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Source: *Ecology*, Vol. 65, No. 6 (Dec., 1984), pp. 1780-1786

Published by: [Ecological Society of America](#)

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GRANIVORY IN A DESERT ECOSYSTEM: EXPERIMENTAL EVIDENCE FOR INDIRECT FACILITATION OF ANTS BY RODENTS¹

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Abstract. Two major groups of desert granivores, ants and rodents, coexist as permanent residents of local desert habitats in southwestern North America. At our Sonoran Desert study site, both of the major taxa exhibited short-term increase in density when the other taxon was experimentally removed. Over the longer term, density compensation continued at a relatively constant level for rodents in the absence of ants. In contrast, beginning ≈ 2 yr after initiation of experiments, ant populations on rodent removal plots showed a gradual but significant decline relative to densities on control plots.

Indirect interactions, mediated through ant and rodent resources, may account for these differences. Removal of harvester ants leads to higher annual plant densities only in small-seeded species. These plants are relatively poor competitors and do not displace the large-seeded annuals, on whose seeds rodents specialize. In contrast, rodent removal leads to a differential increase in large-seeded annuals, which competitively displace the small-seeded resource species of ants.

The decline of ant populations on rodent removal plots preceded by several years the first detectable evidence for competitive suppression of small-seeded annuals. Because ants do not excavate buried seed, they probably experienced resource depression before buried seed reserves were exhausted through germination and subsequent competitive inhibition.

Key words: *ants; Arizona; desert annuals; facilitation; granivory; indirect mutualism; rodents; seed predation; Sonoran Desert.*

INTRODUCTION

Ecologists have long recognized the importance of direct biotic interactions, such as competition, predation, and mutualism, in determining the distribution and abundance of organisms. However, with the notable exception of interactions between a single “keystone” predator and its competing prey (e.g., Paine 1966), few experimental studies have addressed the role of indirect interaction pathways in regulating community structure and diversity. Interactions among desert granivores and their resources hold considerable promise as a model system for studying the indirect effects of plant and animal populations on one another. Strong direct interactions (notably competition and predation) occur among a diverse, yet experimentally manageable, group of consumer and resource species and suggest the likely importance of indirect interaction pathways. Here we report that responses to experimental manipulation of granivore populations change through time as a result of indirect interactions mediated through resource species.

Fig. 1 illustrates that the net interaction between two consumers at the same trophic level may be mutualistic

if each consumer specializes on a different class of resources and those resource classes are in competition. For example, by differentially reducing populations of resource 1, consumer 1 indirectly makes additional resources of type 2 available to consumer 2. Vandermeer (1980) showed mathematically that two factors increase the likelihood of indirect mutualism between the consumers in Fig. 1. These factors are: (1) increased consumer specialization for acquisition (but not assimilation) of distinct resource classes, and (2) intense competition between resource classes. To date, there exists no firm experimental evidence for indirect mutualisms produced in natural ecosystems by consumer-resource interactions similar to those in Fig. 1 (Boucher et al. 1982).

In North American deserts, a diverse group of generalized seed consumers uses the relatively abundant and dependable seeds of annual plants. Much evidence suggests that spatial and temporal variation in seed availability influences the abundances of both migratory avian granivores (Dunning and Brown 1982) and seed-eating ants and rodents that are permanent residents of local deserts (Brown 1973, 1975, Whitford 1976, 1978a, b, Davidson 1977a, b). This reliance on a common resource base links the population dynamics of individual species as well as major classes of granivores (Brown and Davidson 1977, Brown et al. 1979, Munger and Brown 1981, D. W. Davidson, *personal observa-*

¹ Manuscript received 3 August 1983; revised and accepted 12 December 1983.

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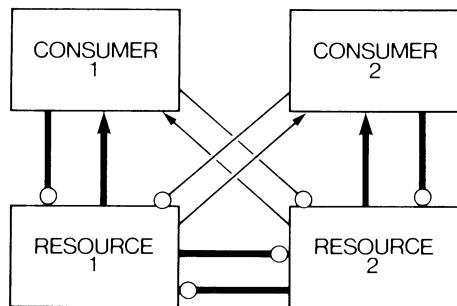


FIG. 1. Diagrammatic representation of interactions leading to indirect mutualism between two groups of consumers and their competing resources (modified from Levine 1976). Population enhancement or damping of particular species is indicated by arrows or circles, respectively, and line width is proportional to interaction strength.

tion). In experiments in the Sonoran Desert, both ants and rodents increased in abundance over the short term when the other major taxon was removed (Brown et al. 1979). Resource levels on experimental and control plots suggested that changes in granivore populations were mediated through exploitative resource competition. Two years after removal experiments were established, measured densities of annual plants and seed levels in soils (across all species) were statistically indistinguishable on plots where either ants or rodents or both groups of granivores were present. Densities of annual plants and seed resources were significantly greater where both ants and rodents had been removed, than on control plots.

Although dietary overlap between harvester ants and seed-eating rodents leads to short-term resource competition between the two groups, both of the criteria favoring long-term indirect mutualism may be met. First, considerable evidence suggests that ants and rodents specialize to some extent on different size-classes of seeds (Brown and Davidson 1977, Brown et al. 1979, Inouye et al. 1980). In the experimental studies, small-seeded annuals increased differentially on ant removal plots, while populations of large-seeded annuals were significantly enhanced by the exclusion of rodents. Second, we had preliminary evidence for competition between resource classes (Inouye et al. 1980) by year 4 of our experiment. On rodent removal plots, increased densities of three species of large-seeded annual (mean seed masses of the species ranging from 1.1 to 1.6 mg) were accompanied by a significant decline in populations of the small-seeded ($\bar{x} = 0.2$ mg) *Euphorbia polycarpa*, a species that lives either an annual or a perennial life history, depending on the favorability of growth conditions in space and time. No significant decline was detected in the densities of small-seeded and strictly annual plant species on rodent removal plots or large-seeded annuals on ant removal plots. However, annual plants exhibit exceptionally large microspatial variation in abundance, and large sample sizes may be

necessary to document significant changes in population densities. Here, we present new data that allow us to reexamine the system of granivores and their resources for relatively long-term indirect pathways of interaction, possibly leading to indirect mutualism between ants and rodents.

HABITAT AND METHODS

Our experimental studies of desert granivores took place at the Silverbell Validation Site of the United States International Biological Program Desert Biome, located ≈ 60 km northwest of Tucson, Arizona, near Marana (Pima County), Arizona. Study plots on the bajada (alluvial outwash plain) at Marana were situated at ≈ 330 m elevation in typical Sonoran Desert habitat, characterized by *Larrea tridentata* and *Ambrosia deltoides* as dominant shrub species. Here, the bimodal distribution of annual rainfall (Fig. 2) regularly produces two distinct seasonal peaks of ephemeral vegetation. Frontal storms in winter stimulate the germination and growth of annual plants that fruit in late winter or early spring, and a second crop of annuals, responding to summer thunderstorms, fruits in late summer. On average, total winter precipitation (November through March) is approximately equal to total summer precipitation (June through August) in amount and predictability (winter mean = 119 mm, and coefficient of variation = 53%; summer mean = 111 mm, and coefficient of variation = 56%). However, high summer temperatures and consequent high rates of evapotranspiration result in markedly lower mean seed productivity in summer than in winter annuals. Mild winter temperatures at this latitude and elevation permit almost year-round activity of most ant and rodent granivores.

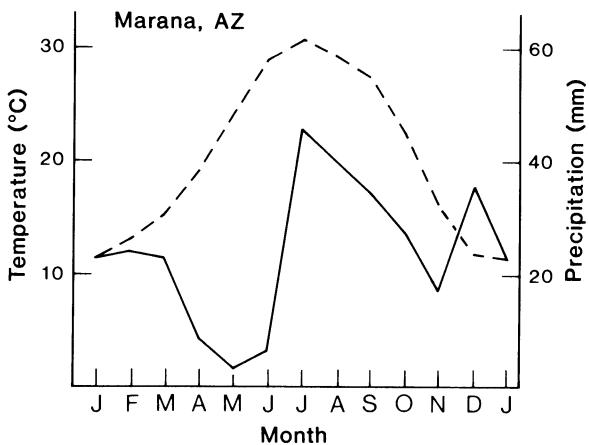


FIG. 2. Climate diagram for vicinity of Marana, Arizona (elevation 800 m): — precipitation; — temperature. Records are from United States Weather Bureau Stations at Silverbell, Arizona (899 m; 1958–1973), and from the University of Arizona at Tucson (802 m; 1974–1980) after the Silverbell station was closed.

TABLE 1. Large-seeded (mean seed mass ≥ 1.10 mg) and small-seeded (mean seed mass ≤ 0.70 mg) winter annuals on the Marana alluvial plain.

Large-seeded annuals	Small-seeded species
<i>Erodium cicutarium</i>	<i>Euphorbia polycarpa</i> *
<i>Erodium texanum</i>	<i>Filago californicus</i>
<i>Lotus humistratus</i>	<i>Pectocarya recurvata</i>
	<i>Eriophyllum lanosum</i>
	<i>Cryptantha barbigera</i>
	<i>Astragalus</i> sp.
	<i>Lappula redowskii</i>

* May be annual or perennial (see Methods).

Details of our methodology have been published elsewhere (Brown and Davidson 1977, Brown et al. 1979, Inouye et al. 1980) with our early results, and here we review only the nature of our experimental treatments and census techniques. Granivore removal experiments were initiated in August (first replicate) and December (second replicate) of 1973. We established two replicates of each of the following experimental treatments on circular plots ≈ 0.1 ha in area: (1) colonies of seed-harvester ants removed twice per year by poisoning with Myrex (Allied Chemical) in the immediate vicinities of nest entrances; (2) seed-eating rodents excluded by trapping from areas fenced with 0.64-cm wire mesh, ≈ 90 cm high and buried to a depth of 15 cm; (3) both ants and rodents removed as above; and (4) unmanipulated control plots. Efficacy of removal treatments was documented in an earlier report (Brown et al. 1979). Unfortunately, ant poisoning was not continued after May of 1978, but low population densities of ants were apparent on ant removal plots at least through the summer of 1979. In the summer of 1980, small entrance holes were cut in the hardware-cloth rodent exclosures to allow recolonization by rodents. Later, a decision was made to prolong the exclusion experiments, and in early winter of 1980, entrance holes were covered with hardware-cloth, and rodents were again trapped out of the fenced plots.

Population densities of ants and rodents were monitored on a regular basis. Twice annually from October of 1974 through August of 1976, and once again in the summer of 1977, we censused colonies of harvester ants by searching plots systematically and repeatedly during the diurnal temperature cycle. Rodents were censused more frequently, because their numbers were low, and many samples were required to establish statistical confidence. Rodents were captured using 20 aluminum live traps ($23.0 \times 7.8 \times 9.0$ cm), set in a standardized geometric pattern on each plot for a single night. Following their identification, animals were released. We used Repeated Measures ANOVA (Biomedical Computer Program BMDP2V) to calculate the probability that trends in granivore population densities differed between control and treatment plots.

Winter annuals were enumerated by species in eight 400-cm² square quadrats per treatment plot on 12

March 1980, 6 yr after initiation of experiments. Census quadrats, located in the same relative positions on each plot, were situated at random with respect to vegetation, except that we displaced them to open microhabitats if designated position were beneath shrub canopies. Plant species had been classified as large seeded or small seeded in an earlier study in 1977 (Inouye et al. 1980). Although individuals of the three large-seeded annuals identified in 1979 could be identified to species in March of 1980, most of the smaller seeded plants were too small to allow accurate species determinations. Table 1 gives the identities of large-seeded annuals enumerated in 1980 and small-seeded annuals known to have been present in 1979 and/or 1980 censuses.

RESULTS

Granivore responses

Ants in the genus *Pheidole* were the most common harvester ants on our plots, regularly comprising 60–98% of colony counts, depending on plot and census date. Occasionally, when the diagnostic major workers were not active, the three *Pheidole* species inhabiting our site could not be safely distinguished. Although we have lumped the three species in our analyses, *P. xerophila tucsonica* predominated in all censuses.

Fig. 3 compares the numbers of *Pheidole* colonies on control plots and rodent removal plots as a function of time. The pattern of change in population density differed significantly between control and rodent removal plots ($P = .029$ in Repeated Measures ANOVA), and this difference was assignable to quartic trends in the data set ($P = .005$ in orthogonal decomposition of the analysis). Populations of *Pheidole* first increased and then declined in response to rodent removal. Repeated Measures ANOVA reveals a significant increase in the densities of ant colonies on rodent removal plots relative to control plots between October 1974 and

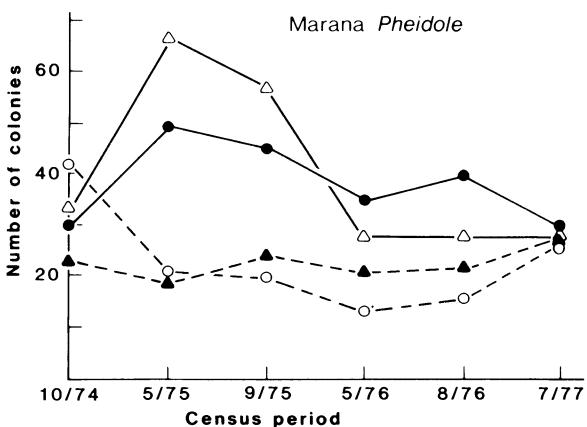


FIG. 3. Changes in density of *Pheidole* spp. (including *P. xerophila tucsonica*, *P. sitarches*, and *P. gilvescens*) on two rodent removal plots (—) and two control plots (---) at Marana, Arizona over a 2 1/4-yr period.

TABLE 2. Mean population densities of large-seeded and small-seeded plants under different regimes of seed predation by ants and rodents.

Rodents	Seed size*	Plant density (no./400 cm ²)†		Effect of ant removal (P‡)	
		Ants present	Ants absent		
Present	L	94.4	72.5	<.414	
		38.5	39.8		
	S	148.6	173.3	<.089	
		347.6	90.0		
Absent	L	176.5	178.0	<.352	
		97.4	157.0		
	S	32.6	114.6	<.002	
		22.1	233.8		
Effect of rodent removal (P):		L	<.001	<.000	
		S	<.001	<.454	

* L = large-seeded annuals and S = small-seeded annuals, as defined in Table 1.

† Two replicates for each experimental treatment.

‡ ANOVA, with replicate plots treated as separate grouping variables.

September 1975 ($P = .037$). In contrast, between May 1975 and July 1977, densities of *Pheidole* colonies on rodent removal plots showed a significant decline relative to densities on control plots ($P = .036$).

Rodent densities remained higher on ant removal plots than on control plots throughout our censuses (Brown et al. 1979). Densities on ant removal plots did not change relative to those on control plots over the duration of our censuses ($P \gg .05$ in Repeated Measures ANOVA; $N = 14$ censuses at approximately regular intervals from December 1973 through January 1977).

Plant responses

Analysis of variance of lognormally distributed plant densities for winter 1980 demonstrates that seed-eating ants and rodents have had differential effects on the densities of large-seeded and small-seeded annuals. Because interaction effects for the combined influence of ants and rodents are significant in both cases ($P < .002$ for large-seeded species and $P < .005$ for small-seeded plants), simple main effects analyses must be undertaken to understand fully the effects of granivores on their resources (Table 2). On plots with ants present, rodent removal is attended by significantly higher densities of large-seeded annuals and lower densities of small-seeded species. Where ants are absent, densities of large-seeded annuals increase in response to rodent removal, but populations of small-seeded species do not differ significantly from those on plots where rodents remain. On plots with rodents present, removal of ants produces no statistically significant change in the densities of small-seeded or large-seeded annuals. Finally, where rodents have been removed, small-seeded plants increase with ant removal, but large-seeded annuals remain at densities equivalent to those on plots containing ants.

The Inouye et al. (1980) data for 1977 winter annuals were reanalyzed using the same ANOVA procedures performed on 1980 data. Relative to their densities on

control plots, populations of small-seeded annuals were significantly higher on ant removal plots ($P = .023$), and large-seeded annuals were significantly more abundant on rodent removal plots ($P < .001$). In neither case, however, was there a significant interaction effect of ants and rodents; for this reason, the ANOVA was not broken down further. At this time, there was no apparent effect of rodents on small-seeded annuals or ants on large-seeded annuals. However, since only four quadrats were censused per treatment pen (just half our sample size in the 1980 census), the likelihood of Type II statistical error was high.

If large-seeded annuals and small-seeded annuals compete for access to water and/or other limiting resources, abundance of annuals in these two functional groups should be negatively correlated across sample quadrats. Densities of the two categories of annuals on unmanipulated control plots are lognormally distributed by Kolmogorov-Smirnov Goodness-of-Fit Tests ($P \gg .20$ for null hypotheses of lognormal distribution). Fig. 4 illustrates the significant inverse relationship between log-transformed densities of large-seeded and small-seeded annuals on control plots at Marana in March 1980 ($P < .01$ in linear regression for ● only). Data for rodent removal plots cannot legitimately be included in the regression analysis, but these data reveal markedly higher densities of large-seeded species and lower densities of small-seeded species in relation to control plots (○, $P < .01$ in two-tailed Mann-Whitney *U* Tests).

DISCUSSION

Long-term studies of plant, ant, and rodent populations strongly support the consumer-resource interaction model shown in Fig. 5. First, as in 1977, winter-annual densities in 1980 documented seed size specialization by ants and rodents. Ant removal produced higher densities only in small-seeded annuals, while rodent removal led to increases only in large-seeded species. These results occurred despite some dietary

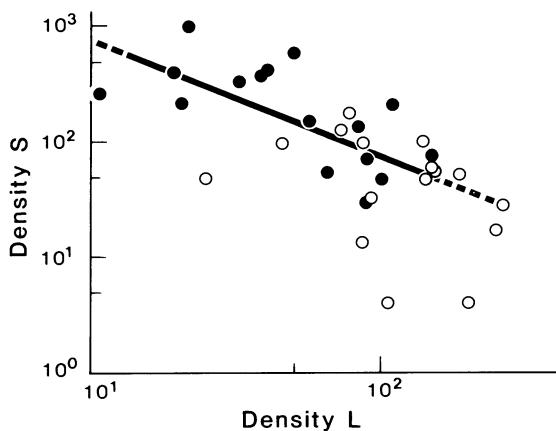


FIG. 4. Inverse logarithmic relationship between the densities (number per 400 cm²) of large-seeded (L) and small-seeded (S) annuals at Marana, Arizona, in March of 1980. ● and regression line = densities in quadrats on control plots only ($r = 0.65$ with 14 df for log-transformed data). ○ = densities in quadrats on rodent exclusion plots.

overlap between the two granivore taxa on both functional categories of seeds (D. W. Davidson, *personal observation*). Rodents consume some small seeds, particularly during the fruiting season when these seeds are packaged in easily harvested fruiting heads. In 1980, the response of small-seeded annuals to ant removal was statistically significant only in the absence of rodents (Table 2). Thus where rodents were present, they apparently compensated for missing ants by maintaining higher densities and biomass on ant removal plots throughout the experiments (Brown and Davidson 1977), and possibly also by altering their diets to include more small seeds. At peak periods of winter seed production, rodents collect almost exclusively the large seeds of *Erodium* and *Lotus* species. Though ants also forage on the seeds of *Erodium*, the genus contributing most prominently to the pool of large seeds at Marana, they are probably less efficient than rodents at reducing these seed populations before seed burial by hygroscopic awns. Unlike rodents, ants do not appear to excavate buried seeds. As measured by their impact on resources, ants compensated for missing rodents in the short term (Brown et al. 1979) but were unable to do so in the longer term because of changes in the plant community.

Second, several kinds of evidence document competition between large-seeded and small-seeded annuals and demonstrate the asymmetry of this competition. (1) The densities of annuals in these two functional groups were strongly and inversely correlated on unmanipulated control plots. (2) Increased densities of large-seeded annuals on rodent removal plots were accompanied by reductions in the densities of small-seeded plants. The decline in populations of small-seeded species was pronounced and statistically significant where these seeds were also harvested by

ants. In contrast, population densities were not reduced significantly in the absence of ants, probably because of the relaxation of predation on small-seeded species. (3) Although ant removal enhanced densities of small-seeded annuals, there was no compensating decrease in densities of large-seeded plants. (4) Finally, the results presented here are consistent with recent direct experimental evidence for the competitive superiority of large-seeded winter annuals (Inouye 1982). Thinning of large-seeded species in mid-January 1980 produced significantly enhanced germination and survivorship of small-seeded annuals in relation to control plots. In contrast, thinning of small-seeded species had no detectable effect on subsequent germination and survivorship of large-seeded species.

Granivore population responses also support the model depicted in Fig. 1. Removal experiments produced short-term reciprocal density compensation between ants and rodents. Over the longer term, however, asymmetric competition between ant and rodent resources led to asymmetry in the net effects of the two granivore groups on one another. In response to rodent removal, populations of the most common harvester ants first increased but later declined, as their small-seeded resource species were competitively replaced by large-seeded annuals. Because small-seeded plants are competitively inferior to large-seeded species, their increase on ant removal plots probably served only to augment the food supply of rodents. Rodents maintained slightly higher densities and biomass on ant removal plots than on control plots, and long-term and short-term responses were not detectably different.

If the reduction in population densities of small-seeded annuals was not detectable on rodent removal plots for 3 yr following the conclusion of our ant censuses, can the decline in *Pheidole* densities be attributed to a reduction in ant resources? Small seeds are readily buried in sandy soils, and a number of years may be required for germination and subsequent inhibition by large-seeded annuals to deplete buried seed

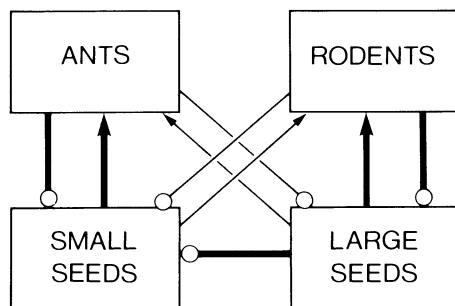


FIG. 5. Diagrammatic representation of interactions among granivores and resources at the Marana site. Representations as in Fig. 1. By reducing densities of large-seeded plants that are competitively superior to small-seeded plants, rodents may indirectly facilitate ant populations.

reserves. Because ants do not excavate buried seed, it is reasonable to suggest that they should encounter resource depression prior to the exhaustion of soil seed reserves for germination. The availability of small seeds should be reduced at the soil surface as soon as large-seeded annuals increase sufficiently to inhibit growth and reproduction of small-seeded plants germinated from soil reserves. Significantly higher densities of large-seeded annuals, apparent on rodent removal plots early in 1977, may have existed even in previous years for which we lack data. Unfortunately, the small sample sizes available for the 1977 census contributed to a high probability of Type II statistical error in detecting lowered densities of small-seeded annuals in this spatially heterogeneous plant community.

The results of our long-term experiments may help to explain biogeographic patterns in the abundances of ant and rodent granivores in desert ecosystems. If granivorous rodents facilitate seed-harvester ants by preying on the competitors of ant resources, we would predict lower densities of harvester ants in the absence of seed-eating rodents. In this context, Mares and Rosenzweig (1978) have attributed the paucity of harvester ants in deserts of the Argentine Monte to the extinction of seed-eating marsupial mammals (Argyrolagidae). They hypothesized that granivorous ants and rodents are "coevolutionary mutualists," and that the absence of mammalian seed consumers permitted plant adaptations reducing susceptibility to seed predation by ants. Unfortunately, they provided no information on the sizes or morphologies of the seeds of desert annuals in the Monte. Small mammalian seed consumers are also unimportant in Australian deserts, but there, unlike the Monte, avian granivores may compensate for the absence of rodents, and within-habitat diversity of harvester ants equals or exceeds that in North American deserts of comparable productivity (Morton 1979, 1982, S. R. Morton and D. W. Davidson, *personal observation*). Finally, asymmetry in the competitive abilities of ant and rodent resource species predicts that ants should be competitors of rodents in the long term as well as short term. Thus, where the harvester ant fauna is particularly impoverished, as in relatively high-elevation and high-latitude deserts of North America, we should expect rodents to compensate for missing ants in abundance and diversity. Brown and Davidson (1977) presented evidence that this is indeed the case.

Recently, we have replicated and expanded our granivore experiments in Chihuahuan desert habitat, on the eastern bajada of the Chiricahua Mountains in southeastern Arizona. Although some of the results in this more recent experimental study (e.g., seed size specialization by ants and rodents) are similar to those at Marana, several factors make the interaction structure much more complex than that depicted in Fig. 5. This desert is characterized by greater seasonality in temperature, in the production of seed resources, and in the use of these resources by granivores. In addition,

the annual plant that dominates this community in both numbers and biomass has a growth period spanning that of both summer and winter annuals, and potentially linking the population dynamics of these 2 seasonally distinct ephemeral floras (Davidson et al., *in press*). Experiments on the Chiricahua bajada should provide an interesting contrast to those at Marana and may permit us eventually to test predictions from theory regarding the effect of consumer dietary specialization and intensity of resource competition on the likelihood of indirect mutualisms (Vandermeer 1980).

ACKNOWLEDGMENTS

We are grateful to the many colleagues, students, and assistants who have participated in this research project and generously shared their time and ideas. In particular, we thank A. Kodric-Brown and K. Brawley, who helped us construct the granivore exclosures. P. Coley and D. Samson provided helpful comments on an earlier draft of the manuscript. The study was supported in part by Grant 551 from the Desert Biome section of the United States International Biological Program and National Science Foundation Grants DEB 76-83858, DEB 79-05488, and DEB 80-21537.

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