HABITAT SELECTION AND COEXISTENCE OF SPECIES OF KANGAROO MICE (*MICRODIPODOPS*)

John C. Hafner, David J. Hafner, and *Mark S. Hafner*

ABSTRACT.— Microhabitat use by sympatric populations of kangaroo mice, *Microdipodops megacephalus* and *M. pallidus*, is assessed at two ecologically dissimilar sites (Penoyer Valley and Sandy Summit) in south-central Nevada. Penoyer Valley exhibits a fine-grain mixture of vegetation and soil types, whereas Sandy Summit is edaphically uniform with a distinctly course-grained (patchy) mixture of plant species. Capture data (from a trapping program involving a combined total of 6,183 trapnights) are evaluated to determine preference for microhabitat by the two species of *Microdipodops* at the two sites. Despite edaphic and floristic differences between the two sites, overall *Microdipodops* density (approximately 5 percent trap success) and proportionate species contribution (about 40 percent *M. megacephalus*; 60 percent *M. pallidus*) are nearly equivalent at the two localities. At Penoyer Valley, these sand-dune specialists seem to be coexisting by selecting different microhabitats based on attributes of both the soil and vegetation; significant differences are found in vegetation height and soil texture when capture stations of *M. pallidus* and *M. megacephalus* are compared. At Sandy Summit, the two species occur in different floral microhabitats; goodness-of-fit tests show significant habitat selection by both *M. megacephalus* (favoring *Artemisia*-dominated microhabitats) and by *M. pallidus* (favoring *Chrysothamnus*-dominated microhabitats).

Key words: habitat selection, *Microdipodops*, coexistence, desert rodents

One of the principle aims of community ecology is to identify the factors that may be responsible for determining the number of coexisting species. In this regard, studies of seed-eating desert rodents in North America have played an especially important role in advancing our understanding of mechanisms that promote species coexistence (for review see Brown, 1975; Brown et al., 1979; Kotler and Brown, 1988; Price and Brown, 1983; Rosenzweig et al., 1975). After several decades of intense study of desert rodent communities, several generalizations may be made: 1) these coexisting species appear to be competitors (Brown and Munger, 1985; Lemen and Freeman, 1983; Munger and Brown, 1981); 2) seed availability and plant productivity may be the important limiting resources that drive competitive interactions and, hence, determine community structure (Brown, 1973, 1975; Hafner, 1977; Reichman, 1979, 1984); 3) coexisting species show differential habitat affinities and, as a consequence, species diversity is directly related to habitat complexity (Rosenzweig and Winakur, 1969; M'Closkey, 1978); 4) coexisting species differ in morphology (Bowers and Brown, 1982; Brown, 1973, 1975; Brown et al., 1979); and, 5) historical biogeographical factors may influence the structure of desert-rodent communities (Brown, 1973, 1975; Brown et al., 1979).

Granivorous rodent communities in North American deserts are overwhelmingly dominated by species of the family Heteromyidae. Although four genera of heteromyid rodents occur in the arid regions of the North American deserts, virtually all studies of species coexistence have focused on granivore guilds involving species of only three genera: kangaroo rats, *Dipodomys*, and pocket mice, *Chaetodipus* and *Perognathus*. Unfortunately, kangaroo mice, *Microdipodops*, have not received a commensurate degree of attention by community ecologists: only one study has examined coexistence of species of kangaroo mice (Ghiselin, 1970). Kangaroo mice probably have not received much attention from heteromyid rodent ecologists because, unlike the other three genera, *Microdipodops* is restricted in distribution (the Great Basin Desert), is depauperate in species number (only two extant species), and its species rarely coexist.

The dearth of information pertaining to the ecology of kangaroo mice has led to some popular misconceptions about their biology. Both species of kangaroo mice are portrayed commonly as "small, bipedal rodents" that favor open microhabitats (e.g., Kotler, 1985; Longland and Price, 1991; Pierce et al., 1992; Price and Brown,

Pp. 249 - 259, Contributions in Mammalogy: A Memorial Volume Honoring Dr. J. Knox Jones, Jr.
Museum of Texas Tech University, 1996, il + 315 pp.

1983). Indeed, kangaroo mice are often treated by heteromyid ecologists as simply down-sized versions of kangaroo rats. As pointed out elsewhere (Hafner and Hafner, 1983, 1988; Hafner, 1993), kangaroo mice differ markedly from kangaroo rats in their morphology, physiology, behavior, and evolutionary history. For example, kangaroo mice rely on the quadrupedal ricochet as their predominant mode of locomotion and not a bipedal gait (Eisenberg, 1963; Hafner, 1993), yet it is common to pigeon-hole kangaroo mice with kangaroo rats as bipedal rodents when examining microhabitat use, predation risk, and coexistence (e.g., Kotler, 1985; Longland and Price, 1991). Also, when kangaroo mice are included in ecological studies, a single species of *Microdipodops* is selected as a generic representative (small, "bipedal" granivore that prefers open areas), despite the paucity of comparative data on the ecology of the species of kangaroo mice. Are the two species of *Microdipodops* essentially identical in ecology?

The two species of kangaroo mice, *M. megacephalus* and *M. pallidus*, are distributed largely in a parapatric fashion with a narrow zone of sympatry (Fig. 1). This distributional pattern may be explained by a combination of historical biogeographical events and present-day ecological requirements of the species; unfortunately, little information is available to evaluate the merits of either explanation. It is clear, however, that *M. megacephalus* is found generally in the upper portions of the Upper Sonoran Life Zone and *M. pallidus* is distributed mainly in the lower portion of the Upper Sonoran Life Zone (Hafner, 1981). Moreover, the species have a shared affinity for sandy soils (Hall and Linsdale, 1929; Hall, 1941; Ghiselin, 1970; Hafner, 1981), and they are very similar morphologically (i.e., they are sibling species; Hafner et al., 1979). Given the available information pertaining to the distribution and ecology of kangaroo mice, it is not surprising that the two species are rarely found in sympatry. Indeed, the principle of limiting similarity (MacArthur and Levins, 1964) and the observed association between morphology and microhabitat affinity in heteromyid rodents in general (Longland and Price, 1991; Price and Brown, 1983) suggest that the species of kangaroo mice should be extremely close competitors where they coexist.

Herein we report on a study designed to investigate the ecology of coexisting species of kangaroo mice. Ecological interactions of kangaroo mice are examined at two areas of sympatry in south-central Nevada. The sites were selected because of their contrasting environmental settings. Our principal goal is to determine whether or not these sibling species show differential microhabitat affinity in sympatry.

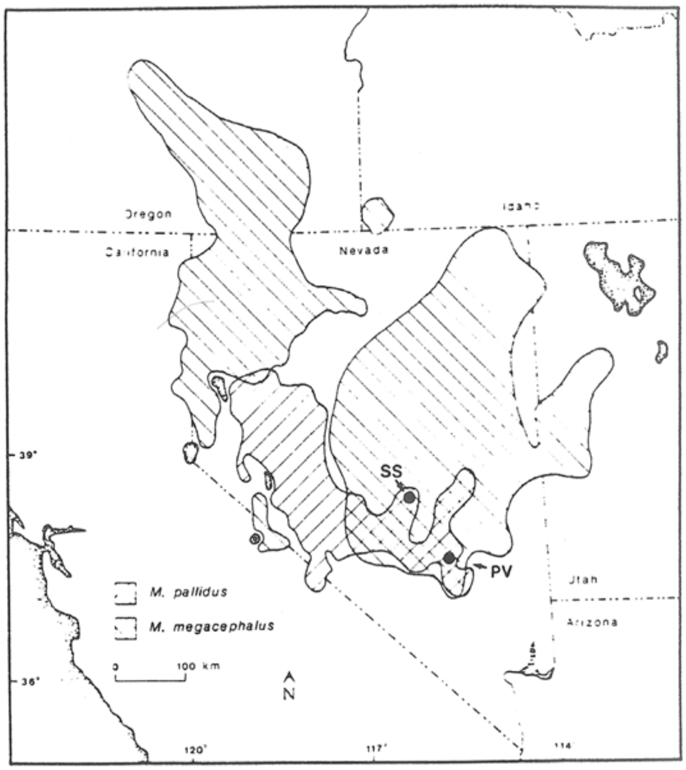

Fig. 1. Distribution of *Microdipodops* species in the Great Basin. Study sites of Sandy Summit (SS) and Penoyer Valley (PV) are indicated.

METHODS

The present study was initiated in 1975 while we collected data for a parallel study that focused on the genetic interactions of the two species in sympatry (Hafner et al., 1979). Ecological data bearing on this study were collected in 1975 and periodically through 1991. Over the duration of the study we observed no gross changes in the environmental conditions (e.g., vegetation density, amount bare ground, disturbance) at the study sites.

The study areas.—The two sites with sympatric populations of *M. megacephalus* and *M. pallidus* were identified during field work in Nevada during the spring of 1975 and chosen for study: Penoyer Valley (= Sand Spring Valley, 9.7 km N, 49.9 km W [= 6 mi N, 31 mi W] Hiko, 1,464 m [= 4,800 ft], Lincoln Co.) and Sandy Summit (30.9 km N, 21.6 km E [= 19.2 mi N, 13.4 mi E] Warm Springs, 1,830 m [= 6,000 ft], Nye Co.). These sites represent environmental extremes of *Microdipodops* habitat: the lower elevational, valley-floor site of Penoyer Valley is more typical of *M. pallidus* habitat and the higher elevational site at Sandy Summit is more typical of *M. megacephalus* habitat. Cursory examination of the sites reveals differences in plant species composition, soil characteristics, and overall patchiness of the environment. Penoyer Valley figured prominently in Hall's (1941) systematic study of *Microdipodops* and Ghiselin's (1970) study of coexistence of the two species. Our study demonstrating that *M. megacephalus* and *M. pallidus* are full biological species (Hafner et al., 1979) was also conducted at Penoyer Valley. To our knowledge, the Sandy Summit locality of sympatry was not known prior to our field reconnaissance in 1975.

Kangaroo mouse trapping.—We used a series of trap lines to census the relative abundance and distribution of kangaroo mice at each of the study localities. A typical trap line comprised 100 traps set at 50 trap stations (two traps per station) and distributed in a linear array; trap stations were set 7 m (eight paces) apart and 5-6 m separated each pair of traps at a station. Detailed notes pertaining to distance measurements (from fixed positions) and compass orientation were taken on the placement of trap lines so as to ensure consistent deployment of trap lines throughout the duration of the study. Kangaroo mice were trapped with either Sherman live traps or snap traps. Trap types were not mixed within a single trap line and we noted no differences between success of the two trap types. The capture position (line number and station number) was recorded for each *Microdipodops* captured.

Nearest-neighbor analysis.—Distances between capture sites within each trap line were recorded for nearest capture of a conspecific and nearest capture of the alternate species. These nearest-neighbor distances provide a relative measure of dispersion for each species at each site and between sites, and between species at both sites. If the species are dispersed randomly relative to one another, then there should be no difference between intra- and interspecific nearest-neighbor distances. But, if interspecific distances are greater than intraspecific distances, conspecifics would be expected to co-occur, in a clumped, nonrandom pattern. Conversely, a hyperdispersed distribution would be expected if intraspecific distances are greater than interspecific distances.

Soil and vegetation analyses.—Soil and plant data were recorded at trap stations. Different methods were used to appraise microhabitat heterogeneity at the two sites because of their dissimilar environments. Plant species identity was noted at each capture point at Sandy Summit because of obvious floral heterogeneity at this site, but these data were not taken at Penoyer Valley because there was a fine, consistent admixture of the same plant species throughout this site. Conversely, soil texture data were collected routinely at each capture point at Penoyer Valley because of obvious edaphic heterogeneity, but not at Sandy Summit, where the soil was judged to be generally uniform across the study site.

At Penoyer Valley, three microhabitat variables were recorded at each trap site that yielded a kangaroo mouse. These parameters included vegetation height (average height [cm] of perennial shrubs), vegetation spacing (average distance [m] between shrubs), and soil texture index (soil scores of 0-4 as follows: 0 = fine, loose, deep, sand-dune like soil devoid of gravel; 1 = more firm, but still deep, fine sandy soil with only rare bits of gravel overlay; 2 = fine, moderately loose, sandy soil with an uneven overlay of generally small-sized gravel; 3 = fine, but relatively firm, sandy soil with uniform overlay of gravel of varying sizes; and 4 = conspicuous cover of gravel over firm-packed, fine sandy soil).

Vegetation transect scores were recorded at every trap station on all of the trap lines at both Penoyer Valley and Sandy Summit. Relative dominance of the five major plant species, *Artemisia* (sagebrush), *Chrysothamnus* (rabbit-brush), *Tetradymia*, *Atriplex* (saltbush), and *Hilaria* (galleta), was recorded using a relative dominance scale (plant dominance scores of 0-4 as follows: 0 = absent; 1 = rare; 2 = secondary; 3 = codominant; and 4 = dominant). Vegetation transect scores from trap stations were used to describe the floral environments at both sites (see principal components analysis below) and to evaluate microhabitat affinity of *Microdipodops* species at Sandy Summit only; due to the monotonous nature of the vegetation transect scores across trap stations at Penoyer Valley, vegetation transect scores from actual capture points of *Microdipodops* at Penoyer Valley were not examined.

Statistical analyses.—Conventional, descriptive statistics and univariate statistics of inference (e.g., analysis of variance, Student's *t*-test) were employed in this study for characters known to be distributed normally. Characters that were not distributed normally were either log-transformed prior to hypothesis testing (i.e., nearest-neighbor distance) or we opted instead for nonparametric testing procedures (i.e., soil texture was compared by use of the Mann-Whitney *U*-test). The *G*-test of goodness of fit (Sokal and Rohlf, 1981) and the traditional chi-square test were used in the analysis of

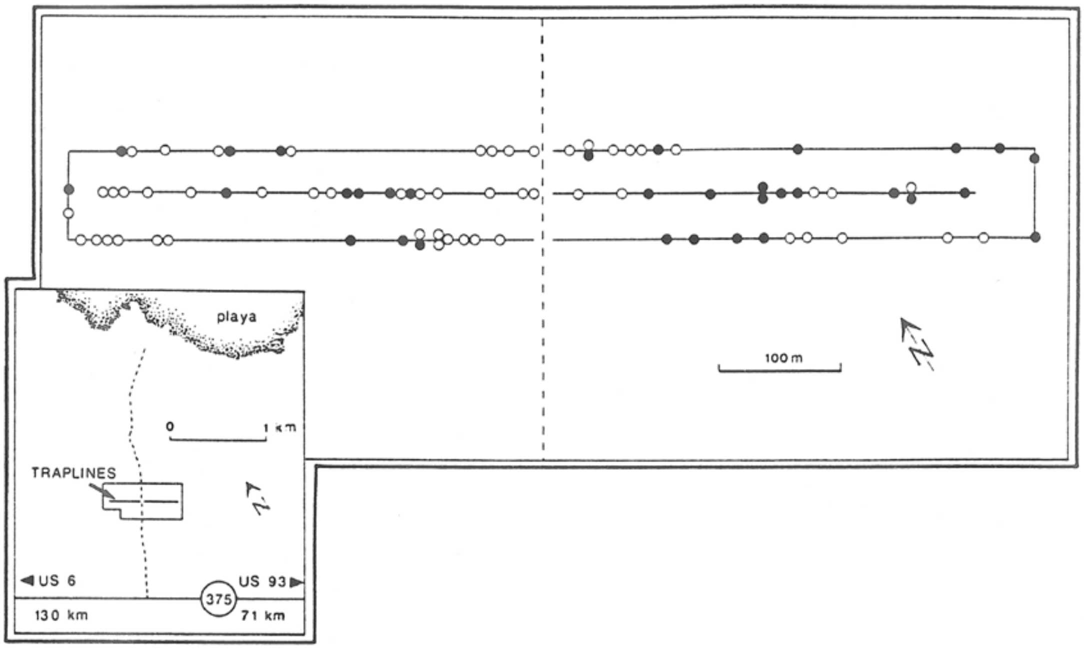

Fig. 2. Penoyer Valley study site, indicating location of trap lines and captures of *M. pallidus* (open circles) and *M. megacephalus* (closed circles).

frequencies. Lastly, the vegetation transect scores were subjected to a principal components analysis (PCA), in combination with kernel density smoothing (Silverman, 1986), to summarize floral microhabitat variability with reduced dimensionality. All statistical analyses except for the goodness-of-fit tests were performed on personal computers with the aid of SYSTAT statistical software (Wilkinson, 1988, 1990).

RESULTS

Penoyer Valley

The Penoyer Valley study site lies immediately south of a large playa, now a dry, alkali-sink lake bed. Vegetation surrounding the playa follows a smooth gradient from large, well-spaced shrubs of *Sarcobatus* (greasewood) in the dunes at the sink edge, towards *Atriplex-Tetradymia* dominated associations away from the sink. Our preliminary trapping located the site of sympatry of *M. megacephalus* and *M. pallidus* in the *Atriplex-Tetradymia* dominated association 1.8 km south of the edge of the playa (= 1.0 km north Nevada Highway 375 [= Highway 25 on older maps]; Fig. 2). Initial trapping around the edge of the playa (in the *Sarcobatus*-dominated dune system) produced only *M. pallidus*.

Floral and edaphic characteristics.—Vegetation in the area of sympatry is a homogeneous mixture of plant species, with *Atriplex* and *Tetradymia* sharing dominance at virtually all trap stations, whereas *Artemisia*, *Chrysothamnus*, and *Hilaria* are either rare or absent at most stations. Station scores plotted on the first two factors of a PCA (Fig. 3A) reflect this vegetational homogeneity: although this analysis maximizes the variation among samples, most stations are included in a single microhabitat assemblage. Loadings for plant species scores, eigenvalues, and percent variance explained for the first two factors are shown in Table 1. Although vegetation height and spacing appear to be homogeneous throughout the transect, mean vegetation height is significantly different at capture sites of the two species ($F_s = 4.806$, $P = 0.036$; Table 2), with *M. pallidus* occurring in higher vegetation. The full range of sandy soils occurs in a fine-grain fashion at the area of sympatry. Cap-

Table 1. Loadings, eigenvalues, and percent variance explained for principal factors (eigenvalue > 1.00) produced by principal component analyses based on floral microhabitat scores from all trap stations at Penoyer Valley and Sandy Summit.

Species	Penoyer Valley Factor		Sandy Summit Factor	
	I	II	I	II
Artemisia	0.115	0.851	-0.939	0.175
Chrysothamnus	-0.496	-0.187	0.798	-0.216
Tetradymia	-0.861	0.238	0.739	0.230
Atriplex	0.960	-0.159	0.015	-0.726
Hilaria	0.206	0.811	0.250	0.713
Eigenvalue	1.965	1.499	2.128	1.166
% Variance Explained	39.29	29.99	42.56	23.21
Total Variance Explained	69.28		65.77	

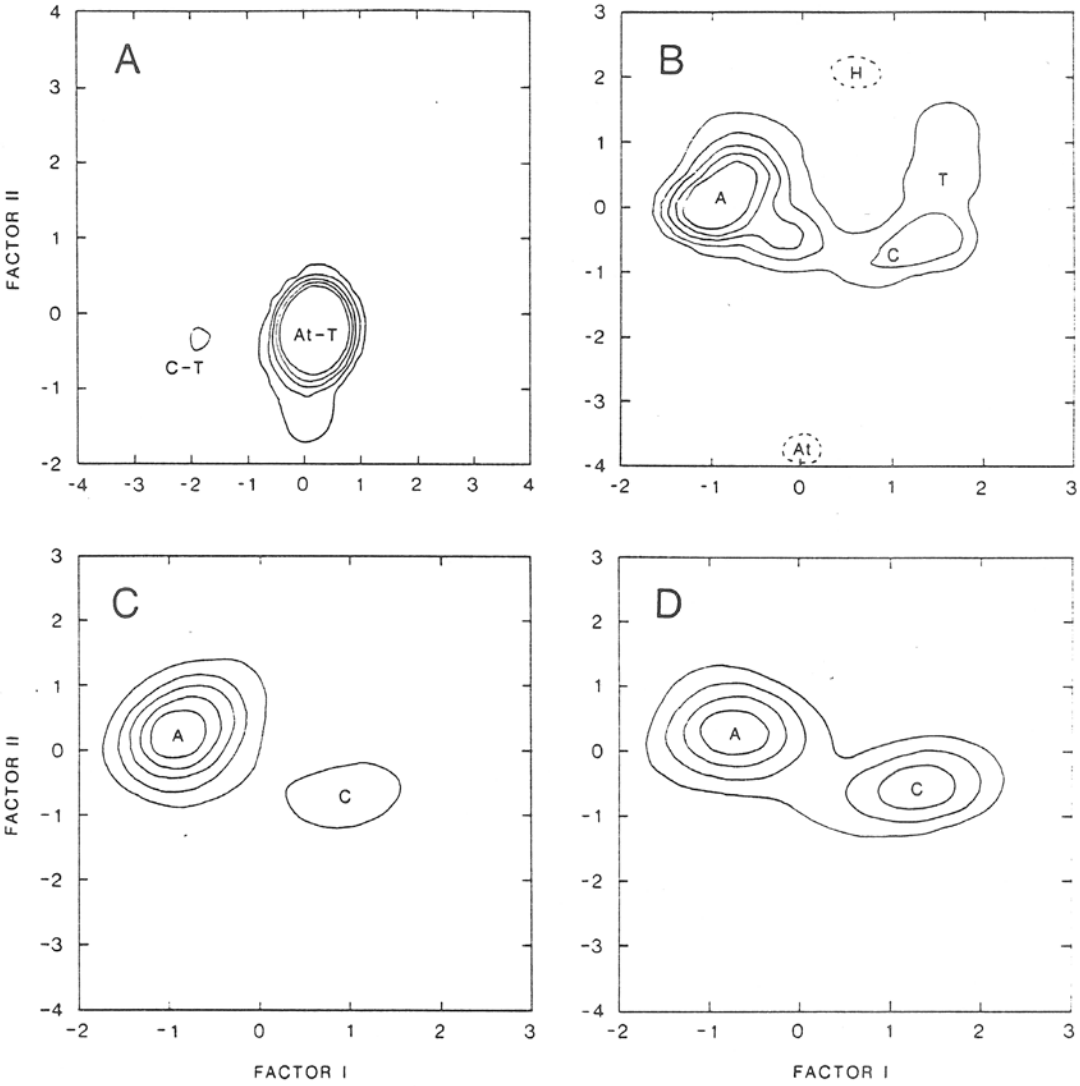

Fig. 3. Distribution of microhabitat scores at Penoyer Valley (A) and Sandy Summit (B-D) relative to the first two factors of two principal components analyses. Density contours produced by kernel smoothing increase in increments of 0.05 relative density. Major microhabitats are indicated: At-T *(Atriplex-Tetradymia)*, C-T *(Chrysothamnus Tetradymia)*, A *(Artemisia)*, C *(Chrysothamnus)*, T *(Tetradymia)*, H *(Hilaria)*. and At *(Atriplex)*. A: Distribution of scores for all stations at Penoyer Valley; contours enclose 86.4% of stations. B: Distribution of scores for all stations at Sandy Summit; contours enclose 93.0% of stations; dotted contours identify densities < 0.05. C: Distribution of scores for *M. megacephalus* at Sandy Summit; contours enclose 94.3% of stations. D: Distribution of scores for *M. pallidus* at Sandy Summit; contours enclose 85.1% of stations.

ture sites of *M. pallidus* tend to be in more loose sand, whereas those of *M. megacephalus* are associated with more gravelly sandy soils (Table 2). Mean soil affinities of the species are significantly different ($U = 193.0$, $P = 0.021$).

Abundance of Microdipodops *species.*—Trapping data from Penoyer Valley show that 100 *Microdipodops* (60.0 percent *M. pallidus*; 40.0 percent *M. megacephalus*) were captured during 3,989 trapnights. Trapping results indicate that during multiple-night trapping, trap success drops quickly as kangaroo mice are removed. Trap success for first-night trapping considered alone (72 captures/1,395 trapnights) varies from 2.8 percent (September 1977) to 11.0 percent (September 1975); seasonal averages for March, May, and September (1975-1977) are remarkably consistent (5.1–5.2 percent).

Table 2. General statistics (means ± SE) and comparisons between means for vegetation characteristics and soil scores at Penoyer Valley capture sites.

Character	*M. megacephalus*	*M. pallidus* ($n = 14$)	Test Statistic ($n = 19$)
Veg. Height (cm)	28.93 ± 1.07	32.11 ± 0.96	$F_s = 4.806$*
Veg. Spacing (m)	1.36 ± 0.11	1.32 ± 0.08	$F_s = 0.099$ ns
Soil Index (0–4)	2.64 ± 0.23	1.90 ± 0.19	$U = 193$*

*$P < 0.05$.

Overall mean trapping success (*Microdipodops* only) over the period 1975-1977 is 5.2 percent.

Mean distance between nearest captures of conspecifics does not differ significantly between the species, but mean interspecific nearest-neighbor distances are significantly different (larger) than intraspecific distances (Table 3). Although both species are captured throughout the trap lines (Fig. 2), the greater interspecific nearest-neighbor capture distances indicate clumped distributions for both species.

Microhabitat affinity.—As stated earlier, *M. megacephalus* and *M. pallidus* segregate according to soil characteristics and vegetational height at the Penoyer Valley locality (Table 2). However, because of the homogeneous plant mixture, there is no obvious microhabitat segregation of the two species based on plant species composition. The apparent overall uniformity of plant species composition among all stations at Penoyer Valley may preclude the opportunity for selection or avoidance of particular floral microhabitats by the two species at the site (or obfuscate our ability to detect it).

Sandy Summit

In contrast to the Penoyer Valley site where the two species meet along a narrow band away from the playa edge, the area of sympatry at Sandy Summit embraces a larger (50 ha) checkerboard of clearly recognizable plant species associations or microhabitats. Both species are represented along 9 of 12 trap lines (Fig. 4).

Floral and edaphic characteristics.—Overall, the vegetation at Sandy Summit is higher and more dense compared to Penoyer Valley. The five major plant species are distributed in evident patches of microhabitats wherein one of five species dominates. A single species is dominant at 83.2 percent of stations (versus 10.4 percent for Penoyer Valley). Density contours of a PCA based on all station vegetation scores (1,097 trap stations) at Sandy Summit delineate the major microhabitats as defined by plant-species composition (see Fig. 3B). A survey of all stations shows that *Artemisia*-dominated microhabitats are most common (52.1 percent), followed by microhabitats dominated by *Chrysothamnus* (21.2 percent), *Artemisia-Chrysothamnus* codominant microhabitats (12.0 percent) and *Tetradymia* (4.7 percent). Loadings for plant species scores, eigenvalues, and percent variance explained for the first two factors are shown in Table 1. In contrast to Penoyer Valley, soil characteristics appear to be uniform throughout the study area, generally of a sandy soil index of about 2.

Table 3. Mean nearest neighbor distances (m) within M. megacephalus (M-M) and M. pallidus (P-P), and between species (M-P) at Penoyer Valley and Sandy Summit. Significance levels (based on t-tests between means) are indicated for each comparison.

Location	Comparison				
	M-M		M-P		P-P
			ns		
Penoyer Valley	44.6	*	61.5	**	39.8
	ns		***		ns
Sandy Summit	39.2	***	115.8	***	29.2
			ns		

$^{*}P < 0.05$
$^{**}P < 0.01$
$^{***}P < 0.001$

Abundance of Microdipodops *species*.—Trapping data reveal that a total of 82 *Microdipodops* (57.3 percent *M. pallidus*; 42.7 percent *M. megacephalus*) was captured at Sandy Summit during 2,194 trapnights. Trap success varies from 1.9 percent (May 1991) to 6.6 percent (May 1977), and is 4.3 percent during September 1977 (3.7 percent overall). Overall trap success (*Microdipodops* only) over the period 1975–1977 is 5.3 percent.

Mean distance between nearest captures of conspecifics does not differ significantly between the species, but mean interspecific nearest-neighbor distances are significantly different (larger) than intraspecific distances (Table 3). Although both species are represented along 9 of 12 trap lines (Fig. 4), the greater interspecific nearest-neighbor capture distances indicate clumped distributions for both species.

Microhabitat affinity.—Goodness-of-fit comparisons of observed frequencies of capture of kangaroo mice in various microhabitats with expected frequencies of occurrence (based on distribution of vegetation transect scores) reveal habitat selection by both species of *Microdipodops*. The distribution of captures of *M. megacephalus* across the different floral microhabitats is significantly different from expectation ($G = 9.636$, $P < 0.05$ [$\chi^2 = 8.051$, $P < 0.05$]; Table 4). Analysis of frequencies indicates that *M. megacephalus*, shows a preference for *Artemisia* and avoidance of other microhabitats.

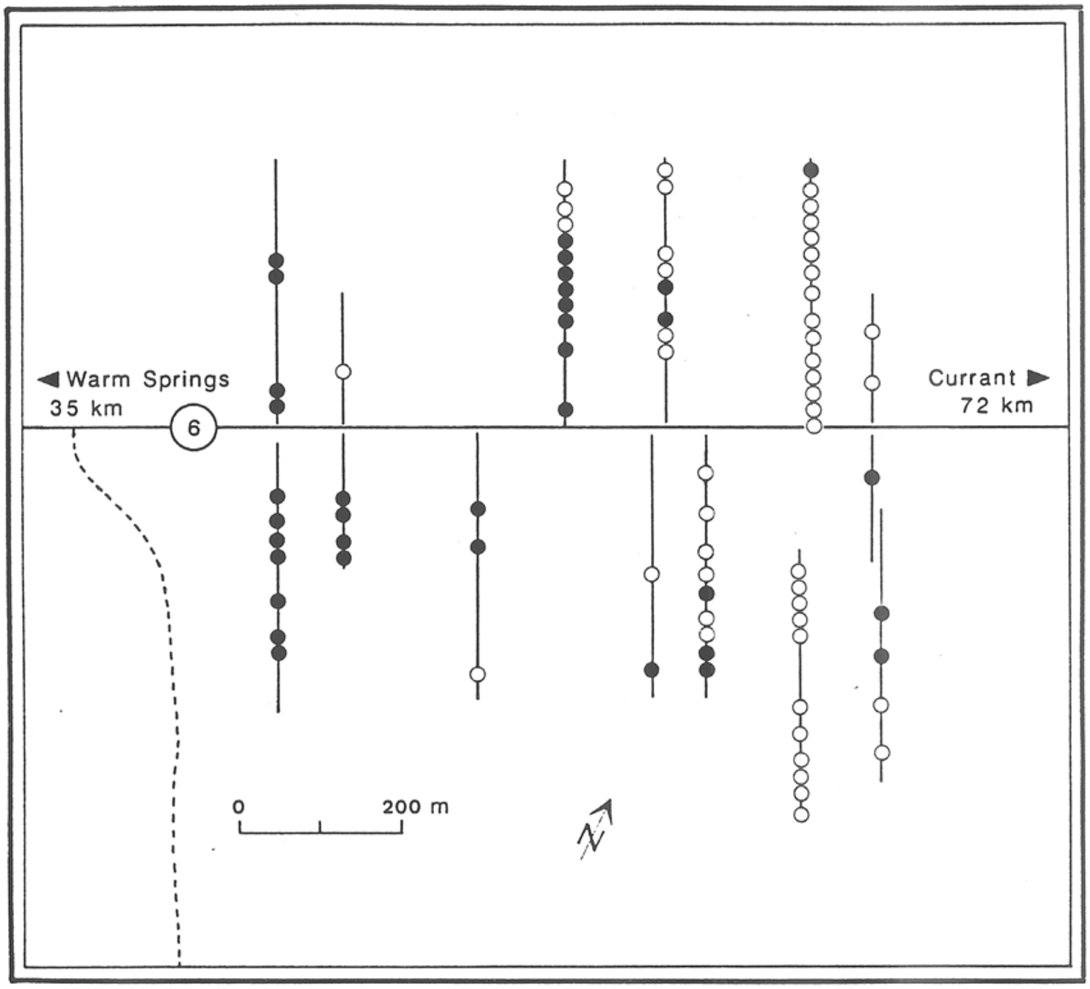

Fig. 4. Sandy Summit study site, indicating location of trap lines and captures of *M. pallidus* (open circles) and *M. megacephalus* (closed circles).

Significant departure from expectation is also observed for *M. pallidus* ($G = 10.368$, $P < 0.05$ [$\chi^2 = 11.447$, $P < 0.01$]; Table 4). Although *M. pallidus* is found most commonly in the most common microhabitat (*Artemisia*), the species occurs disproportionately common (twice that expected) in *Chrysothamnus* microhabitats. Distributions of trap sites (Fig. 3C and 3D) relative to the available trap stations (Fig. 3B) illustrate the respective microhabitat affinities of each species. Both species occur rarely in microhabitats dominated by *Tetradymia*, *Hilaria*, or *Atriplex*.

DISCUSSION

Microhabitat affinity.—Hall (1941) suggested that the distribution of species of kangaroo mice is determined principally by the texture of the soil; *M. pallidus* is restricted to fine sand, whereas *M. megacephalus* occurs more commonly on more coarse soils, but shows a rather broad tolerance for soil type. Ghiselin (1970) tested Hall's (1941) hypothesis that edaphic factors control habitat selection. Ghiselin examined soil affinity at three localities of sympatry of kangaroo mice, including the Penoyer Valley site. Although Ghiselin (1970) could not demonstrate microhabitat affinity at two of the three sympatric localities (including Penoyer Valley), he did demonstrate distinct soil preferences when all three localities were pooled for analysis. Ghiselin's results suggest microhabitat affinity of kangaroo mice is related to texture of soils. However, contrary to Hall's (1941) claims, Ghiselin (1970) found that *M. megacephalus* is not the soil generalist but largely restricted to gravelly soils and *M. pallidus* is not the sandy-soil specialist, but is found commonly on both sandy and more gravelly soils.

The findings of the present study contradict those of Ghiselin (1970) at Penoyer Valley. In the present study, we demonstrate a significant difference in substrate affinity between the species; *M. pallidus* seems to favor the finer, sandy soils and *M. megacephalus* is associated more commonly with sandy soils having a substantial gravel content. It is possible that Ghiselin (1970) was unable to demonstrate habitat selection by the spe-

Table 4. Results for tests for presence and extent of microhabitat selection in two species of Microdipodops *based on cumulative capture data from Sandy Summit.*[a]

Dominant or Codominant Microhabitat (expected probabilities)	*M. megacephalus*			*M. pallidus*		
	f	f'	deviation from f'	f	f'	deviation from f'
Artemisia (0.521)	26	18.25	+	21	24.51	-
Chrysothamnus (0.212)	6	7.40	-	19	9.94	+
Artemisia-Chrysothamnus (0.120)	2	4.21	-	4	5.65	-
Tetradymia (0.047)	0	1.63		1	2.19	
Hilaria (0.027)	0	0.96		0	1.28	
	1	5.14	–	3	6.90	–
Atriplex (0.026)	1	0.089		0	1.20	
Other (0.047)	0	1.66		2	2.23	
Total	35	35.00		47	47.00	
		$G = 9.636$*			$G = 10.368$*	
		$\chi^2_{.05[3]} = 7.815$			$\chi^2_{.05[3]} = 7.815$	

[a] f = observed frequencies of capture; f' = expected frequencies based on expected probabilities obtained from the distribution of vegetation transect (dominance or codominance) scores from all (1097) trap stations surveyed at Sandy Summit.

* $P < 0.05$

cies at Penoyer Valley because he used only two substrate categories: sand and gravel (based on the criterion of whether or not 5 percent by weight of the individual soil samples did not pass through a 2.00 mm sieve). The two soil classes of Ghiselin's (1970) study may have prevented him from detecting the subtle substrate affinities shown by the species at Penoyer Valley (Table 2).

Substrate affinity was not examined at the Sandy Summit locality because the soil seemed uniformly sandy with a gravel overlay. At both study sites, however, we did observe floral microhabitat affinity for both species, despite the gross differences in the environmental settings of the two sites. Kangaroo mice seem to display microhabitat affinity within the monotonous, patternless vegetation of Penoyer Valley by assorting according to shrub height; *M. pallidus* shows an affinity for taller plants and *M. megacephalus* is associated with shorter shrubs. At Sandy Summit, the coexisting species of kangaroo mice show microhabitat affinity on the basis of floral associations; *M. megacephalus* seems to prefer *Artemisia* and avoid other dominant plant associations, whereas *M. pallidus* seems to select *Chrysothamnus* habitats in disproportion to their occurrence at this site.

Although much more information is needed about the coexistence of kangaroo mice, some general conclusions may be drawn at this stage. From our earlier work (Hafner et al., 1979) we know the species coexist as genetically isolated units (biological species) and from the work of Ghiselin (1970) and the present study we know that coexisting species of kangaroo mice show affinities for different soil types and floral associations. However, we have only indirect evidence that they actually compete and we have no evidence that they can actually differentiate among soil and floral types. Accordingly, we cannot explain at this time why the coexisting species show the demonstrated microhabitat affinities.

Abundance of kangaroo mice.—Estimates of trapping success of kangaroo mice at the two areas of sympatry are virtually identical (5.2 percent at Penoyer Valley versus 5.3 percent at Sandy Summit) despite the dissimilar environmental settings. Although overall trap success of kangaroo mice at these sites may seem low, our field experience in the Great Basin shows that it is typical for *Microdipodops* trapping sites. Hafner's (1981) study of kangaroo mice, performed almost exclusively on allopatric populations and involving 18,253 trapnights, showed that mean success of capture of kangaroo mice (at sites yielding kangaroo mice) throughout the Great Basin is 5.24 percent. Hence, kangaroo mice are no less abundant at these areas of sympatry than they are at other places throughout their distribution.

Considering that trap success is about 5 percent at localities where *M. megacephalus* or *M. pallidus* occur in allopatry (Hafner, 1981), one might expect to see approximately 10 percent trap success in areas where these species occur in sympatry. It seems to us that the observed 5 percent trap success in areas of sympatry may indicate that the environment imposes an upper limit to numbers of kangaroo mice at localities across the Great Basin, regardless of species composition. Although we have no direct evidence that competition occurs between these two species in sympatry, these equivalent estimates of abundance of kangaroo mice in allopatry and sympatry provide an indirect clue that competitive interactions must be intense between these coexisting sibling species.

The proportionate contributions of the species at both study sites favor *M. pallidus* in about a 60:40 ratio. *Microdipodops pallidus* is slightly larger than *M. megacephalus* in body size and external characteristics (Hall, 1941; Hafner et al., 1979; Hafner, 1981) and, by virtue of its larger size, it may dominate *M. megacephalus* in behavioral interactions, resulting in numerical predominance in areas of sympatry. However, an examination of relative abundance of kangaroo mice at the 12 localities of sympatry reported in Hall (1941) reveals that the mean number of individuals of *M. megacephalus* and *M. pallidus* in that study is 14.33 and 16.75, respectively, and these means are not significantly different ($F_s = 0.188$; $P = 0.669$); actually, *M. megacephalus* is the more abundant species at five of the sites. Although *M. pallidus* is also numerically dominant at each of Ghiselin's (1970) three study sites, we feel that the observed ratios more likely reflect arbitrary placement of the trap lines within zones of sympatry, rather than actual difference in relative abundance of the species. In the case of this study, we intended simply to identify a zone of sympatry where the species were represented in approximately equal numbers. Until such time as information becomes available on the behavioral interactions of the species in sympatry, our working hypothesis is that neither species is behaviorally dominant and the species are equally abundant at sympatric localities.

Our analysis of the mean distances between nearest captures of kangaroo mice (nearest-neighbor analysis) shows that individuals of both *M. megacephalus* and *M. pallidus* are not distributed randomly, but are more apt to be captured near a conspecific; hence, kangaroo mice are found generally in clumps of one species or the other. This clumping is observed at both localities of sympatry (Figs. 2 and 4; Table 3). As can be seen from inspection of Table 3, mean interspecific distance at Sandy Summit is significantly different from that at Penoyer Valley. Although the intraspecific distances between the localities are not significantly different (two-tailed testing; Table 3), the mean intraspecific distance of individuals of *M. pallidus* at Sandy Summit is significantly shorter than that at Penoyer Valley ($P < 0.05$ for one-tailed test). These data taken together suggest that there is a greater clumping of species of kangaroo mice at Sandy Summit than at Penoyer Valley. This is not surprising inasmuch as the vegetation at Sandy Summit is obviously clumped by plant species (coarse grained) whereas the vegetation at Penoyer Valley is a monotonous mixture of plant species (fine grained).

Morphology.—As we noted before (Hafner et al., 1979), the species of *Microdipodops* are very similar in morphology and represent classical sibling species. One species, *M. pallidus*, is slightly larger and generally more pale in color than the other, but the two are difficult to identify on the basis of morphology alone (see Hall, 1941; Hafner, 1981). Indeed, in an earlier study (Hafner et al., 1979:5) we determined that the two species at Penoyer Valley differed by only about 5 percent in most external and cranial variables.

There are, however, trenchant differences between the species in size and shape of the angular processes, pterygoids, and incisive foramina of the species at Penoyer Valley (Hafner et al., 1979); for example, angular bifurcation differs by about 68 percent between the species. These characters are related to, or are direct components of, the masticatory apparatus and, thus, may suggest that ecological separation between the species is accomplished by differential allocation of the food resource base. The incisive foramina are known to be passageways connecting the mouth with the vomeronasal organ (Jacobson's organ), which serves a chemosensory function. Thus, differences in size and shape of the incisive foramina might signal differential ability to discriminate among food items or between species-specific pheromones. The pterygoid bones and angular processes of the dentary serve as origin and insertion sites for the adductor muscles of the jaw (*m pterygoideus* and *m masseter*) and these skeletal differences may, again, suggest that the species have different food habits. Unfortunately, nothing is known about the food habits of these congeners in sympatry.

Biogeographical considerations.— Clearly, the present geographic distribution of the two species of kangaroo mice is a result of both present-day environmental conditions and largely unknown historical events during the evolution of the genus. Kangaroo mice are restricted to the Upper Sonoran Life Zone in the Great Basin and are known to occur at elevations ranging from 1,190 to 2,318 m (3,900-7,600 ft). The geographic distribution of *M. megacephalus* spans this entire elevational range, but is usually associated with the *Artemisia* floral community in the upper portion of the Upper Sonoran Life Zone. The distribution of *M. pallidus* is much more restricted than that of *M. megacephalus*; it has a geographic range about one-third that of *M. megacephalus*, and is found at sites varying in elevation from only 1,190 to 1,830 m (3,900-6,000 ft).

Hall (1941) explained the distributional differences of the species as being due to a fairly rigid floral and edaphic separation. According to Hall (1941), the distribution of *M. pallidus* is restricted to fine sandy soils in a floral zone that is elevationally beneath the *Artemisia* zone. He also argued that, because fine sands usually accumulate at the bottoms of basins, *M. pallidus* is far less continuous in its distribution than *M. megacephalus*, a species that is often found away from the valley bottoms.

Although we generally agree with Hall's (1941) conclusions about the gross floral and edaphic affinities of the species, the occurrence of *M. pallidus* at the Sandy Summit locality provides new information relevant to our understanding of habitat preference by *M. pallidus*. Importantly, *M. pallidus* is found at Sandy Summit (1,830 m) in a floral association dominated by *Artemisia*; we have shown that it occurs in the *Artemisia* microhabitat in approximately equal abundance relative to *M. megacephalus*. In contrast to the prevalent view in the literature (e.g., Hall, 1941; 1946), the occurrence of *M. pallidus* at Sandy Summit suggests that this species may be rather catholic in its habitat selection. This observation is supported further by Ghiselin's (1970) data, which indicate that *M. pallidus* is not restricted to sandy soil but is found in both sandy and more gravelly soils. Obviously, one should not assume that *M. pallidus* is now, and always has been, restricted to fine sandy soils in the bottoms of basins below the *Artemisia* floral zone.

The region of sympatry between the species of *Microdipodops* (Fig. 1), is defined presently by only 13 localities. It would be interesting to know whether this region represents a stable area of species distributional overlap (hence, evidence of long-term coexistence) or simply represents ephemeral encounters between two intensely competitive sibling species. Unfortunately, only four of these 13 localities have been studied since Hall's (1941) treatise on the genus. In the ensuing years, Ghiselin (1970) trapped both species of kangaroo mice at three localities of sympatry, and we have captured both species at the two sites reported here periodically over the past 20 years. Clearly, these four localities of sympatry are stable, at least in short-term "ecological time", and it is possible that they have persisted as localities of sympatry for hundreds, if not thousands, of years. A thorough study of the geographic distribution of the species is needed to resolve this question of temporal stability of the region of overlap.

As both Ghiselin (1970) and Hafner et al. (1979) observed, much more information is needed on the biology of kangaroo mice in sympatry before we can understand how and why the species are able to coexist. It seems to us that, in addition to further studies of microhabitat affinity, detailed studies of the distribution, diet, behavior, and reproduction of the coexisting species should provide especially fruitful avenues for future research. Given the general dearth of ecological information on *Microdipodops*, it is important to note that studies should also be undertaken on each species where it occurs alone to give a basis for comparison in studies addressing species coexistence.

ACKNOWLEDGMENTS.— Field assistance was generously provided by P. M. Hafner, K. R. LeVering, J. M. Hafner, and R. C. Hafner. We thank J. H. Brown, E. H. Braker and an anonymous reviewer for critical evaluation of the manuscipt

LITERATURE CITED

Bowers, M. A., and J. H. Brown. 1982. Body size and coexistence in desert rodent: chance or community structure? Ecology, 63:391-400.

Brown, J. H. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. Ecology, 54:775-787.

———. 1975. Geographical ecology of desert rodents. Pp.315-341, *in* Ecology and evolution of communities (M. L. Cody, and J. M. Diamond, eds.), Belknap Press of Harvard University Press, Cambridge, Massachusetts, 545 pp.

Brown, J. H., and J. C. Munger. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. Ecology, 66:1545-1563.

Brown, J. H., O. J. Reichman, and D. W. Davidson. 1979. Granivory in desert ecosystems. Annual Review of Ecology and Systematics. 10:201-227.

Eisenberg, J. F. 1963. Behavior of heteromyid rodents. University of California Publications in Zoology, 69:1-100.

Ghiselin, J. 1970. Edaphic control of habitat selection by kangaroo mice (*Microdipodops*) in three Nevadan populations. Oecologia, 4:248-261.

Hafner, D. J., J. C. Hafner, and M. S. Hafner. 1979. Systematic status of kangaroo mice, genus *Microdipodops* : morphometric, chromosomal, and protein analyses. Journal of Mammalogy, 60:1-10.

Hafner, J. C. 1981. Evolution, systematics, and historical biogeography of kangaroo mice, genus *Microdipodops*. Unpublished Ph.D. Dissertation, University of California, Berkeley, 269 pp.

———. 1993. Macroevolutionary diversification in heteromyid rodents: heterochrony and adaptation in phylogeny. Pp. 321-326 *in* Biology of the Heteromyidae (H. H. Genoways and J. H. Brown,eds.), Special Publication, American Society of Mammalogists, Allen Press, Lawrence, Kansas, 10:xii+1-719.

Hafner, J. C., and M. S. Hafner. 1983. Evolutionary relationships of heteromyid rodents. Great Basin Naturalist Memoirs, 7:3-29.

Hafner, J. C., and M. S. Hafner. 1988. Heterochrony in rodents. Pp. 217-235 *in* Heterochrony in Evolution (M.L. McKinney, ed.), Plenum Press, New York, 348 pp.

Hafner, M. S. 1977. Density and diversity in Mojave Desert rodent and shrub communities. Journal of Animal Ecology, 46:924-938.

Hall, E. R. 1941. Revision of the rodent genus *Microdipodops*. Field Museum of Natural History, Zoology Series, 27:233-277.

Hall, E. R., and J. M. Linsdale. 1929. Notes on the life history of the kangaroo mouse (*Microdipodops*). Journal of Mammalogy, 10:298-305.

Kotler, B. P. 1985. Owl predation on desert rodents which differ in morphology and behavior. Journal of Mammalogy, 66:824-828.

Kotler, B. P., and J. S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. Annual Review of Ecology and Systematics. 19:281-307.

Lemen, C., and P. W. Freeman. 1983. Quantification of competition among coexisting heteromyid rodents in the southwest. The Southwestern Naturalist, 28:41-46.

Longland, W. S., and M. V. Price. 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? Ecology, 72:2261-2273.

MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences, 51:1207-1210.

M'Closkey, R. T. 1978. Niche separation and assembly in four species of Sonoran Desert rodents. American Naturalist, 112:683-694.

Munger, J. C., and J. H. Brown. 1981. Competition in desert rodents: an experiment with semipermiable exclosures. Science, 211:510-12.

Pierce, B. M., W. S. Longland, and S. H. Jenkins. 1992. Rattlesnake predation on desert rodents: microhabitat and species-specific effects on risk. Journal of Mammalogy, 73:859-865.

Price, M. V., and J. H. Brown. 1983. Patterns of morphology and resources use in North American Desert Rodent communities. Great Basin Naturalist Memoirs, 7:117-134.

Reichman, O. J. 1979. Desert granivore foraging and its impact on seed densities and distributions. Ecology, 60:1085-1092.

———. 1984. Spatial and temporal variation in seed distributions in desert soils. Journal of Biogeography, 11:1-11.

Rosenzweig, M. L., B. Smigel, and A. Kraft. 1975. Patterns of food, space, and diversity. Pp. 241-268. *in* Rodents in desert environments (I. Prakash and P. K. Ghosh, eds.), W. Junk, The Hague, The Netherlands, 624 pp.

Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology, 50:558-571.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London.175 pp.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second Edition. W. H. Freeman and Company, San Francisco 859 pp.

Wilkinson, L. 1988. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois, 822 pp.

———. 1990. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois, 677 pp.

Moore Laboratory of Zoology and Department of Biology, Occidental College, Los Angeles, CA 90041; New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, NM 87104; Museum of Natural Science and Department of Zoology & Physiology, Louisiana State University, Baton Rouge, LA 70803.