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J.H. Brown

D.W. Davidson

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RODENT SEED-FORAGING STRATEGIES AND COMPETITION WITH ANTS IN THE SONORAN DESERT

J. H. Brown (Project Leader)
and D. W. Davidson
University of Arizona

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Ecology Center, Utah State University, Logan, Utah 84322

ABSTRACT

Exclusion experiments have demonstrated what appear to be significant competitive interactions between seed-eating rodents and ants in a desert ecosystem. In 1973 two replicate sets of experimental plots were established on which four treatments were performed: 1) rodents removed, 2) ants removed, 3) both rodents and ants removed, 4) unmanipulated control. Since then repeated sampling has indicated that number of ant colonies increased 76% on plots where rodents were absent; rodents increased 19% in numbers of individuals and 24% in biomass on plots where ants were removed relative to control plots. On plots where both rodents and ants were removed, O. J. Reichman has observed a large accumulation of seeds in the soil, but no other effects of the experimental treatment on the plant community have been detected. The plant-granivore system on the manipulated plots may not yet have reached equilibrium. This study suggests that competition between unrelated taxa may play a major role in determining the structure and dynamics of natural ecosystems.

INTRODUCTION

Competitive interactions between such distantly related taxa as insects and mammals have received little attention from population and community ecologists. There are numerous studies that document competition between closely related species (usually congeners) and suggest it has played a major role in structuring natural communities (e.g., Cody and Diamond 1975; Grant 1972; Miller 1967). Although it is obvious that distantly related taxa often share requirements for limited resources such as food, the lack of obvious patterns of resource subdivision and character displacement and the taxonomic specialization of many ecologists apparently have inhibited detailed studies of competition among distantly related species.

Long-term analyses of community structure and resource utilization of seed-eating rodents (Brown 1973, 1975; Brown and Lieberman 1973) and ants (Davidson, in prep.) suggested that these two taxa might be important competitors and that their interactions might play an important role in determining the structure and function of desert ecosystems. Among the rodents and ants that occur in desert habitats, the majority of species are primarily granivorous. In a geographic gradient over which precipitation and productivity increased but temperature, latitude and other parameters remained relatively constant, the abundance and species diversity of both ants and rodents increased in a similar fashion. The two taxa overlapped greatly in the sizes and species of seeds on which they foraged and in the microhabitats where they were collected. An experimental study (Brown et al. 1975) indicated that ants and rodents overlapped greatly in their predation on artificial seeds placed in desert habitats. Taken together, these results suggested that rodents and ants might compete strongly for seeds and that an experimental test of such competitive interactions was required.

In 1973, we began a series of exclusion experiments to assess the significance of competition between seed-eating rodents and ants in a desert ecosystem. In addition, we hoped to measure the impact of these granivores on the structure and dynamics of the desert plant community. These experiments now appear to have produced significant results that are reported here for the first time.

METHODS

A series of exclusion experiments were begun on the Silverbell Validation Site (approximately 24 km west of Marana, Pinal County, Arizona) in 1973. In August, a set of four experimental plots was established, and a replicate set was added in December. One of the four plots in each set was treated as follows: 1) fenced with ¼-inch wire mesh to exclude rodents, rodents removed by snap-trapping; 2) ants removed by local application of Mirex or Chlorodane to colonies, and exclusion maintained by repeated poisoning; 3) both ants and rodents removed and excluded by both fencing and poisoning as indicated above; 4) unmanipulated control. Each plot was 18 m in radius. Plots were distributed haphazardly on the area of relatively flat, homogeneous, *Larrea-Ambrosia* habitat on the northeast corner of the Silverbell site. During the first year rodents apparently entered the enclosures via burrows deep beneath the wire fencing, and frequent trapping was required to keep the fenced plots free of rodents. After the first year the fences proved effective in excluding rodents and little trapping within the enclosures was required. Ants were virtually eliminated from the appropriate plots by the initial poisoning and subsequent applications once or twice a year when incipient colonies were detected.

Because rodents and ants differed in abundance and presented different sampling problems, different techniques were employed to sample the two taxa on the experimental plots. Only a few rodents foraged on any particular plot at any one time, so that it was necessary to sample repeatedly to avoid sampling error and accumulate statistically meaningful data. However, too frequent sampling involved the risk of attracting rodents to the baited traps and mitigating the effects of the experimental treatments. Initially, the plots were trapped for one night at intervals of several months, but since April 1975, the plots have been trapped for one night at intervals of one or two months. Each plot was sampled by setting 20 Sherman aluminum live traps (8 x 8 x 22 cm) baited with mixed birdseed in a standardized geometric arrangement.

Ants could be censused accurately by counting the number of active colonies. Since some ant species were active only for short period of the year and there were large numbers of colonies on each plot, it was sufficient to census the ants infrequently, but during periods when most of the colonies were active. It is difficult to estimate accurately the number of ants in a colony. Thus, we are unable to provide figures on the number of individuals or the total biomass of ants on a plot, but we are confident that the number of colonies represents an accurate and probably conservative estimate of the response of ants to the elimination of rodents.

A photographic technique was used to sample the annual plants on the experimental plots. Twenty sample areas were chosen haphazardly by tossing a marker onto each plot. Each sample area of standardized size (75 x 45 cm) was photographed using high speed Ectachrome film in a 35-mm camera. Colored slides were then obtained and projected on a grid to count the number and species of plants present and to obtain an estimate of cover (number of grid squares containing one or more plants).

RESULTS

The results clearly indicate that the presence of either rodents or ants inhibits the other taxon from attaining the numbers it can reach in the absence of these competitors. The response of ants to eliminating rodents was much greater (Tables 1 and 2) than the increase in rodents when ants were removed (Tables 2 and 3). The number of ant colonies increased 76% on plots from which rodents were excluded relative to control plots, and experimental plots had more colonies than controls in five of six possible comparisons. The only exception was for the first census of the second replicate, which was made only eight and one-half months after the treatments were begun. The difference between the number of colonies on rodent-removed and control plots is highly significant (Mann-Whitney U; $P < 0.004$). It should be mentioned that these results are probably conservative. They involve only number of colonies, but ants might very well respond to reduced competition also by increasing the size (number of workers) of preexisting colonies. The primary response of ants to reduced rodent competition was by the three species: *Pheidole sitarches*, *P. xerophila* and *Pogonomyrmex pima* (although *P. pima* was generally inactive during the May 1975 censuses), that were also abundant on the control plots.

Rodents consistently increased slightly on the plots where ants had been removed relative to controls. The aggregate increase in numbers of individuals was 19%, and in 13 of 17 comparisons there were more rodents sampled on ant-removed plots than on controls. These differences are highly significant (Mann-Whitney U; $P < 0.05$; Wilcoxon Pairs Signed Ranks Test; $P < 0.01$). There was a tendency for *Dipodomys merriami*, the most abundant on the control plots and the only species that is active throughout the year, to account for most of the increase when ants were removed. Because *D. merriami* is the largest rodent in this community, biomass showed a greater increase (24%) on ant-removed plots relative to controls than did the number of individual rodents (Table 2). Again, it is likely that these results are conservative. The plots to which the rodents have access are not fenced. Thus, any individual that is attracted onto a census plot during a sampling period is likely to be trapped. Any attractiveness of the baited traps that is effective beyond the boundaries of the plots will tend to obscure differences between ant-removed plots and controls.

Sampling the annual plants on the plots on May 9-13, 1975, failed to reveal any consistent differences between the control plots and those from which ants, rodents or both had been removed (Table 4). The only abundant plant species in these samples was *Euphorbia albomarginata*, although individuals of *Erodium cicutarium*, *Cryptantha angustifolia*, *Eriogonum trichopes*, *Poa* sp. and *Agiostris* sp. were present (many apparently from the previous fall) and were included in the analysis.

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			
	1st Replicate		2nd Replicate		1st Replicate		2nd Replicate		1st Replicate		2nd Replicate	
	-R*	C**	-R	C	-R	C	-R	C	-R	C	-R	C
Pheidole xerophila or P. sitarches	30	23	33	42	49	19	67	21	45	24	57	20
Pogonomyrmex pima	24	12	4	8	1	0	1	0	11	10	16	8
Veromessor pergandei	1	1	2	2	0	1	2	2	0	1	2	2
Solenopsis xyloni	3	1	1	2	0	0	0	0	1	0	0	0
Total Ant Colonies	58	37	40	54	50	20	70	23	57	35	75	30

-R* Plots from which rodents were removed.

C** Control plots.

Table 2. Summary of the results of experiments in which ants or rodents were eliminated from plots and the unmanipulated taxon was repeatedly censused

	Rodents Removed	Ants Removed	Control	% increase relative to control	Number of comparisons experimental > control
Ant Colonies	350	---	199	76	5/6
Rodent Individuals	---	128	104	19	13/17
Rodent Biomass(kg)*	---	4.79	3.66	24	13/17

*Based on body weights 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. Body weight data courtesy of O. J. Reichman.

Table 3. Number of rodent individuals trapped on plots from which ants were excluded and on unmanipulated control plots

Species	15-19 Dec'73 1st Replicate		15-19 May 1974 1st Replicate		15-19 May 1974 2nd Replicate		16-17 April 1975 1st Replicate		16-17 April 1975 2nd Replicate		29-30 June 1975 1st Replicate		29-30 June 1975 2nd Replicate	
	-A*	C**	-A	C	-A	C	-A	C	-A	C	-A	C	-A	C
Dipodomys merriami	8	9	7	5	6	0	7	4	6	5	9	4	5	5
Perognathus baileyi	5	2	1	0	0	0	0	0	0	0	0	0	0	0
P. penicillatus	0	0	0	1	1	2	1	0	0	2	1	2	2	1
P. amplus	0	0	1	1	0	0	2	3	1	2	0	1	1	1
Total Rodents	13	11	9	7	7	2	10	7	7	9	10	7	8	7

Species	29-30 August 1975 1st Replicate		29-30 August 1975 2nd Replicate		4-5 October 1975 1st Replicate		4-5 October 1975 2nd Replicate		8-9 November 1975 1st Replicate		8-9 November 1975 2nd Replicate	
	-A	C	-A	C	-A	C	-A	C	-A	C	-A	C
Dipodomys merriami	10	7	6	6	9	8	6	5	10	10	5	5
Perognathus baileyi	0	0	0	1	0	0	0	1	0	0	0	0
P. penicillatus	2	2	2	1	0	0	1	0	0	0	0	0
P. amplus	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

Species	2-3 January 1976 1st Replicate		2-3 January 1976 2nd Replicate		1-2 February 1976 1st Replicate		1-2 February 1976 2nd Replicate	
	-A	C	-A	C	-A	C	-A	C
Dipodomys merriami	4	1	3	2	4	2	2	1
Perognathus baileyi	0	0	0	0	0	0	0	0
P. penicillatus	0	0	0	0	0	0	0	0
P. amplus	0	0	0	0	0	0	0	0
Total Rodents	4	1	3	2	4	2	2	1

-A* Plots from which ants were removed.

C** Control plots.

Table 4. Numbers of individual plants and cover values for annuals from experimental plots from which rodents, ants, both or neither were excluded

	Ants and Rodents Removed		Ants Removed		Rodents Removed		Unmanipulated Control	
	1st Replicate	2nd Replicate	1st Replicate	2nd Replicate	1st Replicate	2nd Replicate	1st Replicate	2nd Replicate
$\bar{x}$ No. of Plants	7.60	7.45	7.15	9.80	10.35	6.20	9.70	8.45
$\bar{x}$ Cover	11.40	14.15	11.20	5.45*	13.20	3.45**	14.95	15.75

* Value significantly less than either ants and rodents removed or control, $P < 0.05$.

** Value significantly less than either ants and rodents removed or control, $P < 0.005$.

DISCUSSION

Our experimental results clearly indicate that competition between seed-eating ants and rodents plays an important role in limiting the numbers of these two kinds of granivores in desert ecosystems. Although primarily granivorous rodents are know to eat ants (O. J. Reichman, pers. comm.), we suggest that these two taxa affect each other primarily by competing for limited seed resources. The extensive work that we have done on community structure and resource utilization in both rodents (Brown 1973, 1975; Brown and Lieberman 1973) and ants (Davidson, in prep.) demonstrates that both taxa are limited by the availability of seeds and that closely related species coexist by subdividing food resources on the basis of seed size and foraging behavior. The large overlaps between ants and rodents in diet and foraging areas under natural (Davidson, in prep.) and experimental (Brown et al. 1975) conditions, suggest that the two taxa potentially compete by depleting each other's food resources. Further evidence for this comes from the work of O. J. Reichman (pers. comm.) on our plots. He has been sampling the seeds in the soil and has noted that large numbers of seeds accumulated only on the plots from which both rodents and ants had been excluded. This observation also corroborates the experimental observations of Brown et al. (1975), that rodents and ants are the primary consumers of seeds in North American desert ecosystems.

As clear as our results may be, we point out that they may be conservative for three reasons. First, because of the small scale of our manipulations and the inadequacies of our sampling methods, we may be underestimating the real magnitude of the effect of removing the competing taxon on both rodents and ants. Second, there may have been insufficient opportunity for the populations to reach an equilibrial level of response to our experimental manipulations. There have been only two periods of significant precipitation and seed production (summer 1974 and winter 1974-75) since we established our plots, and as yet there is no evidence of any effect of our manipulations on the plants except for the increase of seeds where both rodents and ants were removed. Third, desert ants and rodents probably represent an approximate evolutionary equilibrium in which each taxon has adapted to compete and coexist with the other. These adaptations may limit the ability of both taxa to respond to the short-term elimination of the other.

Despite negative results to date, we remain hopeful that seed-eating rodents and ants may have significant impact on the structure and dynamics of desert plant communities and that we may be able to assess these effects on our experimental plots. Again, we believe that the system may not have reached equilibrium even for annuals and we eagerly await a few more seasons of sufficient precipitation to produce abundant plant germination, growth and seed production. Although we continue to be impressed by the tremendous spatial heterogeneity in plant abundance and distribution in desert ecosystems, we feel confident that our photographic sampling techniques will be adequate to pick up any major differences between our treatments. We are particularly encouraged by Reichman's data on seed accumulation on plots where we have removed both rodents and ants. Unless totally unexpected phenomena are operating, these differential accumulations of seeds should germinate to give rise to significantly different plant communities.

This report suggests that competition between such unrelated taxa as rodents and ants may play a major role in determining the structure and function of natural ecosytems. Such diffuse competition has not received much attention from ecologists, probably in large part because it is so difficult to study empirically and to model theoretically. It probably is not coincidental that we have worked in a desert ecosystem where the system may be simple relative to that in other biomes. In deserts, seeds are a major food source, but they are utilized heavily by sufficiently few taxa that it is possible to think in practical terms of analyzing and experimentally manipulating the major elements of the granivore communiy. However, we do not believe that the sorts of competitive interactions we have demonstrated are unique to desert ecosystems; on the contrary, we expect them to be widespread and important. We suggest that if ecologists want to understand how entire communities and ecosystems function, they must get rid of their taxonomic constraints and study functional groups of often distantly related species that utilize the same resources or interact in other important ways.

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