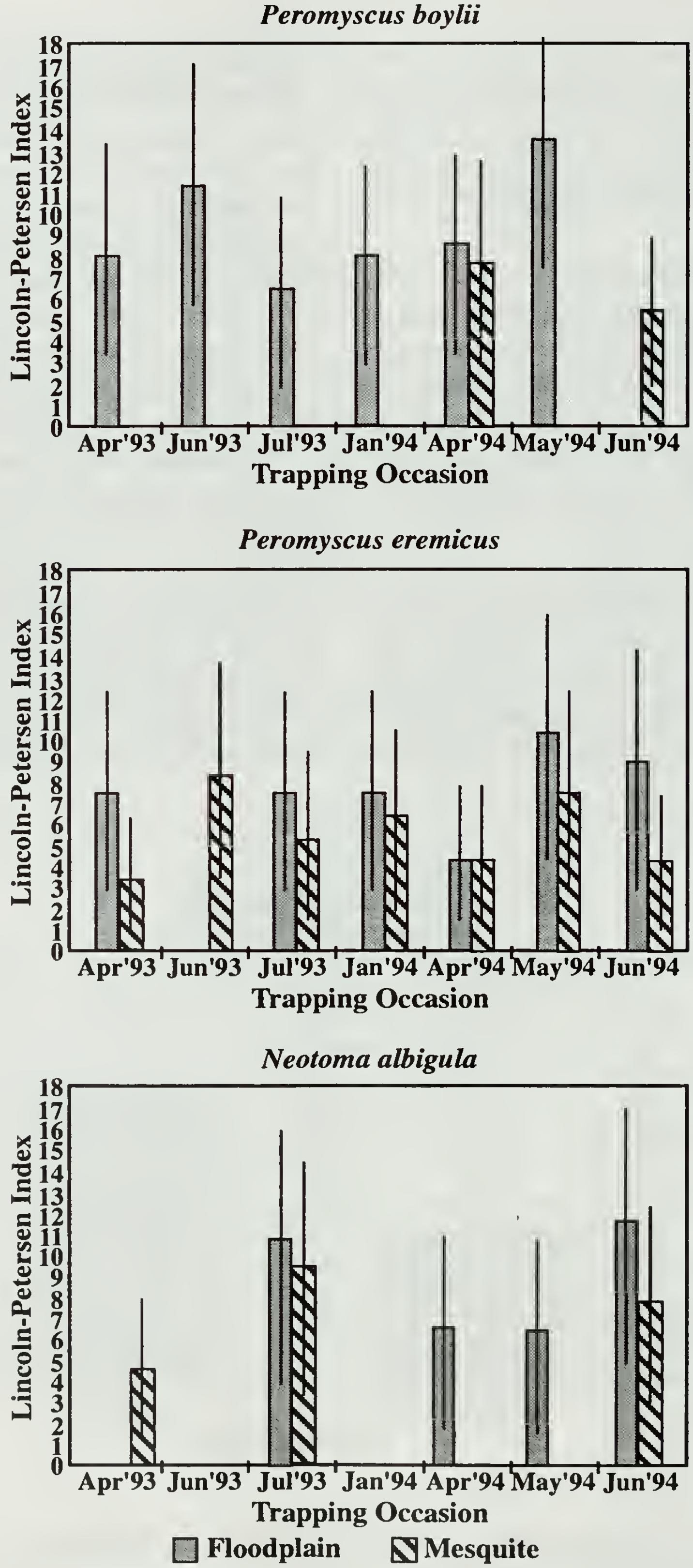

Figure 4. Lincoln-Petersen population estimates for three species of small mammals (*Peromyscus boylii, P. eremicus, and Neotoma albigula*) at Montezume Castle National Monument, Yavapai County, Arizona from April 1993 - June 1994. Bars are 95% confidence intervals.

ing in Figure 4 indicate that sample sizes were insufficient to calculate reliable Lincoln-Petersen estimates.

Body weights

We found that average weight of adult males differed significantly between habitat types only for *N. albigula* (Figure 5). Larger-sized males of this species were found in the mesquite which, again, did not follow our initial prediction.

Age Classes

In the nonbreeding season (January 1994), we captured only six subadults (five *P. eremicus* and one *N. albigula*). No juvenile animals were captured. These sample sizes were insufficient to analyze age proportions for the nonbreeding season. During the breeding season (April - June, both years), juvenile and subadult age classes were combined to increase sample sizes within cells for the G-test. Proportion of juveniles and subadults during the breeding season for each species did not differ significantly between the two habitats except for *N. albigula* (Figure 6). Eight subadults of this species were captured in the floodplain habitat and none in the mesquite (G=10.46, d.f.=1, $p<0.05$).

Reproductive Conditions

We captured no animals in reproductive condition during winter trapping (January 1994). During the breeding season, a significantly larger proportion of *P. eremicus* individuals were reproductively active in the mesquite in proportion to nonreproductive individuals (Figure 7). There was no significant difference in breeding activity between floodplain and mesquite for the other two species.

Longevity and Residency

We expected individuals of a species to live longer in the floodplain, if the floodplain habitat is a source habitat for a species. Proportion of animals surviving between trapping occasions did not differ significantly between habitat types for any species, though. We also expected the mesquite habitat would show a higher proportion of transient animals (those animals captured only once). This was true only for *P. boylii* (Figure 8). We found significantly more transients in proportion to residents in the mesquite for this species (G=4.837, d.f.=1, $p<0.05$).

Dispersal

We observed few instances of large-scale dispersal of animals between habitats over the two years of this study. Three animals, all *P. boylii*, moved between floodplain and mesquite grids in 1994; one adult male moved from mesquite into floodplain at location 1, one adult female moved from floodplain into mesquite at location 1, and one adult female moved from mesquite to floodplain at location 2.

Habitat Results

We found significantly greater percent cover of trees, perennial grasses, and litter in mesquite than in the floodplain (Table 3). Debris pile frequency and percent cover of herbaceous vegetation were higher for floodplain habitats than mesquite. Because floodplain grids included portions of stream channels, we found a greater percent rock substrate in floodplain habitats whereas we found percent exposed soil was higher in the mesquite.

We also found a higher plant species richness in floodplain habitats versus the mesquite (Table 4). A total of 29 species were encountered in the floodplain and only 21 species in the mesquite. For the floodplain, the most frequent shrubs were *Chilopsis linearis*, *Gutierrezia sarothrae*, *Acacia greggii*, *Berberis haematocarpa*, and *Brickellia californica* (pachaba). Predominant trees were *Platanus wrightii*, *Juniperus monosperma*, *Prosopis velutina*, *Fraxinus pennsylvanica*, and *Juglans major* (Arizona walnut). A total of four species of perennial grasses, several species of annual grasses, six species of herbs, and nine different shrub species were found in floodplain habitat.

In mesquite habitat, predominant shrubs were *A. greggii*, *G. sarothrae*, *Atriplex canescens*, *Marrubium vulgare* (common horehound), and *B. haematocarpa*. Tree species were *J. monosperma* and *P. velutina*. A

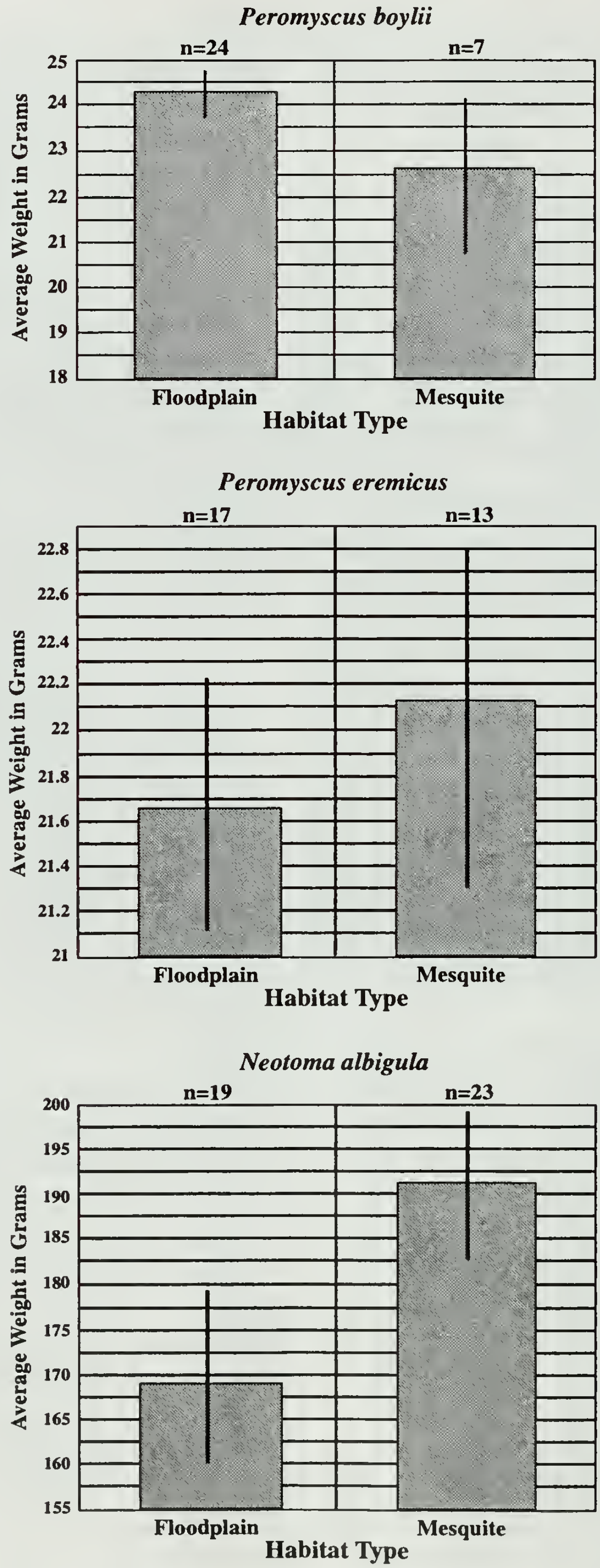

Figure 5. Comparison of average weight in grams of adult male *P. boylii*, *P. eremicus*, and *N. albigula* (both years combined) between floodplain and mesquite habitatat Montezuma Castle National Monument, Yavapai County, Arizona. Numbers above bars are sample sizes (first captures). Lines on bars are standard errors.

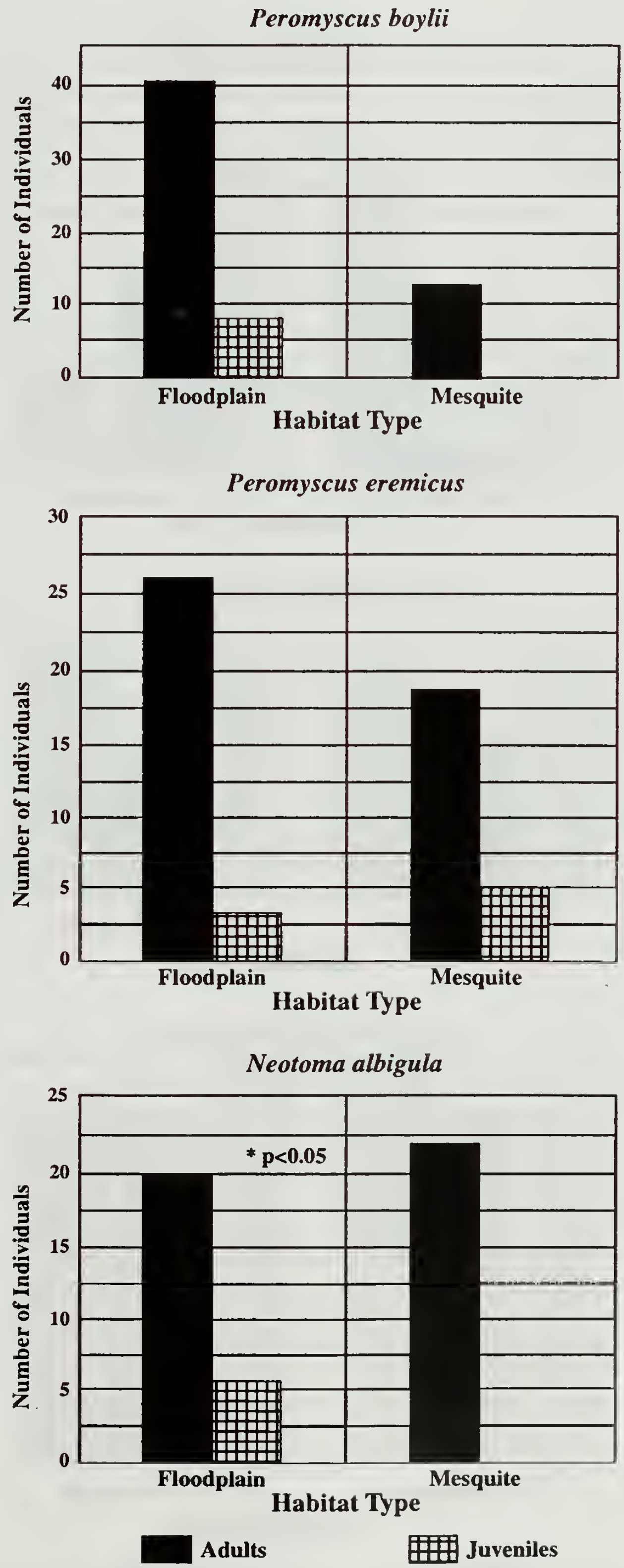

Figure 6. Breeding season age compostition (proportion of adults compared to juveniles and subadults) between floodplain and mesquite habitats at Montezuma Castle National Monument, Yavapai County, Arizona during April 1993 - June 1994 excluding January 1994 trapping occasion. *Log likelihood ratio chi-square value=10.464, d.f.=1, $p<0.05$.

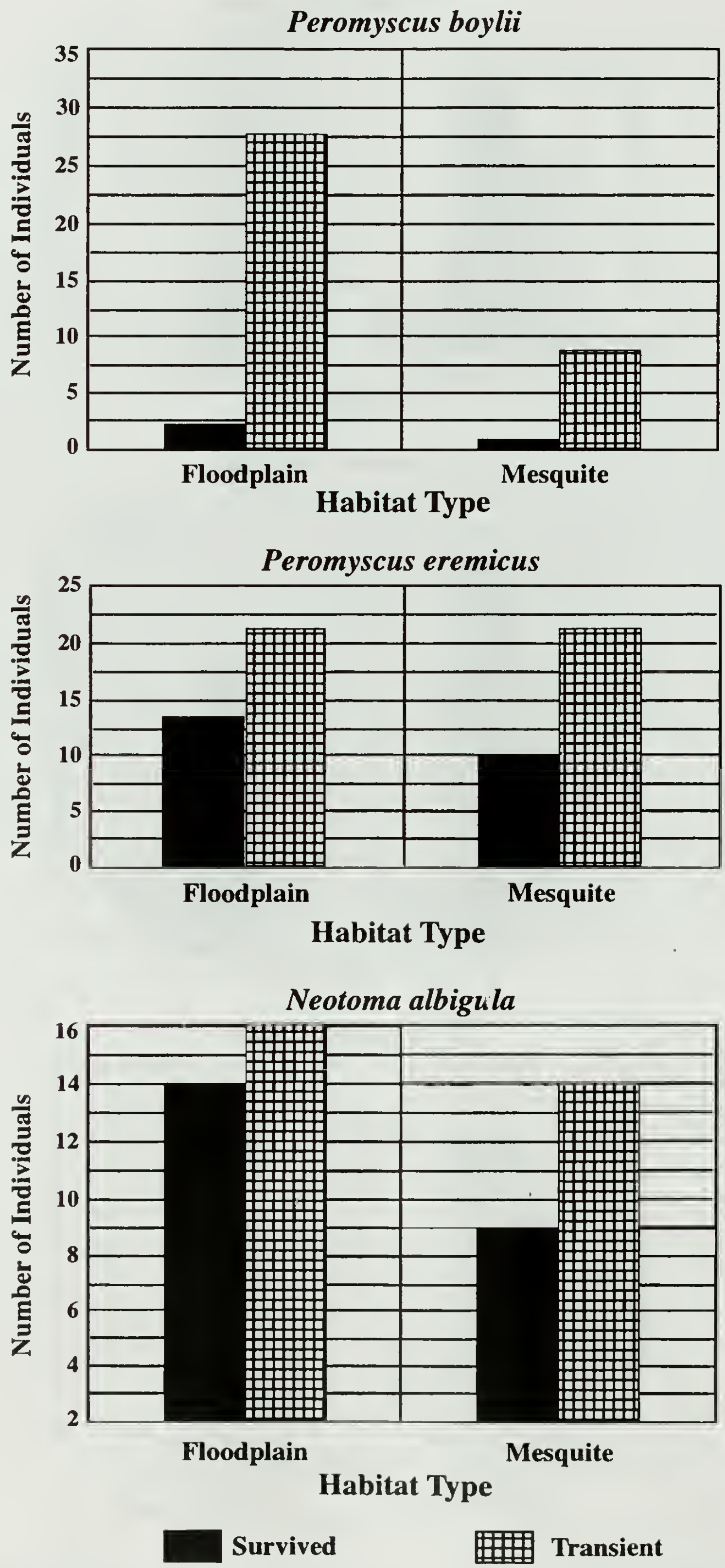

Figure 7. Proportion of adults in reproductive condition during the breeding season for three species of small mammals at Montezuma Castle National Monument, Yavapai County, Arizona during April 1993 - June 1994 excluding January 1994 trapping occasion. *Log likelihood ratio chi-quare value=5.104, d.f.=1, $p<0.05$.

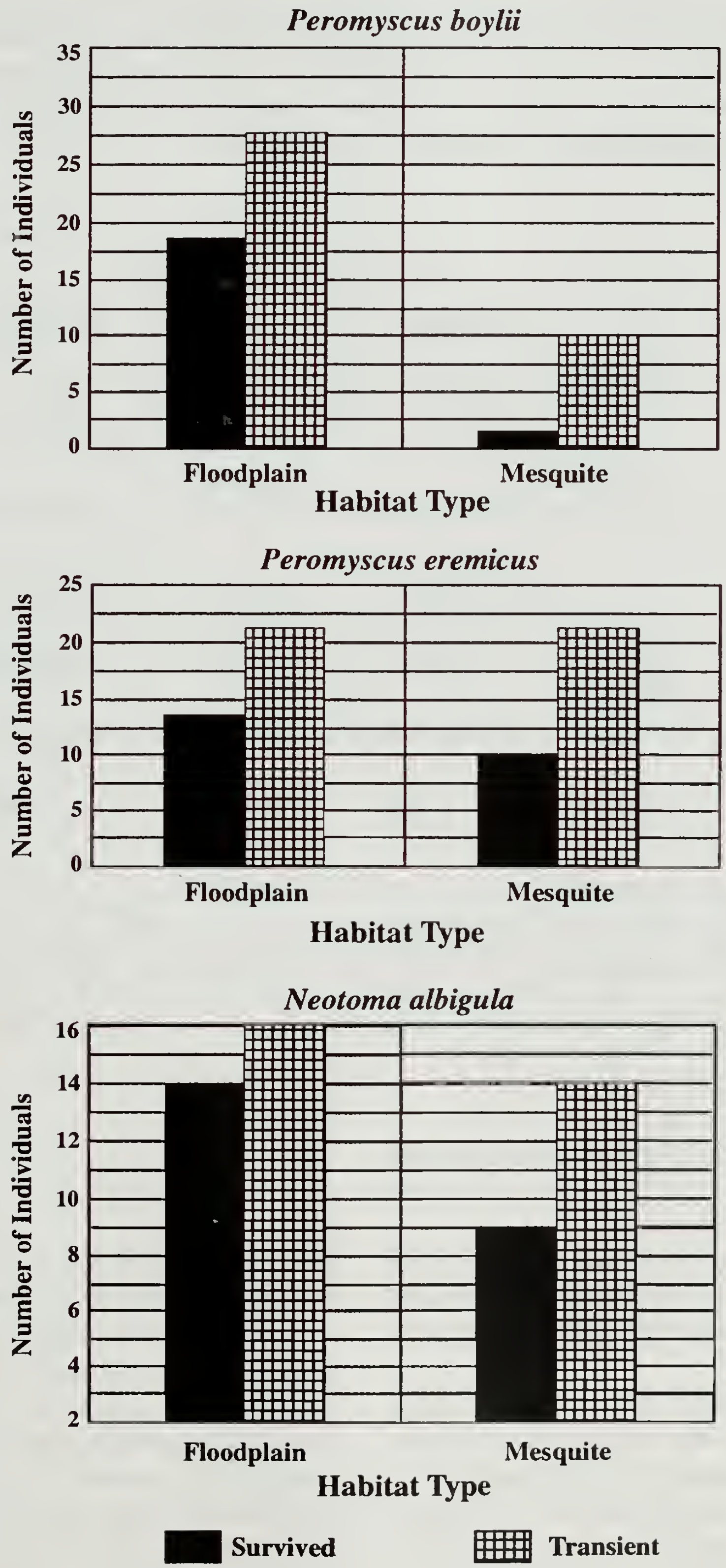

Figure 8. Proportion of animals recaptured within a trapping occasion combined across occasions (Residents) and proportion of first-captures only (Transients) for three species of small mammals at Montezuma Castle National Monument, Yavapai County, Arizona. *Log likelihood ratio chi-square value=4.837, d.f.=1, $p<0.05$.

Table 3. Mean (±SE) percent cover of vegetative strata and ground cover by habitat type (n=200 for each habitat), and frequency of debris piles at Montezuma Castle National Monument, Yavapai County, Arizona. Percent cover by strata were analyzed with a Wilcoxon (Mann-Whitney) signed ranks test. Debris pile frequency differences were analyzed using a G-test.

	Mean percent cover	
Vegetative Strata	**Floodplain**	**Mesquite**
Trees	28.02 ± 3.36	43.35 ± 2.58 *
Shrubs	32.82 ± 2.30	29.62 ± 2.03
Forbs	3.98 ± 0.87	0.03 ± 0.02 *
Perennial grasses	1.82 ± 0.58	6.46 ± 0.93*
Annual grasses	7.49 ± 1.28	8.46 ± 1.24
Debris piles	182	45 **
Ground Cover		
Bare soil	12.42 ± 1.41	19.71 ± 1.36 *
Gravel	4.96 ± 0.93	3.76 ± 0.68
Rock	20.91 ± 2.25	3.74 ± 0.26 *
Litter	48.75 ± 2.38	75.78 ± 2.00 *

* $p<0.05$

** Log likelihood ratio chi-square=110.7; $p<0.05$

total of three species of perennial grasses, several species of annual grasses, two species of herbs, and 12 different shrub species were encountered in mesquite habitat.

In riparian floodplain habitat, the percentage of perennial grass cover was an important environmental variable as indicated by the length of its line relative to other lines (Figure 9). In Figure 9, we projected a perpendicular dotted line from *P. eremicus* to the perennial grass axis in the diagram and the endpoints of this dotted line indicate the relative value of the weighted average of this species with respect to occurrence of perennial grasses. Therefore, we inferred that *P. boylii* has the lowest weighted average with respect to perennial grass cover (this species occurs in areas with high litter content and annual grass cover), *N. albigula* has the second lowest value, and *P. eremicus* is inferred to have the highest weighted average. Hence, *P. eremicus* was captured in areas with a high percentage of perennial grasses, whereas *N. albigula* and *P. boylii* were captured in areas with lower percentages of perennial grasses.

In floodplain habitat, we found percent perennial grass cover, forb cover, tree cover, and frequency of trees were the strongest correlates with

Table 4. Average percent vegetation cover by species by habitat type and species richness by habitat type. Numbers in parentheses are standard error values. (n=200 for each habitat type).

Species	Mean percent cover	
	Floodplain	Mesquite
Perennial grasses		
Bothriochloa barbinodis	0.09(0.05)	-0-
Bouteloua curtipendula	1.60(0.57)	-0-
Aristida purpurea	3.60(1.57)	-0-
Muhlenbergia porteri	-0-	5.78(0.94)
Paspalum distichum	0.14(0.08)	-0-
Sitanion hystrix	-0-	0.65(0.18)
Sporobolus airoides	-0-	0.03(0.03)
Annual grasses		
Bromus spp.	2.30(0.61)	8.37(1.24)
Unknown annual grass	5.19(1.17)	0.09(0.09)
Herbs		
Castilleja chromosa	0.01(0.01)	-0-
Datura meteloides	0.31(0.08)	-0-
Eriodictyon angustifolium	0.14(0.11)	-0-
Eriogonum spp.	-0-	0.01(0.003)
Linaria dalmatica	0.01(0.01)	-0-
Lotus mearnsii	0.09(0.04)	-0-
Solidago wrightii	0.35(0.11)	-0-
Unknown annual herbs	3.35(0.88)	0.02(0.02)
Shrubs		
Acacia greggii	0.71(0.34)	10.26(1.47)
Atriplex canescens	-0-	3.18(0.60)
Baccharis sarothroides	0.28(0.16)	-0-
Berberis haematocarpa	0.67(0.32)	3.75(0.84)
Brickellia californica	0.57(0.30)	-0-
Ceratoides lanata	-0-	0.07(0.05)
Chilopsis linearis	28.66(2.18)	-0-
Ephedra viridus	-0-	0.38(0.21)
Gutierrezia sarothrae	1.22(0.20)	9.42(0.85)
Larrea divaricata	-0-	0.09(0.09)
Lycium pallidum	-0-	0.13(0.08)
Marrubium vulgare	-0-	2.19(0.45)
Opuntia leptocaulis	0.05(0.05)	-0-
Rhus trilobata	0.37(0.27)	-0-
Yucca elata	-0-	0.06(0.05)
Ziziphus obtusifolia	0.01(0.01)	0.03(0.02)
Unknown shrubs	0.03(0.02)	0.07(0.07)
Trees		
Celtis reticulata	0.10(0.07)	-0-
Fraxinus pennsylvanica	5.06(1.42)	-0-
Juglans major	1.52(0.79)	-0-
Juniperus monosperma	5.67(1.44)	0.38(0.37)
Platanus wrightii	9.86(1.96)	-0-
Prosopis velutina	5.61(1.36)	42.98(2.58)
Total cover	77.6%	87.9%
Total number of species	29	21

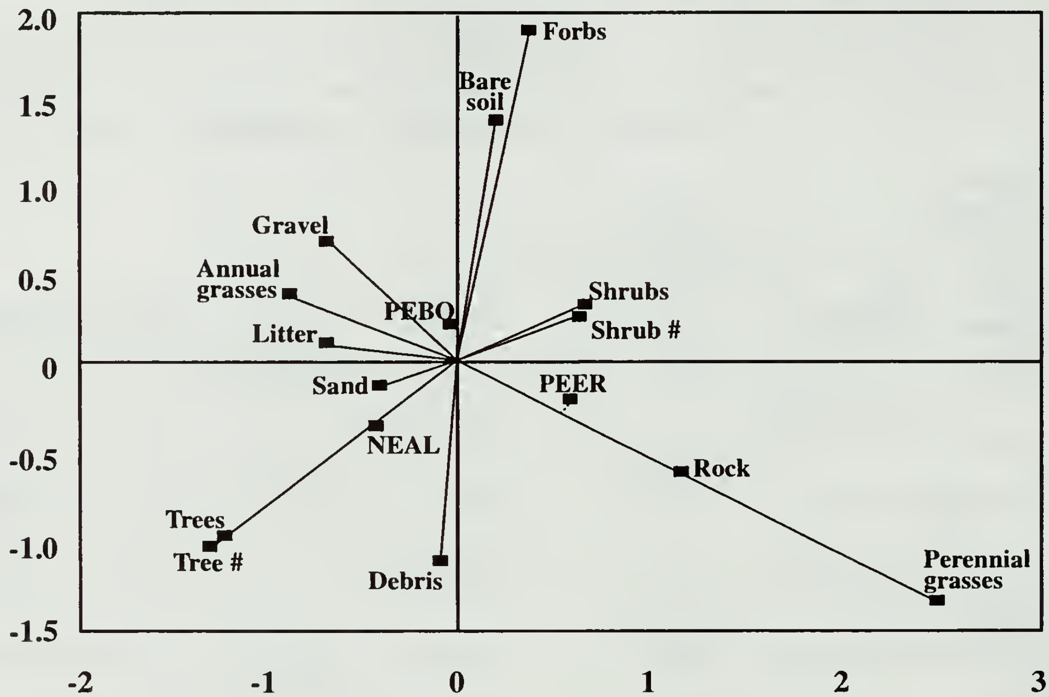

Figure 9. The distribution of three species of small mammals in the riparian floodplain habitat at Montezuma Castle National Monument, Yavapai County, Arizona. Canonical correspondence analysis (CCA) ordination diagram with species as points and environmental variables as lines ending in points; first axis is horizontal, second axis is vertical. Shown also is the projection of the small mammal point labeled **PEER** onto the trajectory of the line Perennial grasses. The endpoint of this projection indicates the approximate weighting of the centers of distributions of this mammal along the variable "perennial grasses", *Peromyscus eremicus* being found in habitats with the highest percentage cover of perennial grasses. The small mammal species are (clockwise from left top quadrant): **PEBO** = *Peromyscus boylii*, **PEER** = *P. eremicus*, and **NEAL** = *Neotoma albigula*. The environmental variables are: Litter = percentage substrate covered by litter, Annual grasses = percentage cover of annual grasses, Gravel = percentage substrate covered by gravel, Bare soil = percentage substrate covered by bare soil, Forbs = percentage cover of herbaceouds vegetation, Shrubs = percentage cover of shrub species, Shrub # = density of shrubs, Rock = percentage substrate covered by rock, Perennial grasses = percentage cover of perennial grasses, Debris = frequency of debris piles, Trees = percentage cover by trees, Tree # = density of trees, and Sand = percentage substrate covered by sand.

small mammal distributions. *Peromyscus eremicus*, displayed in the lower right quadrant of the diagram, was captured mainly in areas with high percentage of cover by perennial grasses and where substrate was fairly rocky. *Peromyscus boylii*, in the left upper quadrant, was captured mainly in areas with high annual grass cover, high litter contents, high percent cover by forbs, and where substrate was mostly exposed soil. *Neotoma albigula*, displayed in the lower left quadrant, occurred in areas with high litter contents, and high tree frequency. For this habitat type, 100.0% of the cumulative variance of the species-environment relationship was accounted for by the first two axes (Table 5).

Microhabitat separation among these three species in the floodplain was significant (Table 5). The 99 random data sets generated by the Monte Carlo permutation test of trap stations yielded a lower eigenvalue with a p-value less than 0.05. Therefore, differences in vegetative strata and habitat

Table 5. Summary of canonical correspondence analysis (CCA) and Monte Carlo permutation test in desert riparian floodplain habitat at Montezuma Castle National Monument, Yavapai County, Arizona. Results are from a CCA of three small mammal species and 13 environmental variables shown in the ordination diagram of Figure 9.

Axes	1	2	3	4	
Eigenvalues:	.130	.064	.521	.351	
Species-environment correlations:	.518	.330	.000	.000	
Cumulative percentage variance					
of species data:	12.2	18.1	67.0	100.0	
of species-environment relation:	67.1	100.0	.000	.000	
Sum of all canonical eigenvalues:					1.066

Monte Carlo permutation test for significance of first canonical axis (1):
Eigenvalue = 0.13
F-ratio = 14.68
* P-value = 0.04

structure found at a trap station significantly determine what species will occur there.

In mesquite habitat, we found *P. eremicus* also occurred in areas with high percentage of perennial grasses, and areas dense with shrubs and herbaceous species (Figure 10). This species was negatively associated with tree cover, tree frequency, litter content, and debris piles. As in floodplain habitat, *N. albigula* occurred most often with debris piles, high percent tree cover, tree density, and high percent litter content. *Peromyscus boylii*, in the upper right quadrant, occurred in areas with high percentage of annual grasses, and where the substrate is mostly rocky. For this habitat, 100% of the cumulative variance of the species-environment relation can be explained by the first two axes (Table 6).

Microhabitat separation among these three species in the mesquite habitat was also significant (Table 6). The Monte Carlo permutation test of trap station again yielded a lower eigenvalue for the first canonical axis indicating significant microhabitat segregation among species within a habitat type.

Across habitat types, the difference between microhabitats where *P. boylii, P. eremicus,* and *N. albigula* were caught and those where these species were never caught was significant (F=5.98, Wilks' Lambda=0.769, d.f.=10, 199, p<0.05; F=2.09, Wilks' Lambda=0.899, d.f.=10, 185, p<0.05; and, F=3.55, Wilks' Lambda=0.761, d.f.=10, 113, p<0.05 respectively) (Appendix B). Results from the univariate F-tests showed that *Peromyscus boylii* was captured at trap stations where the percent shrub cover was significantly higher (F=11.14, d.f.=1, p<0.05), where frequency of debris piles was higher (G=66.34, d.f.=1, p<0.05), and where percent rocky (F=26.49, d.f.=1, p<0.05) and sandy (F=13.18, d.f.=1, p<0.05) substrates were significantly higher than randomly available, but not used, trap stations. *Peromyscus boylii* was also captured at stations with less annual grass cover (F=5.91, d.f.=1, p<0.05), less percent cover by litter (F=20.82, d.f.=1, p<0.05), and lower frequency of trees (G=9.86, d.f.=1, p<0.05).

Peromyscus eremicus was captured at trap stations with greater percent shrub cover (F=8.64, d.f.=1, p<0.05), a greater frequency of shrubs (G=3.80, d.f.=1, p<0.05), significantly 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 greater tree cover (F=6.38, d.f.=1, p<0.05), higher

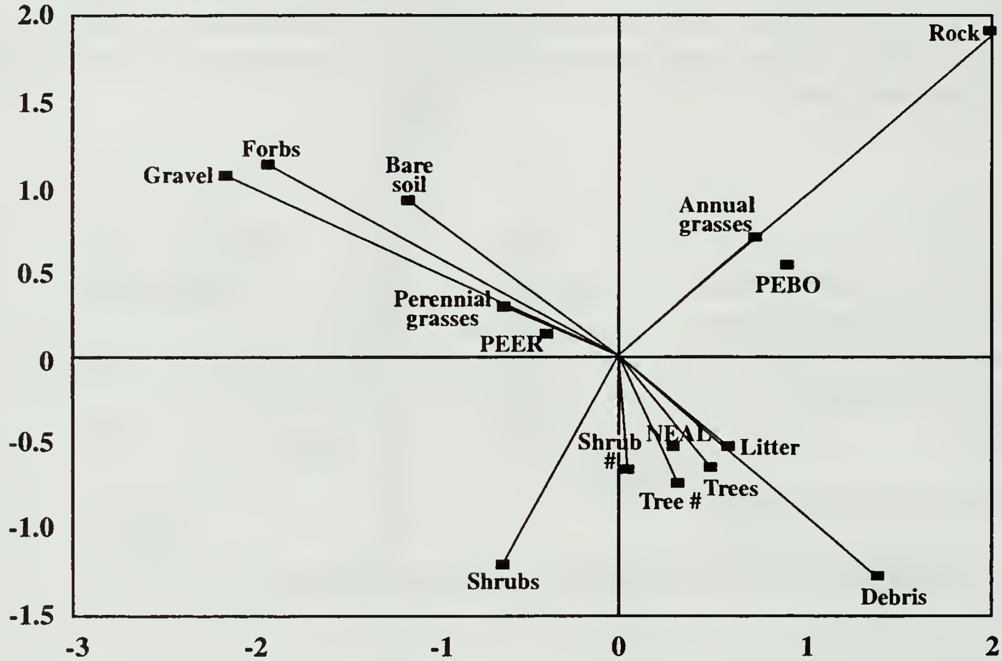

Figure 10. The distribution of three species of small mammals in mesquite habitat at Montezuma Castle National Monument, Yavapai County, Arizona. Canonical correspondence analysis (CCA) ordination diagramwith species as points and environmental variables as lines ending in points; first axis is horizontal, second axis is vertical. The small mammal species are (clockwise from left top quadrant): **PEER**= Peromyscus eremicus, **PEBO**= *P. boylii*, and **NEAL**= *N. albifula*. The environmental variables are: Perennial grasses= percentage cover by perennial grasses, Gravel= percentage substrate covered by gravel, Forbs= percentage cover by herbaceous vegetation, Bare soil= percentage substrate covered by bare soil, Annnual grasses= percentage cover by annual grasses, Rock= percentage substrate covered by rock, Litter= percentage substrate covered by litter, Debris= frequency of debris piles, Trees= percentage cover by trees, Tree #= density of trees, Shrub #= density of shrub species, Shrubs= percentage cover of shrub species.

frequency of debris piles (G=28.81, d.f.=1, $p<0.05$), and higher frequency of trees (G=7.29, d.f.=1, $p<0.05$). This species was also captured in areas with less exposed soil (F=15.52, d.f.=1, $p<0.05$) and less cover by perennial grasses (F=8.66, d.f.=1, $p<0.05$).

Within the floodplain habitat, there were no significant differences in percent cover of vegetative strata for traps used and traps randomly available within a habitat type (Appendix C). Structural characteristics of the habitat did differ between used and randomly available trap stations for *P. boylii* and *N. albigula* with *P. boylii* associated with a higher frequency of debris piles (G=17.81, d.f.=1, $p<0.05$), and *N. albigula* also associated with more debris (G=17.28, d.f.=1, $p<0.05$) and higher density of trees (G=13.70, d.f.=1, $p<0.05$).

Within the mesquite habitat, there were also no significant differences in vegetative strata between used and unused traps (Appendix D). Again, *N. albigula* was associated with more debris (G=4.97, d.f.=1, $p<0.05$), a structural characteristic.

Table 6. Summary of canonical correspondence analysis (CCA) and Monte Carlo permutation test results in mesquite habitat at Montezuma Castle National Monument, Yavapai County, Arizona. Results are from a CCA of three small mammal species and 12 environmental variables shown in the ordination diagram of Figure 10.

Axes	1	2	3	4	
Eigenvalues:	.236	.145	.475	.422	
Species-environment correlations:	.594	.487	.000	.000	
Cumulative percentage variance					
of species data:	18.4	29.8	66.9	100.0	
of species-environment relation:	62.0	100.0	.000	.000	
Sum of all canonical eigenvalues:					1.277

Monte Carlo permutation test for significance of first canonical axis (1):
Eigenvalue = 0.24
F-ratio = 12.67
* P-value = 0.02

CHAPTER 4
DISCUSSION

Habitat quality differences in a heterogeneous landscape can result in a source-sink population structure with net emigration of individuals from better habitats (sources) combined with net immigration into poorer habitats (sinks) (Pulliam 1988; Pulliam and Danielson 1991). This source-sink population structure manifests differences in performance and reproductive success of individuals encountering the source and sink habitats (Kawecki 1995). Hence,we define high quality habitats, or sources, to be those areas that afford conditions necessary for relatively successful survival and reproduction over long periods when compared with other similar environments. Conversely, marginal habitats, or sinks, support individuals, but their rates of survival and reproduction are low relative to high quality habitats. Marginal habitats are usually suitable for occupancy for short, or intermittent, periods (Morrison et al. 1992). In a purely social sense, dispersal sinks can also develop if social interactions prevent subordinate individuals from entering into, or remaining in, high quality habitats (Van Horne 1982, 1983). So, sinks can also be thought of as marginal areas to which surplus individuals disperse due to competitive exclusion from optimal habitats (Lidicker 1976).

Source and sink dynamics within a population have been documented in a variety of taxa, e.g. *Bonasa bonasia* (hazel grouse) (Beshkarev et al. 1994), *Peromyscus maniculatus* (deer mouse) (Van Horne 1982), *Tamias townsendii* (Townsend's chipmunk), *Glaucomys sabrinus* (northern flying squirrel), *Zapus trinotatus* (Pacific jumping mouse) (Doyle 1990), sphingid moths (Janzen 1986), *Rangifer tarandus* (caribou) (Bergerud 1988), and *Haleaetus leucocephalus* (bald eagles) (Swenson et al. 1986). These studies show that the source-sink phenomenon is widespread, but difficult to determine conclusively within a study site unless an excess of local reproduction over immigration can be shown, and active juvenile dispersal is observed (Andersen 1994).

Since source habitats, by definition, are net exporters of individuals, and are presumed of higher quality than adjacent habitats, we made several predictions about the small mammal community structure within a source. These included a greater population density, greater species diversity, larger-sized adults, and a greater proportion of the population in reproductive condition within a source for a given species. In addition, survival of individuals should increase in these high quality habitats, number of transient animals should be minimized, and most importantly, there should be evidence of dispersal from source to sink.

Riparian floodplains are generally considered more productive than adjacent ecosystems because of their unique hydrologic conditions (Mitsch and Gosselink 1993), and this is particularly true in the arid southwest (Johnson 1979). Periodic flooding contributes to a higher productivity by supplying an adequate water supply for the vegetation, supplying nutrients and altering soil chemistry (increasing nitrification, sulfate reduction, and nutrient mineralization), and creating a more oxygenated root zone while also "flushing" waste products.

For these reasons, we predicted that on a regional scale the floodplain would be the source for several small mammal species. But the data that we collected for floodplain and mesquite habitats at Montezuma Castle did not support this prediction. We also predicted a more diverse small mammal community in the floodplains since a habitat of high quality should be able to support a more diverse small mammal assemblage. But we found species diversity greater in the mesquite, due to the presence of burrowing small mammals and habitat-specific species. For instance, *Dipodomys ordii* (Ord's kangaroo rat) was captured only in mesquite where the substrate included a greater amount of sandy, gravelly, and friable soil. The floodplain areas also contained friable soil, but the occurrence of this substrate was patchy due to fragmentation by stream channels. In addition, *Reithrodontomys megalotis* (western harvest mice) was captured only in mesquite habitats.

Although abundance of *P. boylii* was greater in the floodplain, male adults were not significantly larger, nor was there an increase in the number of juveniles and subadults in comparison to mesquite habitat. In addition, reproductive activity was not greater in the floodplain, although non-significance for these latter two criteria may be a reflection of low sample sizes in mesquite habitat. Finally, *P. boylii* did not appear to survive significantly longer in floodplain over mesquite habitats.

Peromyscus boylii was more transient in mesquite. Animals in poor quality habitat or in a sink habitat might continue searching for better habitat and would gain little advantage from the long-term maintenance of a stable home range, whereas stability might well be important for both dominants and subordinates in high quality habitat (Van Horne 1981).

Peromyscus eremicus population size also tended to be larger in the floodplain, but again results from the other criteria were not conclusive. There was some indication that mesquite was a source habitat for *N. albigula. Neotoma albigula* population size was generally larger in the floodplain, but males were significantly larger in the mesquite, and there were more juveniles and subadults in the floodplain which would indicate mesquite is a higher quality habitat for this species. Sinks can exhibit larger population sizes relative to sources (Pulliam 1988; Van Horne 1983).

We could not conclude from our data that riparian floodplain habitat along Wet Beaver Creek acted as a source habitat and that mesquite acted as a dispersal sink for any small mammal species. The fact that our data do not support source-sink dynamics may suggest three things. First, the spatial scale and the number of sampling replications of the study site were both relatively small. On a landscape level, riparian floodplain may act as a source for *P. boylii*, but within our study site, we were not able to detect this pattern. We also did not sample true "upland" habitat. Second, since population densities appeared to be low during the study, interspecific competition or interference among individuals may not have been sufficiently strong to force emigration into inferior habitats. Third, the temporal scale of this study may not have been sufficient to detect a source and sink habitat.

Although we were not able to distinguish a source from a sink for any species, the data that we collected on habitat use provides important information on habitat selection and habitat separation among the species. The distribution of individuals among habitats may be largely determined by habitat selection (Pulliam and Danielson 1991). At low population densities, habitat selectivity is enhanced, but at high densities, habitat selectivity diminishes (Rosenzweig 1991). Habitat selectivity by *P. boylii*, *P. eremicus*, and *N. albigula* was significant between floodplain and mesquite habitats indicating that selection of habitat was probably the most important mechanism structuring the small mammal communities within Montezuma Castle NM.

Peromyscus boylii is a widely distributed species living in a variety of habitats in Arizona. This species is a large-sized *Peromyscus* and frequently climbs in and through trees with ease (Hoffmeister 1986). During this study, we found *P. boylii* to be more abundant in the floodplain where it selected microhabitats with more debris, sandy soils, and a rocky substrate. 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) also found *P. boylii* in high densities along rocky slopes and brush-rock slopes. Association of *P. boylii* with floodplain habitats probably also relates to the herbaceous vegetation in these habitat types. This species has a flexible diet, but the main component is herbaceous vegetation (Goodwin and Hungerford 1979). Percent cover by herbaceous vegetation was significantly higher in the floodplain habitat than in the mesquite in our study, which could partially explain why this species is more abundant in the floodplain.

Peromyscus eremicus is the most typical and widespread desert-dwelling member of the genus *Peromyscus* (King 1968). This species is found among and around cacti, creosote, woodpiles, rocks and rocky slopes, chaparral, and sandy flats, and they often reside in the abandoned burrows of other mammals or in parts of woodrat piles (Hoffmeister

1986). *Peromyscus eremicus* at Montezuma Castle also tended to be more abundant in the floodplain. This species selected microhabitats with significantly more shrub cover, significantly higher density of shrubs, and a rockier substrate than randomly available microhabitats. In coastal sage scrub habitat of California, frequency of capture of *P. eremicus* was also greater in areas of dense vegetation and shrubs (Veal and Caire 1979).

Neotoma albigula is common in a variety of habitats throughout Arizona, building large nests in and around cacti, shrubs such as mesquite or acacia, or rock piles. In mesquite and catclaw vegetation associations, this species feeds on the bark of these shrubs frequently climbing into them to debark certain branches (Hoffmeister 1986). We found that *N. albigula* selected microhabitats with greater tree cover, increased tree density, and greater amount of debris than microhabitats that were available, which follows habitat utilization patterns reported in the literature. Macedo and Mares (1988) also found *N. albigula* in areas with large quantities of debris and dead trees. Large quantities of debris provide sufficient cover for house construction. Olsen (1973) hypothesized that shelter site selection by this species is based on the quantity of ground level vegetation and debris available for cover.

Not only were the above species of small mammals selecting certain habitat characteristics nonrandomly, but we also found evidence of significant microhabitat separation among these species. In floodplain habitat, *N. albigula* was associated with more trees and tree cover, *P. eremicus* with rockier substrates and increased cover by perennial grasses, while *P. boylii* was more highly associated with herbaceous vegetation, exposed soil substrate, and cover by annual grasses. In mesquite, *P. boylii* was associated with more annual grass cover and a rockier substrate, *P. eremicus* with perennial grass cover, herbaceous vegetation, and gravelly soils, while *N. albigula* was again associated with more trees and tree cover. *Neotoma albigula* was also associated more significantly with debris and litter. Coexistence of small mammal species within the same area is facilitated by microhabitat separation (Doyle 1987; Dueser and Shugart 1978), and microhabitat separation has been shown to be a prominent feature in community structure in several studies in the southwest (Holbrook 1979; Rosenzweig and Winakur 1969; Thompson 1982).

Both the importance of habitat selection and the role that microhabitat plays in structuring communities is well documented (Adler 1988; Price 1978). Small mammal community structures in riparian floodplain and mesquite habitats at Montezuma Castle National Monument in central Arizona may depend on several factors, but habitat selection and microhabitat separation appear to be the most influential mechanisms.

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APPENDIX A
LIVE-TRAPPING RESULTS

Appendix A. Trapping results for the three most abundant species at Montezuma Castle National Monument (PEBO = *P. boylii*, PEER= *P. eremicus*, and NEAL=*N. albigula*). Table includes date, species, number of individuals, estimated capture probability (p-hat), model chosen by program CAPTURE, population estimate (± SE), and Lincoln-Peterson estimate of population size with [95% confidence intervals].

Grid Location	Date	Species	Number of Individuals	Estimated Capture Probability p-hat (Model*)	CAPTURE Population Estimate (± SE)	L-P Estimate [CI]
Floodplain I	April 1993	PEBO	5	0.292 ($M_{(tbh)}$)	6 (1.62)	8.1 [2.95, 13.29]
		PEER	6	0.438 ($M_{(o)}$)	6 (0.48)	7.7 [2.61, 12.82]
		NEAL	1	Data set too small		
Mesquite I	April 1993	PEBO	0			
		PEER	2	Data set too small		3.5 [0.36, 6.69]
		NEAL	3	0.200 ($M_{(o)}$)	5 (1.62)	4.5 [0.82, 8.10]
Floodplain II	June 1993	PEBO	7	0.375 ($M_{(bh)}$)	6 (1.28)	11.48 [5.32, 17.63]
		PEER	0	Data set too small		
		NEAL	0	Data set too small		
Mesquite II	June 1993	PEBO	0	Data set too small		
		PEER	6	0.266 ($M_{(o)}$)	6 (0.47)	8.52 [3.28, 13.76]
		NEAL	1	Data set too small		
Floodplain I	July 1993	PEBO	9	0.403 ($M_{(o)}$)	8 (0.26)	6.58 [1.97, 11.18]
		PEER	4	0.250 ($M_{(o)}$)	4 (0.33)	7.72 [2.61, 12.82]
		NEAL	8	0.275 ($M_{(o)}$)	8 (0.58)	10.62 [4.46, 16.77]
Mesquite I	July 1993	PEBO	1	Data set too small		
		PEER	4	0.229 ($M_{(o)}$)	4 (0.41)	5.48 1.37, 9.60]
		NEAL	9	0.240 ($M_{(o)}$)	9 (0.73)	9.10 [3.28, 14.92]
Floodplain II	January 1994	PEBO	7	0.225 ($M_{(o)}$)	10 (2.17)	8.12 [2.95, 13.29]
		PEER	6	0.286 ($M_{(o)}$)	7 (1.37)	7.72 [2.61, 12.82]
		NEAL	1	Data set too small		
Mesquite II	January 1994	PEBO	0			
		PEER	6	0.312(M($_{o}$))	8 (1.62)	6.58 [1.97, 11.18]
		NEAL	0			

Appendix A. continued.

Grid Location	Date	Species	Number of Individuals	Estimated Capture Probability p-hat (Model*)	CAPTURE Population Estimate (± SE)	L-P Estimate [CI]
Floodplain I	April 1994	PEBO	13	0.433 ($M_{(th)}$)	15 (1.53)	8.52 [3.28, 13.76]
		PEER	3	0.438 ($m_{(th)}$)	4 (1.14)	4.46 [0.82, 8.10]
		NEAL	6	0.312 ($M_{(th)}$)	8 (1.62)	6.58 [1.97, 11.18]
Mesquite I	April 1994	PEBO	6	0.469 ($M_{(o)}$)	8 (1.62)	7.72 [2.61, 12.82]
		PEER	4	0.250 ($M_{(h)}$)	6 (1.62)	4.46 [0.82, 8.10]
		NEAL	1	Data set too small		
Floodplain II	May 1994	PEBO	15	0.358 ($M_{(o)}$)	15 (0.72)	13.52 [6.69, 20.34]
		PEER	9	0.375 ($M_{(o)}$)	9 (0.49)	10.62 [4.46, 16.77]
		NEAL	5	0.300 ($M_{(o)}$)	5 (0.92)	6.58 [1.97, 11.18]
Mesquite II	May 1994	PEBO	0			
		PEER	6	0.156 ($M_{(o)}$)	8 (1.81)	7.72 [2.61, 12.82]
		NEAL	2	Data set too small		
Floodplain I	June 1994	PEBO	1	Data set too small		
		PEER	8	0.297 ($M_{(b)}$)	8 (0.07)	9.10 [3.28, 14.92]
		NEAL	9	0.289 ($M_{(o)}$)	9 (0.90)	11.48 [5.32, 17.63]
Mesquite I	June 1994	PEBO	4	0.156 ($M_{(h)}$)	4 (0.72)	5.48 [1.37, 9.60]
		PEER	3	0.208 ($M_{(o)}$)	3 (0.94)	4.46 [0.82, 8.10]
		NEAL	6	0.140 ($M_{(o)}$)	8 (2.79)	7.72 [2.61, 12.82]

* $M_{(b)}$ = capture probabilities vary by behavioral responses.
$M_{(bh)}$ = capture probabilities vary by behavioral responses and by individual animal.
$M_{(h)}$ = capture probabilities vary by individual animal response to capture.
$M_{(tbh)}$ = capture probabilities vary by time (trapping occasion), behavioral responses to capture, and individual animal.
$M_{(o)}$ = capture probability is constant.
$M_{(th)}$ = capture probabilities vary by time (trapping occasion) and by individual animal.

APPENDIX B

HABITAT SELECTION RESULTS

Appendix B. Used versus available habitat results for riparian floodplain and mesquite habitats displaying mean percent cover of 10 environmental variables (five vegetative strata and five substrate variables) (± SE) and frequency of debris, trees, and shrubs for three species of small mammals (*P. boylii*, *P. eremicus*, and *N. albigula*) captured at Montezuma Castle National Monument. Data were analyzed using 1-way MANOVA. Frequency of debris, trees, and shrubs were analyzed with G-tests.

Environmental variables	*P. boylii*[1]		*P. eremicus*[2]		*N. albigula*[3]	
	Used (n = 105)	**Available** (n = 105)	**Used** (n = 98)	**Available** (n = 98)	**Used** (n = 62)	**Available** (n = 62)
Vegetative Strata:						
Annual grass cover	7.58 (1.94)	14.24 (1.94)*	7.17 (1.89)	10.46 (1.89)	8.76 (2.20)	6.98 (2.20)
Perennial grass cover	1.34 (0.81)	3.35 (0.81)	3.64 (1.14)	3.56 (1.14)	1.24 (1.18)	6.17 (1.18)*
Forb cover	2.82 (0.90)	1.16 (0.90)	1.62 (0.98)	1.84 (0.98)	0.91 (0.88)	1.84 (0.88)
Shrub cover	33.59 (2.63)	21.19 (2. 63)*	37.51 (2.99)	25.07 (2.99)*	28.58 (4.00)	30.16 (4.00)
Tree cover	36.48 (4.27)	46.39 (4.27)	39.90 (4.64)	43.80 (4.64)	57.25 (5.75)	36.71 (5.75)*
Structural variables:						
Debris piles	185	60*	109	101	106	89*
Tree frequency	185	244*	191	209	164	112*
Shrub frequency	1120	1706	1495	1271*	770	857
Substrate:						
Litter	57.07 (3.13)	77.29 (3.13)*	63.74 (3.57)	63.88 (3.57)	66.51 (4.37)	64.61 (4.37)
Bare soil	11.20 (2.20)	17.02 (2.20)	10.69 (2.24)	17.71 (2.24)*	6.10 (2.59)	20.54 (2.59)*
Gravel	2.28 (0.60)	1.26 (0.60)	2.73 (1.05)	4.30 (1.05)	2.20 (1.14)	3.31 (1.14)
Sand	9.19 (1.51)	1.44 (1.51)*	4.75 (1.57)	5.24 (1.57)	9.04 (2.34)	4.32 (2.34)
Rock	19.17 (2.27)	2.68 (2.27)*	17.26 (2.74)	8.66 (2.74)*	14.76 (3.18)	7.09 (3.18)

[1] F = 5.98, Wilks' Lambda = 0.769, d.f. = 10, 199, $p<0.05$.
[2] F = 2.09, Wilks' Lambda = 0.899, d.f. = 10, 185, $p<0.05$.
[3] F = 3.55, Wilks' Lambda = 0.761, d.f. = 10, 113, $p<0.05$.
*$p<0.05$.

APPENDIX C

FLOODPLAIN HABITAT SELECTION RESULTS

Appendix C. Used versus available habitat results for riparian floodplain habitat displaying mean percent cover of 10 environmental variables (five vegetative strata and five substrate variables) (± SE) and frequency of debris, trees, and shrubs for three species of small mammals (*P. boylii*, *P. eremicus*, and *N. albigula*) at Montezuma Castle National Monument. Data were analyzed using 1-way MANOVA. Frequency of debris, trees and shrubs were analyzed with G-tests.

Environmental variables	*P. boylii*		*P. eremicus*		*N. albigula*	
	Used (n = 85)	**Available** (n = 85)	**Used** (n = 50)	**Available** (n = 50)	**Used** (n = 40)	**Available** (n = 40)
Vegetative strata:						
Annual grass cover	5.69 (1.92)	8.14 (1.92)	4.60 (2.32)	7.82 (2.32)	7.10 (2.82)	7.76 (2.82)
Perennial grass cover	1.46 (0.96)	2.74 (0.96)	4.42 (1.56)	0.85 (1.56)	1.31 (1.39)	2.73 (1.39)
Forb cover	3.48 (1.30)	3.69 (1.30)	3.18 (1.75)	4.08 (1.75)	1.42 (2.16)	5.92 (2.16)
Shrub cover	37.68 (3.58)	32.57 (3.58)	37.37 (4.72)	34.99 (4.72)	26.74 (5.08)	30.24 (5.08)
Tree cover	30.83 (5.06)	23.71 (5.06)	30.85 (6.28)	23.84 (6.28)	52.60 (8.18)	27.08 (8.18)
Structural variables:						
Debris piles	163	100*	85	73	83	47*
Tree frequency	131	102	78	62	104	52*
Shrub frequency	737	567*	433	355	266	251
Substrate:						
Litter	49.20 (3.57)	47.20 (3.57)	44.67 (4.68)	50.41 (4.68)	51.46 (5.57)	46.48 (5.57)
Bare soil	12.28 (2.16)	13.39 (2.16)	8.75 (2.33)	12.52 (2.33)	6.52 (2.59)	11.25 (2.59)
Gravel	2.76 (1.44)	6.97 (1.44)	2.11 (1.54)	5.58 (1.54)	3.18 (1.04)	3.68 (1.04)
Sand	11.35 (2.48)	11.71 (2.48)	9.31 (3.08)	12.52 (3.08)	14.01 (3.88)	12.88 (3.88)
Rock	23.07 (3.48)	20.09 (3.48)	33.55 (4.80)	18.41 (4.80)*	22.68 (5.32)	25.12 (5.32)

* $p<0.05$

APPENDIX D

MESQUITE HABITAT SELECTION

Appendix D. Used versus available habitat results for mesquite habitats displaying mean percent cover of 10 environmental variables (five vegetative strata and five substrate variables) (± SE) and frequency of debris, trees, and shrubs for three species of small mammals (*P. boylii*, *P. eremicus*, and *N. albigula*) captured at Montezuma Castle National Monument. Data were analyzed using 1-way MANOVA. Frequency of debris, trees, and shrubs were analyzed using G-tests.

Environmental variables	*P. boylii*		*P. eremicus*		*N. albigula*	
	Used (n = 19)	**Available** (n = 19)	**Used** (n = 48)	**Available** (n = 48)	**Used** (n = 23)	**Available** (n = 23)
Vegetative strata:						
Annual grass cover	16.42 (3.99)	11.39 (3.99)	5.58 (2.16)	9.85 (2.16)	16.63 (4.55)	11.28 (4.55)
Perennial grass cover	0.87 (1.86)	1.48 (1.86)	5.68 (1.35)	2.84 (1.35)	1.56 (0.78)	1.07 (0.78)
Forb cover	———	———	———	———	———	———
Shrub cover	17.07 (4.25)	18.44 (4.25)	28.56 (4.35)	37.66 (4.35)	16.85 (5.87)	33.16 (5.87)
Tree cover	57.87 (7.19)	59.37 (7.19)	49.88 (5.44)	49.32 (5.44)	54.56 (7.26)	62.93 (7.26)
Structural variables:						
Debris piles	18	15	24	27	23	11*
Tree frequency	49	53	113	112	63	56
Shrub frequency	381	390	1062	915	525	391
Substrate:						
Litter	90.01 (4.95)	89.26 (4.95)	82.54 (3.40)	83.59 (3.40)	82.51 (4.56)	91.52 (4.56)
Bare Soil	6.94 (4.40)	9.73 (4.40)	15.17 (3.09)	12.71 (3.09)	16.07 (4.32)	7.06 (4.32)
Gravel	0.21 (0.17)	0.10 (0.17)	1.03(0.71)	3.37 (0.71)	1.14 (0.68)	1.06 (0.68)
Sand	———	———	———	———	———	———
Rock	2.74 (1.86)	0.05 (1.86)	1.25 (0.74)	0.29 (0.74)	0.18 (0.20)	0.36 (0.20)

* $p<0.05$

As the nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural and cultural resources. This includes fostering of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for enjoyment of life through outdoor recreation. The department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people. The department also promotes the goals of the Take Pride in America campaign by encouraging stewardship and citizen responsibility for the public lands and promoting citizen participation in their care. The department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

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