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THE ROLE OF MICROHABITAT IN STRUCTURING DESERT RODENT COMMUNITIES[1]

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Abstract. Interspecific competition is thought to be important in determining patterns of resource use and species abundances in natural communities. However, there have been few field tests of competition-based models of community structure. In this study, experiments were conducted with 4 coexisting desert rodent species to see whether competition is a sufficient explanation for their resource use and abundance patterns. Results were consistent with 3 predictions from competition theory. (1) The 4 species differed in their use of a resource, foraging microhabitat, which is potentially limiting to their populations. (2) Each species shifted its use of microhabitats in predicted directions when competitors were removed from or added to outdoor enclosures. (3) Each species was most dense where its preferred microhabitat was abundant, and augmentation of 1 microhabitat led to an increase in the density of the appropriate microhabitat specialist. These results suggest that competition maintains interspecific differences in foraging microhabitat, and that the availability of appropriate microhabitats determines species abundances on a local scale.

Key words: Arizona; community structure; desert rodents; Dipodomys; *enclosure experiments; microhabitat partitioning; niche shifts;* Perognathus; *resource competition; rodents; vegetation manipulation.*

INTRODUCTION

What are the forces determining the species composition of natural communities? This is a central question in ecology, and one whose answer could, in the least tractable of all worlds, be different for each system examined. The hope of ecologists is that a relatively few factors can be built successfully into a predictive general theory of the number and relative abundance of species.

Much recent theoretical treatment of community structure (Levins 1968, MacArthur 1972, May 1973) has followed the pioneering work of Volterra (1928), Lotka (1925), and Gause (1934) in postulating that interspecific competition, the mutually detrimental sharing by 2 species of 1 scarce resource, can be of primary importance in limiting the growth of natural populations. This assumption yields a series of predictions about the number and relative abundances of competitor species that can coexist on a finite array of resources. Because it is difficult to identify and measure the resource(s) for which species compete and the manner in which populations interact, models of competition—and the community structure predictions to which they lead—have only recently begun to be tested experimentally (e.g., Yeaton and Cody 1974; Pulliam 1975; Werner and Hall 1976, 1977; Titman 1976; Tilman 1977). Further tests are needed before we can assess the extent to which competitive interactions explain patterns of species diversity.

It should be possible to detect the influence of competition on natural communities by assessing whether patterns of resource use and species abundances fit those predicted by theory. Three predicted general effects of resource competition are (Schoener 1974):

1) Coexisting species should differ in the way they use a scarce resource (MacArthur and Levins 1967, Seaton and Antonovics 1967, Allard and Adams 1969, Lawlor and Maynard Smith 1976, Roughgarden 1976). Such differences could result from local extinction of species too similar to others, or from competition-mediated selection favoring individuals that differ from interspecific competitors in the way they use resources.

2) If competitive interactions currently maintain divergent specializations among similar species, then resource use by 1 species should shift in predictable ways when competitor densities change (Miller 1967, Vandermeer 1972, Colwell and Fuentes 1975, Lawlor and Maynard Smith 1976).

3) The abundances of coexisting resource competitors should be related to resource abundances so that the total resource utilization of the community fits the resource-availability curve (MacArthur 1970, 1972; May 1973).

The research reported here provides a qualitative test of these 3 predictions with heteromyid rodent species that coexist in desert areas near Tucson, Arizona, USA. Although there is considerable evidence that interspecific competition has molded patterns of resource use and species composition in heteromyid communities, much of it is indirect and observational. From regular spacing of body size among coexisting species, Brown (1973, 1975) inferred that heteromyids partition a size-related resource. Rosenzweig and Winakur (1969) correlated rodent species diversity with complexity of soil and vegetation in Arizona study sites. From this they postulated that the rodents

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subdivide a habitat resource, and that increased habitat complexity enhances rodent diversity by providing suitable habitats for a variety of species. Additional studies (Brown and Lieberman 1973, Wondolleck 1978, Rosenzweig et al. 1975, Lemen 1978) documented in more detail species-specific habitat or microhabitat preferences, and Rosenzweig (1973) showed that 2 species respond differentially to habitat manipulations. Competitive interactions may indeed be important in maintaining preferences and in regulating rodent diversity, but these studies generally lack experimental evidence that this is the case.

In this paper, I present more such experimental evidence. First, I use trapping data from intact 4- and 2-species heteromyid communities to document that coexisting species partition foraging microhabitats. Next, I show that predictable shifts in microhabitat use accompany addition or removal of competitors in outdoor enclosures. This suggests that competitive interactions maintain divergent microhabitat specializations. Finally, I show that augmentation of 1 microhabitat type in a natural community results in predictable shifts in rodent densities.

Throughout this paper I refer to foraging microhabitat as a resource, although it is obscure how microhabitat could limit the growth of heteromyid populations directly. In all probability, structural microhabitats are important to rodents indirectly because they differ in the density, dispersion, or kind of food they contain, and thus, in the energetic costs of foraging in them. Because it is easy to measure, microhabitat use by rodents is a convenient first approximation to their use of other, perhaps more directly limiting, resources.

The Study Area and Species Descriptions

Experiments were carried out at 950-m elevation on ungrazed portions of the Santa Rita Experimental Range (USDA), 50 km south of Tucson, Arizona. The complex vegetation of the study area is classified as Lower Sonoran Desert–Desert Grassland Transition (Lowe 1964), and contains scattered trees (*Prosopis juliflora* and 2 *Cercidium* spp.), large shrubs (*Celtis pallida, Acacia greggii, Ephedra trifurca*), small shrubs (*Haplopappus tenuisectus, Baccharis brachyphylla, Zinnia pumila*), grass clumps (*Aristida* spp., *Andropogon barbinodis, Tricachne californica, Stipa neomexicana*), and periodically abundant low annual plants. Surface soil also is heterogeneous in this region, as washes dissect the bajada and pebbly wash banks alternate with fine sandy soil on small plateaus.

In this area the rodent fauna is dominated by the Heteromyidae, a New World family of nocturnal burrowing rodents. Four heteromyid species are abundant on the Santa Rita Range and are so distributed that all of the 4 can be caught at a single trap position. They include a kangaroo rat (*Dipodomys merriami*) and 3 pocket mice (*Perognathus amplus, Perognathus penicillatus,* and *Perognathus baileyi*), which conform qualitatively to the regular body-size spacing pattern discussed by Brown (1973, 1975) (Fig. 1). Several cricetid rodents (*Neotoma albigula,* 3 *Peromyscus* spp., *Onychomys torridus,* and 3 *Reithrodontomys* spp.),

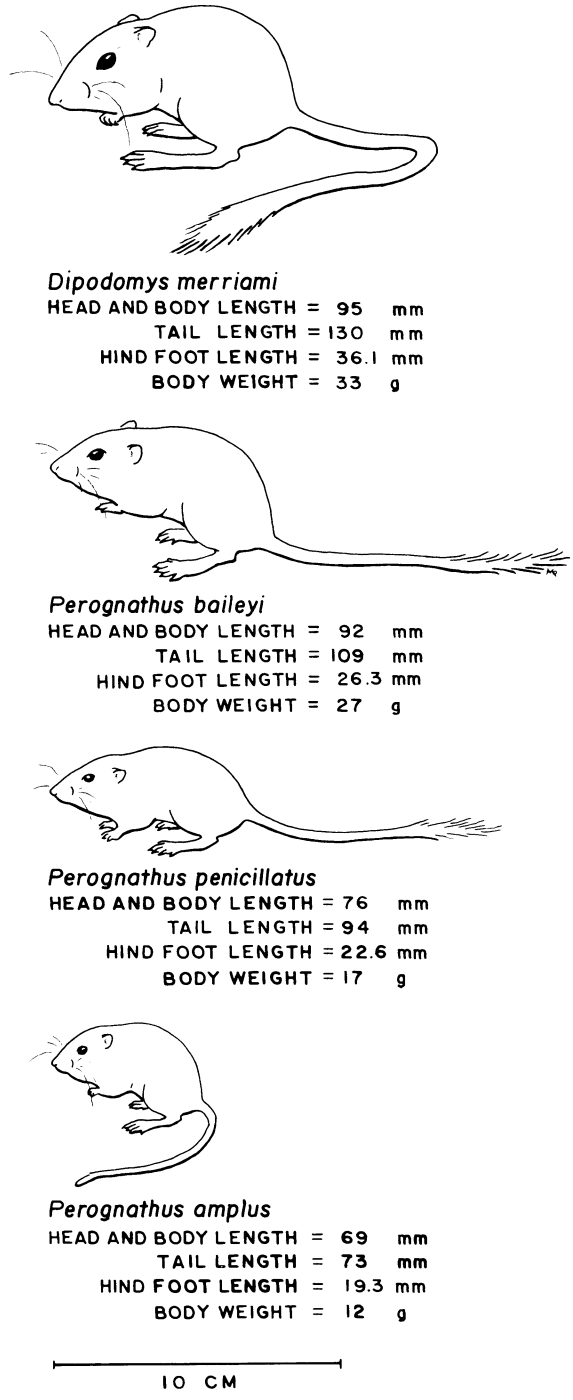

FIG. 1. Body size and morphology of the 4 heteromyid rodent species common to the study site. Body measurements are the means of 10 specimens (equal numbers of ♂♂ and ♀♀) taken from the study area.

and 1 sciurid rodent (*Ammospermophilus harrisii*) occur in the area but altogether comprised <10% of all individuals caught. The most numerous cricetid species, *Onychomys torridus*, is locally abundant, but was excluded from study because its primarily insectivorous diet is very different from that of the granivorous heteromyids.

Subdivision of Foraging Microhabitats by Coexisting Rodent Species

I first tested the prediction that coexisting rodents should differ in their use of microhabitats if foraging space is, or is correlated with, a limiting resource. The test consisted of observing whether there were interspecific differences in microhabitat use in an intact 4-species community.

Methods

I measured microhabitat use by placing equal numbers of live traps in 4 qualitatively distinct microhabitats and tallying microhabitat-specific capture frequencies for each rodent species. This provided a measure of the frequency with which each species foraged in different microhabitats, because foraging effort and capture frequency are strongly correlated in heteromyids (Price 1977).

Rodent activity was sampled on a 60-m × 135-m grid consisting of 33 stations arranged in 4 lines with 15-m intervals between stations. Four 25 × 10 × 10 cm rectangular metal live traps were placed within a 5-m radius of the center of each station, 1 in each of 4 microhabitats. I chose microhabitat categories which would sample many of the structural vegetation features that might be distinguished by a rodent while foraging for seeds on the ground, ignoring vertical categories because preliminary data suggested that heteromyids in this area rarely climb. The other 4 were defined as follows: "large open" (a space of bare ground at least 2 m in diameter), "small open" (a space of bare ground between 0.25 and 0.5 m in diameter), "large bush" (the ground under a shrub at least 1 m tall and 2 m in diameter), and "tree" (the ground under a *Prosopis* or *Cercidium* tree at least 1.7 m tall). All traps were placed carefully to sample as consistently as possible the defined microhabitats.

I estimated the overall availability of each microhabitat by making radial line transects 8 m long in 4 compass directions from the center of each trapping station, and averaging estimates of percent cover over the whole grid. I sampled rodent microhabitat use for 12 nonconsecutive nights during the period 6 June to 30 September 1974, and for 6 nonconsecutive nights during the following November, December, and January. Traps were baited with rolled oats at dusk, checked at 2200 h and 0600 h, and then closed for the day. During the winter months, they were checked and closed at 2200 h to avoid torpor deaths. Animals were toe-clipped for individual recognition and each capture event was scored for species, individual, station, and microhabitat. The intensity with which each species used each microhabitat was expressed as the relative number of captures, and of individuals, recorded in each category during a season's trapping.

Results

Relative microhabitat availability on the 33-station grid was as follows: large open, 0.29; small open, 0.44; large bush, 0.10; tree 0.17. Proportional use of these microhabitats was calculated for each rodent species from the distributions both of total captures and of individuals. However, because microhabitat distributions measured in the 2 ways were homogeneous ($X < 2$, df = 3, $p > .5$ for all species), and because "total captures" data yield larger sample sizes than "individuals" data, only the former are considered in the analyses that follow (Fig. 2).

During the summer season, no species except perhaps *P. baileyi* was equally active in the 4 microhabitats ($X > 17$, $p < .005$ for *D. merriami*, *P. amplus*, and *P. penicillatus*; $X = 7.67$, $p = .055$ for *P. baileyi*), nor did capture frequencies reflect the availability of microhabitats on the grid ($X > 11$, df = 3, $p < .025$ for all species). The 4 species differed in their overall summer microhabitat use ($X = 112$, df = 9, $p < .005$) (Fig. 2). *Dipodomys merriami* was most active in large open spaces, and *Perognathus amplus* in small open spaces. *Perognathus penicillatus* and *P. baileyi* were most active in the same microhabitats, both preferring large bushes and trees.

Microhabitat use did not change during June, July, August, and September. However, winter capture distributions of the 2 winter-active species, *D. merriami* and *P. baileyi*, were significantly different from summer distributions ($X > 9.3$, df = 3, $p < .025$ for both species) (Fig. 2). Despite shifts in activity, both species maintained distinct capture distributions ($X = 22$, df = 3, $p < .005$) and distinct preferred microhabitats; small open spaces in the case of *D. merriami* and large bushes in the case of *P. baileyi*. These seasonal shifts are interesting in that both species increased use of microhabitats that had been preferred in the summer by another species; *P. amplus* had used small open spaces and *P. penicillatus* large bushes. Such shifts could result from seasonal differences in food distribution or from an increased energetic advantage to foraging in a sheltered microhabitat in the winter. They also could be due to reduced interspecific competition from hibernating species.

To summarize, these 4 heteromyid species were not caught randomly in 4 microhabitats. Each species maintained a capture distribution largely distinct from those of other simultaneously active rodents even though preferences shifted from summer to winter. These and previous data (Rosenzweig and Winakur

1969, Brown and Lieberman 1973, Rosenzweig 1973, Wondolleck 1978) indicate that heteromyid rodents partition microhabitats, and that such partitioning can be remarkably fine-tuned.

Microhabitat Use Shifts in Response to Changing Competitor Density

If competitive interactions currently maintain divergent microhabitat specializations, then specializations may be expected to diminish when competitors are removed, given that the animals retain sufficient behavioral flexibility. Conversely, specializations may become more marked when a competitor is added as a result of decreased use by each species of competitor-preferred microhabitats. I tested these predictions first by placing each species alone in artificial enclosures and comparing its microhabitat use under this condition to that in the intact community. Second, individuals of a competitor species were added to some enclosures, and microhabitat use of each species compared with that in control enclosures to which no competitors had been added.

Methods

I partitioned a pre-existing 1.84-ha rectangular rodent enclosure into 6 contiguous enclosures ranging in area from 0.26–0.34 ha. Partition walls consisted of aluminum window screening 1.4 m high that was buried 0.5 m in the soil and supported every 1.5 m by aluminum poles. Outside enclosure walls consisted of sheet, of the same height and buried similarly, that was supported by wooden stakes. The enclosures were situated immediately adjacent to the study grid described previously. The relative cover of trees, large bushes, small bushes, and grass was homogeneous between the 6 enclosures ($X = 19.6$, df = 15, $p > .1$) (Table 1), and between the enclosures as a whole and the adjacent unenclosed study grid ($X = 6.5$, df = 3, $p > .05$).

I removed all rodents resident in the enclosures prior to the start of the experiments. Experimental animals were collected in live traps from within 1.6 km of the enclosures and housed indoors in cages under a 12 h light:dark regime pending release in the enclosures. Individuals were maintained in the laboratory for varying lengths of time, but at most for 2 consecutive mo, and most rodents were kept <1 mo.

Because microhabitat use did not change significantly between June and September in the intact community, I felt that it was reasonable to initiate the enclosure experiments in April 1975, when the seeding of spring annuals was nearly over and hibernating *P. amplus* and *P. penicillatus* had emerged for the summer. Microhabitat use (measured as capture frequency) was determined for each species first at a density of 8 individuals per enclosure when no other species was present (Treatments 1a and b), second when 4 individuals of another species were present (Treatment 2), and finally when 8 individuals of the second species were present (Treatment 3). I chose *D. merriami*, the largest of the 4 species, as the competitor to be placed with each of the 3 *Perognathus* spp. as it seemed likely that this kangaroo rat would be behaviorally dominant over each of the smaller pocket mice (MacMillan 1964) and would elicit an especially noticeable response in microhabitat use. Table 2 summarizes the experimental design.

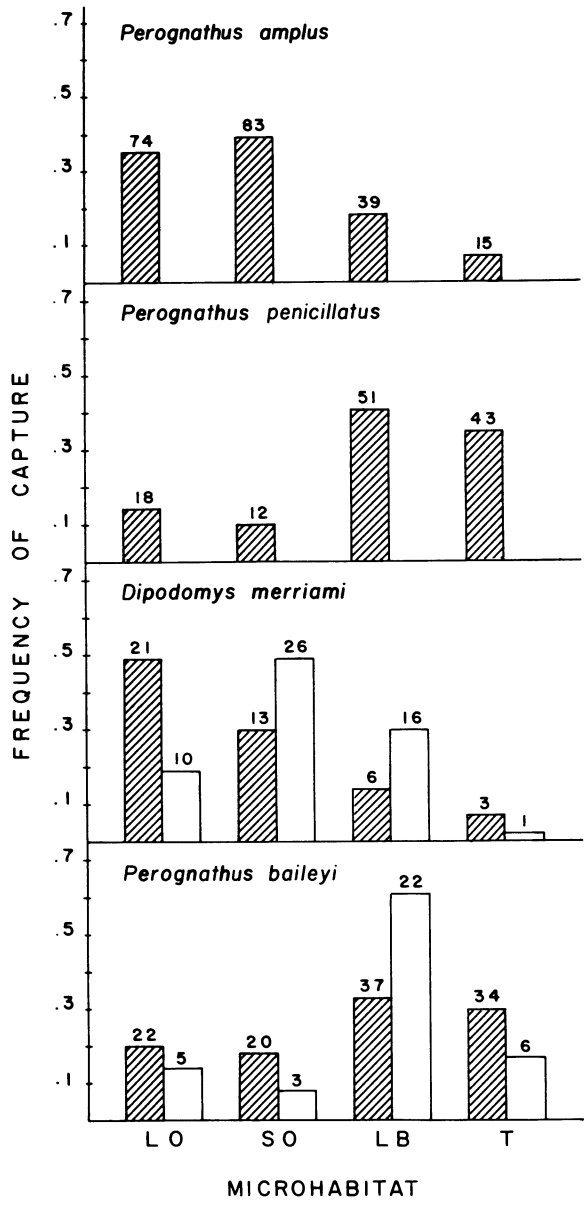

FIG. 2. Summer (cross-hatched bars) and winter (white bars) microhabitat distributions of 4 heteromyid rodent species. Only 2 species were winter-active. Relative capture frequencies in 4 microhabitats are given for the summer and winter sampling periods. Numbers above bars are the total captures obtained in each habitat. LO = large open; SO = small open; LB = large bush; T = tree.

TABLE 1. Size and vegetation characteristics of the enclosures. Grass and small bush cover was estimated from a 1-metre wide transect running the width of each enclosure. Tree and large bush cover was estimated by counting the number of each in an enclosure, multiplying by the mean canopy area of 10 randomly chosen individuals, and dividing by the area of the enclosure

Enclosure Number	Area (m^2)	Tree cover (%)	Large bush Cover (%)	Grass cover (%)	Small bush Cover (%)
1W	3150	14	3	12	5
2W	2847	9	2	22	8
3W	2700	8	2	12	5
1E	2868	12	2	12	8
2E	2559	10	2	15	8
3E	3431	13	1	8	15

In all enclosures, 8 traps were placed in each microhabitat. Trap positions were rotated every 4 nights and individuals were released at least 10 paces from capture locations to reduce their tendency to return immediately to known reward locations. Traps were baited with rolled oats at dusk and checked at 2200 h and 0600 h, except during April and May 1975 when they were closed at 2200 h. Animals were toe-clipped, and each capture event was scored for species, individual, trap location, and microhabitat. Traps were never set on rainy nights and never for more than 2 consecutive nights as captives tended to lose weight.

I continued each experimental treatment until at least 35 legitimate captures had been recorded in each enclosure (i.e., within-night recaptures of an individual at a trap and captures of escapees from other enclosures were not counted), keeping density variations releasing new animals to compensate for known mortality or for individuals that had not been captured for 4 consecutive trapping sessions. The occasional animals which escaped from 1 enclosure to another were re-established in the proper enclosure, or replaced if they proved to be habitual fence-climbers. The few unmarked animals that appeared in the enclosures were removed. After being added to the enclosures at the start of a treatment, animals were allowed 3 to 4 days to equilibrate in their new environment before sampling resumed. Only adults in good health were used in the experiments, and approximately equal numbers of males and females were maintained in each enclosure.

I chose enclosure densities to be consistent with normal field densities for the area. In the summer of 1975, there were ≈67 heteromyids per ha on the Santa Rita Range (M. Courtney, *personal communication*), which corresponds to ≈20 individuals per enclosure. The highest densities used were 16 individuals per enclosure. Because the rodents remained in excellent condition and even gained weight after being released from the laboratory, these were considered reasonable densities.

Although enclosures are known to influence rodent population dynamics (Krebs et al. 1969), they should not affect the factors which go into foraging microhabitat choices by optimally foraging rodents, e.g., microhabitat encounter rate and expected reward per microhabitat (MacArthur and Pianka 1966, Charnov 1976, Pulliam 1976). My enclosures probably con-

TABLE 2. Experimental design and timetable of the 1975 enclosure experiments. The species present at each time are given for each enclosure. *D. m.* = *Dipodomys merriami; P. a.* = *Perognathus amplus; P. p.* = *Perognathus penicillatus; P. b.* = *Perognathus baileyi*

	11 April	Treatment 1a (8 nights)	22 May	Treatment 1b (8 nights)	21 June	Treatment 2 (6 nights)	3 July	Treatment 3 (4 nights)	20 July
Enclosure Number	*D. m.* added to all enclosures		*D. m.* removed *Perognathus* added		4 *D. m.* added to experimental enclosures		4 more *D. m.* added to experimental enclosures		trapping ended
1W		8 *D. m.*		8 *P. a.*		8 *P. a.* + 4 *D. m.*		8 *P. a.* + 8 *D. m.*	
2W		8 *D. m.*		8 *P. a.*		8 *P. a.* (control)		8 *P. a.* (control)	
2E		8 *D. m.*		8 *P. p.*		8 *P. p.* + 4 *D. m.*		8 *P. p.* + 8 *D. m.*	
3W		8 *D. m.*		8 *P. p.*		8 *P. p.* (control)		8 *P. p.* (control)	
1E		8 *D. m.*		8 *P. b.*		8 *P. b.* + 4 *D. m.*		8 *P. b.* + 8 *D. m.*	
3E		8 *D. m.*		8 *P. b.*		8 *P. b.* (control)		8 *P. b.* (control)	

TABLE 3. The effect of competitor density on use of 4 microhabitats. The number and (in parentheses) the relative frequency of captures in each microhabitat are given for each species in enclosures and in the intact community. Intact community values are taken from Fig. 2. LO = large open; SO = small open; LB = large bush; T = tree

Species	Enclosure	Micro-habitat	Intact community	Treatment 1 11 Apr–21 Jun 1975	Treatment 2 21 Jun–3 Jul 1975	Treatment 3 3 Jul–20 Jul 1975
A. *Microhabitat use in experimental enclosures and in the unenclosed intact community*						
Dipodomys merriami	1W	LO	21 (.49)	17 (.31)	8 (.36)	24 (.49)
		SO	13 (.30)	10 (.18)	4 (.18)	10 (.20)
		LB	6 (.14)	19 (.35)	6 (.27)	12 (.24)
		T	3 (.07)	9 (.16)	4 (.18)	3 (.06)
	2E	LO		19 (.33)	5 (.25)	22 (.52)
		SO		23 (.40)	9 (.45)	11 (.26)
		LB		12 (.21)	5 (.25)	8 (.19)
		T		4 (.07)	1 (.05)	1 (.02)
	1E	LO		20 (.45)	11 (.31)	15 (.42)
		SO		8 (.18)	8 (.22)	10 (.28)
		LB		9 (.20)	12 (.33)	11 (.31)
		T		7 (.16)	5 (.14)	0 (.00)
Perognathus amplus	1W	LO	74 (.35)	26 (.31)	16 (.26)	6 (.17)
		SO	83 (.39)	22 (.26)	14 (.23)	11 (.31)
		LB	39 (.18)	22 (.26)	12 (.20)	11 (.31)
		T	15 (.07)	15 (.18)	19 (.31)	8 (.22)
Perognathus penicillatus	2E	LO	18 (.14)	24 (.30)	25 (.40)	6 (.18)
		SO	12 (.10)	20 (.25)	8 (.13)	10 (.30)
		LB	51 (.41)	22 (.28)	17 (.27)	9 (.27)
		T	43 (.35)	14 (.18)	12 (.19)	8 (.24)
Perognathus baileyi	1E	LO	22 (.20)	13 (.14)	16 (.21)	3 (.08)
		SO	20 (.18)	31 (.34)	22 (.29)	10 (.27)
		LB	37 (.33)	26 (.29)	22 (.29)	5 (.14)
		T	34 (.30)	21 (.23)	16 (.21)	19 (.51)
B. *Microhabitat use in control enclosures*						
Perognathus amplus	2W	LO		24 (.37)	14 (.31)	6 (.24)
		SO		20 (.31)	12 (.27)	7 (.28)
		LB		14 (.23)	12 (.27)	9 (.36)
		T		6 (.09)	7 (.16)	3 (.12)
Perognathus penicillatus	3W	LO		14 (.26)	18 (.31)	11 (.31)
		SO		7 (.13)	9 (.15)	4 (.11)
		LB		16 (.30)	17 (.29)	7 (.20)
		T		16 (.30)	15 (.25)	13 (.37)
Perognathus baileyi	3E	LO		20 (.24)	16 (.23)	9 (.17)
		SO		24 (.29)	18 (.26)	14 (.26)
		LB		25 (.30)	20 (.29)	20 (.37)
		T		15 (.18)	16 (.23)	11 (.20)

strained the total area traversed by individuals and may have contained relatively low densities of terrestrial predators. I do not know if this has any effect on the results.

Results

Results were compared with the following predictions. (1) In the absence of competitors (Treatments 1a and 1b), microhabitat specializations of each species should decrease; that is, captures should tend toward a uniform distribution with relative capture frequencies of .25 in all microhabitats. This means we expect each species to decrease use of microhabitats that contained >25% of all captures in the intact community, and to increase use of those that contained <25%. (2) When *D. merriami* is added to single-species populations of *Perognathus* (Treatments 2 and 3), microhabitat specializations should increase; that is, capture distributions of the 2 competitors should diverge by decreased use of microhabitats most preferred by the competitor and increased use of microhabitats least preferred by the competitor. It is difficult to predict what shifts, if any, should occur in microhabitats of intermediate preference. Because *D. merriami* highly prefers large open spaces, and also because it may be the behaviorally dominant member of the community, all *Perognathus* spp. should decrease their use of this microhabitat and compensate by increasing their use of others. In particular, they should increase use of tree microhabitats because *D. merriami* prefers these least of all. *Dipodomys merriami*, in turn, should respond to *Perognathus* spp. by increasing its use of large open spaces and decreasing its use of trees. The magnitudes of microhabitat shifts

TABLE 4. Magnitudes of between-treatment changes in capture frequencies of *Perognathus* spp. in large open and tree microhabitats as a function of enclosure type.—**Top:** mean magnitudes, standard deviations, and sample sizes of changes in control vs. experimental enclosures between treatments 1 and 2 (T1–T2), 1 and 3 (T1–T3), and 1, 2, and 3 (All). **Bottom:** results of a 2-way analysis of variance using values from all treatments normalized with an arcsin transformation

ENCLOSURE TYPE						
	Experimental			**Control**		
	T1–T2	T1–T3	All	T1–T2	T1–T3	All
$\bar{x}$	0.063	0.117	0.109	0.050	0.063	0.055
s	0.0463	0.0889	0.0828	0.0219	0.0392	0.0333
n	6	6	18	6	6	18

Source of Variation	df	F	P
Species	2	0.20	NS
Enclosure Type (control vs. experimental)	1	6.30	<.01
Interaction	2	1.07	NS
Error	30		

by *Perognathus* spp. should be greater at high than at low *D. merriami* density.

Shifts accompanying decreased competitor density.—Treatment 1 microhabitat use differed significantly from that in the intact community for the 3 *Perognathus* spp. ($X > 7.82$, df = 3, $p < .05$, pooling captures from replicate enclosures) but not for *D. merriami* ($X = 4.7$, df = 3, $p > .1$). Between-treatment comparisons of relative capture frequencies in each microhabitat show that, in general, each species decreased its use of microhabitats that contained >25% of its captures in the intact community, and increased its use of those that contained <25%. Thirty-two of 36 comparisons were in the predicted direction (Table 3), significantly more than would be expected if changes were in random directions (binomial $p = .003$). These changes resulted in more generalized and even use of microhabitats in the absence of competitors.

Despite these increases in the evenness of microhabitat use, the Treatment 1 microhabitat distributions of the 4 species remained significantly heterogeneous ($X = 28$, df = 9, $p < .005$, pooling captures from replicate enclosures). No species except *P. penicillatus* was caught equally often in all microhabitats when alone in the enclosures ($X > 8.4$, df = 3, $p < .05$ for 3 species, pooling captures from control and Treatment 1 enclosures). This implies that microhabitat preferences are not solely functions of competitive interactions, but are maintained to a lesser extent even in the absence of other species. Maintained preferences could reflect morphological and behavioral specializations that cause each species to forage more efficiently in some microhabitats than in others, or could be artifacts of the short time scale of the experiment.

Shifts in large open and tree microhabitats accompanying increased competitor density.—We can assess the effect on *Perognathus* spp. of increasing *D. merriami* numbers by comparing experimental and control enclosures with respect to both the magnitude and direction of changes in large-open and tree capture frequencies. For each *Perognathus* sp., the magnitudes of these changes were greater in experimental than in control enclosures, especially between treatments 1 and 3, and these differences were significant over all 3 species in a 2-way ANOVA (Table 4). The directions of changes for *Perognathus* spp. were not significantly different from random in either experimental or control enclosures between treatments 1 and 2. Three of 6 changes in experimental, and 4 of 6 in control enclosures were in expected directions. However, between treatments 1 and 3, directions of changes in use of large open and tree microhabitats were consistently in expected directions. In this case, 6 of 6 changes in experimental, and 3 of 6 in control enclosures were in expected directions. The binomial probability of 6 of 6 changes in expected directions occurring by chance alone is only .012. As expected, there appeared to be a larger response by *Perognathus* spp. to high than to low *D. merriami* density, with respect to both magnitude and directions of shifts in microhabitat use. In fact, there appeared to be a threshold *D. merriami* density below which there were no substantial microhabitat shifts.

Dipodomys merriami responded to the presence of *Perognathus* spp. by increasing use of large open spaces and decreasing use of trees. Between treatments 1 and 3, 5 of 6 changes were in these expected directions (binomial $p = .109$). Therefore, over all 4 species, 11 of 12 changes between treatments 1 and 3 in use of these microhabitats were in expected directions (binomial $p = .003$).

These effects cannot be artifacts of using traps to sample microhabitat use. It could be argued that reciprocal changes in capture frequencies of *D. merriami* and *Perognathus* spp. were due solely to saturation of traps in large open and tree microhabitats by members of the other species, because multiple captures in 1 trap were impossible. Suppose, for example, that kangaroo rats entered large-open traps preferentially before the less mobile pocket mice could find them. Were this to happen, *D. merriami* could make most of the large-open traps in enclosures unavailable, and all captures of *Perognathus* spp. would necessarily occur in traps placed in other microhabitats even if no changes occurred in their use of large open spaces. The magnitude of this effect can be estimated using the capture data in Table 3. Assuming that my perception of "similar microhabitat" is like that of a heteromyid, then changes in trap availability caused by *D. merriami* can be calculated for each enclosure as follows. Subtract the total *D. merriami* captures that occurred in each microhabitat during a treatment from

the total number of captures that were possible in that microhabitat (2 trap checks per night × 8 traps per microhabitat × the number of nights per treatment). This gives the minimum number of open traps potentially able to capture pocket mice during a treatment. The new relative availability of traps in a microhabitat is calculated by dividing this number by the number of available traps in all microhabitats. We can estimate similarly the effect of *Perognathus* spp. captures within each enclosure on the availability of traps to *D. merriami*.

If all between-treatment changes in capture frequencies in large open and tree microhabitats were caused solely by changes in the relative availabilities of unoccupied traps, their average magnitude would have been 0.024 ($s = 0.0202$, $n = 24$) for all species. Actual changes in experimental enclosures ($\bar{x} = 0.107$, $s = 0.0762$, $n = 24$) were significantly greater (using arcsin-transformed values, $t = 4.46$, df = 17, $p < .001$ for pooled *Perognathus* spp.; and $t = 4.95$, df = 5, $p < .01$ for *D. merriami* pooling experimental enclosures). Thus, changes in trap availability cannot account for the magnitudes of observed between-treatment changes in capture frequencies.

In summary, none of the 3 *Perognathus* spp. responded noticeably to a low density of *D. merriami*. However, high *D. merriami* density led to consistent reductions in their use of large open spaces and increases in use of trees. Magnitudes of these between-treatment shifts were significantly greater over all *Perognathus* species in experimental than in control enclosures. In turn, *D. merriami* increased its use of large open spaces and decreased its use of trees in the presence of *Perognathus* spp. These changes in microhabitat use agree with predictions from competition theory.

Response of Rodent Densities to Changing Availability of Foraging Microhabitats

Competition theory suggests that once competitive interactions have caused coexisting species to diverge in the subset of a resource spectrum each exploits efficiently, their equilibrium abundances should be determined by the shape of the curve of available resources (MacArthur 1970, 1972). I made a qualitative test of this prediction as follows.

In July 1975, I set up a 7 × 7 station grid with 30-m intervals between stations near the study area described in the first section of this paper. Vegetation and topographic heterogeneity was such that the grid covered a mosaic of intermixed microhabitat patches, and rodent abundances varied considerably between stations.

The study consisted of 2 phases. First, microhabitat abundances were measured and rodents censused at each of the 49 stations. Rodent densities were regressed on the principal components of microhabitat variables to see whether the abundance of the preferred foraging microhabitat of each species seemed to determine its local abundance. Second, the availability of large open spaces was increased at randomly selected stations, and rodents were again censused to see if this microhabitat manipulation changed the community inhabiting treated stations in a predictable way. Short-term increases in the abundance of *D. merriami*, the large open-space specialist, would indicate that rodent communities can adjust to changes in the spectrum of available microhabitats.

Methods

Rodents were censused before and after manipulation of large, open microhabitats for 7 nonconsecutive nights. The first census occurred from 27 June through 19 July 1975, and the second occurred 6 wk after manipulation from 9–20 September 1975. By the seventh night of each census, the number of unmarked rodents caught per night had levelled off at 13–16% of total per-night captures. Each station comprised 4 live traps spaced evenly in a circle 6 m from the center of the station. Trap positions were rotated counterclockwise by 2 m between trapping nights to reduce the impact of repeated returns by some individual rodents to a known reward location. Traps were rotated and baited with rolled oats at dusk, checked at 0600 h, and closed for the day. Animals were toe-clipped, and each capture event was scored for species, individual, and station. Data in final form were expressed by station as the total number of individuals of each species that were caught at least once during the 7-night census. For the postmanipulation census, the number of new individuals not previously recorded in July as well as the number of resident individuals disappearing between census periods were tallied also for each station.

After the premanipulation rodent census, 24 of the 49 grid stations were chosen from a random-numbers table for manipulation and the other 25 were left as controls for possible overall seasonal shifts in rodent activity or density. At each manipulated station, ½ of the bushes that were between 60 and 100 cm in height and had a canopy diameter >0.5 m were chopped off at ground level, and the brush hauled at least 100 m off the study grid. This was done by rotating a 10-m string around the center of each station and removing every other bush of appropriate size that the string contacted in its sweep. The gaps created by bush removal were big enough to qualify as large open spaces. The canopy diameter of each bush was recorded before its removal to provide an estimate of the total area of large open spaces added to each station. This averaged 4.3% of their area, so that an average of 2.34 m were added to the premanipulation mean (estimated from line transects) of 15.23 m large open spaces per manipulated station. Because the bush species chosen for removal (mostly *Haplopappus tenuisectus* and

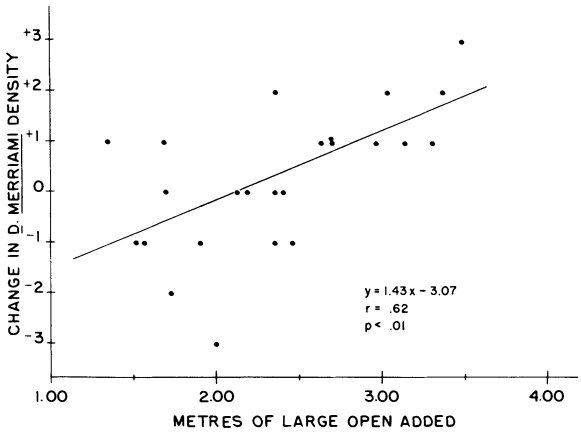

FIG. 3. Response of *Dipodomys merriami* to augmentation of large open spaces. The change in *D. merriami* density is measured as the number of individuals recorded at a station in the postmanipulation census minus the number recorded there in the premanipulation census.

Baccharis brachyphylla) did not produce seeds until after the 7-day postmanipulation rodent census, it was unlikely that their removal had any direct effect on overall seed density at manipulated stations.

Results

Premanipulation species compositions.—I summarize here the results from premanipulation correlations between rodent density and microhabitat availability. I will gladly supply more detailed descriptions of methodology and results on request.

TABLE 5. Species composition of manipulated and control stations before and after manipulation.—Means ($\bar{x}$) are expressed as the number of individuals recorded per station; s = standard deviation of the per-station number of individuals; N = total number of individuals recorded from manipulated or control stations, and (in parentheses) the percentage of all rodents which each species comprised

Species		Premanipulation		Postmanipulation	
		Manipulated stations	Control stations	Manipulated stations	Control stations
Dipodomys merriami	$\bar{x}$	1.417	1.360	1.708	1.240
	s	.970	.995	.954	1.268
	N	25 (21%)	28 (19%)	35 (32%)	28 (25%)
Perognathus amplus	$\bar{x}$	1.167	1.200	.750	.440
	s	.761	.913	.737	.651
	N	26 (22%)	29 (20%)	15 (14%)	11 (10%)
Perognathus penicillatus	$\bar{x}$	1.917	1.880	1.875	1.800
	s	1.472	1.641	1.035	1.190
	N	33 (28%)	38 (26%)	38 (35%)	39 (35%)
Perognathus baileyi	$\bar{x}$	1.667	2.280	1.000	1.360
	s	1.129	1.100	.722	.638
	N	35 (29%)	49 (34%)	20 (19%)	33 (30%)

All multiple regressions of rodent density on microhabitat availability were significant at the .04 level at least. For all 4 species, the variable with the highest positive regression coefficient reflected the availability of microhabitats that were preferred in the previous studies (Fig. 2). *Dipodomys merriami* was abundant in stations having many large open spaces. *Perognathus amplus* was abundant where scattered low bushes provided many small open spaces between bush canopies. *Perognathus penicillatus* was abundant in sandy-soil stations with trees, and *P. baileyi* was abundant in pebbly-soil stations with trees. These results suggest that the availability of preferred foraging microhabitats in part determines the local abundance of each of these species.

Postmanipulation species compositions.—The effect of the manipulation on microhabitat abundance was twofold, because bush cover was removed to create large open spaces. Because *D. merriami* strongly preferred and was associated with large open spaces, we predict it should increase in density in response to the manipulation. From the premanipulation regression equation, we further predict it should increase by $\approx$1.3 individuals per metre of large open space added. *Perognathus penicillatus* and *P. baileyi* should not respond strongly to the manipulation, because neither large open spaces nor small bushes were their preferred microhabitats. There is no unambiguous prediction for *P. amplus*, because the manipulation could have 2 opposite effects. On the one hand, removal of bushes from dense clumps probably creates some of the small open spaces preferred by this species; on the other hand, removal of scattered bushes converts existing small open spaces between bush canopies to large open spaces. These 2 effects should cancel one another to some extent, so that we predict at most a small net response by *P. amplus* to the manipulation.

Results were generally consistent with these predictions (Table 5). *Dipodomys merriami* increased in density by 21% at manipulated stations, but declined by 9% at control stations. These proportional changes were significantly different ($p < .005$, t-test of difference of proportions, Sokal and Rohlf 1969, p. 607), and postmanipulation mean density at manipulated stations was higher than at controls ($t = 1.48$, $p = .077$, 1-tailed). In addition, the changes in *D. merriami* density at manipulated stations were significantly ($r = .62$, $p < .01$) correlated with the amount of large open space added (Fig. 3); and the slope of this relationship (1.4 individuals per metre large open space) was very close to that predicted from the premanipulation multiple regression.

This increase in kangaroo rat density at manipulated stations relative to controls primarily resulted from selective invasion of these sites both by immigrants that had not been recorded on the grid in the first census and by individuals moving from control sta-

tions. At manipulated sites, the number of such invaders was significantly ($r = .48$, $p < .05$) correlated with the amount of large open space added. In addition, fewer individuals moved away from manipulated than from control stations (0.25 *versus* 1.04 individuals, $t = 3.95$, $p < .001$, 1-tailed).

In contrast to *D. merriami*, all 3 *Perognathus* spp. decreased in density at both station types. This decline was largely due to the beginning of their winter period of inactivity in September. The proportional decline in density was the same at both station types for *P. penicillatus* and *P. baileyi*, but slightly less at manipulated than control stations for *P. amplus* (-0.357 *versus* -0.633, $t = 1.96$, $p = .051$). Absolute changes in density and immigration and emigration rates were not significantly different between station types for any *Perognathus* spp., nor were they correlated with amount of large open space added to manipulated stations. *Perognathus amplus* may have responded indirectly to the manipulation by avoiding stations with increased *D. merriami* density because changes in *P. amplus* density were negatively correlated ($r = -.329$, $p < .05$) with those for *D. merriami*.

These results are consistent with predictions. *Dipodomys merriami* clearly responded to the manipulation by increasing in density. Although there may have been a response by *P. amplus* to the manipulation, it was small and perhaps an indirect effect of interactions with *D. merriami*. No other *Perognathus* spp. appeared to be influenced by increased availability of large open spaces.

The manipulation had a significant effect on the relative proportions of the 4 species inhabiting manipulated stations as a whole (Table 5). The proportion of *D. merriami* increased by 5% more in manipulated than in control sites, a change coincident with the 4% average increase in large open microhabitat at these stations. Overall, the species proportions changed significantly between censuses at manipulated ($X = 8.5$, $df = 3$, $p < .05$), but not at control stations.

These results substantiate the hypothesis that the species composition of this heteromyid rodent community can shift in a fine-tuned and predictable manner to accommodate small changes through time and space in the spectrum of available resources. Only *D. merriami* responded clearly to the augmentation of its preferred foraging microhabitat. This resulted in a rodent community having relatively more large open-space specialists than before, and therefore one which provided a better fit to the changed microhabitat availability curve at manipulated stations.

Discussion

The experiments reported here lend strong support to the hypothesis that interspecific competition molds patterns of resource use and relative abundance in heteromyid rodent communities. Their results show that accurate predictions of small variations in species abundances can be obtained by matching the resource utilizations of individual species to resource availability.

The findings of earlier studies that heteromyid distributions are correlated to vegetation (Rosenzweig and Winakur 1969, Rosenzweig et al. 1975, Reynolds 1950), that resource use differences exist between coexisting species (Brown and Lieberman 1973), and that faunal changes accompany changes in vegetation structure (Rosenzweig 1973, Beatley 1975), are in general agreement with those reported here. This agreement suggests that heteromyid communities may be structured by competition for foraging microhabitats throughout North American deserts.

Habitat availability may also control rodent abundances in nonheteromyid communities. Cricetid rodents compete for space (Grant 1972, Douglass 1976, Crowell and Pimm 1976), and habitat selection appears to be a major mechanism allowing regional coexistence of cricetid species with similar nutritional requirements (Grant 1972, M'Closkey and Fieldwick 1975).

The microhabitat utilizations measured in this study are very broadly overlapping. Real interspecific differences may be much larger for the following reasons: (1) Trapping methods do not measure foraging microhabitat precisely because a rodent can be captured while traveling through an inappropriate habitat patch to reach an appropriate one (Schroder and Rosenzweig 1975). Microhabitat affinities measured by other methods tend to show stronger preferences than does trapping, so that actual affinities are probably stronger than this study suggests (cf. Price 1977). (2) The range of categories defined for this study is unlikely to coincide with all those discriminated by the rodents. For example, *D. merriami* probably uses open spaces larger than those sampled, and therefore its high overlap with *P. amplus* may be an artifact of sampling only 1 portion of the microhabitat spectrum. The high overlap between *P. baileyi* and *P. penicillatus* may similarly be a result of neglecting to include surface soil texture in the definition of microhabitat categories.

Heteromyid rodents may partition resources other than foraging microhabitat. Indeed, because seeds directly limit their populations (Brown 1975, Pearson 1975, Whitford 1976, E. L. Cockrum, *personal communication*), one might predict that heteromyids directly or indirectly partition seeds and thereby coexist. Brown and Lieberman (1973) suggested that coexisting heteromyids eat seeds of different size. However, others have failed to find evidence that heteromyids eat seeds of different weight (Lemen 1976) or even different species (Reichman 1975, Smigel and Rosenzweig 1974, Rosenzweig and Sterner 1970). Most evidence suggests that any partitioning of seeds is an indirect result of microhabitat specializations. Microhabitats differ in the seeds they contain (Goodall and Morgan 1974) because patterns of seed density and clumping

coincide with local variations in soil-surface microtopography and structural features of vegetation (Reichman 1976). This study suggests that if rodents eat different seed resources, it is because they forage in different microhabitats. Indeed, the ultimate reason that microhabitats are discriminated by heteromyids may be that 1 particular body size and morphology is maximally efficient for collecting only 1 particular spatial array of seeds which happens to be associated with a particular microhabitat.

To test this hypothesis, we need to know the energetic cost of collecting seeds as a function of rodent morphology and seed dispersion. Preliminary data from experiments in my laboratory suggest that clump-size preferences vary between rodents of divergent morphology, and that the preferences may be based on foraging efficiencies. I have found (Price 1978) that kangaroo rats, which are bipedal, and pocket mice, which are quadrupedal, differ in their preferences for seed-clump sizes. *Dipodomys merriami* strongly selects big clumps and *Perognathus* spp. select small clumps or scattered seeds. This fits well with Reichman's (1976) finding that seeds are more clumped in open spaces than under bushes. Reichman and Oberstein (1977) have also found differences between species in their foraging efficiencies on various seed spatial arrays.

Once the functional relationship between microhabitat and morphology is understood, it will perhaps be possible to predict the "morpho-species" of resident rodents from measurements of vegetation structure. Brown (1975) has documented remarkably consistent patterns in the body sizes of the heteromyids coexisting in sandy-substrate environments throughout the deserts of North America. It remains to be seen whether such patterns can be predicted solely from a knowledge of variations in availability of different microhabitats in desert environments. If they can, we will have gained support for the general theory that competitive divergence and resource availability are principles structuring communities of competing species, as well as a better understanding of the behavior of an important group of desert organisms.

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Literature Cited

Allard, R. W., and J. Adams. 1969. Population studies in predominately self-pollinating species. XIII. Intergenotypic competition and population structure in barley and wheat. American Naturalist **103**:621–645.

Beatley, J. C. 1976. Environments of kangaroo rats (*Dipodomys*) and effects of environmental change on populations in southern Nevada. Journal of Mammalogy **57**:67–93.

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. Pages 315–341 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press, New Haven, Connecticut, USA.

———, and G. L. Lieberman. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. Ecology **54**:788–797.

Charnov, E. L. 1976. Optimal foraging, the Marginal Value Theorem. Theoretical Population Biology **9**:129–136.

Colwell, R. K., and E. R. Fuentes. 1975. Experimental studies of the niche. Annual Review of Ecology and Systematics **6**:281–310.

Crowell, K. L., and S. L. Pimm. 1976. Competition and niche shifts of mice introduced onto small islands. Oikos **27**:251–258.

Douglass, R. J. 1976. Spatial interactions and microhabitat selections of two locally sympatric voles, *Microtus montanus* and *Microtus pennsylvanicus*. Ecology **57**:346–352.

Gause, G. F. 1934. The struggle for existence. Williams and Wilkins, Baltimore, Maryland, USA.

Goodall, D. W., and S. J. Morgan. 1974. Seed reserves in desert soils. United States/International Biological Program, Desert Biome Research Memorandum 74-16. Utah State University, Logan, Utah, USA.

Grant, P. R. 1972. Interspecific competition among rodents. Annual Review of Ecology and Systematics **3**:79–106.

Krebs, C., B. Keller, and R. Tamarin. 1969. *Microtus* population biology. Ecology **50**:587–607.

Lawlor, L. R., and J. Maynard Smith. 1976. The coevolution and stability of competing species. American Naturalist **110**:79–99.

Lemen, C. A. 1978. Seed size selection in heteromyids. Oecologica **35**:13–19.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.

Lotka, A. J. 1925. Elements of physical biology. Williams and Wilkins, Baltimore, Maryland, USA.

Lowe, C. H. 1964. The vertebrates of Arizona. University of Arizona Press, Tucson, Arizona, USA.

MacArthur, R. H. 1970. Species packing and competitive equilibrium for many species. Theoretical Population Biology **1**:1–11.

———. 1972. Geographical ecology. Harper and Row, New York, New York, USA.

———, and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist **101**:377–385.

MacArthur, R. H., and E. Pianka. 1966. On optimal use of a patchy environment. American Naturalist **100**:603–609.

MacMillan, R. E. 1964. Population ecology, water relations, and social behavior of a southern California semidesert rodent fauna. University of California, Publications in Zoology **71**:1–59.

May, R. H. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

M'Closkey, R. T., and B. Fieldwick. 1975. Ecological separation of sympatric rodents (*Peromyscus* and *Microtus*). Journal of Mammalogy **56**:119–129.

Miller, R. S. 1967. Patterns and process in competition. Advances in Ecological Research **4**:1–72.

Pearson, O. R. 1975. An outbreak of mice in the coastal desert of Peru. Mammalia **39**:375–586.

Price, M. V. 1977. Validity of live-trapping as a measure of foraging activity of heteromyid rodents. Journal of Mammalogy **58**:107–110.

———. 1978. Seed dispersion preferences of coexisting desert rodent species. Journal of Mammalogy **59**:624–626.

Pulliam, H. R. 1975. Coexistence of sparrows: a test of community theory. Science **189**:474–476.

———. 1976. The principle of optimal behavior and the theory of communities. Pages 311–332 *in* Bateson, P. P. G. and P. H. Klopfer, editors. Perspectives in ethology. Plenum Press, New York, New York, USA.

Reichman, O. J. 1975. Relation of desert rodent diets to available resources. Journal of Mammalogy **56**:731–751.

———. 1976. Effects of rodents on germination of desert annuals. United States/International Biological Program, Desert Biome Research Memorandum 76-20. Utah State University, Logan, Utah, USA.

———, and D. Oberstein. 1977. Selection of seed distribution types by *Dipodomys merriami* and *Perognathus amplus*. Ecology **58**:636–643.

Reynolds, H. 1950. Relation of Merriam kangaroo rats to range vegetation in southern Arizona. Ecology **31**:456–463.

Rosenzweig, M. L. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. Ecology **54**:111–117.

———, B. Smigel, A. Kraft. 1975. Patterns of food, space, and diversity. Pages 241–268 *in* Prakash, I. and P. K. Ghosh, editors. Rodents in desert environments. Dr. W. Junk, The Hague, The Netherlands.

Rosenzweig, M. L., and P. W. Sterner. 1970. Population ecology of desert rodent communities: body size and seed husking as bases for heteromyid coexistence. Ecology **51**:217–224.

Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology **50**:558–752.

Roughgarden, J. 1976. Resource partitioning among coexisting species—a coevolutionary approach. Theoretical Population Biology **9**:388–424.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science **185**:27–39.

Schroder, G. E., and M. L. Rosenzweig. 1975. Perturbation analysis of competition and overlap in habitat utilizations between *D. ordii* and *D. merriami*. Oecologia **19**:9–28.

Seaton, A. P. C., and J. Antonovics. 1967. Population interrelationships. I. Evolution in mixtures of *Drosophila* mutants. Heredity **22**:19–34.

Smigel, B. W., and M. L. Rosenzweig. 1974. Seed selection in *Dipodomys merriami* and *Perognathus penicillatus*. Ecology **55**:329–339.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California, USA.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology **58**:338–348.

Titman, D. 1976. Competition between algae: experimental confirmation of resource-based competition theory. Science **192**:463–465.

Vandermeer, J. H. 1972. Niche theory. Annual Review of Ecology and Systematics **3**:107–132.

Volterra, V. 1928. Variations and fluctuations of the number of individuals in animal species living together. Pages 409–448 *in* R. Chapman, editor. Animal ecology. McGraw-Hill, New York, New York, USA.

Werner, E. E., and D. J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science **191**:404–405.

———. 1977. Competition and habitat shift in two sunfishes. (Centrarchidae). Ecology **58**:869–876.

Whitford, W. G. 1976. Temporal fluctuations in density and diversity of desert rodent populations. Journal of Mammalogy **57**:351–369.

Wondolleck, J. T. 1978. *in press*. Forage area separation and overlap in heteromyid rodents. Journal of Mammalogy.

Yeaton, R. I., and M. L. Cody. 1974. Competitive release in island song sparrow populations. Theoretical Population Biology **5**:42–58.