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MICRO- AND MACROHABITAT ASSOCIATIONS IN MOJAVE DESERT RODENT COMMUNITIES

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Characterizing habitat associations of species is fundamental to understanding the mechanistic basis of community organization. Typically, investigators estimate microhabitat characteristics that account for significant amounts of variation in species composition. Nonetheless, highly resolved microhabitat characteristics may account for no more variation in species composition than coarse macrohabitat distinctions, particularly in heterogeneous environments. We describe micro- and macrohabitat associations of 13 species of nocturnal rodents distributed across 31 communities within the Mojave Desert. Rodent species composition, biomass of 81 perennial plant species, representation of 9 soil and rock classes, and the percent cover of annuals and grasses were quantified. Communities also were assigned to macrohabitats based on qualitative characteristics. Multivariate analysis of variance indicated highly significant community-wide differences among macrohabitats and species-specific analyses of variance substantiated differences for all but 1 species analyzed. Microhabitat characteristics accounted for approximately 55% of the variation in rodent species composition. Moreover, microhabitat characteristics accounted for 17% variation in rodent species composition over and beyond that shared with macrohabitat distinctions. Micro- and macrohabitat perspectives provide complimentary insights into species composition of rodent communities. Edaphic features in particular represented important environmental heterogeneity that likely acts both directly on rodent species composition and indirectly through influencing variation in plant species composition. Indeed, the Mojave Desert is represented by a spatial mosaic of species-rich and compositionally dynamic rodent communities that will provide many insights into the coexistence of species at regional spatial scales.

Key words: community structure, desert rodent, habitat selection, macrohabitat, metacommunity, microhabitat, scale, scale-dependence, spatial processes

Of the 4 great North American deserts (Chihuahuan, Great Basin, Mojave, and Sonoran), the Mojave has received the least focus in terms of organization of mammalian communities. This is especially true of rodents despite the fact that they are an important component of the mammalian fauna in many desert systems. In the Mojave Desert, rodents are represented by approximately 58 taxa (Patterson et al. 2005). Rodents play important ecological roles as consumers, secondary producers, and mechanical processors (Brown 1986). In particular, rodents are important seed and spore dispersers, consumers of vegetation, seeds, and fruits (Reichman and Price 1993), and represent a substantial resource base for many other predators (Kotler 1984).

Most of the area of North American deserts falls within the Basin and Range province of western North America (MacMahon 1979). Accordingly, regular alternation of desert basins and mountain ranges combined with predictable but complex toposequences create considerable spatial heterogeneity (Whitford 2002). This is especially true in the Mojave Desert, the driest and least productive desert in North America. Even within a particular toposequence, edaphic characteristics and microclimates can be variable across short distances, further increasing spatial heterogeneity. Minute differences in relative humidity between different mountain slopes affect distribution of dominant plant species such as blackbrush (*Coleogyne ramosissima*), thereby creating substantial habitat heterogeneity across sharp but short gradients (Beatley 1975). Abundance of desert rodents has been demonstrated to exhibit strong relationships with environmental characteristics, and a better understanding of quantitative environmental characteristics important to distribution and abundance of desert rodents can greatly inform basic biology of poorly known desert systems.

Microhabitat characteristics commonly are used to understand variation in abundance of species and to identify important quantifiable niche dimensions. Particular microhabitat

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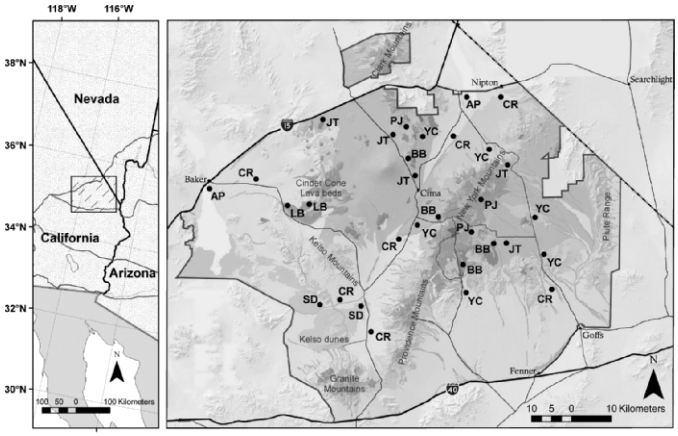


Fig. 1.—Map of the Mojave National Preserve demonstrating sampled communities. Acronyms are as follow: AP, alkali playa; BB, blackbrush woodland; CR, creosote bajada; JT, Joshua tree woodland; LB, lava bed; PJ, piñon–juniper woodland; SD, sand dune; YC, Mojave yucca woodland.

characteristics that are correlated with variation in abundance are inferred to reflect important decisions made by individuals that maximize fitness (i.e., density-dependent habitat selection—Rosenzweig 1991). Nonetheless, microhabitat characteristics are not the only salient forms of environmental heterogeneity. Macrohabitat features—more gross and discrete habitat differences typically defining different plant communities or life zones—also can affect consumer densities yet are not necessarily completely embodied by underlying microhabitat characteristics (Morris 1987). Variation among macrohabitats often is greater than variation among microhabitats within a macrohabitat. Accordingly, microhabitat variables may have limited ability to predict the abundance of consumer species, especially at large spatial scales. Distinction between microhabitat and macrohabitat selection has made evident the degree to which individuals are actively selecting particular microhabitat characteristics or are simply preferentially responding to coarser differences reflected in macrohabitats (Morris 1987). Indeed, before effects of specific microhabitat characteristics can be implicated as important in determining abundance of populations and ultimately the diversity of communities, effects of macrohabitat should be evaluated.

We describe the comparative community ecology of nocturnal rodents in the eastern Mojave Desert. Specifically, we examine 31 communities occurring in a series of interdigitating macrohabitats. We quantify microhabitat characteristics that are important in predicting abundance of common species and we evaluate the degree to which microhabitat characteristics predict rodent abundances over and beyond expectations from simple macrohabitat delimitations.

Materials and Methods

Study site and sampling.—The Mojave National Preserve comprises close to 600,000 ha and its northern border is located approximately 80 km southwest of Las Vegas, Nevada, in San Bernardino County, California (Fig. 1). Our study area was located on a broad alluvial fan complex consisting of 4 different materials: limestone, mixed plutonics, quartz monzonite, and mixed volcanics (Young et al. 2004). Elevation ranges from 85 to 2,417 m (Beever et al. 2006). Average precipitation ranges from 130 to 230 mm annually (Young et al. 2004). Dominant vegetation (Brooks et al. 2004) is *Larrea tridentata* (48% of study site), *Yucca brevifolia* (26%), and *Yucca schidigera* (18%).

Between September and November 2005, we sampled 31 communities from 8 of the most extensive macrohabitats within the Mojave National Preserve: creosote bajada (7 communities), Joshua tree woodland (5), blackbrush scrub (4), Mojave yucca woodland (6), piñon–juniper woodland (3), lava bed (2), sand dune (2), and alkali playa (2). Herein we refer to macrohabitats as large, coarse-grained discontinuities associated with discrete plant associations whereas we refer to microhabitat as small-scale, fine-grained, and quantifiable variation in floral and edaphic characteristics of communities. We sampled rodent species composition using paired 500-m transects separated by approximately 100 m. One Sherman live trap (H. B. Sherman Traps, Inc., Tallahassee, Florida) was placed every 5 m for a total of 101 traps on each transect and 202 traps sampling each community. Sampling was conducted for 3 nights (606 total trap-nights of effort) and animals were marked and released each morning. Rodent relative abundance data was based on the number of unique individuals caught during the 3 nights (i.e., recaptures not counted). Rodent relative abundances were square-root transformed before analyses to normalize the count data and so that dominant species did not dominate results (Legendre and Legendre 1998). Pocket mice (*Chaetodipus* and *Perognathus*) can become inactive during the coldest portions of the year (Kenagy and Bartholemew 1985). Although we caught pocket mice during the entire field season, this does not ensure that no individuals became inactive during our sampling; estimates of relative abundance for these 2 genera may be conservative. The ground squirrels *Spermophilus tereticaudus* and *Ammospermophilus leucurus* are primarily diurnal and as such their relative abundance more reflects the amount of time traps were open in the morning and afternoon than their actual relative abundance on the sampling transects. Sciurids were not considered in any analysis. *Reithrodontomys megalotis* was captured at 2 communities and had relative abundances too low to make meaningful species-specific analyses; this species was excluded from analyses focusing on species-specific patterns. Rodent sampling adhered to Louisiana State University Institutional Animal Care and Use Committee protocol 06-033 based on guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). Voucher specimens are deposited in the Museum of Natural Science, Louisiana State University. Data are available from the authors upon request.

Sampling of vegetative characteristics of each community was based on a total of 4 additional transects, each 2 m wide and 50 m long, running perpendicular to each mammal transect. The positions of these vegetation transects were evenly spaced, located at 0-, 167-, 333-, and 500-m marks along the

mammal transects. On each transect, length, width, and height of each perennial plant were determined to estimate the sum of the biomass of each species. Within each vegetation transect, we calculated the percent cover of all grasses and all annual plants inside two 5 × 2-m quadrats set between 15 and 20 m from the center of the vegetation transect. We estimated mean percent values in each quadrat based on independent assessments by 2 observers.

Soil microprofile was characterized based on ten 1-dm^3 samples evenly spaced along mammal transects. Each sample was manually sieved and separated based on particle size into 9 categories: <1.4 mm, 1.4–<3.18 mm, 3.18–<4.75 mm, 4.75–<6.3 mm, 6.3–<12.5 mm, 12.5–<25 mm, 25–<50 mm, 50–<120 mm, and >120 mm. Each portion was weighed and mean proportional contribution of each particle size class was used for analyses.

We characterized species diversity of each macrohabitat using additive forms of α, β, and γ (Lande 1996). Specifically, mean α is the number of species shared among communities within a macrohabitat type, β is the mean number of unique species within communities, and γ is the sum of mean α and β.

Macrohabitat effects.—One-way multivariate analysis of variance (MANOVA) was used to evaluate significant differences among macrohabitats based on rodent species composition of replicated communities. We also used discriminant function analysis (DFA) to illustrate significant differences determined by MANOVA. We conducted a posteriori least significant difference tests (Sokal and Rohlf 1995) to determine pairwise differences among macrohabitats based on site scores from the DFA. We also conducted 1-way analyses of variance (ANOVA) on each rodent species separately to determine which likely contributed to the significant MANOVA.

Microhabitat effects.—We characterized microhabitat using biomass of 81 perennial plant species, 9 soil microprofile classes, percent cover of grasses, and percent cover of annuals. We conducted a cluster analysis to investigate the similarity in the response of different rodent species to environmental gradients spanning our study system. Based on standardized Pearson correlation coefficients (Sokal and Rohlf 1995) of the relationship between each environmental variable and the relative abundance of each rodent species, we calculated a matrix of Euclidean distances among all species. Using these distances and an unweighted pair group method with arithmetic mean (UPGMA) algorithm, we built a dendrogram of relationships among rodent species that depicts their hierarchical clustering in terms of similarities or differences in their association to environmental characteristics.

We used principal component analysis (PCA) based on a covariance matrix to reduce redundancy and hence dimensionality of perennial and soil microprofile data sets separately. Perennials were square-root transformed so as to normalize data and reduce influence of species with very high biomass. PCA reduced perennial and soil microprofile data sets to 6 and 1 variables (principal components [PCs]), respectively, based on those derived axes that had eigenvalues greater than expected based on a broken-stick model (Jackson 1993).

For the community-wide focus we conducted a redundancy analysis (RDA) whereby perennial PCs, soil profile PC, annual percent cover, and grass percent cover were independent variables and rodent relative abundances at each community were dependent variables. RDA selects a combination of independent variables that maximally accounts for variation in dependent variables (Jongman et al. 1995). This analysis also provides amount of variation accounted for by dependent variables (i.e., adjusted R^2) as well as statistical significance of the result based on 10,000 permutations of the original data. This RDA was conducted using Matlab routines written by Peres-Neto et al. (2006). For species-specific analyses, stepwise multiple regression determined the linear combination of 9 (6 perennial PCs, 1 soil PC, grass variable, and annual variable) microhabitat variables that could best predict relative abundance of each species of nocturnal rodent.

We also were interested in amount of unique variation accounted for by microhabitat associations after controlling for macrohabitat affiliation of each community and whether microhabitat variables can explain significantly more variation in rodent relative abundances after accounting for simple macrohabitat designations. We conducted a partial RDA where microhabitat variables were the independent matrix and macrohabitat associations represented the covariate matrix. Macrohabitats were coded as dummy variables in a covariate matix according to Legendre and Legendre (1998). Significance was based on 10,000 permutations of the original data. We used Matlab routines written by Peres-Neto et al. (2006) to conduct these analyses.

Results

Our sampling of 31 communities from 8 different macrohabitats resulted in 18,786 trap-nights that generated 6,108 unique captures (i.e., not counting recaptures) of 15 species. Species were not distributed uniformly across macrohabitats or communities (Table 1). *Dipodomys merriami* and *Neotoma lepida* occurred in the greatest number of macrohabitats and communities, whereas *R. megalotis* exhibited the narrowest distribution, occurring in only 2 macrohabitats and 2 communities. On average, species occurred in 5.15 macrohabitats and 15 communities. Gamma diversity of macrohabitats ranged from 6 to 10 and mean α was always greater than β and varied from 4 to 7.25.

Macrohabitats differed significantly in terms of rodent species composition ($F = 8.48$, $d.f. = 91,77$, $P < 0.001$, $R^2 = 0.52$). Least significant difference tests performed on DFA scores on the first 2 DFA axes for communities indicated that all macrohabitats were significantly different from at least 4 other macrohabitats (Fig. 2). Species-specific ANOVAs indicated that 11 of 12 species exhibited significant differences among macrohabitats (Table 2). *Perognathus longimembris* exhibited no significant differences in relative abundance across the 8 macrohabitats.

Relative abundances of rodents exhibited numerous and varied associations with microhabitat characteristics (Appendix I). However, species could be aggregated into 4 major groups

Table 1.—Presence or absence of nocturnal rodent species across 8 macrohabitats examined and estimates of α, β, and γ diversity. Occurrence within a macrohabitat is denoted with ××. γ refers to the total number of species found in all communities within a macrohabitat. Mean α refers to the average number of species within communities representing a macrohabitat. β refers to the number of unique species. Incidence represents the proportion of all 31 communities in which a species was encountered.

	Playa	Blackbrush	Creosote	Joshua tree	Lava	Piñon–juniper	Dune	Yucca	Incidence
Species									
Chaetodipus formosus		××	××	××	××	××	××	××	0.45
Chaetodipus penicillatus	××		××				××		0.13
Dipodomys deserti	××						××		0.10
Dipodomys merriami	××	××	××	××	××	××	××	××	0.97
Dipodomys panamintinus		××	××	××		××		××	0.61
Neotoma lepida	××	××	××	××	××	××	××	××	0.97
Onychomys torridus	××	××	××	××	××	××	××	××	0.84
Perognathus longimembris	××	××	××	××			××	××	0.52
Peromyscus crinitus		××			××				0.10
Peromyscus eremicus		××	××	××	××	××		××	0.68
Peromyscus maniculatus	××	××	××	××		××		××	0.71
Peromyscus truei		××		××		××			0.16
Reithrodontomys megalotis				××		××			0.06
Diversity									
γ	7	10	9	10	6	9	7	8	
Mean α	4	7.25	6	7	5.5	6.33	6.5	6.3	
β	3	2.75	3	3	0.5	2.67	0.5	1.7	

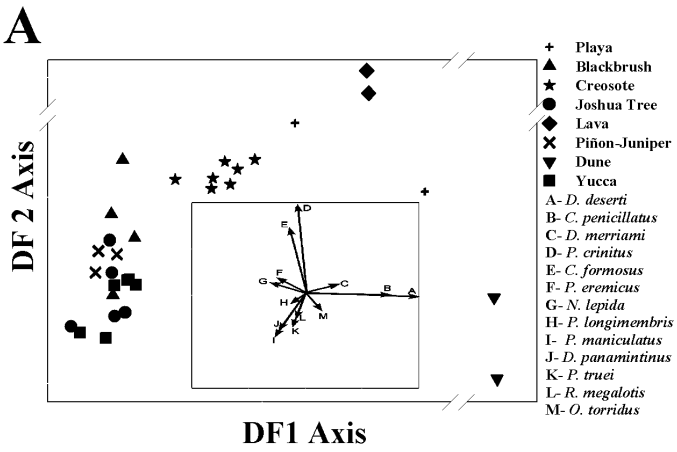
corresponding to their microhabitat preferences (Fig. 3). The 1st group contains only *Peromyscus truei*. This species has the most dissimilar microhabitat preference, and is almost solely found in high-elevation communities, typically characterized by the presence of juniper (*Juniperus*) and rocky soils. The 2nd group contains *Chaetodipus formosus*, *Peromyscus crinitus*, *N. lepida*, and *Peromyscus eremicus* (Fig. 3). *C. formosus* and *P. crinitus* are associated with rocky habitats, and are particularly abundant in lava beds, and in the case of *C. formosus* also in rocky creosote bajadas. *N. lepida* and *P. eremicus* also were very abundant in mid- to low-elevation rocky sites, but they are more general in their habitat use, being present in a large number of communities (Table 1). The 3rd group consists entirely of heteromyid rodents: *Dipodomys deserti*, *Chaetodipus penicillatus*, *Perognathus longimembris*, and *D. merriami*. This group of species generally prefers communities of low elevation and fine to intermediate soil particles. *C. penicillatus* and *D. deserti* share the most similar habitat preferences; they are strongly associated with fine-particle substrates, such as sandy soils of sand dunes, or clayey soils of alkali playas. However, *P. longimembris*, and especially *D. merriami* are usually more generalist species, occurring in a large variety of habitats. The 4th and final group is formed by *Dipodomys panamintinus*, *Peromyscus maniculatus*, and *Onychomys torridus*. These species frequently are found in midelevation communities, associated mostly with yucca woodlands, Joshua tree woodlands, and blackbrush scrub (see also Table 1, Fig. 4, and Appendix I).

Relative abundance of each species of rodent was correlated with at least 4 microhabitat characteristics (Appendix I). *D. merriami* exhibited the greatest number of significant correlations (36). Moreover, its response was different from other species in that it exhibited primarily negative correlations with vegetative characteristics. All other species primarily exhibited positive correlations with vegetative characteristics, although the identity of which perennial species was correlated with which rodent species was quite variable.

Principal component analysis reduced the 81 perennial shrub variables to 6 derived variables that accounted for 83.5% of the variation among communities. Correlations of original plant species with PCs can be used to interpret identity of derived variables (Appendix II; Table 3). All 6 PCs have straightforward interpretations reflecting transitions from one macrohabitat to another. A 2nd PCA reduced 9 soil particle sizes to 1 derived variable that accounted for 77% of the variation among communities. Correlations of original soil variables with this PC indicated that it represented an axis ranging from sandy soils at low values to rocky soils at high values.

Multiple regression indicated numerous significant relationships between microhabitat PCs and rodent relative abundances (Table 4). All species except *P. longimembris* could be significantly related to some form of microhabitat variation. Significant coefficients ranged from 0.20 for *O. torridus* to 0.87 for *D. merriami*. The soil PC significantly loaded into multiple regression models for 7 of 11 species, perennial PCs for 9 of 11 species, annuals for 2 of 11 species, and grasses for 9 of 11 species exhibiting significant relationships. Soil PC1 was the most frequent variable to load 1st, doing so for 5 species.

When all species were analyzed together, microhabitat PCs accounted for approximately 55% of the variation among communities in terms of rodent species composition. Sites with similar macrohabitat affinity tended to be ordered similarly in the multivariate space defined by the RDA (Fig. 4). The soil PC and the 1st perennial PC were the most important microhabitat variables accounting for rodent species composition across our study area (Fig. 4A). *O. torridus*, *P. longimembris*, *P. truei*, and *R. megalotis* exhibited weak relationships with the first 2 derived axes from RDA, whereas all other species exhibited moderate to strong relationships (Fig. 4B).



B

	Playa	Blackbrush	Creosote	Joshua Tree	Lava	Piñon-Juniper	Dune	Yucca
Playa		***	***	***		***	***	***
Blackbrush	***		***		***		***	
Creosote		***		***	***	***	***	***
Joshua Tree	***	***	***		***		***	
Lava	***	***	***	***		***	***	***
Piñon-Juniper	***		***		***		***	
Dune	***	***	***		***	***		***
Yucca	***	***	***		***			

FIG. 2.—Results from discriminant function analysis illustrating differences among macrohabitats based on rodent abundances. A) Communities are arranged according to their positions on discriminant functions axes. Vector plot indicates the contribution of species to differences on each axis (inset, upper figure). B) Matrix indicates significant pairwise differences (asterisk, $P < 0.05$) between macrohabitats based on least significant difference tests conducted on discriminant function scores. Differences along axis 1 are represented in the upper triangle, whereas differences along axis 2 are represented in the lower triangle.

Microhabitat characteristics explained variation in rodent species composition beyond that expected from simple macrohabitat associations. Partial RDA indicated that when shared variation between microhabitat and macrohhabitat variables is controlled, microhabitat still accounts for an additional 17% of the variation in rodent species composition ($P < 0.001$).

DISCUSSION

Our understanding of North American desert rodent community organization comes primarily from studies in the Chihuahuan and Sonoran deserts (Brown and Munger 1985; Heske et al. 1994; Price 1978; Rosenzweig and Winakur 1969) and to a lesser degree from the Great Basin (Parmenter and MacMahon 1983; Patterson and Brown 1991). Within the Mojave, investigators have tended to focus on the structure of communities in single habitat types such as creosote bajadas (Chew and Butterworth 1964; Garland and Bradley 1984), saltbush flats (Kenagy 1973; Kenagy and Bartholomew 1985), Joshua tree woodlands (Price et al. 2000), or sand dunes (Brown 1973). Our study represents a comprehensive examination of comparative community ecology of rodents across multiple habitats in this region. Moreover, this study demonstrates that not only is the inclusion of numerous macrohabitats necessary to more comprehensively characterize rodent community structure in this desert but also that description based on fine-grained microhabitat characteristics significantly contributes to such a characterization.

TABLE 2.—Results from 1-way ANOVA evaluating differences among 8 macrohabitats regarding abundances of 13 species of rodents.

Species	*F*	*P*-value
Chaetodipus formosus	3.861	0.014
Chaetodipus penicillatus	4.310	0.015
Dipodomys deserti	391.963	<0.001
Dipodomys merriami	7.812	<0.001
Dipodomys panamintinus	3.965	0.005
Neotoma lepida	5.166	0.001
Onychomys torridus	2.516	0.041
Perognathus longimembris	0.935	0.484
Peromyscus crinitus	46.48	0.002
Peromyscus eremicus	3.536	0.011
Peromyscus maniculatus	8.910	<0.001
Peromyscus truei	6.176	0.010

Importance of edaphic characteristics.—Soil microprofile characteristics contributed greatly to canonical microhabitat axes important in explaining spatial variation in rodent species composition. Moreover, soil characteristics commonly were important microhabitat features for particular species (11 of 13 taxa). Although the examination of the importance of soil characteristics has been fairly common in studies of rodent community structure conducted outside North America (Corbalan 2006; Krasnov et al. 1996; Rogovin et al. 1994; Scott and Dunstone 2000; Shenbrot 1992; Shenbrot and Rogovin 1995), these characteristics have been only infrequently examined in North American deserts in general and the Mojave Desert in particular (Hardy 1945; Root et al. 2000). That soil micro-

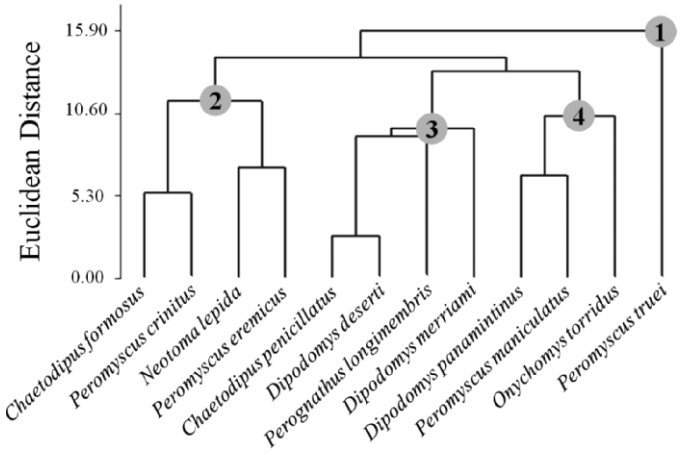


FIG. 3.—Dendrogram produced by cluster analysis based on standardized Pearson correlation coefficients of the abundance of each species with the original environmental variables. Numbers mark the nodes that give origin to the 4 major clusters of species (see text for interpretation).

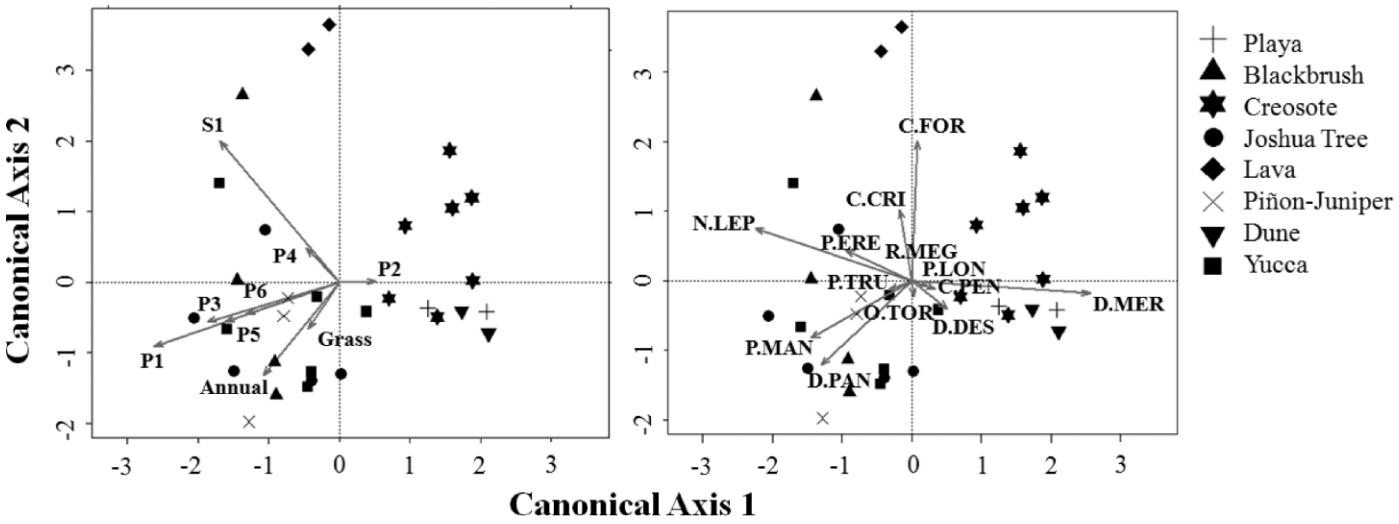


Fig. 4.—Results from redundancy analysis examining the relationship between rodent species composition and microhabitat variables. Symbols represent communities from particular macrohabitats. Arrows represent vectors describing the relationship of A) microhabitat variables and B) rodent species density to relationships defined by the redundancy axes. Microhabitat variables are as follows: P1–P6, 6 perennial principal components (PCs); S1, soil PC; Annual, annual percent cover; Grass, grass percent cover. Rodent vectors are as follow: C.FOR, *Chaetodipus formosus*; C.PEN, *Chaetodipus penicillatus*; D.DES, *Dipodomys deserti*; D.MER, *Dipodomys merriami*; D.PAN, *Dipodomys panamintinus*; N.LEP, *Neotoma lepida*; O.TORR, *Onychomys torridus*; P.LON, *Perognathus longimembris*; P.CRI, *Peromyscus crinitus*; P.ERE, *Peromyscus eremicus*; P.MAN, *Peromyscus maniculatus*; P.TRU, *Peromyscus truei*; R.MEG, *Reithrodontomys megalotis*.

profile affects rodent species composition is logical. Direct effects might include appropriate substrates within which to construct burrows (Luna et al. 2002; Romanach et al. 2005), substrates matching in color so as to enhance evasion of predators (Dice 1939; Krupa and Geluso 2000), and particle size that affects seed foraging efficiency (Wasserberg et al. 2005). Soils also may have indirect effects such as providing the proper substrate for important resource plants thereby enhancing productivity (Huerta-Martinez et al. 2004; Ward et al. 1993) and ultimately seed rain that provides a dietary source for many species. Indeed, edaphic characteristics are significant contributors to rodent community structure in this system and better appreciation of the relative contributions of direct and indirect effects of soil microprofile may greatly add to our mechanistic understanding of spatial variation in the distribution and relative abundance of rodents in North American deserts.

Macrohabitat and microhabitat perspectives.—Interesting species-specific patterns emerged from our analyses. For example, *P. truei* exhibited only minor associations with DFA and RDA axes that summarized important variation in terms of rodent species composition. Nonetheless, this species fell out as the most distinct based on the cluster analysis. This species was restricted to high-elevation sites primarily in piñon–juniper woodlands. In fact, Hoffmeister (1981:4) pointed out that ''no other species of *Peromyscus*, or any other small rodent, is as exclusively confined to the piñon–juniper belt or occurs as abundantly in it as does *P. truei*.'' Although 8 other species occur in this macrohabitat, they tend to do so with relatively low relative abundance and tend not to have strong correlations with microhabitat characteristics found there. Thus, habitat specialization of *P. truei* makes it distinct from others in the Mojave Desert. Moreover, the low proportional representation of the piñon–juniper macrohabitat likely explains weak associations with major axes of variation defined by RDA and DFA.

Dipodomys merriami exhibited a quite distinct response to microhabitat variables. Although this species occurred in approximately 97% of the communities we examined, it was different from all other species in its negative response to habitat variables. All significant correlations with vegetative characteristics except that with *L. tridentata* were negative, reflecting the well-known affinity of this species for open microhabitats (Rosenzweig and Winakur 1969). This is further demonstrated by the extreme position of this species on the 1st RDA axis. Use of more-open microhabitats has been related to foraging economics (Reichman and Oberstein 1977) or a response to minimize risk of predation (Bowers 1988; Kotler 1984; Price et al. 1984) or competitive interactions (Bowers et al. 1987; M'Closkey 1981; Price 1978). Nonetheless, *D. merriami* grouped with a relatively large assemblage of heteromyids in the cluster analysis and was not highly differentiated from others based on the DFA. These contrasting results highlight differences between microhabitat and macrohabitat perspectives.

Significant differences in relative abundances of rodents among macrohabitats demonstrate this important determinant of community organization in the Mojave Desert. Macrohabitat selection occurs when the precise mix and amount of resources required by an organism are related primarily to discontinuities at larger spatial scales. For example, production of seed and mast consumed by granivores can exhibit more variation among macrohabitats than among microhabitats within a macrohabitat. This is even more true as differences in plant species composition and age structure between macrohabitats increase

Table 3.—Results from principal component analysis on 81 perennial plant species. PC refers to a particular principal component, Variance explained refers to the amount of unique variation accounted for by that component, and Cumulative variance refers to the cumulative variation accounted for by a particular PC and all other PCs extracted prior. Gradient represents the interpretation of a particular PC.

PC	Variance explained	Cumulative variance	Gradient
1	33.8	33.8	Creosote to Joshua tree
2	17.6	51.4	Joshua tree/yucca to piñon–juniper
3	11	62.4	Amount of Joshua tree
4	9	71.4	Sage to piñon–juniper
5	7.5	78.8	Saltbush to piñon–juniper
6	4.7	83.5	Yucca to saltbush

(Morris 1987). Macrohabitat variables account for much of the variation embodying density-dependent habitat selection. In many cases macrohabitat associations account for more variation in species relative abundance than quantitative microhabitat variables (Coppeto et al. 2006; Jorgensen and Demarais 1999; Morris 1984, 1987), and in some cases the effect of microhabitat completely disappears once macrohabitat is accounted for (Morris 1984, 1987).

Considerations of macrohabitat distinctions alone can substantively account for spatial variation in rodent species composition. Thus, from a practical perspective, considering only differences among macrohabitats can account for more than the majority of variation in species composition among sites. Although for predictive and mechanistic purposes it is necessary to know the underlying microhabitat characteristics that drive spatial variation in species composition, such highly resolved information may not be necessary to account for major differences in species composition. Alternatively, results from partial RDA demonstrate that microhabitat variables do account for substantive unique variation not shared with macrohabitat distinctions. Indeed, micro- and macrohabitat represent complimentary perspectives that provide insight into variation in rodent species composition in the Mojave Desert.

Spatial and temporal dynamics at the regional scale.—Our results provide a perspective complementary to more typical intensive examinations of single communities, a perspective that can provide valuable insights into the mechanistic bases of community organization. Patterns described here have implications not only to spatial variation in community structure but also the coexistence of species of rodents at regional scales. For example, almost one-half of the species occurred in less than half of the communities. Moreover, the average Spearman rank correlation of pairwise relative abundances was close to 0 ($\bar{X}$ = 0.041, 95% confidence interval = −0.032–0.114, upper and lower extremes = −0.65, 0.79), suggesting that although some relatively strong correlations do exist among species, relative abundances generally are not highly correlated. Idiosyncratic responses of species also are indicated by multivariate analyses. DFA and RDA indicate some concordance among rodent species in terms of microhabitat and macrohabitat preferences. Nonetheless, strong concordance would be indicated if all species had response vectors (arrows) of similar length and direction. In contrast, response vectors are distributed throughout the space defined by these 2 analyses. Species do not appear to co-occur in a strongly coordinated fashion across this study area. Strong positive covariation would suggest concerted responses of species to spatial variation in environmental conditions across the landscape (Houlahan et al. 2007), whereas strong negative covariation can characterize competitive interactions (Stevens and Willig 2000; Tello et al. 2008) or compensatory dynamics (Goheen et al. 2005). Such a weak pattern of co-occurrence suggests a Gleasonian pattern of species distributions characterized by highly individualistic responses of species to the environment, the same type of pattern that has been demonstrated for other North American deserts (Brown and Kurzius 1987) as well as in comparative analyses of deserts around the world (Kelt et al. 1996).

Table 4.—Results of stepwise multiple regression analysis of the relationship between rodent species abundances and soil and perennial principal components (SPC and PPC, respectively), grass, and annual (ANN) variables.

Dependent variable	Independent variable(s)	Coefficient of determination	*P*-value
Chaetodipus formosus	SPC1, PPC1	0.471	<0.001
Chaetodipus penicillatus	SPC1	0.237	0.006
Dipodomys deserti	SPC1	0.319	0.001
Dipodomys merriami	PPC1, SPC1, grass, PPC6	0.867	<0.001
Dipodomys panamintinus	PPC1, PPC3	0.325	0.004
Neotoma lepida	PPC3, SPC1, PPC2	0.637	<0.001
Onychomys torridus	PPC2	0.198	0.012
Perognathus longimembris	No variables selected		
Peromyscus crinitus	SPC1, ANN, grass, PPC6	0.513	0.001
Peromyscus eremicus	SPC1, PPC2, PPC1	0.494	<0.001
Peromyscus maniculatus	PPC1, ANN	0.538	<0.001
Peromyscus truei	PPC1, PPC2, PPC6 PPC5, PPC3	0.767	<0.001

Low α diversity is thought to be the rule for desert rodent communities, at least in North America (Brown and Kurzius 1987—mean species richness of 202 communities = 3.24). Moreover, local communities even when in close proximity are highly variable in terms of species composition because they do not share many species (Brown and Kurzius 1987), a pattern indicative of high β diversity. Most rodent species in the southwestern deserts were demonstrated to occur in <30% of the communities within their geographic range and almost one-half of all species examined occurred at <10 of 202 examined communities (Brown and Kurzius 1987). Similar patterns were not present in this Mojave Desert system. Species richness was relatively high (mean species richness across 31 communities = 6.29), communities shared many species, and β diversity was relatively low. Differences could be for a number of reasons. For example, many previous data have been collected at low-productivity communities not necessarily characteristic of the entire Mojave Desert. Moreover, even intensive, focused studies in the Mojave have been conducted on low-productivity

communities such as creosote bajadas or dunes (Brown 1973, 1975; Brown and Kurzius 1987; Hafner 1977); only the work of Price et al. (2000) has included higher-productivity habitats such as Joshua tree woodlands and reported a total of 10 species. Another possibility is the greater sampling effort employed here. Each community in our study was characterized using 606 trap-nights of effort. Other studies have typically used less effort and this may have made estimates of α diversity conservative. Lastly, these data were collected following a year of above-average precipitation in the Mojave Desert. Thus, an overall increase in α diversity and resultant decrease in β diversity could be the result of responses to a regional increase in productivity. Nonetheless, such a simple causal link has been questioned, at least in other North American deserts (Brown and Ernest 2002).

As exemplified by patterns of α and β diversity across our study area, the Mojave Desert is a dynamic biotic mosaic. This complexity manifests in other characteristics as well. For example, the Mojave Desert is highly heterogeneous in terms of climate. Temperature and the amount of winter snow vary regularly from north to south and the rain shadow effect creates large differences in precipitation from west to east (Ruffner 1978). Our study area occurs in the central Mojave and is characterized by relatively high precipitation and some of the greatest standing plant biomass in the desert (McAuliffe and McDonald 1995). Climate is temporally heterogeneous and unpredictable as well (Davidowitz 2002). Such variability creates conditions of ''feast and famine'' in terms of resources available to desert rodents (Polis 1991) that ultimately affects distribution. Based on overlapping species range maps obtained from Patterson et al. (2005), with the Mojave ecoregion defined by Olson et al. (2001), it becomes apparent that most rodent species occurring in the Mojave are not endemic. In fact, representative species occur in other ecoregions and tend to have large geographic distributions that do not overlap the entire Mojave Desert but terminate there (53 of 58 or 91%). Because most species are at the edge of their geographic distribution in the Mojave Desert, such fluctuations in productivity likely correspond to dramatic fluctuations in the distribution of desert rodents in this system. Indeed, this study represents a single point estimate in time and species–habitat relationships are likely to fluctuate as plant species richness and individual plant biomass fluctuates across macrohabitats and within microhabitats in response to variable precipitation. Dispersal-mediated changes in species composition in response to fluctuations in productivity may drive spatial and temporal patterns of community structure. Such spatial and temporal complexity suggests that large landscape-scale studies in general and the bourgeoning metacommunity concept (Holyoak et al. 2005; Leibold and Miller 2004; Leibold et al. 2004) in particular may add greatly to our understanding of desert rodent community ecology, especially in the Mojave Desert.

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APPENDIX I

Significant relationships among environmental variables (plants and soil particle size) and rodent species abundances. Pearson product-moment correlation coefficients describe degree of association between a particular rodent species' relative abundance and microhabitat characteristics (2 right columns). Stepwise multiple regression is based on microhabitat variables that were significantly correlated with rodent relative abundances (middle 3 columns). Variables in bold accounted for a significant amount of unique variation in a particular principal component (PC) and loaded into the stepwise multiple regression.

	Regression			Pearson correlation	
Species/environmental variable	Adjusted R^2	*P*-value	Standardized β	*r*	*P*-value
Chaetodipus formosus	0.671	<0.001			
Eriogonum inflatum			**0.559**	**0.710**	**<0.001**
Ambrosia dumosa			**0.354**	**0.434**	**0.015**
6.3–12.5 mm			**0.290**	**0.528**	**0.002**
50–120 mm				0.653	<0.001
25–50 mm				0.646	<0.001
12.5–25 mm				0.588	<0.001
<1.4 mm				−0.496	0.005
Atriplex hymenelytra				0.460	0.009
Encelia farinosa				0.460	0.009
Opuntia basilaris				0.407	0.023
Ericameria cooperi				−0.395	0.028
Ephedra cf. *trifurca*				0.391	0.030
Chaetodipus penicillatus	0.639	<0.001			
Argemone munita			**0.605**	**0.745**	**0.000**
1.4–3.18 mm			**−0.357**	**−0.594**	**0.000**
Machaeranthera canescens				0.625	0.000
3.18–4.75 mm				−0.547	0.001
<1.4 mm				0.532	0.002
Stephanomeria				0.509	0.003
4.75–6.3 mm				−0.441	0.013
Dipodomys deserti	0.988	<0.001			
Petalonyx thurberi			**−0.404**	**0.678**	**<0.001**
Machaeranthera canescens			**1.235**	**0.964**	**<0.001**
1.4–3.18 mm			**−0.057**	**−0.596**	**<0.001**
<1.4 mm			**0.064**	**0.610**	**<0.001**
Stephanomeria				0.733	<0.001
Argemone munita				0.701	<0.001
3.18–4.75 mm				−0.546	0.001
4.75–6.3 mm				−0.492	0.005
6.3–12.5 mm				−0.433	0.015
Dipodomys merriami	0.754	<0.001			
<1.4 mm			**0.451**	**0.593**	**<0.001**
Larrea tridentata			**0.537**	**0.697**	**<0.001**
Opuntia acanthocarpa			**−0.228**	**−0.603**	**<0.001**
Ephedra nevadensis				−0.619	<0.001
Echinocereus engelmannii				−0.651	<0.001
Eriogonum fasciculatum				−0.654	<0.001
Ericameria linearifolia				−0.572	0.001
Opuntia erinacea				−0.555	0.001
Prunus fasciculate				−0.533	0.002
Ambrosia dumosa				0.532	0.002
4.75–6.3 mm				−0.531	0.002
Menodora spinescens				−0.527	0.002
Yucca baccata				−0.525	0.002
Gutierrezia microcephala				−0.520	0.003
Opuntia chlorotica				−0.508	0.004
Yucca brevifolia				−0.506	0.004
Salvia dorrii				−0.493	0.005
6.3–12.5 mm				−0.490	0.005
3.18–4.75 mm				−0.482	0.006
Opuntia phaeacantha				−0.454	0.010
Thamnosma montana				−0.438	0.014
Juniperus osteosperma				−0.437	0.014
Purshia tridentata				−0.433	0.015

APPENDIX I.—Continued.

Species/environmental variable	Regression			Pearson correlation	
	Adjusted R^2	*P*-value	Standardized β	*r*	*P*-value
Opuntia basilaris				−0.408	0.023
Fallugia paradoxa				−0.401	0.025
Pinus monophylla				−0.400	0.026
Salazaria mexicana				−0.390	0.030
>120 mm				−0.386	0.032
50–120 mm				−0.378	0.036
Verbena gooddingii				−0.377	0.037
Rhus trilobata				−0.377	0.037
Artemisia ludoviciana				−0.377	0.037
Pellaea mucronata				−0.377	0.037
Quercus turbinella				−0.377	0.037
Baccharis sergiloides				−0.374	0.038
Coleogyne ramosissima				−0.372	0.039
Dipodomys panamintinus	0.745	<0.001			
Chaetopappa ericoides			**0.494**	**0.396**	**0.027**
Tetradymia stenolepis			**0.408**	**0.537**	**0.002**
Ephedra nevadensis			**0.392**	**0.580**	**0.001**
Hymenoclea salsola			**0.260**	**0.527**	**0.002**
Ericameria cooperi				0.568	0.001
1.4–3.18 mm				0.538	0.002
Larrea tridentata				−0.468	0.008
Eriogonum fasciculatum				0.442	0.013
25–50 mm				−0.399	0.026
Artemisia tridentata				0.396	0.027
Thamnosma montana				0.375	0.037
Ambrosia dumosa				−0.374	0.038
Neotoma lepida	0.723	0.001			
Opuntia basilaris			**0.414**	**0.530**	**0.002**
Physalis hederifolia			**0.319**	**0.380**	**0.035**
Salazaria mexicana			**0.349**	**0.647**	**0.000**
Ephedra nevadensis			**0.305**	**0.633**	**0.000**
Opuntia acanthocarpa				0.588	0.001
Yucca brevifolia				0.553	0.001
3.18–4.75 mm				0.535	0.002
Yucca shidigera				0.509	0.003
4.75–6.3 mm				0.453	0.011
Lycium andersonii				0.450	0.011
Echinocereus engelmannii				0.444	0.012
<1.4 mm				−0.433	0.015
Menodora spinescens				0.428	0.016
Ericameria cooperi				0.426	0.017
1.4–3.18 mm				0.424	0.018
Encelia virginensis				0.413	0.021
Opuntia echinocarpa				0.374	0.038
Ferocactus cylindraceus				0.368	0.042
Onychomys torridus	0.499	<0.001			
Krascheninnikovia lanata			**0.538**	**0.504**	**0.004**
Tetradymia stenolepis			**0.400**	**0.365**	**0.043**
Purshia tridentata			**−0.320**	**−0.410**	**0.022**
Adenophyllum cooperi				0.453	0.011
>120 mm				−0.404	0.024
Senecio flaccidus				0.400	0.026
12.5–25 mm				−0.383	0.033
25–50 mm				−0.381	0.034
Opuntia chlorotica				−0.378	0.036
Perognathus longimembris	0.399	0.001			
Mirabilis multiflora			**0.419**	**0.398**	**0.026**
Datura wrightii			**0.388**	**0.421**	**0.018**
Eriogonum fasciculatum			**−0.338**	**−0.382**	**0.034**
Unknown sp. 2				0.398	0.026

APPENDIX I.—Continued.

Species/environmental variable	Regression			Pearson correlation	
	Adjusted R^2	*P*-value	Standardized β	*r*	*P*-value
Peromyscus crinitus	0.968	<0.001			
Atriplex confertifolia			**−4.289**	**0.591**	**<0.001**
Ephedra* cf. *trifurca			**4.749**	**0.685**	**<0.001**
Sphaeralcea ambigua			**0.142**	**0.481**	**<0.001**
Eriogonum inflatum			**0.126**	**0.764**	**<0.001**
Opuntia basilaris			**0.124**	**0.730**	**<0.001**
Atriplex hymenelytra				0.741	<0.001
Encelia farinosa				0.741	<0.001
>120 mm				0.660	<0.001
50−120 mm				0.622	<0.001
Psorothamnus fremontii				0.591	<0.001
25−50 mm				0.441	0.013
12.5−25 mm				0.422	0.018
<1.4 mm				−0.389	0.031
1.4−3.18 mm				−0.356	0.049
Peromyscus eremicus	0.625	<0.001			
Hymenoclea salsola			**0.408**	**0.379**	**0.035**
Eriogonum inflatum			**0.397**	**0.529**	**0.002**
Menodora scoparia			**0.313**	**0.459**	**0.009**
Opuntia basilaris			**0.260**	**0.559**	**0.001**
Yucca brevifolia				0.546	0.001
Menodora spinescens				0.526	0.002
Encelia virginensis				0.510	0.003
Ferocactus cylindraceus				0.488	0.005
Salvia mohavensis				0.459	0.009
Unknown sp. 3				0.459	0.009
Unknown sp. 4				0.459	0.009
Mirabilis pumila				0.459	0.009
Viguiera parishii				0.455	0.010
Lotus rigidus				0.454	0.010
<1.4 mm				−0.443	0.013
Yucca baccata				0.439	0.013
Sphaeralcea ambigua				0.437	0.014
Lycium andersonii				0.428	0.016
Ephedra nevadensis				0.419	0.019
Gutierrezia microcephala				0.416	0.020
Baileya multiradiata				0.412	0.021
Opuntia acanthocarpa				0.410	0.022
Salazaria mexicana				0.383	0.033
Echinocereus triglochidiatus				0.380	0.035
12.5−25 mm				0.362	0.045
Peromyscus maniculatus	0.745	<0.001			
Ephedra nevadensis			**0.544**	**0.727**	**<0.001**
Adenophyllum cooperi			**0.319**	**0.480**	**0.006**
Mean annuals			**0.254**	**0.479**	**0.006**
Eriogonum fasciculatum			**0.222**	**0.490**	**0.005**
3.18−4.75 mm				0.588	0.001
Larrea tridentata				−0.566	0.001
Yucca brevifolia				0.543	0.002
Salazaria mexicana				0.542	0.002
Ambrosia dumosa				−0.541	0.002
1.4−3.18 mm				0.526	0.002
Hymenoclea salsola				0.520	0.003
Gutierrezia microcephala				0.515	0.003
Ericameria cooperi				0.461	0.009
Thamnosma montana				0.451	0.011
4.75−6.3 mm				0.447	0.012
Yucca baccata				0.442	0.013
Unknown sp. 2				0.402	0.025
Mirabilis multiflora				0.402	0.025
Opuntia acanthocarpa				0.385	0.032

APPENDIX I.—Continued.

Species/environmental variable	Regression			Pearson correlation	
	Adjusted R^2	*P*-value	Standardized β	*r*	*P*-value
Lycium andersonii				0.373	0.039
Coleogyne ramosissima				0.371	0.040
Senecio flaccidus				0.356	0.049
Peromyscus truei	0.899	<0.001			
Salvia dorrii			**0.626**	**0.886**	**<0.001**
Echinocereus engelmannii			**0.218**	**0.430**	**0.016**
Juniperus osteosperma			**0.234**	**0.736**	**0.000**
Opuntia phaeacantha			**0.170**	**0.541**	**0.002**
Purshia tridentata				0.824	0.000
Opuntia erinacea				0.745	0.000
Ephedra viridis				0.665	0.000
Ericameria linearifolia				0.659	0.000
Fallugia paradoxa				0.637	0.000
Yucca baccata				0.620	0.000
Opuntia chlorotica				0.592	0.000
Pinus monophylla				0.562	0.001
Gutierrezia microcephala				0.553	0.001
Quercus turbinella				0.552	0.001
Artemisia ludoviciana				0.552	0.001
Verbena gooddingii				0.552	0.001
Rhus trilobata				0.552	0.001
Pellaea mucronata				0.552	0.001
>120 mm				0.500	0.004
Prunus fasciculata				0.483	0.006
<1.4 mm				−0.466	0.008
Eriogonum fasciculatum				0.443	0.013
Menodora spinescens				0.442	0.013
Larrea tridentata				−0.385	0.032
Atriplex canescens				0.377	0.036
Reithrodontomys megalotis	1.000				
Opuntia phaeacantha			**0.907**	**0.357**	**0.049**
Chaetopappa ericoides			**0.453**	**0.891**	**<0.001**
Artemisia tridentata				0.891	<0.001
Juniperus osteosperma				0.570	0.001
Unknown sp. 1				0.428	0.016
Escobaria vivipara				0.423	0.018
Opuntia erinacea				0.408	0.023
Eriogonum fasciculatum				0.386	0.032
Echinocereus triglochidiatus				0.362	0.046

Appendix II

Relationships of perennial plant species to perennial principal components (PCs). Species listed for each PC were significantly correlated with that axis. Species in bold accounted for a significant amount of unique variation in a particular PC and loaded into the stepwise multiple regression.

	Regression			Pearson correlation	
Perennial PC/plant species	Adjusted R^2	*P*-value	Standardized β	*r*	*P*-value
Perennial PC1	0.995	<0.001			
Larrea tridentata			**−0.629**	**−0.880**	**<0.001**
Salvia dorrii			**0.099**	**0.600**	**<0.001**
Ephedra nevadensis			**0.238**	**0.768**	**<0.001**
Ericameria linearifolia			**0.101**	**0.665**	**<0.001**
Yucca baccata			**0.232**	**0.828**	**<0.001**
Prunus fasciculata			**0.143**	**0.421**	**0.018**
Ambrosia dumosa			**−0.094**	**−0.756**	**<0.001**
Thamnosma montana			**0.055**	**0.450**	**0.001**
Opuntia acanthocarpa			**0.048**	**0.607**	**<0.001**
Coleogyne ramosissima				0.570	0.001
Echinocereus engelmannii				0.582	0.001
Echinocereus triglochidiatus				0.430	0.016
Eriogonum fasciculatum				0.558	0.001
Gutierrezia microcephala				0.741	<0.001
Juniperus osteosperma				0.484	0.006
Menodora spinescens				0.596	<0.001
Opuntia chlorotica				0.461	0.009
Opuntia erinacea				0.554	0.001
Purshia tridentata				0.461	0.009
Yucca brevifolia				0.659	<0.001
Perennial PC2	0.954	<0.001			
Fallugia paradoxa			**0.856**	**0.851**	**<0.001**
Hymenoclea salsola			**−0.167**	**−0.396**	**0.027**
Yucca shidigera			**−0.200**	**−0.388**	**0.031**
Juniperus osteosperma			**0.500**	**0.598**	**<0.001**
Salvia dorrii			**−0.324**	**0.407**	**0.023**
Ericameria linearifolia			**−0.182**	**0.464**	**0.008**
Artemisia ludoviciana				0.840	<0.001
Baccharis sergiloides				0.557	0.001
Eriogonum fasciculatum				0.402	0.025
Opuntia chlorotica				0.481	0.006
Opuntia erinacea				0.740	<0.001
Opuntia phaeacantha				0.806	<0.001
Pellaea mucronata				0.840	<0.001
Pinus monophylla				0.842	<0.001
Prunus fasciculata				0.744	<0.001
Purshia tridentata				0.791	<0.001
Quercus turbinella				0.840	<0.001
Rhus trilobata				0.840	<0.001
Verbena gooddingii				0.840	<0.001
Perennial PC3	0.910	<0.001			
Ericameria cooperi			**0.407**	**0.804**	**<0.001**
Salazaria mexicana			**0.311**	**0.754**	**<0.001**
Yucca shidigera			**0.343**	**0.700**	**<0.001**
Eriogonum fasciculatum			**0.210**	**0.512**	**0.003**
Acacia greggii				0.380	0.035
Hymenoclea salsola				0.480	0.006
Krameria spp.				0.456	0.010
Opuntia acanthocarpa				0.567	0.001
Opuntia parishii				0.487	0.005
Unknown sp. 5				0.487	0.005
Tetradymia stenolepis				0.663	<0.001
Yucca brevifolia				0.406	0.023
Perennial PC4	0.835	<0.001			
Artemisia tridentata			**−0.688**	**−0.521**	**0.003**
Prunus fasciculata			**0.557**	**0.501**	**0.004**

APPENDIX II.—Continued.

Perennial PC/plant species	Regression			Pearson correlation	
	Adjusted R^2	*P*-value	Standardized β	*r*	*P*-value
Echinocereus triglochidiatus			**−0.262**	**−0.358**	**0.048**
Eriogonum fasciculatum			**0.248**	**0.417**	**0.020**
Artemisia ludoviciana				0.686	<0.001
Baccharis sergiloides				0.487	0.005
Chaetopappa ericoides[a]				−0.521	0.003
Fallugia paradoxa				0.664	<0.001
Opuntia chlorotica				0.645	<0.001
Opuntia phaeacantha				0.481	0.006
Pellaea mucronata				0.686	<0.001
Pinus monophylla				0.680	<0.001
Purshia tridentata				0.527	0.002
Quercus turbinella				0.686	<0.001
Verbena gooddingii				0.686	<0.001
Rhus trilobata				0.686	<0.001
Perennial PC5	0.920	<0.001			
Juniperus osteosperma			**0.622**	**0.620**	**<0.001**
Yucca shidigera			**0.395**	**0.418**	**0.019**
Atriplex polycarpa			**−0.314**	**−0.502**	**0.004**
Thamnosma montana			**0.218**	**0.604**	**<0.001**
Acacia greggii			**0.195**	**0.413**	**0.021**
Artemisia tridentata				0.466	0.008
Chaetopappa ericoides				0.466	0.008
Datura wrightii				−0.360	0.047
Ephedra nevadensis				0.367	0.042
Ephedra viridis				0.427	0.017
Ericameria linearifolia				0.586	0.001
Eriogonum fasciculatum				0.421	0.018
Opuntia acanthocarpa				0.519	0.003
Opuntia echinocarpa				0.393	0.029
Opuntia erinacea				0.364	0.044
Salvia dorrii				0.388	0.031
Perennial PC6	0.807	<0.001			
Yucca brevifolia			**0.730**	**0.812**	**<0.001**
Atriplex canescens			**0.301**	**0.410**	**0.022**
Atriplex polycarpa			**−0.230**	**−0.394**	**0.028**
Echinocereus triglochidiatus				0.521	0.003
Ephedra nevadensis				0.562	0.001
Ephedra viridis				0.516	0.003
Gutierrezia microcephala				0.671	<0.001
Hymenoclea salsola				0.473	0.007
Lycium andersonii				0.573	0.001
Lycium cooperi				0.475	0.007
Menodora spinescens				0.633	<0.001
Mirabilis multiflora				0.407	0.023
Salazaria mexicana				0.368	0.041
Salvia dorrii				0.613	<0.001
Unknown sp. 2				0.407	0.023
Yucca baccata				0.635	<0.001

[a] Variable not considered because of high multicolinearity.