

HABITAT HETEROGENEITY, HABITAT ASSOCIATIONS, AND RODENT SPECIES DIVERSITY IN A SAND–SHINNERY-OAK LANDSCAPE

MICHAEL J. CRAMER* AND MICHAEL R. WILLIG

Program in Ecology, Department of Biological Sciences and The Museum, Texas Tech University,
Lubbock, TX 79409-3131

Present address of MJC: Department of Biological Sciences, University of Cincinnati,
Cincinnati, OH 45221-0006

The habitat-heterogeneity hypothesis states that an increase in habitat heterogeneity leads to an increase in species diversity. Although community-level analyses of effects of habitat heterogeneity on species diversity are important, they do not reveal the mechanism through which heterogeneity affects diversity. In contrast, habitat associations of particular species suggest a potential mechanism whereby diversity is affected by habitat heterogeneity. The sand–shinnery-oak ecosystem of southwestern United States contains 2 habitat types: blowouts and matrix. Blowouts are small and infrequent wind-formed open patches without shrubs. These disturbances are surrounded by a dense shrub-dominated matrix, mostly containing the low stature oak, *Quercus havardii*. Habitat associations of particular species with respect to blowouts versus matrix were assessed using capture frequencies and species abundances. Only *Dipodomys ordii* was more abundant in blowouts than in surrounding matrix, and this only occurred during summer. This seasonal change could be a consequence of competition or predation. All other species showed a preference for the matrix. Considerations of scale and edge effects between blowouts and matrix may provide additional insight into habitat associations of rodents, leading to a deeper understanding of the mechanistic basis of diversity in this ecosystem.

Key words: community ecology, habitat associations, habitat heterogeneity, rodents, species diversity

The habitat-heterogeneity hypothesis, developed initially by MacArthur and MacArthur (1961), proposes that an increase in number of different habitats can lead to an increase in species diversity. One way in which habitat heterogeneity could enhance diversity occurs when habitats are large enough to support distinct populations. In ecosystems where many habitats can support populations of species, diversity should be high because of the presence of specialists that exhibit distinct habitat preferences (sensu Rosenzweig 1981). In contrast, diversity may be low in systems where alter-

native habitats are fragmented and of low areal extent because of lack of specialization and intense competition among generalists. Nonetheless, the presence of small habitat patches may increase overall quality of the matrix by supplying predator-free space or complementary resources. Although not sufficiently large to support distinct populations, the presence of alternative habitat types may provide unique resources that improve habitat quality for particular species. In certain circumstances, species that cannot defend these small habitat patches may specialize on alternate resources to remain in the community, lead-

* Correspondent: cramerm@email.uc.edu

ing to shared habitat preferences (sensu Rosenzweig 1991). Either way, the presence of multiple habitats can lead to an increase in species diversity.

Habitat associations provide a useful way to determine how different species respond to environmental heterogeneity. Because habitat selection has an adaptive basis (Martin 1998), it is reasonable to assume that individuals demonstrating preference for high-quality habitats have a reproductive advantage over conspecifics in low-quality habitats. This ultimately would lead to particular species being more abundant in some habitats than in others. Consequently, investigation of habitat associations of each species in a community enhances understanding of how the presence of different habitats ultimately affects species diversity. If habitat heterogeneity increases species diversity in a manner consistent with the habitat-heterogeneity hypothesis, then species should specialize in different habitats because of strong competitive or predation pressures or because abiotic conditions are more suitable.

Habitat associations of rodents have been studied extensively in desert (Heske et al. 1994; Kotler and Brown 1988) and grassland (Kaufman and Fleharty 1974; Lacher and Alho 1989; Moulton et al. 1981; Snyder and Best 1988) systems. Many of these studies examine direct responses of 1 species to the removal of a competitor (Bowers et al. 1987; Heske et al. 1994; Price 1978; Rebar and Conley 1983), to assess whether competition plays a role in determination of habitat associations. Few studies directly assess effects of habitat heterogeneity on species diversity (but see Grant and Birney 1979 and Hall and Willig 1994), although many make inferences about rodent community structure on the basis of demographic and behavioral responses of a few common species in the community (Brown 1989; Brown et al. 1994; Kotler 1984; Kotler and Brown 1988; Rosenzweig 1973; Rosenzweig and Abramsky 1997).

The ecosystem of sand-shinnery-oak

(*Quercus havardii*) of the southwestern United States is an appropriate system for addressing questions of habitat heterogeneity and species diversity. This system contains 2 distinct habitat types: open blowouts surrounded by a dense and brushy sand-shinnery-oak matrix (Willig and McGinley 1999). The blowouts, formed by wind, are areas of open sand with little vegetation (Holland 1994). Previous studies of mammals in this system provide evidence of the importance of habitat heterogeneity, with total rodent density and species composition differing between areas that had been cleared of shrubs and those that were undisturbed (Colbert 1986; Willig et al. 1993). These studies concentrate on large-scale anthropogenic disturbance but do not address the influence of habitat heterogeneity at smaller spatial scales.

Our objective was to determine the mechanism through which diversity is affected by the presence of multiple habitats in the sand-shinnery-oak ecosystem. The scale at which rodents perceive heterogeneity in their environment was investigated to determine whether the community comprises habitat specialists or whether the presence of blowouts increases overall habitat quality for some species.

MATERIALS AND METHODS

Study area and site selection.—The study area is approximately 19 km southwest of the town of Sundown (33°19'N, 102°37'W) in Yoakum County, Texas. The soil consists of aeolian deposits, or cover sands, and has good water retention (Dhillion et al. 1994). The climate is warm-temperate and semiarid, with fluctuating temperatures during the winter (Willig et al. 1993). Annual precipitation averages 41 cm, with most rainfall occurring from May through October (Dhillion et al. 1994). The study site consists of 2 adjacent fields separated by a barbed-wire fence. The eastern field (approximately 500 km²) was grazed by cattle from September through March. The western field (approximately 200 km²) was ungrazed during the study.

The plant community is dominated by sand-

shinnery-oak (Dhillion et al. 1994). This oak is a low-growing clonal shrub that has a large proportion of its biomass occurring belowground. Other common plant species at the site include sand sagebrush (*Artemisia filifolia*), plains yucca (*Yucca campestris*), mesquite (*Prosopis glandulosa*), little bluestem (*Schizachyrium scoparium*), sand bluestem (*Andropogon hallii*), purple three-awned needlegrass (*Aristida purpurea*), sand dropseed (*Sporobolus cryptandrus*), sand paspalum (*Paspalum setaceum*), wild buckweed (*Eriogonum annuum*), plains blackfoot (*Commelina erecta*), Fendler's euphorbia (*Euphorbia fendleri*), James rushpea (*Caesalpinia jamesei*), and Russian thistle (*Salsola kali*). Rodents at the site (Cramer 1998) include Ord's kangaroo rat (*Dipodomys ordii*), plains pocket mouse (*Pergnathus flavescens*), hispid pocket mouse (*Chaetodipus hispidus*), deer mouse (*Peromyscus maniculatus*), western harvest mouse (*Reithrodontomys megalotis*), plains harvest mouse (*Reithrodontomys montanus*), northern grasshopper mouse (*Onychomys leucogaster*), hispid cotton rat (*Sigmodon hispidus*), southern plains woodrat (*Neotoma micropus*), house mouse (*Mus musculus*), and spotted ground squirrel (*Spermophilus pilosoma*).

Ten random sites were selected in the study area, each consisting of a blowout paired with undisturbed sand–shinnery-oak habitat. Blowouts were selected by 4 criteria: the blowout was larger than the trapping configuration (14 by 12 m); the blowout was at least 30 m from other selected sites (to minimize the likelihood of rodents traveling among sites); the blowout was of recent origin (not overgrown with oak); and the blowout was generated by natural forces rather than by anthropogenic activity (i.e., roads and man-made ditches are not blowouts).

Rodent sampling.—Trapping was conducted in 3 seasons: summer, autumn–winter (hereafter referred to as winter), and spring. Seasons were defined by the phenology of the plant community (Colbert 1986). Summer (July–September) is the time of maximum plant development and reproduction, winter (November–March) is the period of oak defoliation, and spring (April–June) is the period of oak refoliation. Trapping was not conducted on the full moon night and on the 2 nights before and after it because some nocturnal rodents curtail activity during this period (Carley et al. 1970).

A census and assessment period characterized

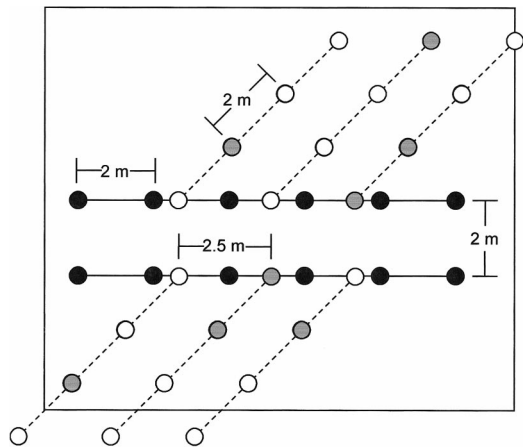


FIG. 1.—Schematic representations of census lines (bold), assessment lines (dashed), and area of effect (bold rectangle) on the basis of method of O'Farrell et al. (1977). Black dots represent census trapping stations, open dots represent assessment trapping stations, and gray dots represent assessment trapping stations where a particular animal was captured. The boundary of the area of effect is defined as 1 m (0.5 times the interstation distance) past the outermost capture station on the assessment lines. Area of effect in this example is 108 m².

each season of sampling. Two pairs of parallel census lines were established at each site, 1 pair in the blowout and the other in adjacent, undisturbed sand–shinnery-oak habitat (the matrix). Census lines were 2 m apart and 10 m in length (Fig. 1). Each census line contained 6 trapping stations. One Sherman live trap was located at each station (12 traps in each of 2 habitats). Census trapping continued at each site until number of unmarked animals was <5% of number of previously marked animals at that site (Lacher and Alho 1989). Traps were closed for at least 2 nights after the census period. The assessment period was used to determine distance traveled by marked rodents from census lines, providing an estimate of the area used by each species. Each of 3 parallel assessment lines extended at 45° angles away from each of a pair of parallel census lines (Fig. 1). Four trapping stations were established on each assessment line (48 traps per site). The assessment period lasted 3 nights.

Traps were baited with a mixture of sunflower seeds, rolled oats, and peanut butter. All captured rodents were marked by toe-clipping, iden-

tified to species and sex, weighed, and then released. Trapping was not conducted when expected overnight minimum temperature was $<2^{\circ}\text{C}$, to reduce mortality of rodents in traps. Rodent trapping conformed to guidelines sanctioned by the American Society of Mammalogists (Animal Care and Use Committee 1998). Voucher specimens were collected in a nearby area before the initiation of the study and are deposited at the Museum, Texas Tech University, Lubbock, Texas.

Density and population estimation.—Density of each species in each habitat was calculated following the method of O'Farrell et al. (1977). The proportion of marked animals captured on the assessment lines (R_p) was estimated using the formula $R_p = M/T$, where M is the number of recaptures and T is the total number of animals (new captures and recaptures) on the assessment lines. The number of animals in the area of effect (N_A) is estimated by $N_A = N_G/R_p$, where N_G is the number of animals marked during the census trapping period.

For each pair of census lines, the boundary of the area of effect (A) equaled 0.5 times the interstation distance beyond the outermost capture of an individual of a given species along the assessment lines (O'Farrell et al. 1977). Area of effect was determined by extending a line perpendicular to the census line, 1 m past the outermost recapture station on the assessment line (Fig. 1). This was done for each census line in a given pair. Area of this rectangle is area of effect for each pair of census lines. Density (D) for each species was then estimated in each habitat by $D = N_A/A$.

This approach provides an accurate estimate of ecological density, or the amount of space per individual that is used for ecological activities such as foraging, reproduction, and social interactions. However, a bias is introduced when considering rare species. Species not captured on both census and assessment lines cannot be included in community-level analyses. If there were no captures for a particular species on assessment lines, then T would equal 0, and R_p would be mathematically undefined. Alternatively, if a species was captured only during the assessment period, then M would be 0, making R_p equal to 0, and N_A would be mathematically undefined. Because of the bias introduced by eliminating rare species, an alternative estimate of abundance was considered for each species.

We assumed that populations were closed within each site during a trapping season and that no new individuals were added through births and immigration or subtracted through deaths and emigration. This assumption is justified by the short trapping periods at each site in each season. We used mean Chapman's Modified Lincoln-Petersen index (\bar{N}):

$$\bar{N} = \frac{\sum_{i=1}^x N_i^*}{x},$$

because it is accurate, is mathematically simple to calculate, and makes few assumptions about the organisms in question (Mares et al. 1981). The estimate is simply an average for a number of consecutive Chapman's Modified Lincoln-Petersen estimates (N_i^*):

$$N_i^* = \left[\frac{(M_i + 1)(n_i + 1)}{(m_i + 1)} \right] - 1,$$

where n_i refers to the number of individuals captured in sample i , m_i is the number of marked individuals in sample i , and M_i is the number of previously marked individuals in the population during the period of sample i . Only captures along the census lines were used to calculate the population estimate.

Statistical analysis.—A repeated-measures analysis of variance (SPSS, Inc. 1988) was used to assess differences between habitats and among seasons for ecological densities and population estimates of common species. Repeated measures were necessary because the assumption of independence was violated in 2 ways. First, the location of sand-shinnery-oak matrix was paired with a blowout. Second, measurements were taken at the same sites in different seasons. Separate analyses were conducted for each species, and probabilities were modified using Bonferroni's sequential adjustment (Rice 1989). In the presence of a significant seasonal effect independent of season, 2 orthogonal a priori contrasts were used to identify seasonal effects. The 1st tested the difference in abundance (either ecological density or population size) between summer and winter. The 2nd tested the difference between spring and average of summer and winter. A significant season-by-habitat interaction indicated that seasonal differences were dependent on habitat, and orthogonal

a priori contrasts were used to identify which seasonal effects were habitat specific. One compared the difference between summer and winter in the blowouts with the same seasonal difference in the matrix. The other compared the difference between spring and the average of summer and winter in the blowouts with the same difference in the matrix.

Habitat preferences were analyzed for common species. If a species shows no preference, then the proportion of captures in each habitat should be equal. Any significant deviation from this null hypothesis indicates habitat preference. Deviations were assessed using a replicated goodness-of-fit test (Sokal and Rohlf 1981). Because G -tests are based on the logarithm of captures, unity (1) was added to both capture frequencies when observed values for 1 of the 2 habitats was 0.

RESULTS

Community composition.—Eight species (3 heteromyids—*D. ordii*, *P. flavescens*, and *C. hispidus*; 4 murids—*O. leucogaster*, *R. montanus*, *S. hispidus*, and *N. micropus*; and 1 sciurid—*S. spilosoma*) were captured over 3,120 trap nights during summer (18 July to 20 September 1996). *S. spilosoma* was excluded from analyses because it is diurnal (Streubel and Fitzgerald 1978). Mean species richness was higher in sand-shinnery-oak ($\bar{X} = 3.5$) than in blowout ($\bar{X} = 2.3$) habitats (paired t -test, $t = -3.34$, $d.f. = 9$, $P = 0.009$). *D. ordii*, *P. flavescens*, and *O. leucogaster* were the most frequently captured and abundant species during summer.

Eight taxa were captured in 3,336 trap nights during winter (5 November 1996 to 29 March 1997), including 2 heteromyids (*D. ordii* and *P. flavescens*) and 6 murids (*O. leucogaster*, *R. montanus*, *R. megalotis*, *N. micropus*, *M. musculus*, and *Peromyscus*). Two species of *Peromyscus* (*P. maniculatus* and *P. leucopus*) occur in Yoakum County (Davis and Schmidly 1994), but individuals of these 2 taxa are difficult to differentiate using external characteristics (Rich et al. 1996). As a result, individuals of this genus were not identified to species

but instead were pooled (*Peromyscus*). Because both of these species were uncommon at the study site, pooling abundances had a negligible effect on measures of diversity. Mean species richness was higher in matrix ($\bar{X} = 3.7$) than in blowout ($\bar{X} = 2.5$) habitats (paired t -test, $t = -2.71$, $d.f. = 9$, $P = 0.024$). *D. ordii* and *O. leucogaster* were the most abundant species during winter.

Three heteromyids (*D. ordii*, *P. flavescens*, and *C. hispidus*), 6 murids (*O. leucogaster*, *R. montanus*, *R. megalotis*, *S. hispidus*, *Peromyscus*, and *N. micropus*), and 1 sciurid (*S. spilosoma*) were captured in 3,000 trap nights during the spring period (1–29 May 1997). Mean species richness was higher in the sand-shinnery-oak ($\bar{X} = 4.2$) than in blowout ($\bar{X} = 3.2$) habitats (Wilcoxon matched-pairs signed-ranks test, $Z = -2.37$, $d.f. = 9$, $P = 0.018$). *D. ordii*, *P. flavescens*, and *O. leucogaster* were the most common species during the spring.

The effect of season and habitat on species abundance of each of 4 species was similar for measures of ecological density and population estimates. Season or habitat affected the ecological density and population estimate of *D. ordii*, *O. leucogaster*, and *P. flavescens* (Tables 1 and 2). In contrast, neither season nor habitat affected ecological density or population estimate of *R. montanus*. Although ecological density of *Peromyscus* was affected by habitat (Table 1), there were no significant effects of either habitat or season on abundance of *Peromyscus* in terms of population estimate (Table 2). Densities of *D. ordii* differed consistently among seasons without a habitat effect (Table 1). Densities were higher in winter than in summer, and densities were higher in spring than in winter and summer as a group. There was a significant interaction between season and habitat in terms of population estimate: the discrepancy between habitats was greater in winter than in summer (Table 2). Densities of *P. flavescens* did not differ seasonally but were consistently higher in the matrix re-

TABLE 1.—Ecological densities of common species in blowouts and matrix during each of 3 phenological seasons in the sand–shinnery-oak system. When results (S, season; H, habitat, S × H, season-by-habitat interaction) of repeated-measures analysis of variance (SPSS, Inc. 1988) indicated consistent seasonal effects, a priori contrasts were used to identify instances when differences occurred (A, comparison between summer and winter regardless of habitat; B, comparison between spring and average of summer and winter regardless of habitat). Similarly, when seasonal effects were habitat specific (a significant S × H interaction), a priori contrasts were used to identify instances when differences occurred (C, comparison of difference between summer and winter in blowouts with the same difference in the matrix; D, comparison of difference between spring and average of summer and winter in blowouts with the same difference in the matrix). Probabilities were corrected for multiple comparisons using Bonferroni's sequential adjustment (Rice 1989).

Season	Blowout		Matrix		Total	
	\bar{X}	SD	\bar{X}	SD	\bar{X}	SD
<i>Dipodomys ordii</i> (S**, H*, S × H*; A**, B**)						
Summer	0.0457	0.0318	0.0318	0.0112	0.0387	0.0173
Winter	0.0984	0.0592	0.1018	0.0261	0.1001	0.0446
Spring	0.0896	0.0206	0.0912	0.0192	0.0904	0.0194
Total	0.0779	0.0435	0.0749	0.0367		
<i>Perognathus flavescens</i> (S*, H**, S × H*)						
Summer	0.0098	0.0197	0.0305	0.0335	0.0189	0.0277
Winter		undefined	0.0056	0.0126	0.0028	0.0091
Spring		undefined	0.0341	0.0193	0.0199	0.0226
Total	0.0038	0.0128	0.0218	0.0254		
<i>Onychomys leucogaster</i> (S**, H**, S × H**, C**, D*)						
Summer	0.0095	0.0142	0.0291	0.0322	0.0187	0.0254
Winter	0.0197	0.0204	0.0593	0.0174	0.0430	0.0270
Spring	0.0305	0.0111	0.0683	0.0324	0.0528	0.0317
Total	0.0195	0.0173	0.0548	0.0310		
<i>Peromyscus</i> (S*, H**, S × H*)						
Summer		absent		absent		
Winter		absent	0.0046	0.0075	0.0024	0.0058
Spring		absent	0.0098	0.0148	0.0059	0.0122
Total		absent	0.0071	0.0115		
<i>Reithrodontomys montanus</i> (S*, H*, S × H*)						
Summer		absent	0.0013	0.0042	0.0007	0.0030
Winter		absent	0.0047	0.0085	0.0024	0.0063
Spring		undefined	0.0038	0.0102	0.0017	0.0067
Total		undefined	0.0200	0.0961		

* $P > 0.05$, ** $P \leq 0.05$.

ardless of season (Table 1). Analysis of population estimates revealed a significant interaction between season and habitat: differences between habitats were greater in summer (Table 2). Differences among seasons were dependent on habitat for densities and population estimates of *O. leucogaster* (Tables 1 and 2). Differences between winter and summer were more profound in the matrix than in blowouts for

both measures of abundance. Densities of *Peromyscus* were higher in the matrix regardless of season (Table 1). Because no *Peromyscus* were captured in summer, a priori contrasts could not be conducted for this species.

Habitat associations.—Replicated goodness-of-fit tests evaluated the null hypothesis that proportional captures in each habitat were equal during summer (Table 3).

TABLE 2.—Population estimates of common species in blowouts and matrix during each of 3 phenological seasons in the sand–shinnery-oak system. When results (S, season; H, habitat; S × H, season-by-habitat interaction) of repeated-measures analysis of variance (SPSS, Inc. 1988) indicated consistent seasonal effects, a priori contrasts were used to identify instances when differences occurred (A, comparison between summer and winter regardless of habitat; B, comparison between spring and average of summer and winter regardless of habitat). Similarly, when seasonal effects were habitat specific (a significant S × H interaction), a priori contrasts were used to identify instances when differences occurred (C, comparison of difference between summer and winter in blowouts with the same difference in the matrix; D, comparison of difference between spring and average of summer and winter in blowouts with the same difference in the matrix). Probabilities were corrected for multiple comparisons using Bonferroni’s sequential adjustment (Rice 1989).

Season	Blowout		Oak		Total	
	\bar{X}	SD	\bar{X}	SD	\bar{X}	SD
<i>Dipodomys ordii</i> (S**, H*, S × H**, C**, D*)						
Summer	2.62	0.68	1.83	0.96	2.22	0.90
Winter	5.96	1.66	7.03	1.76	6.50	1.76
Spring	8.67	2.50	9.48	1.82	9.07	2.17
Total	5.75	3.04	6.11	3.58		
<i>Perognathus flavescens</i> (S**, H**, S × H**, C*, D*)						
Summer	0.36	0.62	1.72	1.44	1.04	1.28
Winter	absent		0.59	0.74	0.30	0.59
Spring	0.04	0.13	1.06	0.88	0.55	0.81
Total	0.13	0.39	1.12	1.13		
<i>Onychomys leucogaster</i> (S**, H**, S × H**, C**, D*)						
Summer	0.25	0.52	1.26	1.42	0.75	1.17
Winter	0.86	1.29	3.86	1.35	2.36	2.00
Spring	1.69	1.58	3.67	1.31	2.68	1.74
Total	0.93	1.32	2.93	1.78		
<i>Peromyscus</i> (S*, H*, S × H*)						
Summer	absent		absent			
Winter	0.23	0.56	0.46	0.61	0.34	0.58
Spring	absent		0.65	0.92	0.32	0.71
Total	0.12	0.55	0.41	0.76		
<i>Reithrodontomys montanus</i> (S*, H*, S × H*)						
Summer	absent		0.05	0.16	0.03	0.11
Winter	0.09	0.29	0.24	0.39	0.17	0.34
Spring	0.10	0.32	0.16	0.33	0.13	0.32
Total	0.06	0.24	0.15	0.31		

* $P > 0.05$, ** $P \leq 0.05$.

TABLE 3.—Results of analyses of habitat association for selected species of rodents in each of 3 seasons. Proportions of captures in blowouts are reported for each species in each season. Replicated goodness-of-fit tests were conducted in all cases, in which total, pooled, and heterogeneity G -statistics are reported. If only a total G -statistic is listed, then simple G -tests using Williams’ correction are reported because of small sample sizes (Sokal and Rohlf 1981).

Season	Proportion of captures in blowouts	G -statistics		
		Total	Pooled	Heterogeneity
<i>Dipodomys ordii</i>				
Summer	0.59	44.6****	9.5****	35.1****
Winter	0.42	45.3****	24.7****	20.6**
Spring	0.45	26.1***	12.8****	13.3*
<i>Perognathus flavescens</i>				
Summer	0.22	45.6****	39.1****	6.5*
Winter	0.05	18.0****		
Spring	0.17	41.4****	36.8****	4.6*
<i>Onychomys leucogaster</i>				
Summer	0.38	69.7****	6.3**	63.4****
Winter	0.15	181.5****	150.7****	30.8****
Spring	0.37	56.9****	21.1****	35.8****
<i>Peromyscus</i>				
Winter	0.24	7.2***		
Spring	0.24	6.5**		
<i>Reithrodontomys montanus</i>				
Winter	0.15	10.6***		

* $P > 0.05$, ** $0.05 \geq P > 0.01$, *** $0.010 \geq P > 0.001$, **** $P \leq 0.0001$.

Only *D. ordii*, *P. flavescens*, and *O. leucogaster* were captured frequently enough to warrant analysis. *D. ordii* demonstrated a preference for blowouts (pooled $G = 9.45$, $d.f. = 9$, $P = 0.002$; Table 3); however, this preference was not consistent across replicates because 1 site had a significantly higher proportion of captures in the matrix (heterogeneity $G = 35.14$, $d.f. = 9$, $P < 0.001$; Table 3). In contrast, *P. flavescens* was captured more frequently in the matrix than in blowouts (pooled $G = 39.13$, $d.f. = 9$, $P < 0.001$; Table 3), and this preference was consistent across sites (heterogeneity $G = 6.474$, $d.f. = 9$, $P =$

0.692; Table 3). *O. leucogaster* showed a preference for matrix (pooled $G = 6.32$, $d.f. = 9$, $P = 0.012$; Table 3), but this preference was not consistent across sites because more captures occurred in the blowout at 1 site (heterogeneity $G = 63.42$, $d.f. = 9$, $P < 0.001$; Table 3).

Because of considerations of abundance, replicated goodness-of-fit tests for winter were conducted only for *D. ordii* and *O. leucogaster*. *D. ordii* showed a preference for matrix (pooled $G = 24.73$, $d.f. = 9$, $P < 0.001$; Table 3), but magnitude of preference was not consistent across sites (heterogeneity $G = 20.57$, $d.f. = 9$, $P = 0.015$; Table 3). Similarly, *O. leucogaster* showed a preference for matrix (pooled $G = 150.67$, $d.f. = 9$, $P < 0.001$; Table 3), and degree of habitat preference differed among sites (heterogeneity $G = 30.81$, $d.f. = 9$, $P < 0.001$; Table 3). G -tests for goodness of fit, modified using Williams' correction (Sokal and Rohlf 1981), were conducted for those species that were not captured at all sites but had high overall capture frequencies (*P. flavescens*, *R. montanus*, and *Peromyscus*). All 3 taxa showed a significant preference for the matrix (Table 3).

Replicated goodness-of-fit tests were conducted for species captured frequently enough during spring in each site to facilitate analysis (*D. ordii*, *P. flavescens*, and *O. leucogaster*). *D. ordii* showed a preference for the matrix (pooled $G = 12.81$, $d.f. = 9$, $P < 0.001$; Table 3) that was consistent across sites (heterogeneity $G = 13.27$, $d.f. = 9$, $P = 0.151$; Table 3). Similarly, *P. flavescens* demonstrated a preference for the matrix (pooled $G = 36.82$, $d.f. = 9$, $P < 0.001$; Table 3) that was the same regardless of site (heterogeneity $G = 4.59$, $d.f. = 9$, $P = 0.869$; Table 3). *O. leucogaster* exhibited a preference for the matrix (pooled $G = 21.09$, $d.f. = 9$, $P < 0.001$; Table 3). However, this preference was inconsistent among sites because proportion of captures in 1 blowout was higher than in the corresponding matrix (heterogeneity $G = 35.80$, $d.f. = 9$, $P < 0.001$; Table 3). *Peromyscus*

was captured more often in the matrix, according to a G -test for goodness of fit for total captures (Table 3).

DISCUSSION

Habitat associations of rodents in the sand-shinnery-oak system provide mixed support for the habitat-heterogeneity hypothesis. Our results and those of others (Brown 1989; Price 1978) indicate that habitat selection and the spatial organization of diversity are seasonally variable. *D. ordii* preferred blowouts only in summer, whereas other species demonstrated preferences for the matrix in all seasons. This could be a consequence of biotic interactions concerning *D. ordii* or could reflect a community-level response to the distribution of resources.

Biotic interactions.—Competition or predation could be invoked to explain habitat shifts by *D. ordii*. Every species in the rodent community, with the exception of *D. ordii*, has a generalized body plan (Rosenzweig 1973) that may be better adapted for foraging in the matrix; these species can have a strong effect on *D. ordii* via diffuse competition (Pianka 1974). The fact that populations of *P. flavescens* were highest in the summer (Table 2) is consistent with a competitive explanation, as has been suggested in other studies (Brown 1989; Price 1978; Rosenzweig 1973; Rosenzweig and Winakur 1969). *D. ordii*, the only bipedal rodent in the community, may use blowouts efficiently when denied access to the sand-shinnery oak (Brown 1989; Thompson 1982). However, food resources are common in summer, likely resulting in weak competitive pressures at that time. In addition, the observation that *D. ordii* was associated with oak habitat in winter, when resources are most limiting, is not consistent with a competitive explanation.

Although this study was not designed to examine density-dependent habitat selection, a form of isodar analyses based on multiple regression can be used to assess the relationship between densities of spe-

cies in different habitat types (Morris 1989a; Ovadia and Abramsky 1995; Rosenzweig and Abramsky 1997). In this case, the number of kangaroo rats in the blowouts can be explained by the number of quadrupedal rodents and kangaroo rats in the matrix. On the basis of isodar analyses (P -values corrected for multiple comparisons using Bonferroni's sequential adjustment—Rice 1989), no single species had an effect on abundance of *D. ordii* in blowouts in any season. The same nonsignificant result occurred from the perspective of diffuse competition (i.e., all other rodents). However, the power of these tests was low (0.059–0.659). If competitive effects are real, a much larger number of blowouts need to be sampled to statistically demonstrate these effects.

Risk of predation affects habitat selection in desert rodents (Bouskila 1995; Kotler 1984; Price et al. 1984). Predation by snakes may be the most plausible explanation for the switch in habitat association by *D. ordii*. Because of thermoregulatory constraints at other times, summer is the peak period of snake activity and the only season when snakes were encountered in the study area. Kangaroo rats may alter their behavior to avoid these predators. Brown (1989) found similar results: *D. merriami* switched habitat preferences to open habitats in summer, the period when rattlesnake activity was highest.

Distribution of resources.—All other rodent species in the sand–shinnery-oak system avoided blowouts, regardless of season. This may be a response to heterogeneous distribution of resources. In fact, edges may alter resource distributions by acting as a sink for seeds that are relocated from blowouts through wind action. Consequently, edges may contain more resources than either of the other 2 habitats because seeds collect under shrubs along the perimeter of blowouts. As a result, the edge may attract more individuals of granivorous species, and these individuals may wander into both blowouts and sand–shinnery-oak habitats

while foraging. This would homogenize the distribution of species in each habitat, frequently masking habitat associations. Overall, species may avoid blowouts but use resource-rich edges. Thus, the presence of blowouts may be important because the edge they create alters resource distributions.

The absence of distinct habitat preferences by rodent species in the sand–shinnery-oak system differs from results of other studies of rodents in semiarid systems, in which species demonstrate preferences for open microhabitats (Kotler and Brown 1988). This discrepancy may be a consequence of a reversal of the dominant habitat type. In deserts, open space is dominant, with small patches of shrubs; in the sand–shinnery-oak system, shrub-dominated matrix is pervasive, with small patches of open space. This may have an important effect on composition of the rodent community. Because open space in the sand–shinnery-oak system occupies a small areal proportion of the landscape, species such as *D. spectabilis* cannot successfully specialize on blowouts and still persist in the system.

Scale affects diversity and habitat selection (Jorgensen and Demarais 1999; Lyons and Willig 1999, 2002; McIntyre 1997; Morris 1989b; Poizat and Pont 1996). Indeed, discovering the scale at which animals perceive the environment is essential in understanding community structure. Likewise, considerations of scale may affect detection of habitat associations. Many of the species in the sand–shinnery-oak system have home range sizes that are greater than the size of the blowouts (Garner 1974; McCarty 1978; Wilkins 1986). Additionally, distances between blowouts are smaller than reported sizes of home ranges; so several blowouts may be encountered by an individual during its daily activities. Consequently, species may not be associated clearly with distinct habitats because individuals traverse both habitat types.

Even though blowouts are too small to support populations, they may still have im-

portant effects on population structure. Blowouts could be viewed as patches within a landscape that are sink habitats, unable to support growing populations, whereas the matrix is a source area, allowing species to persist (*sensu* Danielson 1991). The presence of blowouts within an individual's home range may increase overall habitat quality by contributing some resource or feature necessary for persistence, such as unique food types, or space for behavioral activities, such as dustbathing (Eisenberg 1963). However, the importance of blowouts may not be reflected in habitat associations, *per se*, especially if the amount of time spent in a given habitat is disproportional to the importance of that habitat for survival.

Although habitat-specific changes in species composition were not detected in this study, inclusion of species abundances revealed differences in species diversity between habitats (Cramer 1998). Nonetheless, it is unclear whether habitat associations are the major mechanism affecting species diversity. Behaviorally oriented studies are necessary to resolve more precisely how blowouts contribute to the persistence and diversity of rodents in this system.

ACKNOWLEDGMENTS

This study could not have been completed without the help of many people, especially A. Acrey and D. Hall. Additionally, S. Cox, J. Dever, D. Hart, J. Homan, C. López-González, E. Richards, J. Roberts, R. Stevens, M. Stringer, and D. Yee assisted in the field. Some traps were provided by M. Rylander, and F. Yancey helped with taxonomic identification of rodents. R. Bradley provided advice concerning field techniques, and C. Jones and M. McGinley were instrumental in developing the project. We also thank J. Fitzgerald, C. Caswell, and J. Grey for allowing access to their land. Comments on earlier versions of this manuscript were provided by C. Bloch, G. Cameron, S. Cox, S. Presley, J. Roberts, and 2 anonymous reviewers. M. J. Cramer was supported by the Department of Biological Sciences at Texas Tech University

through various teaching assistantships and a summer minigrant.

LITERATURE CITED

- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- BOUSKILA, A. 1995. Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology* 76:165–178.
- BOWERS, M. A., D. B. THOMPSON, AND J. H. BROWN. 1987. Spatial organization of a desert rodent community: food addition and species removal. *Oecologia* 72:77–82.
- BROWN, J. S. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. *Ecological Monographs* 59:1–20.
- BROWN, J. S., B. P. KOTLER, AND W. A. MITCHELL. 1994. Foraging theory, patch use, and the structure of a Negev desert granivore community. *Ecology* 75:2286–2300.
- CARLEY, C. J., E. D. FLEHARTY, AND M. A. MARES. 1970. Occurrence and activity of *Reithrodontomys megalotis*, *Microtus ochrogaster*, and *Peromyscus maniculatus* as recorded by a photographic device. *Southwestern Naturalist* 15:209–216.
- COLBERT, R. L. 1986. The effect of the shrub component on small mammal populations in a sand shinnery oak ecosystem. M.S. thesis, Texas Tech University, Lubbock.
- CRAMER, M. J. 1998. The effects of spatial and temporal heterogeneity on rodent diversity in a semi-arid environment. M.S. thesis, Texas Tech University, Lubbock.
- DANIELSON, B. J. 1991. Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. *American Naturalist* 138:1105–1120.
- DAVIS, W. B., AND D. J. SCHMIDLY. 1994. The mammals of Texas. Texas Parks and Wildlife Press, Austin.
- DHILLION, S. S., M. A. MCGINLEY, C. F. FRIESE, AND J. C. ZAK. 1994. Construction of sand shinnery oak communities of the Llano Estacado: animal disturbances, plant community structure, and restoration. *Restoration Ecology* 2:51–60.
- EISENBERG, J. F. 1963. The behavior of heteromyid rodents. University of California Publications in Zoology 69:1–100.
- GARNER, H. W. 1974. Population dynamics, reproduction, and activities of the kangaroo rat, *Dipodomys ordii*, in western Texas. Graduate Studies, Texas Tech University 7:1–28.
- GRANT, W. E., AND E. C. BIRNEY. 1979. Small mammal community structure in North American grasslands. *Journal of Mammalogy* 60:23–36.
- HALL, D. L., AND M. R. WILLIG. 1994. Mammalian species composition, diversity, and succession in conservation reserve program grasslands. *Southwestern Naturalist* 39:1–10.
- HESKE, E. J., J. H. BROWN, AND S. MISTRY. 1994. Long-term experimental study of a Chihuahuan Desert ro-

- dent community: 13 years of competition. *Ecology* 75:438–445.
- HOLLAND, M. 1994. Disturbance, environmental heterogeneity, and plant community structure in a sand shinnery oak community. M.S. thesis, Texas Tech University, Lubbock.
- JORGENSEN, E. E., AND S. DEMARAIS. 1999. Spatial scale dependence of rodent habitat use. *Journal of Mammalogy* 80:421–429.
- KAUFMAN, D. W., AND E. D. FLEHARTY. 1974. Habitat selection by nine species of rodents in north-central Kansas. *Southwestern Naturalist* 18:443–452.
- KOTLER, B. P. 1984. Risk of predation and the structure of desert rodent communities. *Ecology* 65:689–701.
- 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.
- LACHER, T. E., JR., AND C. J. R. ALHO. 1989. Microhabitat use among small mammals in the Brazilian Pantanal. *Journal of Mammalogy* 70:396–401.
- LYONS, S. K., AND M. R. WILLIG. 1999. A hemispheric assessment of scale dependence in latitudinal gradients of species richness. *Ecology* 80:2483–2491.
- LYONS, S. K., AND M. R. WILLIG. 2002. Species richness, latitude, and scale-sensitivity. *Ecology* 83:47–58.
- MACARTHUR, R. H., AND J. W. MACARTHUR. 1961. On bird species diversity. *Ecology* 42:594–598.
- MARES, M. A., K. E. STREILEIN, AND M. R. WILLIG. 1981. Experimental assessment of several population estimation techniques on an introduced population of eastern chipmunks. *Journal of Mammalogy* 62:315–328.
- MARTIN, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* 79:656–670.
- MCCARTY, R. 1978. *Onychomys leucogaster*. *Mammalian Species* 87:1–6.
- MCINTYRE, N. E. 1997. Scale-dependent habitat selection by the darkling beetle *Eleodes hispilabris* (Coleoptera: Tenebrionidae). *American Midland Naturalist* 138:230–235.
- MORRIS, D. W. 1989a. Habitat-dependent estimates of competitive interaction. *Oikos* 55:111–120.
- MORRIS, D. W. 1989b. The effect of spatial scale on patterns of habitat use: red-backed voles as an empirical model of local abundance for northern mammals. Pp. 23–32 in *Patterns in the structure of mammalian communities* (D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds.). Texas Tech University Press, Lubbock.
- MOULTON, M. P., J. R. CHOATE, S. J. BISSELL, AND R. A. NICHOLSON. 1981. Associations of small mammals on the central high plains of eastern Colorado. *Southwestern Naturalist* 26:53–57.
- O'FARRELL, M. J., D. W. KAUFMAN, AND D. W. LUNDAHL. 1977. Use of live-trapping with the assessment line method for density estimation. *Journal of Mammalogy* 58:575–582.
- OVADIA, O., AND Z. ABRAMSKY. 1995. Density-dependent habitat selection: evaluation of the isodar method. *Oikos* 73:86–94.
- PLANKA, E. R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences* 71:2141–2145.
- POIZAT, G., AND D. PONT. 1996. Multi-scale approach to species-habitat relationships: juvenile fish in a large river section. *Freshwater Biology* 36:611–622.
- PRICE, M. V. 1978. The role of microhabitat in structuring desert rodent communities. *Ecology* 59:910–921.
- PRICE, M. V., N. M. WASER, AND T. A. BASS. 1984. Effects of moonlight on microhabitat use by desert rodents. *Journal of Mammalogy* 65:353–356.
- REBAR, C., AND W. CONLEY. 1983. Interactions in microhabitat use between *Dipodomys ordii* and *Onychomys leucogaster*. *Ecology* 64:984–988.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- RICH, S. M., C. W. KILPATRICK, J. L. SHIPPEE, AND K. L. CROWELL. 1996. Morphological differentiation and identification of *Peromyscus leucopus* and *P. maniculatus* in northeastern North America. *Journal of Mammalogy* 77:985–991.
- ROSENZWEIG, M. L. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. *Ecology* 54:111–117.
- ROSENZWEIG, M. L. 1981. A theory of habitat selection. *Ecology* 62:327–335.
- ROSENZWEIG, M. L. 1991. Habitat selection and population interactions: the search for mechanism. *American Naturalist* 137:S5–S28.
- ROSENZWEIG, M. L., AND Z. ABRAMSKY. 1997. Two gerbils of the Negev: a long-term investigation of optimal habitat selection and its consequences. *Evolutionary Ecology* 11:733–756.
- ROSENZWEIG, M. L., AND J. WINAKUR. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* 50:558–572.
- SNYDER, E. J., AND L. B. BEST. 1988. Dynamics of habitat use by small mammals in prairie communities. *American Midland Naturalist* 119:128–136.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2nd ed. W. H. Freeman and Company, New York.
- SPSS, INC. 1988. *SPSS-X advanced statistics guide*. 2nd ed. SPSS, Inc., Chicago, Illinois.
- STREUBEL, D. P., AND J. P. FITZGERALD. 1978. *Spermophilus spilosoma*. *Mammalian Species* 101:1–4.
- THOMPSON, S. D. 1982. Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents. *Ecology* 63:1303–1312.
- WILKINS, K. T. 1986. *Reithrodontomys montanus*. *Mammalian Species* 257:1–5.
- WILLIG, M. R., R. L. COLBERT, R. D. PETIT, AND R. D. STEVENS. 1993. Response of small mammals to conversion of a sand shinnery oak woodland into a mixed mid-grass prairie. *Texas Journal of Science* 45:29–43.
- WILLIG, M. R., AND M. A. MCGINLEY. 1999. The response of animals to disturbance and their roles as agents of disturbance. Pp. 651–675 in *Ecology of disturbed ground* (L. R. Walker, ed.). Elsevier Science, Amsterdam, The Netherlands.

Submitted 6 February 2001. Accepted 3 December 2001.

Associate Editor was Thomas J. O'Shea.