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Competitive release in microhabitat use among coexisting desert rodents: a natural experiment

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Summary. Competitive release among desert rodents on sand dunes of differing species richness was examined in the Great Basin and Mohave Deserts, USA. Expansions in microhabitat use were exhibited by the kangaroo rats *Dipodomys ordii* and *D. merriami* (granivorous heteromyid rodents, weighing 49 and 42 g, respectively) as the number of coexisting heteromyid species decreased geographically. *Perognathus longimembris*, the only common small heteromyid species (7 g) exhibited no competitive release. This may be due either to the absence of competitive interactions that affect the use of space by *P. longimembris* or to an unacceptable increase in risk of predation that precludes the use of more open microhabitats even in the absence of kangaroo rats. The breadth of microhabitat use of an omnivorous cricetid, *Peromyscus maniculatus*, decreased as the density of *Perognathus longimembris* increased, and increased as the density of conspecifics increased. The evidence for competitive release in *Dipodomys* and not in *Perognathus* is consistent with the hypothesis that species in the same guild and of similar size compete more intensely than species of disparate size.

Considerable evidence suggests that granivorous rodents of the North American Desert compete (see review by Brown et al. 1979). Data consistent with the competition hypothesis follow several lines of evidence: species richness of granivores increases as productivity increases (Brown 1973, 1975; Whitford 1976; Brown and Davidson 1977), the arrays of body sizes in Sonoran and Great Basin Desert granivore communities are similar, although the species are different (Brown 1975; MacMahon 1976), granivores of similar size co-occur less frequently than expected by chance (Brown 1973; Simberloff and Boecklen 1981; Bowers and Brown 1982), granivorous rodents exhibit microhabitat partitioning (Rosenzweig and Winakur 1973; Brown and Lieberman 1973; Rosenzweig 1973; Schroder and Rosenzweig 1975; Price 1978a; Wondolleck 1978; Kotler 1984; but see Thompson 1982a), granivores partition seeds or seed clumps on the basis of a positive seed size-rodent size correlation (Brown and Lieberman 1973; Reichman and Oberstein 1977; Mares and Williams 1977; Hutto 1978; Price 1978b; M'Closkey 1980; but see Lemen 1978; and Frye and Rosenzweig 1980), and some species increase in population density when other species are experimentally removed (Munger and Brown 1981; Brown and Munger 1985).

Many of these patterns are descriptive and the extent to which the competition hypothesis accounts for them remains largely untested experimentally. In particular, if habitat partitioning is mediated by ongoing interactions, competitive release in habitat use should be evident locally (e.g., Price 1978a; Wondolleck 1978) and across the geographic range of a species as the number of competing species decreases. If competition is not important between or within species, or if habitat partitioning is the result of competition in the past (see Schroder and Rosenzweig 1975; Connell 1980), shifts in microhabitat use should not be observed as the number of species or their abundances change geographically.

Habitat partitioning among granivores has been demonstrated on isolated sand dunes in the Great Basin and Mohave Deserts where Brown and Lieberman (1973) found that kangaroo rats (*Dipodomys* spp.) and kangaroo mice (*Microdipodops* spp.) preferentially use open microhabitats, whereas pocket mice (*Perognathus* spp.) preferentially use microhabitats under or near shrubs, and deer mice (*Peromyscus* spp.) use all microhabitats with no apparent preference. Brown and Lieberman infer that the differences in these three strategies of microhabitat use are due to competition.

In the present paper, *a priori* predictions of the competition hypothesis are tested using Brown's original data (Brown 1973, 1975; Brown and Lieberman 1973) and similar data collected at a later date by another investigator, BP Kotler (unpublished). The hypotheses were formulated directly from Brown and Lieberman's (1973) work and prior to obtaining the data. Hypothesis 1. If competition significantly affects the microhabitat use of a species, the breadth of microhabitat use will decrease as the number of competing species increases (the niche compression hypothesis, MacArthur and Wilson 1967). If the use of space among desert rodents is closely tied to food resources, then changes in microhabitat use among heteromyids (granivores) will be associated with changes in heteromyid diversity, not total rodent diversity or cricetid diversity (omnivores). Conversely, the breadth of microhabitat use among cricetids will be associated with changes in cricetid diversity, not heteromyid diversity. Hypothesis 2. The breadth of microhabitat use will increase as the number of conspecifics increases (expansion of microhabitat use under pressure from conspecifics, Fretwell and Lucas 1970).

Methods and materials

The data are from 20 isolated sand dunes in the Great Basin and Mohave Deserts: 17 were censused during 1970–71, 1 during 1972 (Brown 1973, 1975) and 7 were re-trapped in 1978 along with 2 additional sites (Kotler, unpublished data) (Fig. 1). Details of the censusing method are reported elsewhere (Brown 1973, 1975; Brown and Lieberman 1973), and are essentially the same for the 1978 data (Kotler, personal communication). In Brown's published data (hereafter referred to as the 1970–71 data) rodents were snap-trapped with Museum Specials, whereas all but one of the sand dunes were sampled with Sherman live-traps in the unpublished 1978 data. (see Appendix 1 for trapping localities and dates).

Trap lines were run through the most vegetatively homogeneous portions of each sand dune. Stations were approximately 15 m apart, and four traps were set at each station. Single traps were placed at the center of a shrub, at the shrub canopy perimeter, and at 1 m and 2 m from the edge of the shrub canopy. The average shrub canopy radius was estimated to be 0.5 m (JH Brown, personal communication), hence the four trap positions were assigned distances from the center of the shrub canopy of 0.1 m, 0.5 m, 1.5 m, and 2.5 m, respectively. The trap at the center of the shrub was assigned the distance of 0.1 m, rather than 0.0 m because the distances were transformed to natural logs for use in estimating the breadth of microhabitat use for each species on each sand dune censused.

Microhabitat is operationally defined as some distance from a shrub center along a gradient extending away from the shrub. In more complex environments where substrate texture and vegetation change dramatically over relatively short distances (e.g., Sonoran Desert bajadas), more variables may be needed to describe adequately the microhabitat use of each species. However, the variation in substrate texture and hardness is minimal on sand dunes, and the sites were chosen to minimize within and between site variability in substrate and vegetation (Brown 1973). Distance to the nearest perennial shrub is the visually dominant aspect of microhabitat in this environment, and different rodent species exhibit distinctive patterns of distribution with respect to this variable (see Brown and Lieberman 1973; Price 1978a; Rosenzweig 1973).

The number of rodent species present on each sand dune was taken to be the number of species trapped. Density of species was estimated by dividing the number of individuals caught by the number of trap nights. Most dunes were trapped for two nights. For dunes trapped more than two nights, only the first two were used in the analyses. *Dipodomys deserti*, a large kangaroo rat (ca. 100 g) was considered present if individuals of the species were seen or if active *D. deserti* burrows were present, even if not trapped. This protocol was used because *D. deserti* is large enough to escape from the Museum Special snap-traps used by Brown and may not appear in the trap data (Brown 1973).

Dipodomys ordii, *D. merriami*, *Perognathus longimembris* (Heteromyidae), and *Peromyscus maniculatus* (Cricetidae) were sufficiently well represented in Brown's data for analysis of microhabitat use, whereas only *D. ordii* microhabitat use could be analysed in the 1978 data. All of the heteromyids are granivores (Morton 1979; Brown 1973). *Peromyscus maniculatus* is considered to be an omnivore (Morton 1979; Bowers and Brown 1982), although it has been considered a granivore elsewhere (Brown and Lieberman 1973; Munger and Brown 1981; Kotler 1984; Brown and Munger, in press). (*Peromyscus* will not be abbreviated to avoid confusion with *Perognathus*. When *Peromyscus* is referred to it should be taken to mean *Peromyscus maniculatus*.)

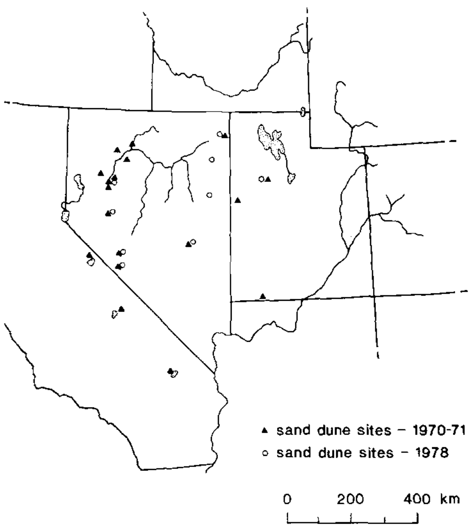

Fig. 1. Study area in the Great Basin and Mohave Deserts. Triangles are sites trapped by Brown in 1970–71. Open circles are sites trapped by Kotler in 1978. Two or fewer species of heteromyid rodents were trapped on the sites near the Utah-Nevada border, whereas as many as six species were trapped on the sites in western Nevada

Variability in microhabitat use

Microhabitat partitioning is employed here in a restrictive sense. It is not meant to imply spatial separation of individuals or species into habitats containing perennial vegetation of differing species composition or density, or across substrates of differing texture or firmness. All species were caught throughout the transects and in all microhabitats, but differed in their distribution of captures across the microhabitat gradient (see Brown and Lieberman 1973). Therefore, tests for changes in microhabitat use are not tests for changes in the range of microhabitats used, but in the distribution of microhabitat use. The statistical variance of the distribution of captures across the four trap locations (log transformed) for each species on each sand dune is used as the measure of breadth of microhabitat use (MUV). MUV is regressed pair-wise and in step-wise multiple regression against the following diversity and abundance variables: total number of species present; number of heteromyid species present; number of cricetid species present; density of conspecifics; for heteromyids, density of non-conspecific heteromyids; for *Peromyscus maniculatus*, the only cricetid, density of non-conspecific cricetids. Mean annual precipitation and the number of trap nights were included to examine the effects of productivity and sampling. Due to the small number of observations in 1978, only pair-wise correlations were computed.

Results

MUV for the two species of *Dipodomys* in 1970–71 is more highly negatively correlated with the number of coexisting

Table 1. Pair-wise correlation coefficients between the variance in microhabitat use (MUV) for each species and the dependent variables

	Variance in Microhabitat Use (MUV)			
N	*Dipodomys ordii* (12)	*D. merriami* (10)	*Perognathus longimembris* (8)	*Peromyscus maniculatus* (11)
HETSP	−0.77**	−0.48	0.158	0.319
HETDEN	−0.587*	0.189	0.407	−0.518
CONDEN	0.225	0.320	−0.485	0.363
CRISP	0.210	0.158	0.378	−0.174
TOTSP	−0.535	−0.235	0.412	−0.163
PPT	0.379	−0.408	−0.477	0.018
TRPNTS	0.060	0.294	0.019	0.164

HETSP = number of heteromyid species, HETDEN = density of non-conspecific heteromyids, CONDEN = density of conspecifics, CRISP = number of cricetid species, TOTSP = total number of species (heteromyid and cricetid), PPT = mean annual precipitation, TRPNTS = number of trapnights

* $P<0.05$, ** $P<0.01$

heteromyid species (HETSP) than any other variable (Table 1), but only *D. ordii* exhibits a significant pair-wise correlation. The MUV of *D. ordii* decreases markedly as the number of coexisting species of heteromyids increases (Fig. 2). No significant variation is accounted for by additional variables in the MUV of *D. ordii* after the initial portion is explained by variation in heteromyid diversity (Table 2). The increase in the MUV of *D. ordii* with the decrease in heteromyid density (Table 1) may be an artifact of the inter-correlation between heteromyid diversity and heteromyid density (Brown 1973) and plays no role in the multiple regression. MUV for *D. merriami* is significantly negatively correlated with the number of heteromyid species if its own density is held constant in partial regression analysis ($r = -0.684$, $P<0.05$). In step-wise multiple regression analysis the effect of heteromyid diversity on the MUV of *D. merriami* is significantly negative and the effect of *D. merriami* density is significantly positive (Table 2). In 1978, again heteromyid species diversity is negatively correlated with MUV for *D. ordii*, but only if both snap-trap and live-trap data are considered (Fig. 2). No similar relationships are evident for variation in the MUV of *P. longimembris* in pair-wise (Table 1) or multiple regression analyses (Table 2).

The MUV of *Peromyscus maniculatus* exhibited trends with respect to the density of heteromyids and conspecifics (Table 1). In multiple regression, heteromyid density ($P = 0.078$) and *Peromyscus maniculatus* density ($P = 0.171$), together account for 43% of the variation in MUV ($P = 0.106$). If the density of *P. longimembris* is included in the array of independent variables in the analysis, heteromyid density is superceded. The MUV of *Peromyscus maniculatus* decreases as the density of *P. longimembris* increases, and increases as the density of conspecifics increases (Table 2). This suggests that even though *Peromyscus* may not be a strong competitor with granivores for seeds (e.g., Bowers and Brown 1982; Morton 1979), its microhabitat use is still affected, although weakly, by inter- and intraspecific interactions. Note that the MUV of *Peromyscus* is correlated with density variables, intra- and interfamilial, in contrast to the MUV of *Dipodomys* spp. that are correlated with diversity variables (Tables 1, 2).

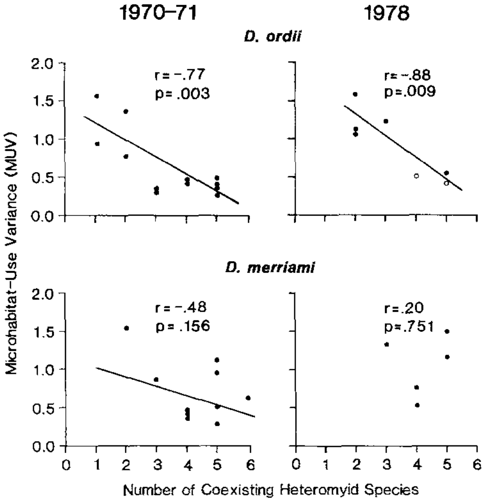

Fig. 2. Correlations between MUV and heteromyid species diversity for 1970–71 (snap-trap data) and 1978 (live-trap data, closed circles; snap-trap data, open circles)

Table 2. Analyses of variance and multiple regression equations for the effects of species diversity and relative abundance on MUV for data collected during 1970–71

Source	df	MS	F	r^2	*P*
Dipodomys ordii					
Regression	1	1.256	14.57	0.59	0.003
HETSP	1				
Residual	10	0.086			
Regression equation	MUV = 1.43 − 0.22(HETSP)				
D. merriami					
Regression	2	0.464	7.51	0.68	0.018
HETSP	1		12.66		0.009
CONDEN	1		9.84		0.016
Residual	7	0.062			
Regression equation	MUV = 1.33 − 0.23(HETSP) + 6.0 (CONDEN)				
Perognathus longimembris					
Regression	1	0.869	1.84	0.235	0.224
CONDEN	1				
Residual	6	0.472			
Regression equation	MUV = 1.87–7.46(CONDEN)				
Peromyscus maniculatus					
Regression	2	0.630	4.79	0.54	0.043
LONDEN	1		7.14		0.028
CONDEN	1		3.26		0.109
Residual	8	0.131			
Regression equation	MUV = 1.49 − 15.36(LONDEN) + 4.26 (CONDEN)				

The possibility that some of these statistically significant interactions could be the result of sampling, or precipitation-productivity effects can be ruled out. There are no significant correlations between MUV and trap-nights (Table 1), or density and diversity with trap-nights (Table 3). Nor were there any significant correlations between mean annual precipitation and any diversity or density variable (Table 3).

Table 3. Pair-wise correlation coefficients among the independent variables used in the multiple regression analysis

	TRPNTS	PPT
ORDEN	−0.232	−0.255
MERDEN	−0.49	0.104
LONGDEN	−0.008	−0.042
MANDEN	−0.181	0.133
HETSP	0.064	−0.141[a] (0.584[b])
TOTSP	−0.011	−0.085
TOTDEN	−0.423	−0.039

[a] Sand dunes where *D. ordii* is present

[b] Sand dunes where *D. merriami* is present

TRPNTS = the number of trapnights, PPT = mean annual precipitation, ORDEN = density of *D. ordii*, MERDEN = density of *D. merriami*, LONGDEN = density of *P. longimembris*, MANDEN = density of *Peromyscus maniculatus*, HETSP = the number of heteromyid species, TOTSP = the number of heteromyid and cricetid species, TOTDEN = the density of heteromyids and cricetids

Discussion

The hypothesis that the breadth of microhabitat use (MUV) should decrease as the number of presumed competing species increased (i.e., within the same guild) was supported by the analyses of MUV for both species of *Dipodomys* on Great Basin Desert sand dunes (Table 2, Fig. 2). The hypothesis that MUV should increase under intraspecific population pressure was generally supported by *D. merriami* and *Peromyscus maniculatus* (Table 2). However, only *D. merriami* significantly expanded its use of microhabitats with increases in its own density, suggesting a strong role of intraspecific competition in addition to interspecific competition in this species (Table 2). The hypothesis that interactions within guilds should be more pronounced than interactions between guilds was generally supported by all species in the analysis. There is no evidence that heteromyid MUV is affected in the slightest by cricetid diversity or abundance, but the MUV of heteromyids is affected by the presence or absence of other granivorous heteromyids (Tables 1, 2). In contrast to both species of *Dipodomys*, *Peromyscus maniculatus* MUV is affected more by the frequency of encounters than it is by the identity of individuals encountered (Table 2), which seems appropriate for an omnivore. The relative absence of inter-guild interactions is consistent with other investigations (Hallet 1982), but contrasts with the report by Rebar and Conley (1983) of a microhabitat shift in *D. ordii* in response to high densities of *Onychomys leucogaster*, a carnivorous cricetid.

The assumption that differences in microhabitat use among desert rodents are due to competition is supported by the analyses presented here. Significant competitive release in microhabitat use of two species of *Dipodomys* in the absence of presumed competitor species is strong evidence that habitat partitioning in heteromyid rodents is subject to competitive constraints. This is not to say that competition is solely responsible for habitat partitioning, but that competition affects the breadth of microhabitat use and the degree of overlap between species. Habitat partitioning is likely to be the result of several factors acting in combination, such as adaptative responses to predation risk, morphological constraints and foraging strategies (see Rosenzweig 1973; Kotler 1984; Thompson 1982b; and review by Price and Brown 1983).

The absence of significant correlations between diversity and abundance variables with the MUV of *P. longimembris* suggests that this species exhibits relatively inflexible foraging behavior with respect to microhabitat or that its habitat use is not affected by significant competitive interactions with other desert rodents. However, there are alternative hypotheses that are difficult to eliminate without manipulative experiments. The absence of a detectable response by *P. longimembris* may be due to constraints imposed by predation or a lack of statistical power. *Perognathus* may be constrained to forage for seeds beneath or near shrub canopies because of increased risk of predation in the open (Rosenzweig 1973; Kotler 1984; Price and Brown 1983), so no net benefit would be derived from expanding its MUV to include more open microhabitats. Additionally, species of *Perognathus* are generally only present on sand dunes of high rodent diversity and are relatively rare even where they occur (Brown 1973, 1975). The relative rarity is probably due to generally recognized preferences of *Perognathus* for habitats with denser vegetation than *Dipodomys* (Rosenzweig and Winakur 1969; Brown and Lieberman 1973; Rosenzweig 1973; Lemen and Rosenzweig 1973; Price 1978a; Wondolleck 1978). The vegetation on the sand dunes is sparse (Brown 1973) and therefore probably not optimal for *Perognathus*. The result is that MUV for *P. longimembris* is estimated over a relatively narrow range of community sizes which might not provide sufficient statistical power to reveal a pattern should one exist (Fig. 2).

Species diversity, productivity and competition

Even though significant correlations between heteromyid diversity and habitat use for *Dipodomys* are consistent with the hypothesis of competitive interactions, further analyses are necessary because productivity is confounded with diversity in the 1970–71 data. That is, predictable yearly rainfall $(\bar{X}-\sigma)$ is positively correlated with total species diversity (Brown 1973, 1975; Brown and Davidson 1977) and can therefore be involved indirectly with the MUV-heteromyid diversity correlations (Fig. 2). When resources are more abundant, species might be expected to specialize on those that can be exploited most efficiently (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971). This would result in the same relationship between MUV and heteromyid diversity as observed (Fig. 2). The question now becomes, what is responsible for changes in MUV, increased productivity allowing species to become more specialized, or competition forcing species to specialize?

Again, a natural experiment provides an opportunity to examine the question in a way experimental manipulations cannot. The eastern Great Basin sand dunes are depauperate in heteromyid species compared with the western sand dunes (Brown 1973, 1975). This appears to be due to high north-south mountain ranges through eastern Nevada preventing many of the heteromyids from colonizing the eastern portion since the restriction of their distributions to lower latitudes during the Pleistocene, rather than being due to heteromyids in the west lacking the physiological ability to survive in the east (Brown 1973, 1975). *D. merriami* is one such species restricted to the western portion, whereas *D. ordii* is not. There is no correlation between productivity and the number of heteromyid species on sand dunes where *D. ordii* is present ($r=-0.141$, $P>0.05$, Table 3), indicating that for this species the effects of productivity and competition are decoupled. If only the western dunes accessible to *D. merriami* are considered, the correlation between diversity and precipitation is marginal ($r=0.584$, $P<0.1$, Table 3). Because the relationship between diversity and rainfall does not exist across the range of sand dunes where *D. ordii* occurs, the decrease in MUV for this species can be attributed to species, interactions, rather than productivity. [Note that Brown (1973, 1975) reported a significant correlation between the number of common rodent species, both heteromyids and cricetids, and predictable yearly rainfall ($\bar{X}-\sigma$) across all sand dunes sampled. Some of those sand dunes are not included in the present analysis due to the absence or rarity of the four species considered here.]

Additional evidence supporting the role of competition comes from the 1978 live-trapping. The variation in rainfall on the sand dunes censused in 1978 is about one half that of the sites censused in 1970–71, because sites with similar rainfall were chosen intentionally (BP Kotler, personal communication). The animals were usually live-trapped and multiple captures of individuals are included in the estimates of MUV. Even so, the slope of the regression line for *D. ordii* is virtually identical to that for Brown's more geographically widespread 1970–1971 sample (Fig. 2), further supporting the competition hypothesis. Unfortunately, the sample size for *D. merriami* in 1978 is too small for meaningfull interpretation.

Body size similarity and competition

That ecologically similar species compete more intensely than less similar species is a paradigm, perhaps even a tautology, of community ecology. Body-size relationships among coexisting heteromyid species suggest that body size may provide an indirect measure of ecological similarity (Brown 1973, 1975; Bowers and Brown 1982), but the single direct experimental test of this hypothesis is ambiguous (see Schroder and Rosenzweig 1975). However, in this analysis of a natural experiment, the species co-occurring with competitors of similar size exhibited competitive release (*D. ordii* 49 g, and *D. merriami* 42 g), whereas there is no evidence that the species (*P. longimembris* 7 g) co-occurring with much larger species was affected by their presence or absence (Tables 1, 2).

Two experiments seeming to refute the hypothesis that *Dipodomys* and *Perognathus* do not compete intensely involve removals or manipulation of the lone species of *Dipodomys* and monitoring the response of three species of *Perognathus* in the Sonoran Desert. Wondolleck (1978) found that only *P. amplus*, the smallest species present, responded to the removal of *D. merriami* by expanding into habitats previously used by *D. merriami*. This is in direct opposition to the results for *P. longimembris* on Great Basin sand dunes and may be related to differences in perceived predation risk on the sparcely vegetated dunes and the relatively dense vegetation of Sonoran Desert bajadas. Price (1978a) compared the microhabitat use of heteromyids in enclosures with that in unenclosed communities and found that all the three species of *Perognathus* present tended to increase their use of the open microhabitat in the enclosures in the absence of *D. merriami*. In contrast, the microhabitat use of *D. merriami* alone in the enclosure was not different from its microhabitat use in the unenclosed community in the presence of the three species of *Perognathus*.

Analysing Price's data by contingency tables and residual analysis (Everitt 1977) using all four microhabitats examined reveals a more complex interaction (see Appendix 2). Only *P. penicillatus* significantly expanded into open habitats in the absence of *D. merriami*. The other two species of *Perognathus* significantly expanded their use of microhabitats which other species of *Perognathus* appeared to prefer in the unmanipulated community, not *Dipodomys* (Appendix 2). This suggests that the observed expansions in habitat use are due to the absence of congeners rather than the absence of *D. merriami* for two of the three species of *Perognathus*. The situation investigated by Wondolleck and Price is the converse of the situation on Great Basin sand dunes in that there are several species of *Perognathus* and one *Dipodomys*. However, on both Great Basin Desert sand dunes and Sonoran Desert bajadas the more diverse genus exhibits evidence for competitive release and not the other. Thus, data from both regions generally support the hypothesis that the interactions among species of similar body size (within genera) are more intense than among species of more disparate body size (between genera).

Over the last two decades considerable evidence has been produced supporting the hypothesis that competition is important in structuring desert rodent communities, particularly the guild of granivorous rodents comprised nearly exclusively of the family Heteromyidae. However, this evidence is not completely consistent. Why do *D. merriami* and *D. ordii* exhibit competitive release in some investigations (Table 1, Fig. 1), but not in others (Schroder and Rosenzweig 1975; Hallett 1982)? Why is there no apparent response by P. *longimembris* to the absence of *Dipodomys* on Great Basin Desert sand dunes, when other *Perognathus* species in other habitats exhibit competitive release in habitat use (Wondolleck 1978; Appendix 2), or in population density (Munger and Brown 1981; Brown and Munger 1985) when *Dipodomys* are removed? How much of the disparity is due to differences in structure of the habitat and apparent risk of predation (Rosenzweig 1973; Kotler 1984; Thompson 1982b), or inherent variation in competitive intensity between and within genera? Much of the current competition research in desert rodents appears to focus on exploitation competition nearly to the exclusion of considering interference (but see Frye 1983), even though the relative importance of each is unknown. An effort to understand the mechanisms behind these patterns and determine the relative importances of habitat structure, and exploitation vs. interference competition, will do much to advance the understanding of granivorous desert rodents and further their usefulness as a model system in community ecology.

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Appendix 1. Trapping dates and locations of sand dune sites in the Great Basin and Mohave Deserts

Dune[a]	Location	Date
1.	29 km WSW Winnemucca, Humbolt Co., Nev.	8/3–4/70
2.	15 km NE Lovelock, Pershing Co., Nev.	8/1/70
3.	34 km WNW Lovelock, Pershing Co., Nev.	7/30–31/70
4.	11 km S Lovelock, Pershing Co., Nev.	7/13–14/71 6/19–20/78[b]
5	37 km SE Fallon, Churchill Co., Nev.	8/5–6/70 7/16–17/78[b]
6.	21 km S Mina, Mineral Co., Nev.	9/1–2/70 7/15/78
7.	21 km N Dyer, Esmeralda Co., Nev.	9/5–6/70 6/4–5/78[b] 7/22/78
8.	7 km NW Keeler, Inyo Co., Calif.	9/13–14/71
9.	25 km S Baker, San Bernadino Co., Calif.	3/27–28/71
14.	11 km NE Montello, Elko Co., Nev.	8/19–20/70 7/1–2/78[b]
15.	2 km NE Dugway, Tooelė Co., Ut.	8/16/71 7/4–5/78[b]
16.	13 km S Currant, Nye Co., Nev.	8/30–31/71 7/12–13/78[b]
17.	16 km W Kanab, Kane Co., Ut.	8/9–10/71
18.	NE shore of Mono Lake, Mono Co., Calif.	9/3–4/70
19.	14 km S Lovelock, Pershing Co., Nev.	8/2–3/70
20.	10 km NW Mill City, Pershing Co., Nev.	7/15/70
21.	13 km N Winnemucca, Humbolt Co., Nev.	7/16/70
22.	15 km N Gandy, Juab Co., Ut.	9/5–6/72
23.	49 km SE Wells, Elko Co., Nev.	6/28–29/78[b]
24.	32 km N McGill, White Pine Co., Nev.	7/9–10/78[b]

[a] Numbering system through dune 18 follows Brown (1973)

[b] Rodents were live-trapped, on all other occasions snap-trapping was employed

Appendix 2. Contingency table analysis of the number of captures in each microhabitat of four species of heteromyids in the natural community and in single species enclosures from Price (1978a). Significance of the deviation from random from each cell in the contingency tables was determined by residual analysis (Everitt 1977). Upward pointing arrows indicate more captures than expected by chance, downward pointing arrows indicate fewer captures than expected by chance, $P<0.05$

	Habitat					
	LO	SO	LB	T	X^2	P
Dipodomys merriami						
Unmanipulated community	21	13	6	3	4.66	0.199
Enclosure	56	41	40	20		
Perognathus amplus						
Unmanipulated community	74↑	83↑	39↓	15↓	12.64	0.0003
Enclosure	70↓	61↓	57↑	31↑		
Perognathus penicillatus						
Unmanipulated community	18↓	12↓	51↑	43↑	17.94	0.0004
Enclosure	67↑	40↑	62↓	58↓		
Perognathus baileyi						
Unmanipulated community	22	20↓	37	34↑	7.08	0.069
Enclosure	58	87↑	91	63↓		

LO = large open microhabitats, SO = small open microhabitats, LB = large shrub microhabitats, and T = tree microhabitats

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