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## Spatial organization of a desert rodent community: food addition and species removal

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**Summary.** From 1977 through 1983 we conducted experiments on a desert rodent community where supplemental seeds were added or certain rodent species and ants were removed from 0.25-ha fenced plots in a Chihuahuan Desert site in southeastern Arizona, USA. In this paper we examine the patterns of microhabitat use relative to vegetative cover by 11 rodent species. The results show that: i) removal of the largest seed-eating species, *Dipodomys spectabilis*, produced the most pervasive and dramatic shifts in microhabitat use by the remaining rodent species; ii) adding seeds or removing ants had little effect on the spatial use of microhabitats by rodents in this community; and iii) non-granivores were just as likely as granivores to shift microhabitat use when other granivores were removed. We believe these results indicate that both food and foraging microsites are limited but the relegation of subdominant species to less-preferred microhabitats by the large *Dipodomys spectabilis* is the major factor underlying the spatial organization of this community. Results also demonstrate that strong interactions among species increase the probability that pathways of indirect interactions through intermediary species are important; these complex linkages may include species that overlap little in food preferences.

**Key words:** Desert – Rodent community – Food addition

Locally co-occurring species of North American desert rodents characteristically forage in structurally distinctive microhabitats with respect to perennial vegetation. This has been interpreted as evidence that these communities possess a high degree of spatial organization that is related to the spatial segregation of species and the exploitation of a spatially varying and limited resource (e.g., M'Closkey 1978; Brown et al. 1979). Bipedal species (*Dipodomys*, *Microdipodops*) are usually associated with open, vegetation-free, microhabitats whereas species with quadrupedal gaits (*Perognathus*, *Peromyscus*, *Reithrodontomys*) more frequently are observed in shrubbier areas. This general pattern has been documented repeatedly for communities in all four of the major North American deserts by many different investigators (Rosenzweig and Winakur 1969; Rosenzweig 1973; Brown and Lieberman 1973; Brown 1975; Price 1978; M'Closkey 1978; Reichman 1980; Price and Brown 1983; Price 1984; Price and Waser 1984; Harris 1984; Bowers 1986).

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The proposed mechanisms underlying this pattern include economic scenarios of foraging energetics (bipedal forms may better exploit widely dispersed but rich seed aggregates in open microhabitats) and susceptibility to predation (bipeds can escape predators in the open, but quadrupeds can not and are restricted to cover). In addition to these species specific traits are competitive interactions among rodent species that vary in intensity according to body-size differences (Bowers and Brown 1982) and resource availability (Congdon 1974); together these play a role in reinforcing spatial segregation and appear to be directly responsible for the patterns of microhabitat use at the community level (cf., Hoover et al. 1977; Price 1978; Wondolleck 1978; Rebar and Conley 1983; Bowers 1986).

Little is known of the mechanisms by which these competitive interactions are resolved. Do rodent species interact through the exploitation of commonly preferred food (seed) resources or are aggressive interactions involving behavioral dominance responsible for the spatial segregation of species and their use of spatially available resources? In complex communities organization may be based on a combination of both exploitative and interference modes of interaction among species. Detailing the interplay between these types of competitive interactions in natural communities should reveal much about the processes affecting local populations and the organization of communities.

In this paper we describe the patterns of microhabitat use of 11 Chihuahuan Desert rodents over a span of almost seven years. We experimentally manipulated both species composition and food supply and measured resulting shifts in microhabitat utilization. Our results enable us to identify important elements of the network, magnitude, and mode of competitive effects underlying organization in this community.

### Study site and methods

The present paper details changes in microhabitat use in response to long-term experimental manipulation of rodent composition and food supply. Our study site was located in a relatively homogeneous desert shrub habitat in southeastern Arizona, USA. Manipulations were performed in twenty 0.25-ha plots. Each plot was fenced with 0.64-cm mesh hardware cloth, extending 0.7-m above and buried 0.2-m below ground. In addition to an unmanipulated fenced control (see below), the remaining treatments consisted of two general classes: treatments where one or more

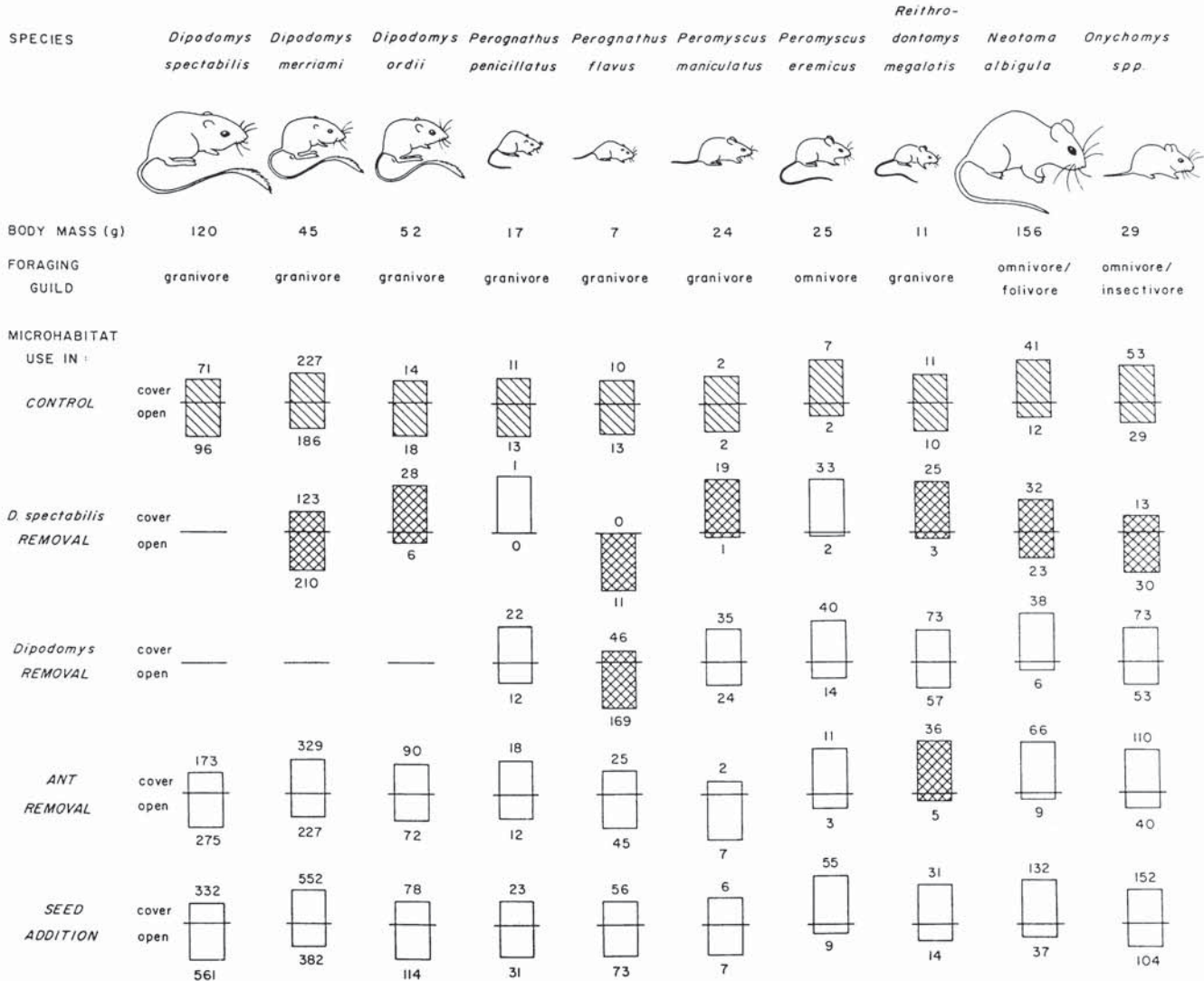


Fig. 1. Rodent species commonly captured at our Chihuahuan Desert study site, their body weights, foraging guilds and microhabitat use in the five treatments. A total of 6,353 individual captures (over an almost seven year period) are scored here relative to two microhabitat categories: captures in greater-than-median (cover) and less-than-median (open) perennial shrub cover. Patterns of microhabitat use in manipulated treatments were tested against those observed in the control (bars with simple hatching); where microhabitat use differed from that in the control ( $\beta < 0.05$ ) cross-hatching is used. Numbers above and below each bar indicate the number of captures for that species in particular microhabitats. The most marked and pervasive shifts accompanied the removal of *Dipodomys spectabilis*

species were removed, potentially, changing both food availability and potential for direct behavioral interactions; and food alteration treatments where supplementary millet seeds were added at a rate of 96 kg per year or seed-eating ants were removed. Sixteen equally-spaced gates in each plot allowed the selective exclusion of rodent species above a threshold body size. These gates varied in size among the treatments. Large gates (3.7 × 5.7-cm) allowed all rodent species access to control (2 plots), ant removal (4 plots), and seed addition plots (8 plots); medium-sized gates (2.6 × 3.0-cm) excluded only the largest seed-eating species, *Dipodomys spectabilis* (2 plots); and small gates (1.9 × 1.9-cm) excluded *D. spectabilis* as well as two smaller species, *Dipodomys merriami* and *Dipodomys ordii* (4 plots). Fourteen rodent species, of which 11 were common, inhabited the study site, and all except those mentioned above had equal access to all plots.

Rodents were censused monthly during the week of the new moon (moonlight has been shown to effect microhabitat use by desert rodents; see Price et al. 1984) using live traps placed in each plot in 7 × 7 grids with 6.5-m between trap stations. Traps were opened for one night per month with plot gates closed so that only plot residents would be captured. For more details concerning the experimental design, procedures and methodology see Munger and Brown (1981), Brown and Munger (1985), Brown et al. (1986).

Following the lead of many previous studies on desert rodent communities we used the percent cover of perennial plants to characterize the microhabitat at each of the 980 trap stations (e.g., Price 1978). Percent cover within a 2-m radius of each trap station was measured by ocular estimates using reference disks of known percent coverage. Cover was measured in 1978, 1981, and 1983. There was

no significant change in cover over this four year period (Mann-Whitney U-test;  $P > 0.05$ ), so we use here the data from 1983 to characterize microhabitats.

Fence installation was completed in June, 1977, pre-manipulative trapping was conducted from July–September, and manipulations were initiated in October, 1977. In this paper we treat just the post-manipulative patterns of microhabitat use from October, 1977, through December, 1983.

We used two methods to estimate microhabitat use; both use trap station data broken into two microhabitat categories: i.e., trap stations with greater or lesser vegetative cover than the median available at trap stations for that treatment. Accordingly, each microhabitat type was represented by an equal number of trap stations in each treatment category. One method of estimating microhabitat use employed trap data to estimate capture frequencies relative to the two cover categories. This was done on a species by species basis. A second measure of habitat use by rodents was obtained by monitoring removal of single millet seeds placed on  $2 \times 2$ -cm plexiglass plates positioned at each trapping station. Seed removal was recorded between dusk and dawn during the winter months (November to April) when rodents were the only actively foraging granivores. There were 49 single millet seeds available on each plot during the seed removal experiments. Seed removal was monitored on six different nights between November 1981 and January 1984.

## Results

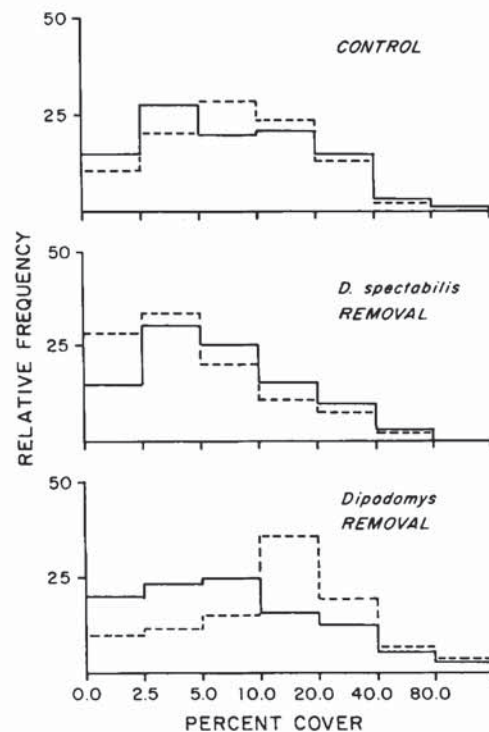
Results are based on differences among the experimental treatments in two measures of microhabitat use: 1) the number of individual rodents captured, by species, in the two microhabitat types; and 2) the microhabitat specific rates of seed removal by the rodent community as a whole. The seven year study resulted in 6,353 captures of the 11 most abundant rodent species and a total of 3,679 individual millet seeds were removed by rodents in six sampling periods.

We first examine capture data on control plots with the null hypothesis that if rodents use microhabitats indiscriminately, they should be trapped in equal frequencies at stations in the two microhabitat categories. Figure 1 shows the distribution of trap captures relative to microhabitat for the different treatments and species. In control plots only *Neotoma albigula* used microhabitats in proportions significantly different than those predicted by the stated null hypothesis; this species exhibited a preference for trap sites with high cover using the median test (Siegel 1956) with  $P = 0.05$  (Fig. 1). *Dipodomys merriami*, the two *Onychomys*, and *Peromyscus eremicus* also displayed a tendency to prefer sites with greater-than-median cover, whereas *Dipodomys spectabilis* was captured most often in open microhabitats.

Microhabitat use by rodents in the four treatments was then tested against those on the control using a chi-square test for homogeneity ( $P < 0.05$ ). Results of this test (Fig. 1) showed that microhabitat selection became more marked relative to that on control plots when rodent and ant species were removed. Significant shifts in microhabitat use was observed for seven species on *D. spectabilis* removal plots, one species on plots where all *Dipodomys* were removed, and one species where ants were removed. Adding supple-

**Table 1.** Results of experiments where the removal of individual millet seeds placed at 980 trap stations was scored relative to perennial shrub cover. Values represent the number of seeds removed at stations with greater-than-median and less-than-median cover for the five experimental treatments. Data were taken over six periods between November and April, 1981–1984. Note that a greater proportion of seeds was removed in the *D. spectabilis* removal treatment relative to seed removal in the other four treatments (Chi-square,  $DF = 4$ ,  $P < 0.05$ )

Treatment	Number of seeds (plots)	Number of seeds removed	
		greater	lesser
Control	588 (2)	234	221
<i>Dipodomys spectabilis</i> removal	588 (2)	205	260
<i>Dipodomys</i> removal	1,176 (4)	271	251
Ant removal	1,176 (4)	446	393
Seed addition	2,352 (8)	703	695



**Fig. 2.** Distribution of trap captures (broken line; all species combined) and available trap sites (solid line) relative to vegetative cover on i) control, ii) *D. spectabilis* removal and iii) *Dipodomys* removal plots. See Fig. 1 and text for sample sizes and more specific details

mental seeds did not significantly affect the use of microhabitats by any of the species.

Table 1 shows the results of the seed removal experiment. There were significant differences between treatments relative to rates of seed removal in the two microhabitats ( $\chi^2 = 10.61$ ,  $DF = 4$ ,  $P < 0.05$ ). The heterogeneous treatment was the *D. spectabilis* removal: the remaining four treatments were statistically indistinguishable in the proportion of seeds removed from each microhabitat ( $\chi^2 = 1.77$ ,  $DF = 3$ ,  $P > 0.30$ ). These results show that a greater proportion of seeds were removed in open microhabitats for the *D.*

*spectabilis* removal treatment relative to seed removal in the remaining treatments where *D. spectabilis* was present.

Using the distribution of trap captures (all species combined) as a measure of the use of space by the entire community and comparing this to the distribution of available microhabitats provides another view of the factors influencing the use of space in this community (Fig. 2). This shows that the distribution of captures in control, *D. spectabilis* removal, and *Dipodomys* removal plots all differ significantly from that expected if the use of microhabitats was random with respect to vegetative coverage (Kolmogorov-Smirnov two-sample tests;  $P < 0.05$ ). However, there are very characteristic ways in which these distributions differ from that expected. On control plots there were fewer captures in trap locations with  $< 5\%$  cover than expected if the use of microhabitats was random with respect to vegetation; on *D. spectabilis* removal plots there was a greater-than-expected usage of these same open sites; and on *Dipodomys* removal plots most rodents were captured in microhabitats with greater than 10% cover. Together these results support some of our earlier analyses: i.e., that when *D. spectabilis* is present open sites are underutilized by the community as a whole; that when *D. spectabilis* is removed the other *Dipodomys* shift to use open sites; but they also show that when all *Dipodomys* are removed the remaining rodent species are unable to fully utilize the vacated microhabitats and that compensation in this community is incomplete as discussed by Munger and Brown (1981).

## Discussion

The results suggest that one species, *D. spectabilis*, controls the use of microhabitats by most other species in the community. Whenever it is present, regardless of experimentally manipulated seed availability or ant density, the effect was the same: *D. spectabilis* was able to preempt resources by preventing other rodents from foraging in the open microhabitats it apparently prefers. This is evidenced by the increased removal rates of seeds from open sites when *D. spectabilis* was removed and the coincident shift in microhabitats used by the numerically dominant *D. merriami* (and by the community as a whole; see Fig. 2), towards open microhabitats when *D. spectabilis* was removed.

The differences in microhabitat use among the control, *D. spectabilis*, and *Dipodomys* removal treatments confirm the hypothesis that interspecific competition affects the distribution of rodent activities in space, but is the exploitation of spatially variable resources the mechanism of competition or is it direct interference between species? From optimal foraging and patch use theory it is predicted that consumers should specialize on their preferred resource and forage in patches where such resources are most available (MacArthur and Pianka 1966; Schoener 1971). Exploitation can change the use of patches by changing the distribution of food resources among each patch type. Accordingly, the data presented here is consistent with that expected if the removal of *D. spectabilis* resulted in the redistribution of resources among open and cover microhabitats and the remaining rodents shifted foraging microsites in response to these changes in resource availability. However, if resource availability and its distribution among microhabitats determines foraging sites shifts in microhabitat use should have occurred in seed addition treatments where overall seed abundance was elevated in all microhabitats. Figure 1

shows that such shifts did not occur. In fact, adding seeds had no effect on the use of microhabitats by any of the rodents. As an alternative, competitors of large body size may directly restrict the foraging activities of smaller species through interference. Under an interference mode of competition adding seeds should not alter the preemption of space and the patterns of microhabitat use should be determined solely by the presence of the dominant species. Because most significant shifts in microhabitat occurred in the *D. spectabilis* removal treatment and seed addition had no effect on the use of microhabitats, we believe our results point to aggressive interference by *D. spectabilis* as the major determinant of the use of space by rodents in this community.

The effects of interference by *D. spectabilis* on the foraging of smaller rodent species are also evident in the rates of seed removal. First, the results suggest that the single millet seeds used to monitor foraging activity may be too small to be consistently collected by *D. spectabilis*, perhaps because the rewards of collecting a single seed are low for an animal of its body size. Consequently, during the seed removal experiments a large proportion of single seeds remain unharvested in the open microhabitats preferred by *D. spectabilis*. However, on *D. spectabilis* removal plots the single seeds in the open are collected by the smaller sized rodents. Thus, as the seed addition and *D. spectabilis* removal treatments indicate, it is not the abundance of seed resources alone that attracts smaller rodents to the open microhabitats, rather it is the absence of interference from *D. spectabilis*.

Our results also suggest that the majority of the shifts in microhabitat use can be traced back to the *D. spectabilis*-*D. merriami* interaction, but at the community level may also include indirect interactions involving many of the other species. The most striking shift was the increased use of open areas by the numerically dominant *D. merriami* when *D. spectabilis*, which had formerly used these microhabitats, was removed. Most of the other shifts in the smaller rodents, including the increased use of open microhabitats by *Perognathus flavus*, *Peromyscus maniculatus* and *Reithrodontomys megalotis* when all *Dipodomys* was removed suggest that these species responded directly to *D. merriami* and only indirectly to *D. spectabilis*. Hence there appears to be a hierarchy of interactions that originate with interactions between the behavioral dominant species, *D. spectabilis*, and the numerically dominant *D. merriami*. Interestingly, a consequence of this interactive hierarchy is that the strong microhabitat preferences of species become apparent only when the behaviorally dominant *D. spectabilis* is removed. Other studies have noted the potential for interference between *D. spectabilis* and *D. merriami* (Frye 1983) and we believe our study shows how this one interaction can resound through the community to affect many other species.

Many of these experimentally induced microhabitat shifts were accompanied by changes in local species densities (Munger and Brown 1981; Brown and Munger 1985; Brown et al. 1986), which lend additional support to the notion that *D. spectabilis* controls the dynamics of this community through a combination of direct and indirect effects. For example, increasing food levels by adding seeds resulted in an increase of *D. spectabilis* and a decrease in *D. merriami* densities. Removal of *D. spectabilis* resulted in positive density compensation of *D. merriami* but no changes in the

smaller seed-eater densities; removal of all *Dipodomys*, however, resulted in large density increase in several of the smaller rodents even though Fig. 2 shows that only partial utilization of habitats vacated by removing all *Dipodomys* occurred. Taken together, microhabitat use and density responses to the experimental treatments indicate that interference competition for foraging sites is an important factor regulating local rodent densities and is largely responsible for the spatial organization of this community.

These results not only provide a clear, direct, demonstration that interspecific competition has a major influence on the foraging behavior and microhabitat use of desert rodents, they also show how a single species, through both the direct and indirect effects of its aggressive interference, can influence the use of space and foraging behavior of many other species. Previous studies of competition among desert rodents have reported that 1) coexisting species differ in where they forage with respect to vegetative cover (e.g., Rosenzweig and Winakur 1969; Brown and Lieberman 1973; M'Closkey 1978; Lemen and Rosenzweig 1978), 2) individuals are interspecifically aggressive and larger species usually dominate agonistic encounters (e.g., Congdon 1974; Blaustein and Riser 1976; Frye 1983; Lemen and Freeman 1986), and 3) species change their microhabitat use when other species are experimentally removed (e.g., Price 1978; Wondolleck 1978; Rebar and Conley 1983; Bowers 1986). The importance of our study is that it shows how all of these processes are interrelated in a single community of many coexisting species.

Four aspects of interspecific interference warrant further comment. First, aggressive dominance typically results in highly asymmetrical interactions among competing species. Aggressive species can defend space, monopolize rich resources, and keep subordinate species at low densities, but the reciprocal effect of subordinate species on dominant ones occurs primarily through the exploitation of resources. Second, the effects of interference are mediated by habitat structure. For example, the effect of interference will depend on the availability of refuges that give smaller species the opportunity to escape from an aggressive larger species. Thus, although the dominant *D. spectabilis* uses both open and cover microhabitats it apparently is only able to reduce the foraging activities of subordinates in open microhabitats. Third, the effects of interference need not be restricted to those species that potentially compete for the same resources. For example, in our study, insectivorous *Onychomys* and folivorous *Neotoma* species shifted their microhabitat use when almost exclusively granivorous *D. spectabilis* was removed. It is interesting that these nongranivorous species exhibited shifts in microhabitat use when granivorous *Dipodomys* were removed, but showed no increase in density. Hence, while interference may play a role in determining the use of microhabitats by rodents in several guilds, its effects appear to be most significant for ecologically similar species. Fourth, the existence of strong aggressive interactions among species increases the possibilities for important pathways of indirect interactions among species that overlap very little in resource utilization. Unfortunately these consequences of interference make most contemporary two-species models of interspecific competition inapplicable to understanding how these interactions meld at the community level; they also make it hazardous to attempt to understand the mechanisms and effects of interspecific competition through comparative, nonexperimental

studies. Comprehensive field experiments, such as we have described here for desert rodents, appear to offer the best prospects for understanding the complex kinds of interactions that determine the structure and dynamics of ecological communities.

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## References

- Blaustein AR, Riser AC (1974) Dominance relationships of the dark kangaroo mouse (*Microdipodops megacephalus*) and the little pocket mouse (*Perognathus longimembris*) in captivity. *Great Basin Natur* 34:312-314
- Bowers MA (1986) Geographic comparison of microhabitats used by three heteromyids in response to rarefaction. *J Mamm* 67:46-52
- Bowers MA, Brown JH (1981) Coexistence of desert rodents: chance or community structure? *Ecology* 63:391-400
- Brown JH (1975) Geographical ecology of desert rodents. In: Cody ML, Diamond JM (eds) *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts
- Brown JH, Lieberman GA (1973) Resource utilization and coexistence of seed-eating rodents in sand-dune habitats. *Ecology* 54:788-797
- Brown JH, Munger JC (1985) Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology* 66:1545-1563
- Brown JH, Davidson DW, Munger JC, Inouye RS (1986) Experimental community ecology: the desert granivore system. In: Diamond JM, Case TJ (eds) *Community ecology*. Harper and Row, New York
- Brown JH, Davidson DW, Reichman OJ (1979) Granivory in desert ecosystems. *Ann Rev Ecol System* 10:201-227
- Congdon J (1974) Effect of habitat quality on distributions of three sympatric species of desert rodents. *J Mamm* 55:659-662
- Frye RJ (1983) Experimental field evidence of interspecific aggression between two species of kangaroo rats (*Dipodomys*). *Oecologia* (Berlin) 59:74-78
- Harris JH (1984) An experimental analysis of desert rodent foraging ecology. *Ecology* 65:1579-1584
- Hoover KD, Whitford WG, Flavill P (1977) Factors influencing the distribution of two species of *Perognathus*. *Ecology* 58:877-884
- Lemen CA, Freeman PW (1976) Interference competition in a heteromyid community in the Great Basin of Nevada, USA. *Oikos* 46:390-396
- Lemen C, Rosenzweig ML (1978) Microhabitat selection in two species of heteromyid rodents. *Oecologia* (Berlin) 33:127-135
- MacArthur RH, Pianka EC (1966) On optimal use of a patchy environment. *Amer Natur* 100:603-609
- M'Closkey RT (1978) Niche separation and assembly in four species of Sonoran Desert rodents. *Amer Natur* 112:683-694
- Munger JC, Brown JH (1981) Competition in desert rodents: an experiment with semipermeable membranes. *Science* 211:510-512
- Price MV (1978) The role of microhabitat in structuring desert rodent communities. *Ecology* 59:910-921
- Price MV (1984) Microhabitat use in rodent communities: predator avoidance or food partitioning. *Netherlands J Zool* 34:63-80
- Price MV, Brown JH (1983) Patterns of morphology and resource use in North American desert rodent communities. *Great Basin Natur Memiors* 7:117-134
- Price MV, Waser NM (1985) Microhabitat use by heteromyid rodents: effects of artificial seed patches. *Ecology* 66:211-219

- Price MV, Waser NM, Bass TA (1984) Effects of moonlight on microhabitat use by desert rodents. *J Mamm* 65:353-356
- Rebar C, Conley W (1983) Interactions in microhabitat use between *Dipodomys ordii* and *Onychomys leucogaster*. *Ecology* 64:894-899
- Reichman OJ (1980) Factors influencing foraging in desert rodents. In: Kamil A, Sargent (eds) *Foraging behavior: ecological, ethological, and physiological approaches*. Garland STM Press, New York
- Rosenzweig ML (1973) Habitat selection experiments with a pair of coexisting heteromyid species. *Ecology* 54:111-117
- Rosenzweig ML, Winakur J (1969) Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* 50:558-572
- Schoener TW (1971) The theory of foraging strategies. *Ann Rev Ecol System* 2:369-404
- Siegel S (1956) *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York
- Wondolleck JT (1978) Forage-area separation and overlap in heteromyid rodents. *J Mamm* 59:510-518

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