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An Experimental Study of Competition Between Seed-eating Desert Rodents and Ants

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SYNOPSIS. Reciprocal increases in rodent and ant densities on 0.1 ha plots from which the other taxon had been excluded demonstrate that these distantly related desert granivores compete for seeds. Relative to unmanipulated control plots, numbers of ant colonies increased 71% on plots where rodents were excluded; rodents increased 20% in numbers of individuals and 29% in biomass in the absence of ants. Comparisons of seed levels in the soil and of annual plant densities on experimental and control plots provide evidence that the rodent and ant populations are limited by and compete for food. Greater numbers of seeds and annuals occurred on plots where rodents and ants had been excluded than on plots where both taxa were present. Particular species of annuals were reduced in density by foraging of rodents. Ants increased species diversity by differentially harvesting seeds of the most common species. Results of these and other recent studies suggest that competition among distantly related organisms plays a major role in the organization of ecological communities.

INTRODUCTION

Much evidence suggests that interspecific competition influences the abundances and distributions of species populations (*e.g.*, Gause, 1934; Connell, 1961) and the structure and function of natural communities (*e.g.*, Cody and Diamond, 1975; see Wiens, 1977, for another view). Virtually all of this evidence comes from studies of closely related, often congeneric species. Because such species share similar evolutionary constraints, the potential for close competition between them is implicitly assumed. However, if food, space, or other resources are sufficiently limiting to result in competition

among close relatives, then these organisms also should compete with distantly related organisms which use the same resources. Recent investigations have demonstrated substantial similarities in diet or other aspects of resource utilization between different classes of vertebrates and between vertebrates and invertebrates (*e.g.*, Hansen and Ueckert, 1970; Brown *et al.*, 1975; Pearson, 1975, 1977; French *et al.*, 1976; Lister 1976; Fisler, 1977; Reichman, in preparation). Although these studies demonstrate the potential for competition, more direct, preferably experimental evidence is required to determine the extent to which distantly related taxa actually compete for limited resources and to assess the effects of these interactions on the organization of natural communities.

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Similarities in seed utilization and community organization between seed-eating desert rodents and ants (Brown, 1975; Brown *et al.*, 1975; Davidson, 1977a; Brown

and Davidson, 1977) led us to investigate possible effects of competition between the two taxa. In 1973 Brown and Davidson established replicated rodent and ant exclusion experiments in the Sonoran Desert near Tucson, Arizona. In the present paper we describe the effects of these treatments on abundances of rodents and ants, on densities of annual plants, and on quantities of seeds in the soil.

Desert seed-eaters provide an excellent system for analyzing the effects of competition between distantly related organisms. Rodents, ants and birds are abundant in deserts, and species of each taxon have specialized to feed primarily on seeds. These granivores are the primary consumers of seeds of annual and perennial plants. Granivorous birds are highly mobile and travel to forage in areas where seeds are locally abundant (e.g., Raitt and Pimm, 1976; Pulliam and Parker, 1979). In contrast, rodents and ants maintain permanent populations in local desert habitats. Although they store seeds to use in times of scarcity, rodent and ant abundances vary temporally and geographically in response to seed production, which in turn depends on precipitation (Brown, 1973, 1975; Whitford, 1976, 1978a,b; Davidson, 1977a,b; Reichman, 1978). Granivorous rodents and ants lend themselves to field studies in which their populations and food resources are manipulated experimentally.

METHODS

Study site

The experiment was conducted on the Silver Bell Validation Site of the Desert Biome, US/IBP, located approximately 60 km NW of Tucson, Arizona. The specific site was a small, relatively homogeneous area of several hectares located on the NE corner of the Validation Site which was characterized by relatively level, sandy soil and desert shrub vegetation dominated by *Larrea tridentata* and *Ambrosia deltoides*. Diverse communities of winter and summer annuals flourished on the site during brief periods when sufficient moisture was available.

Experimental treatments

Eight circular experimental plots, each 36 m in diameter (approximately 0.1 ha in area), were established in the area with the most level substrate and homogeneous vegetation. The experiment consisted of two replicates of four plots each. Plots were assigned at random to each of the following treatments:

1. Rodents excluded: These plots were fenced with 1/4 inch (0.64 cm) wire mesh to exclude rodents. Wire screening 3 ft (92 cm) wide was buried 15 cm in the ground and secured to wooden stakes to enclose the plots. Approximately 9 cm of wire was extended outward at an angle of 90° at the fence bottom to discourage digging, and another 9 cm was extended outward and downward to form an angle of 60° at the top to discourage climbing. Rodents were removed from these fenced plots, and their exclusion was maintained by periodic trapping.

2. Ants excluded: Individual ant colonies were poisoned by minute (0.25 cm³) applications of Mirex (Allied Chemical Corporation) in the immediate vicinities of their entrances. Colonies were located during periods of warm temperatures and high humidities when they were maximally active. Poisoning was repeated whenever careful periodic searches discovered active colonies. These plots were not fenced.

3. Rodents and ants excluded: These plots were both poisoned to eliminate ants and trapped and fenced to exclude rodents, as described above.

4. Control: These plots were not fenced or manipulated in any way.

The procedures described above resulted in extremely effective, but not absolute exclusion of rodents, ants or both from the appropriate plots. Most ant colonies were eliminated by the first poisoning, and repeated applications of Mirex kept the numbers of colonies and foraging workers very low. The combination of fencing and trapping resulted within a few months in the complete removal of the largest, most abundant seed-eating rodent, *Dipodomys merriami*. However, a small number of pocket mice, *Perognathus penicillatus*, *P.*

baileyi and *P. amplus* occasionally entered the fenced plots and were removed by periodic trapping. Our treatments reduced numbers of ants by more than 95% and numbers of rodents by more than 90% on appropriate exclusion plots.

The two replicate sets of plots were established at different times. On the first replicate, set up 1–7 August, 1973, relatively complete elimination of both ants and rodents from appropriate plots was accomplished immediately. When the second replicate was established, 14–20 December, 1973, most ant colonies were inactive and *Perognathus* spp. were hibernating; these granivores were not removed until the following spring (19–21 May, 1974).

Censuses of rodents and ants

Rodents and ants were censused at intervals which took into account their seasonal activity patterns and the amount of replication required to estimate accurately their population densities. Because their numbers were low and many samples were required to establish statistical confidence, rodents were censused more frequently than ants. Periodic rodent trapping was accomplished with 20 aluminum live traps (23.0 × 7.8 × 9.0 cm), set in a standardized geometric pattern on each ant-excluded and control plot for one night. Captured rodents were identified, recorded and released the following morning.

Ants were censused approximately twice each year at widely separated intervals during the warm months. Whenever possible ant colonies were counted during periods of high humidity and soil moisture within a few days after a rain, because most species were maximally active under these conditions. Individual nest entrances were marked, identified and counted by systematic search. Repeated searching of the plots during a daily temperature cycle insured that species with different activity temperatures were recorded. Three species of the genus *Pheidole* occurred on the plots, but occasionally these could not be distinguished because the diagnostic major workers were not active.

Sampling for seeds

A large number of soil samples were collected at intervals between September, 1974, and December, 1976. During each sampling period 50 samples were taken at 0.5 m intervals in a line across each of the four plots in the first replicate. Each sample site was marked with a small pebble, and during the next sampling period, soil was collected from new sites 0.5 m from the previous ones. Soil samples were collected by pressing a vial (39 mm in diameter) into the soil to a depth of 20 mm, sliding a cap over the open end of the vial, and depositing the contents in a coin envelope.

After drying and weighing of soil samples, the seeds were removed by a flotation technique (Reichman, 1976) and separated from organic debris by hand, using a dissecting microscope. Seeds were identified, counted and weighed. Because excessive clumping of minute seeds resulted in large sampling errors, our analyses do not include seeds weighing less than 0.4 mg each.

Census of annual plants

On 9–13 May, 1975, we used a photographic technique to sample annual plants which had germinated and grown on the experimental plots in response to rains during the previous winter. Plants were counted from colored photographic slides. On each experimental plot we photographed 20 sample sites of standardized area (0.33 m²). Five sample sites were chosen at random at approximately 2.5 m intervals along four radial lines running from the center of the plot to each of the cardinal compass directions. If a sample site fell under the canopy of a perennial plant, it was moved the shortest distance possible to obtain an uncovered site. Reference specimens of common annual plant species were collected and identified. Later the slides were projected and individual annuals were counted by species. Annual plants on the study site were censused and studied in detail in the winter (January to April) of 1977. Results of this study are described in detail in Inouye, Byers and Brown (1980).

RESULTS

Rodent and ant densities

Rodents and ants increased and maintained higher densities on plots from which the other taxon had been excluded, compared to unmanipulated control plots where the two taxa coexisted (Tables 1–3, see also Brown and Davidson, 1976, 1977). Increase of ants in the absence of rodents was particularly dramatic. The total number of ant colonies was 71% greater on rodent excluded plots than on controls (Tables 1 and 3); this increase was highly significant (Wilcoxon Matched-Pairs Signed Rank Test, $P < 0.01$). In only 1 of 10 possible comparisons between rodent-removed and control plots was the number of ant colonies greater on the latter. That comparison involved the first census of the second replicate made in August, 1974, only a few months after the onset of any activity, and perhaps too soon to expect significant response to our treatments. Species of the genus *Pheidole* showed particularly large increases in numbers of colonies in the absence of rodents. There were too few colonies of the other harvester ants to detect significant responses of individual species.

Rodents increased 20% in total numbers of individuals and 29% in total biomass on plots from which ants were excluded, relative to controls (Tables 2 and 3). Out of 27 simultaneous paired censuses, 17 had more rodents on ant-excluded plots than on controls, while 5 showed equal numbers under the two treatments. Despite the small sample sizes (and resulting sampling error) and the modest magnitude of the response, the increase of rodents in the absence of ants was highly significant (Wilcoxon Matched Pairs Signed Test, $P < 0.01$). The greater increase in rodent biomass than in numbers of individuals resulted from a differential increase in *Dipodomys merriami*, the largest granivorous rodent inhabiting the study site, on the ant exclusion plots.

Quality of seeds in the soil

If increased densities of rodents and ants in the absence of the other taxon reflect

exploitative competition for seeds, then seed density and biomass should be lower on plots where rodents and ants were excluded. Figure 1 shows that this was, indeed, the case. Seed densities were highest on the plot from which both granivores were excluded, intermediate on the plots where either ants or rodents had been removed, and lowest on the control plot where all granivores were present. Differences among plots were not consistent or significant when sampling was first begun, about a year after the granivore removal treatments were initiated. However, after late 1975, the effects of granivore exclusion were dramatic and consistent. The plot from which both rodents and ants were excluded, consistently contained 2–4 times higher density and biomass of seeds than plots where one or both classes of granivores were present.

Densities of annual plants

The seasonal pattern of rainfall in the Sonoran Desert is bimodal with peaks in winter (November to March) and summer (June and July). Quantity of these rains is highly unpredictable, but if sufficient precipitation falls in a season, a crop of annuals is produced. Winter and summer annuals constitute distinctive communities composed of almost completely different species.

Artificial exclusion of granivores resulted in increasing differences in abundance and species composition of annuals among plots as the study progressed. No differences were apparent when winter annuals were first censused in May, 1975 (Table 4). Since all of these plants had germinated several months previously, this similarity among plots corresponds well to data on seed levels in the soil in September and December, 1974 (Figure 1). Two seasons later, in 1977, there were significant differences among the granivore exclusion treatments (Table 4). These results, even more dramatically than the data on soil seed reserves, show the impact of granivores. Compared to control plots where both classes of seed-eaters were present, densities of annuals were about 1.5 times greater on plots where either rodents

TABLE 1. Number of ant colonies counted on plots from which rodents were excluded and on unmanipulated control plots.

Species	7-9 August, 1974		10-13 May, 1975		18-21 September, 1975		18-21 May, 1976		29 July-1 August, 1976											
	1st Replicate -R ^a	2nd Replicate -R	1st Replicate -R	2nd Replicate -R	1st Replicate -R	2nd Replicate -R	1st Replicate -R	2nd Replicate -R	1st Replicate -R	2nd Replicate -R										
<i>Pheidole xerophila</i> , <i>P. sitarches</i> , or <i>P. givescens</i>	30	23	33	42	49	19	67	21	45	24	57	20	35	21	28	13	40	22	28	16
<i>Pogonomyrmex</i> <i>pima</i>	24	12	4	8	1	0	1	0	11	10	16	8	17	8	8	7	16	8	9	6
<i>Pogonomyrmex</i> <i>rugosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0
<i>Veromessor</i> <i>pergandei</i>	1	1	2	2	0	1	2	2	0	1	2	2	1	0	1	3	0	0	2	2
<i>Novomessor</i> <i>cockerelli</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
<i>Solenopsis</i> <i>xyloni</i> ^c	3	1	1	2	0	0	0	0	1	0	0	0	3	1	2	3	1	2	0	2
Total Ant Colonies	58	37	40	54	50	20	70	23	57	35	75	30	57	31	39	27	59	34	41	27

^a Plots from which rodents were removed (-R).

^b Control plots (C) both rodents and ants present.

^c Number of nest entrances, which may not necessarily represent different colonies.

TABLE 2. Number of rodent individuals trapped on plots from which ants were excluded and on unmanipulated control plots.

Species	15-19 December, 1973		15-19 May, 1974		16-17 April, 1975		29-30 June, 1975						
	1st Replicate -A ^a	C ^b	1st Replicate -A	2nd Replicate C	1st Replicate -A	2nd Replicate C	1st Replicate -A	2nd Replicate C					
<i>Dipodomys merriami</i>	8	9	7	5	6	0	7	4	5	9	4	5	5
<i>Perognathus baileyi</i>	5	2	1	0	0	0	0	0	0	0	0	0	0
<i>P. penicillatus</i>	0	0	0	1	1	2	1	0	0	2	1	2	2
<i>P. amplus</i>	0	0	1	1	0	0	2	3	1	2	0	1	1
Total Rodents	13	11	9	7	7	2	10	7	7	9	10	7	8
	29-30 August, 1975		4-5 October, 1975		8-9 November, 1975		21-22 May, 1976						
	1st Replicate -A	2nd Replicate C	1st Replicate -A	2nd Replicate C	1st Replicate -A	2nd Replicate C	1st Replicate -A	2nd Replicate C					
<i>Dipodomys merriami</i>	10	7	6	6	9	8	6	5	10	10	5	5	
<i>Perognathus baileyi</i>	0	0	0	1	0	0	0	1	0	0	0	0	
<i>P. penicillatus</i>	2	2	2	1	0	0	1	0	0	0	0	0	
<i>P. amplus</i>	0	1	0	1	0	0	0	0	0	0	0	0	
Total Rodents	12	10	8	9	9	8	7	6	10	10	5	5	
	2-3 January, 1976		1-2 February, 1976		19-20 March, 1976		2-3 January, 1977						
	1st Replicate -A	2nd Replicate C	1st Replicate -A	2nd Replicate C	1st Replicate -A	2nd Replicate C	1st Replicate -A	2nd Replicate C					
<i>Dipodomys merriami</i>	4	1	3	2	4	2	2	1	2	1	2	0	2
<i>Perognathus baileyi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. penicillatus</i>	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>P. amplus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
Total Rodents	4	1	3	2	4	2	2	1	2	1	2	0	2
	23-24 June, 1976		10-11 August, 1976		2-3 January, 1977								
	1st Replicate -A	2nd Replicate C	1st Replicate -A	2nd Replicate C	1st Replicate -A	2nd Replicate C	1st Replicate -A	2nd Replicate C					
<i>Dipodomys merriami</i>	0	0	1	1	1	0	2	1	5	4	2	0	0
<i>Perognathus baileyi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. penicillatus</i>	0	1	1	1	1	0	1	1	1	0	0	0	0
<i>P. amplus</i>	3	1	2	2	0	2	1	1	0	0	0	0	0
Total Rodents	3	2	4	4	2	2	4	3	5	4	2	0	0

^a Plots from which ants were removed (-A).
^b Control plots, both rodents and ants present (C).

TABLE 3. Summary of the results of experiments in which ants or rodents were eliminated from plots and the unmanipulated taxon was repeatedly censused.^a

	Rodents removed	Ants removed	Control	% increase relative to control	Fraction of comparisons experimental/4 control
Ant colonies	543	—	318	70.8	9/10
Rodent Individuals	—	151	126	19.8	17/27 (5 equal)
Rodent Biomass (kg) ^b	—	5.41	4.21	28.5	17/27 (3 equal)

^a Values in the first three columns are totals of all censuses. Ants were censused five times and there were two replicates of each treatment for a total of ten comparisons. There were 27 comparisons for rodents, 14 censuses of the first replicate (established in August, 1973) and 13 censuses of second set (established in December, 1973).

^b Based on average body weights on the study area of 41.1 g for *Dipodomys merriami*, 28.1 g for *Perognathus baileyi*, 16.9 g for *P. penicillatus*, and 11.4 g for *P. amplus*.

or ants had been removed, and 2 times greater on those plots where both classes had been excluded (Tables 4 and 5).

When densities of particular plant species are compared among treatments, it is apparent that rodents and ants had different effects on the annual community (Table 5, Inouye *et al.*, 1980). Rodents, by foraging selectively on large-seeded species, increased the evenness with which biomass was distributed among species. When rodents were present, they differentially reduced densities of *Erodium* and *Lotus*; when rodents were removed, these large seeds accumulated in high densities and germinated to produce robust seedlings which grew rapidly and dominated the community in terms of biomass (Inouye *et al.*, 1980). Ants, on the other hand, increased annual species diversity by selectively harvesting the small seeds of *Filago californica*, the most abundant winter herb on the study site (Table 5). It is probably not coincidental that the most abundant ant on the site was *Pheidole xerophila* which has tiny workers and harvests small seeds (Davidson, 1977a,b). Davidson (unpublished data) has independent evidence that seed abundance accounts for the greatest proportion of the variance in seed choice in *Pheidole* foraging on native seeds. Species diversity, H' (where $H' = 1/p_i^2$) and the evenness of species abundances, H'/H'_{\max} were both significantly greater on plots where ants were present than on plots where they had been excluded. For a more complete anal-

ysis of the effects of granivore exclusion and other manipulations on the annual plants in the experimental plots, see Inouye *et al.* (1980).

DISCUSSION

Problems of sampling and experimental design

There has been much recent emphasis on the use of field experiments in ecology. In general this influence has been healthy because it has encouraged rigorous testing of hypotheses and contributed to the fruitful interplay of theory and empiricism. However, it is not as simple as it may appear to manipulate natural ecological systems so as to obtain repeatable and pertinent results. Heterogeneity of the environment, the diversity and complexity of ecosystems, and the spatial and temporal scale of ecological processes present the experimental ecologist with challenges undreamed of by most laboratory biologists and physical scientists. Although our competition experiment was conceptually simple, it illustrates some of the problems encountered in attempting to do rigorous, meaningful experimental ecology.

Because of the spatial scale necessary for our experiments and limitations of money and manpower, extensive replication of treatments was impossible. For this reason, it would have been desirable to obtain accurate pretreatment estimates of rodents, ants, seeds and plants on each plot, rather

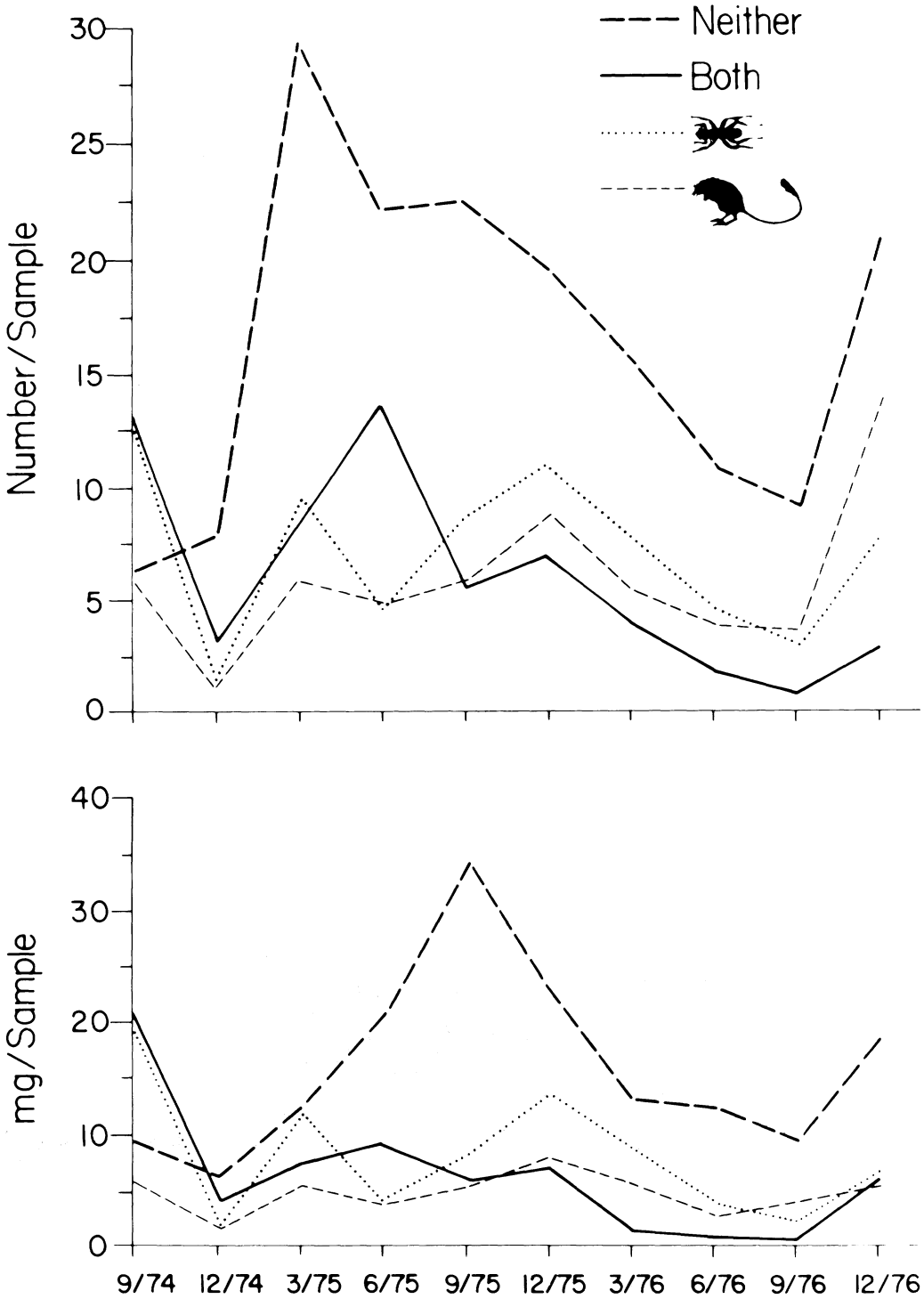


FIG. 1. Comparison of mean number (above) and biomass (below) of seeds weighing more than 0.4 mg in 24 cm³ soil samples collected at different times from plots from which ants (+R-A), rodents (-R+A), both taxa (-R-A), and neither taxon (+R+A, control) had been removed. Note that when granivores were excluded, seeds accumulated in the soil. The pattern is particularly clear for seed biomass.

TABLE 4. *Effects of experimental exclusion of rodents and ants on densities of winter annuals in 1975 and 1977.**

Treatment	+R+A	+R-A	-R+A	-R-A
1975 Density	26.7±15.7	18.5±16.4	20.3±29.4	22.7±19.5
Ratio experimental/ control	1.00	0.69	0.76	0.85
1977 Density	224.1±102.8	371.9±183.9	319.7±204.1	512.0±263.6
Ratio experimental/ control	1.00	1.66	1.43	2.28

* Densities are expressed as number of plants/m² ± 1 standard error; differences in densities on control plots (+R+A) between 1975 and 1977 are owing to differences in rainfall between years. In 1975, about one year after treatments were initiated, there were no significant differences between experimental and control plots, but two years later there were significantly more annuals on granivore removal plots than on controls. From Inouye *et al.* (1980).

than to rely on post-treatment comparisons between manipulated and control plots. However, to do so would have required 1–2 years of frequent sampling to determine whether there were significant differences in rodent, ant and plant populations between plots even before any treatments were begun. However, similarities among treatments in soil seed reserves and annual plant densities early in the study followed by increasing differences as the study progressed and the granivores began to affect the seed bank and plant community, are adequate evidence that the plots were good replicates and the differences we report here were the result of our experimental manipulations.

In conducting an experiment, it is desirable to hold all variables except the one under investigation constant. We would have liked to have excluded ants, rodents and both from our plots without changing anything else. Unfortunately, it was necessary to fence plots in order to exclude rodents, but to have fenced in rodents on those plots where they were supposed to be present would almost certainly have created more artifacts than no fencing at all. Artificially enclosed rodent populations are likely to go extinct if they are small, as in the present case (French *et al.*, 1974); alternatively, they sometimes increase to pathologically high densities (Krebs *et al.*, 1969). We chose the lesser evil, and fenced only those plots from which rodents or both rodents and ants were excluded, but we are aware that the fencing itself may have created artifacts: Most seriously, the fences may have excluded small to medium-sized

mammalian herbivores (*i.e.*, ground squirrels and rabbits) and ant predators (particularly horned lizards of the genus *Phrynosoma*), and they may have interfered with movement of wind and water and thereby with the dispersal of seeds. Fortunately, our data suggest that none of these effects was significant. The only horned lizard on the study site was a large species, *Phrynosoma solare*. The large horned lizards feed primarily on large ants, such as species of *Pogonomyrmex* (Davidson, unpublished data; Whitford and Bryant, 1979), but the ants that increased in density on fenced plots from which rodents had been removed were *Pheidole* spp which have tiny workers. Inouye *et al.* (1980) found no effects of our experimental treatments on the survival of winter annuals and suggested that neither mammalian nor insect herbivores had significant impact on the annual plants. Data on quantities of seeds in the soil (Fig. 1) and densities of winter annuals (Tables 4 and 5, Inouye *et al.*, 1980) show large differences between control plots and those where either or both taxa of granivores were excluded, but no effect of fencing.

Accurate sampling of rodents, ants, plants and seeds also presents problems. The most obvious problem is created by microspatial heterogeneity which drastically influences the local abundance of annual plants and seeds. This difficulty can be overcome in part by taking large numbers of samples, as we have tried to do. Some of the variance in the measurements of annuals is probably attributable to this cause.

Our census techniques may have caused

TABLE 5. Effects of experimental removal of rodents, ants, or both on densities of certain plant species, densities and biomass of all plants, and two measures of plant species diversity for winter annuals in 1977^a.

Density of:	Seed weight (mg)	Treatment				Effect of removal of	
		+R+A	+R-A	-R+A	-R-A	Rodents	Ants
<i>Erodium cicutarium</i>	1.6	1.00 (1.75)	1.83	7.03	16.11	increase $P < 0.01$	not significant
<i>Erodium texanum</i>	1.6	1.00 (0.59)	0.88	2.07	0.78	increase $P < 0.05$	not significant
<i>Lotus humistratus</i>	1.5	1.00 (11.4)	1.14	2.43	5.22	increase $P < 0.01$	not significant
<i>Filago californica</i>	0.04	1.00 (142.1)	1.90	1.43	2.59	not significant	increase $P < 0.05$
All plants ^b		1.00 (209.6)	1.35	1.34	1.94	increase $P < 0.05$	increase $P < 0.01$
Species diversity (H')		1.00 (2.78)	0.73	0.99	0.89	not significant	decrease $P < 0.05$
Evenness (H'/H' _{max})		1.00 (0.53)	0.77	1.99	1.04	not significant	decrease $P < 0.05$
Biomass (g dry weight/m ²)		1.00 (15.80)	1.07	2.09	2.17	increase $P < 0.01$	not significant

^a Values given under the four treatments are ratios of experimental to control (+R+A) means. Numbers in parentheses are average values for control plots. Statistical analysis was by analysis of variance. From Inouye *et al.* (1980).

^b These values are somewhat different from those in Table 4, because they include plots which received supplemental water. Their inclusion does not change the qualitative pattern, but increases sample size and statistical power (see Inouye *et al.*, 1980 for details).

us to underestimate the magnitude of the response of rodents, ants and plants to our experimental manipulations. Since plots containing rodents were unfenced and rodents were sampled using baited traps, it is possible that the traps attracted animals which did not normally forage on the plots. This would have the effect of diminishing real differences in rodent densities between control and ant-excluded plots. We might also have missed some of the rodent response, if rodents responded to ant removal by temporarily increasing foraging activity in the brief periods when the plants were setting and dispersing their seeds. We censused ants by counting the number of colonies, because it was impractical to attempt to estimate the number of individuals in the colonies. If some of the response of ants to exclusion of rodents was to increase the size of individual colonies, as well as to increase the number of colonies, then we did not detect it.

Despite these and other more minor problems with sampling and experimental design, the consistency of our results for rodents, ants, seeds and annual plants gives us great confidence in our results. If anything, we suspect that we may have underestimated the magnitude of the response of both rodents and ants to the experimental removal of the other taxon.

Competition between rodents and ants

Reciprocal density compensations between rodents and ants in response to experimental removal of the other taxon provide direct evidence for competitive interactions between these two kinds of desert granivores. Increases both in quantity of seeds in the soil and in number of summer annuals which germinated and grew out of this seed bank on plots from which rodents, ants or both were excluded provide additional evidence that the changes in granivore populations reflect competition between the two taxa. This evidence is significant for two reasons. First, as Colwell and Fuentes (1975) have pointed out, much of the existing evidence for exploitative competition is indirect or inferred, and even where resource competition can be demonstrated

experimentally, it is extremely difficult to exclude the possibility that some subtle or unrecognized form of interference interaction is the major mechanism of the competition. Our results clearly demonstrate that a significant component of the competition is exploitative. Secondly, recent analyses suggest that indirect interspecific interactions might produce anomalous results in simple exclusion experiments (Levins, 1975; Holt, 1977; Davidson, 1980). Because we have measured changes in resource levels coincidentally with population responses in competing consumers, we are confident that we have interpreted the mechanism of our experimental results correctly.

All of our results consistently support the interpretation that granivorous rodents and ants have overlapping requirements for limited seeds, that the two taxa compete and inhibit each other when they co-occur, and that each taxon is able to harvest more seeds and to increase in population density when the other is excluded experimentally. Bryant *et al.*, (1976) independently performed granivore exclusion experiments in the Chihuahuan Desert near Las Cruces, New Mexico and obtained gratifyingly similar results. Although they did not test for the response of rodents to removal of ants, they did observe similar increases of ants when rodents were excluded and increases of annual plants when both rodents and ants were excluded. These sorts of exclusion experiments may underestimate the magnitude of potential competition between rodents and ants. Seed-eating rodents and ants probably have coexisted in arid habitats for at least 2 million years, so the two groups have had sufficient time to evolve adaptations to avoid competition. Such coevolutionary adjustments would limit the short-term numerical response of the granivores to artificial removal of competitors.

Our experimental data support and complement results of earlier studies which showed that seed-eating rodents and ants: 1) are food limited, and increase in population density and species diversity in geographic gradients of increasing productivity; 2) show patterns of character displacement, community convergence and resource util-

ization which suggest that competition has played a major role in determining community organization; and 3) have large overlaps in diet and foraging areas which indicate the potential for significant ongoing competition, both within and between the two distantly related taxa (Brown, 1973; Brown and Lieberman, 1973; Brown *et al.*, 1975; Brown and Davidson, 1977; Davidson, 1977*a,b*, 1978; Reichman, 1975, 1977; Reichman and Oberstein, 1977; Whitford, 1978*a,b*). In addition, geographic patterns of species diversity and population density in seed-eating rodents and ants provided circumstantial evidence that these two taxa compete for seed resources (Brown and Davidson, 1977). We now have direct, experimental evidence for competition between rodents and ants, and for the impact of these two kinds of granivores as seed predators on the soil seed bank and on annual plant populations.

Current theories of competition and community structure suggest that stable coexistence of competing species depends on differential utilization of limited resources (*e.g.*, MacArthur, 1972 and included references). Closely related species are so similar in most respects that a good naturalist can often guess which of the few differences are involved in subdividing resources (for seed-eating desert rodents and ants see Brown, 1975, and Davidson, 1977*a,b*). Distantly related taxa such as ants and rodents differ in so many ways that it is difficult to determine which are ecologically most important. However, fundamental differences between rodents and ants in life history and body size have numerous behavioral and ecological consequences which appear to promote differential seed utilization and coexistence. Seed-eating rodents live and reproduce as independent individuals weighing 7–120 g as adults. Harvester ants live in highly organized colonies containing a reproductive queen and hundreds or even thousands of sterile workers, each weighing 0.5 to 50 mg. Rodents have relatively short life spans, but they must survive periods of seed scarcity and reproduce as large, energetically expensive individuals. Established ant colonies are long lived and successful founding of new col-

onies occurs infrequently, but ants can adjust foraging activity to resource availability, allow portions of the colony to die back selectively when food is scarce, and produce new workers rapidly and facultatively in response to new seed crops. Both rodents and ants collect seeds when they are abundant and store them for use when they are scarce. Rodents forage selectively for large, clumped, often buried seeds which they collect in cheek pouches. Ants collect seeds singly from the surface of the ground, but they can forage profitably for smaller and more scattered seeds than rodents. Clearly, the two taxa differ significantly in their capacities to utilize various sizes and spatial and temporal distributions of seeds for their maintenance and reproduction, but further study will be required to identify the exact mechanisms of competition and coexistence.

Our data suggest that rodents and ants compete primarily by exploiting common food resources and reducing their availability, but we have some evidence that the two classes also actively interfere with each other. Seed-eating rodents sometimes eat ants (Reichman, 1978) and dig into their nests to steal seeds stored in graineries. We have also seen ants interfering with rodents foraging at seed clumps by climbing over their bodies and apparently biting and stinging them. Although we doubt that such interclass interference plays a major role in structuring desert granivore communities, it warrants further investigation.

General implications

It is widely appreciated that distantly related organisms may compete. Any experienced naturalist can cite examples of distantly related taxa that compete either by aggressive interference or by exploiting limited resources such as food, nest sites or space. Much of modern agricultural practice is devoted to controlling plant, insect and vertebrate pests that compete either directly with man himself or with his domesticated animals and plants.

Despite all the obvious examples, ecologists have been slow to investigate the importance of competition between distantly

related organisms. This is surprising because ecologists have been studying competition since the pioneering work of Gause (1934), Lotka (1925) and Volterra (1926). Much evidence has been accumulated to show that competition among closely related species often plays a major role in determining patterns of coexistence and organization of communities (*e.g.*, see Cody and Diamond, 1975; for a dissenting view see Wiens, 1977). Only in the last few years have ecologists begun to obtain data which suggest that competition among distantly related species might be of great importance in natural communities. Most of the evidence is circumstantial and comes from biogeographic patterns or observed overlaps in diet between such organisms as leaf-eating insects and mammals (Hanson and Ueckert, 1970; Sinclair, 1975; French *et al.*, 1976), insectivorous lizards and birds (Lister, 1976), seed-eating rodents, ants and birds (Brown *et al.*, 1975; Brown, 1975; Davidson, 1977a, Mares and Rosenzweig, 1978), bird and mammal frugivores (Pearson, 1975, 1977), and various taxa of detritivores (Janzen, 1977). Although many kinds of plants are known or suspected to compete for space, light, water or nutrients (*e.g.*, Harper, 1977), and distantly related taxa compete for space in intertidal and other aquatic communities (*e.g.*, Dayton, 1971; Paine, 1971), to our knowledge the present study represents the first direct, experimental documentation of competition for food among distantly related kinds of terrestrial heterotrophs (also see Brown *et al.*, 1975; Brown and Davidson, 1977).

Distantly related taxa differ in a plethora of ways that may influence their roles in the community as competitors, predators, prey or mutualists. Like rodents and ants, many sets of potentially competing, distantly related species differ greatly in body size, energy requirements, trophic structures, and foraging behavior. In terrestrial ecosystems, competition between vertebrates and arthropods must be particularly widespread. Obvious examples include nectar-feeding birds and insects, leaf-eating insects and grazing mammals and fly catching birds, spiders and dragonflies. Comparative studies of these systems may

suggest general mechanisms which enable distantly related taxa to play sufficiently different functional roles within their ecosystems in such a way that they simultaneously compete and coexist as members of a stable community.

We suggest that the general failure of ecologists to study and appreciate the importance of competition among distantly related organisms reflects the lack of an adequate conceptual basis for evaluating this kind of interaction. For decades after Gause's (1934) original experiments with *Paramecium*, empirical studies of competition almost invariably consisted of attempts to test the generality of "Gause's axiom" with yet another pair of superficially similar, closely related species. The most widely used current theories of competition and community structure are based directly on the equations of Lotka (1925) and Volterra (1926). These formalisms are based on the logistic equation of population growth and use the competition coefficient, α , to express the inhibitory effect of a heterospecific individual relative to a conspecific one. Presumably α can be measured directly or estimated indirectly from overlaps in utilization of limiting resources, and there has been some progress applying this approach to communities of closely related species (*e.g.*, Pulliam, 1975; Culver, 1976; Davidson, 1980). However, for organisms which differ as much and in as many ways as vertebrates and arthropods, the Lotka-Volterra model and its derivatives such as the community matrix and limiting similarity concept, simply do not suggest operational criteria and testable hypotheses which are useful for studying interactions in natural communities. Much of the criticism of studies purporting to show the importance in nature of competition among even closely related species stems largely from attempts to interpret patterns in terms of models based on Lotka-Volterra equations (*e.g.*, Wiens, 1977). At this time we have no alternative models to offer. However, we hope that as ecologists learn more about community level interactions among species, patterns will emerge, and these will lead to general concepts and theories.

Wiens (1977) recently has questioned the widely held view that competition plays a major role in determining the structure and function of ecological communities, and he has criticized many of the studies purporting to demonstrate the occurrence and importance of competition. Wiens argues that food and other resources are usually abundant and that competition is likely to occur only during infrequent "ecological crunches" when resources are temporarily in short supply. We conclude by taking issue with Wiens' viewpoint. Probably no other terrestrial habitat experiences such large, unpredictable fluctuations in availability of food, water and other resources as occur in deserts. Unpredictable variation in precipitation and primary production are reflected in pulses of seed availability and in fluctuating population sizes of seed-eating rodents (Whitford, 1976), activity patterns of harvester ants (Davidson, 1977*b*; Whitford, 1978*a*), and foraging behavior of granivorous finches (Raitt and Pimm, 1976). Despite great variation in food availability, rodents and ants appear to be limited by and to compete for seeds almost continuously. The two taxa responded rapidly to our exclusion experiments and they maintained relatively constant levels of compensation; this is most apparent for ants which could be sampled with greater accuracy (Table 1). In addition, both taxa continuously maintained low levels of seed availability despite periodic pulses of seed production and the great accumulation of seeds on plots where both taxa had been removed (Fig. 1). Many adaptations of these granivores such as torpor in rodents, curtailment of surface activity in ants, and accumulation of stored seeds by both taxa appear to be adaptations to diminish adverse effects of widely fluctuating food resources. If desert rodents and ants are food limited and compete strongly with each other, it does not seem unreasonable to argue, as we have on the basis of other independent evidence (Brown and Lieberman, 1973; Brown, 1975; Davidson, 1977*a,b*, 1978, 1980), that competition within these taxa has played a major role in determining the number and characteristics of coexisting species. The present study suggests that

competitive interactions may be far more widespread and important in desert communities than we had ever suspected. This is not to say that predator-prey interactions and variation in the physical environment are not also important; indeed, we suspect that these factors interact with competition to influence community structure and stability (Inouye, *et al.*, 1980). On the basis of our work on desert granivores, we predict that further work on competitive interactions will rapidly advance our understanding of community ecology, particularly as increasing numbers of investigators use experiments to dissect relationships among distantly related species.

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