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GRANIVORY IN THE CHIHUAHUAN DESERT: INTERACTIONS WITHIN AND BETWEEN TROPHIC LEVELS[1]

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Abstract. We investigated the effects of Chihuahuan Desert granivores on three seasonal classes of plant resource species, the effects of these resource classes on one another, and the ways in which interactions through plant resources affect the abundances of seed consumers. At our study site, three seasonally distinct classes of annual plants produce the seeds used by ants and rodents, the two major taxa of resident granivores. Winter annuals and summer annuals have temporally nonoverlapping growth periods. However, one numerically prominent annual, *Eriogonum abertianum,* germinates with winter annuals, reproduces with summer annuals, and may link the population dynamics of plants in the two groups. Experiments showed that high densities of winter annuals inhibit populations of *E. abertianum* and that populations of this species can strongly suppress those of summer annuals. Densities of all three classes of annuals are regulated by the combined effects of competition and seed predation. In *E. abertianum,* interspecific and intraspecific competition appeared to predominate in alternate years and to produce 2-yr abundance cycles, accentuated in magnitude where ants, the major seed predators, had been removed. The period of these cycles appeared to lengthen where rodent removal intesified the effects of interspecific competition.

Granivore removal and seed addition experiments showed that competition also helps to regulate some granivore populations. Although rodents reduced ant resources through their effects on seeds of both summer annuals and winter annuals, ants were competitors of rodents only for seeds produced during the weaker winter resource peak. Seeds of *E. abertianum* were used almost exclusively by ants. Rodents facilitated this plant species indirectly by reducing densities of other winter annuals. Ants and rodents were affected differently by one another's removal. After an initial time delay, workers of *Pheidole xerophila* increased in numbers and/or activity on rodent removal plots, but colony densities of a second ant species, *Pogonomyrmex desertorum,* simultaneously declined. Rodents did not compensate measurably in abundance, biomass, or reproductive activity where ants had been eliminated. The explanation for these responses is complex and includes such factors as: (1) seasonality in the production of seed resources and in their use by the two taxa; (2) specialization by ants and rodents on different density distributions of seeds; (3) "diffuse compensation," or compensation spread over many species populations; and (4) indirect interaction pathways, mediated through competing resource classes.

In general, our experiments show that, despite the climatic variability and unpredictability of desert environments, populations respond to the steady deterministic processes of competition and predation. Nevertheless, comparison of the results of similar experimental studies in the Sonoran and Chihuahuan Deserts demonstrates how climate and seasonality can alter the structure and intensity of interactions in ecosystems.

Key words: annual plant; ant; competition; community; desert; ecosystem structure; experiment; granivore; indirect interaction; rodent; population cycles; seed predation.

INTRODUCTION

The literature on experimental studies of competition is now sufficiently large to support generalizations on both its findings and its strengths and shortcomings (reviewed in Connell 1983, Schoener 1983). Three common limitations of these studies restrict our ability to characterize the complex dynamics of natural populations, whose numbers inevitably are determined by a diversity of biotic and abiotic factors. First, aside from studies of plants and sessile marine invertebrates, most experimental analyses of competition focus on small sets of closely related and ecologically similar species (but see Erikssen 1979). However, natural ecosystems provide many examples of coexistence between taxonomically unrelated and ecologically very different groups of species that consume the same resources. Cases include nectar-feeding insects and birds (Carpenter 1979, Kodric-Brown and Brown 1979), granivorous insects, birds, and mammals (Brown et al. 1979*a*, Smith and Balda 1979), frugivorous microbes, insects, birds, and mammals (Janzen 1977), insectivorous lizards and birds (Pianka 1975, Wright 1979,

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Adolph and Roughgarden 1983, Moermond 1983), and marine mammals and birds that feed on microcrustaceans (May et al. 1979). In each of these examples, unrelated taxa are potentially limited by the same resources and capable of compensating for natural or imposed fluctuations in one another's abundance. Second, the majority of experimental studies of competition tend to ignore the dynamics of resource species and predators that may strongly affect the manner in which species respond to manipulations (e.g., Levine 1976, Holt 1977, Vandermeer 1980). Again, the principal exceptions to this generalization are studies of space-limited intertidal plants (Paine and Vadas 1969, Lubchenco 1978, 1983) and invertebrates (e.g., Paine 1966, 1980), whose herbivores or predators often alter the outcome of competition. Finally, the mean tenure of experimental competition studies, ≤3-yr, is probably inadequate to reveal respones that are intermittent, time-delayed, or indirect and mediated sequentially through populations of intermediary species. Clearly, there is a need for long-term experimental studies of phylogenetically broad consumer-resource systems in other than marine environments.

A promising model system for such experiments is that of the desert granivores and their resources. In the southwestern deserts of North America, the seeds of annual plants constitute a major fraction of the resources available to higher trophic levels and support a diverse assemblage of granivores in three major taxa: ants, rodents, and birds. Most avian granivores are seasonal migrants, exploiting seed resources when and where they are abundant (Brown et al. 1979*b*, Dunning and Brown 1982). In contrast, both ants and rodents are permanent residents of local desert sites and are constrained to feed on resources that are produced and available locally. Seed-eating ants and rodents increase in abundance and diversity along gradients of increasing precipitation and productivity in North American deserts (Brown 1975, Davidson 1977*a*). These biogeographic patterns suggest that granivores are limited in part by their food resources. In addition, extensive dietary overlap between the two granivore groups (Brown and Davidson 1977) suggests that ants and rodents may compete exploitatively for seed resources.

Removal experiments in the Sonoran Desert have demonstrated resource competition between ant and rodent granivores (Brown et al. 1979*a*). Although the two granivore taxa exhibited reciprocal density compensation over the short term, ants later declined on rodent removal plots in relation to their densities on control plots. The most likely explanation for this decline is that increasing densities of large-seeded annuals on rodent removal plots over time led to reduced densities of the small-seeded annuals that provide the primary resources of ants (Davidson et al. 1984). Thus, over the longer term, rodents appear to facilitate ants indirectly by feeding differentially on the seeds of competitively superior large-seeded annuals.

The potential for resource competition between ants and rodents may depend on dietary separation by criteria other than seed size. For example, because temperature, precipitation, and resource production are all markedly seasonal in the southwestern deserts, seasonal differences in the activity schedules of ants and rodents may influence the extent of resource overlap and the intensity of competition. In the Chihuahuan Desert, the foraging activities of ants are highly skewed toward the late summer (Davidson 1977*b*: Fig. 3) and coincide with the higher of two annual peaks in seed production. In contrast, many rodents forage here year-round (Munger and Brown 1981: Fig. 1). In the experiments reported below, we investigated the effects of seed predation by ants and rodents on seasonally distinct resource classes, the effects of these resource classes on one another, and the manner in which direct and indirect interactions through resource species influence ant-rodent competition. Comparisons of these and earlier experiments in the Sonoran Desert enable us to assess how geographic variation in climate affects the structure of interactions in this consumer-resource system.

HABITAT AND METHODS

Long-term experiments

In late summer 1977, we initiated long-term experimental studies 6.5 km east of Portal (Cochise County), Arizona, on the lower alluvial plain, or bajada, of the Cave Creek drainage of the Chiricahua Mountains. We used barbed-wire fencing to exclude domestic grazers from ≈20 ha of superficially homogeneous Chihuahuan Desert shrubland, and established 24 ¼-ha plots within the fenced area. Treatment plots, 16 of these relevant to the present study, were separated from each other by distances of at least 25 m and were positioned on level ground away from the few arroyos or temporary watercourses that cross the site. All plots were fenced with 0.6-mm wire mesh, 0.9 m wide and buried to a depth of 0.2 m. A 0.1-m strip at the base of the buried fencing was turned outward to discourage digging by rodents, and aluminum flashing (0.15 m wide) was riveted to the top edge of the fences to prevent rodents from climbing over the exclosures. Fences were supported at intervals by steel reinforcement bars. Among the grazers native to this site, only *Lepus californicus* was excluded from treatment plots, while both *Sylvilagus audubonii* and *Odocoileus hemionus* made use of the plots.

Two replicate plots were assigned at random to each of the following eight treatments. (1) – A: We removed granivorous ants by repeated application of insecticide (Mirex [Allied Chemical Corporation] through 1980 and later AMDRO [American Cyanamide Company]). Poison (in treated grain) was broadcast generally over the plots as well as applied to individual colony entrances. In comparisons between these treatment plots

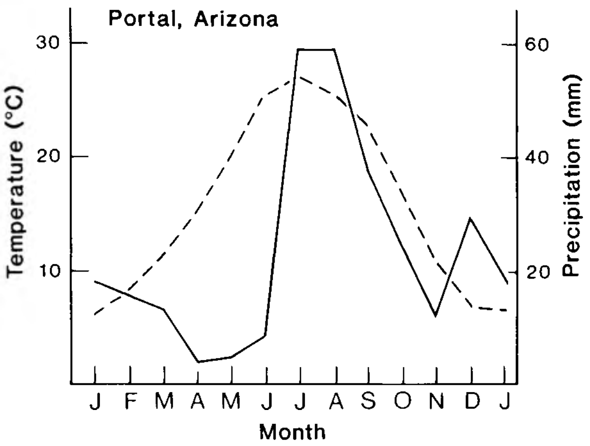

FIG. 1. Climate diagram with approximate long-term weather records for Cave Creek Bajada study site (United States Climatological Data 1958–1980). --- temperature; - precipitation. Data are from nearby weather stations (within 50 km radius) whose elevations most closely approximate that of the study site (1410 m). These stations were Rodeo, New Mexico (1351 m) through 1977, and later Animas, New Mexico (1448 m), after the Rodeo station was closed.

and control plots, continuous monthly capture records on individually marked rodents gave no evidence of any adverse effects of the poison on rodents. (2) −R: Seed-eating rodents (including seed-eating omnivores) were trapped and removed. (3) −A, −R: Both ants and rodents were removed by the procedures described above. (4–7) Natural seed reserves were supplemented by application of 96 kg/yr of *Sorghum vulgare* (milo) seed (September 1977 through August 1980) or *Panicum miliaceum* (millet) seed (September 1980 through September 1983) according to one of the following regimes: CS = continuous addition ($\frac{1}{12}$ of the total amount was applied each month) of small seeds, cracked to ≈1 mg particle mass; CL = continuous addition of large or whole seeds, ≈6 mg particle mass; CSL = continuous addition of both size-classes (50% of total seeds in each size-class); or PSL = pulsed addition of both size-classes as in CSL, with the entire annual seed supplement applied in 2–6 equal installments over a 2-mo period during peak seed-set by summer annuals. All seed supplements were scattered by hand. (8) C: Two plots remained unmanipulated as controls. On all plots except −R plots, 16 equally spaced holes, each 6.5 cm in diameter, were cut in the wire mesh at ground level to permit entry and exit by all species of seed-eating rodents.

All plots were treated identically except with respect to the eight treatments listed above. In an effort to hold disturbance to minimal and equivalent levels across all treatment plots, investigator access was confined to a regular trail system, spatially removed from permanent ant and plant census quadrats, and all plots received equal sampling effort in granivore and plant censuses.

Plant phenology and plant censuses

Two major peaks of precipitation and seed production occur at our study site (Figs. 1 and 2). Winter precipitation (November through March) stimulates germination and growth of winter annuals, which bloom and set fruit in March and April. The three most arid months, April through June, are followed by relatively dependable rains in the form of convective summer thunderstorms in July, August, September, and occasionally, October. A taxonomically different set of annuals germinates in response to these warm, wet conditions. These annual species, and some perennial herbaceous species, continue to grow throughout the summer and set seed in late August, September, or October. Summer rains (July through October) exceed winter rains (December through March) in both amount and predictability (summer mean = 181 mm, or ≈65% of annual mean precipitation, with a coefficient of variation [CV] = 36; winter mean = 67 mm, or ≈24% of yearly mean, CV = 75). For this reason, and because low temperatures inhibit growth during periods of winter precipitation, biomass production of summer annuals at this site probably exceeds that of winter annuals, on average.

A second factor promoting high seed production in summer is the peculiar life history of *Eriogonum abertianum*, an abundant and key plant species on the Cave Creek Bajada (Fig. 2). After germinating concurrently with winter annuals, individuals of this species pass the predictable droughts of late spring and early summer in relative dormancy. Mortality is high during this period, but some plants persist and resume growth with the advent of summer rain. These plants flower and set fruit in late summer with the more typical summer annuals. Thus, a major proportion of winter biomass production is not realized as seed production until the summer months, and large quantities of *E. abertianum* seed are available to seed predators only briefly (approximately October through December).

Twice yearly, from the winter of 1978 through the winter of 1983, annual plants were enumerated in eight permanent census quadrats per ¼-ha experimental plot. The two censuses were timed to coincide approximately with maximum standing crops of live (photosynthetic) winter (March or April) and summer (August or September) annuals, respectively. Initially, separate sets of quadrats were censused in summer and winter so that thinning experiments in one season would not affect densities of annuals counted in the other season. Quadrat size, initially 0.50 m^2, was halved beginning in the summer of 1981. In calculations comparing densities in these quadrats across years, plant densities were standardized to the larger area by doubling densities in the smaller quadrats.

Repeated sampling of plant densities in permanent census quadrats permitted data analysis by the powerful technique of Repeated Measures ANOVA (RMA). We used RMA analysis (BMD statistical package P2V

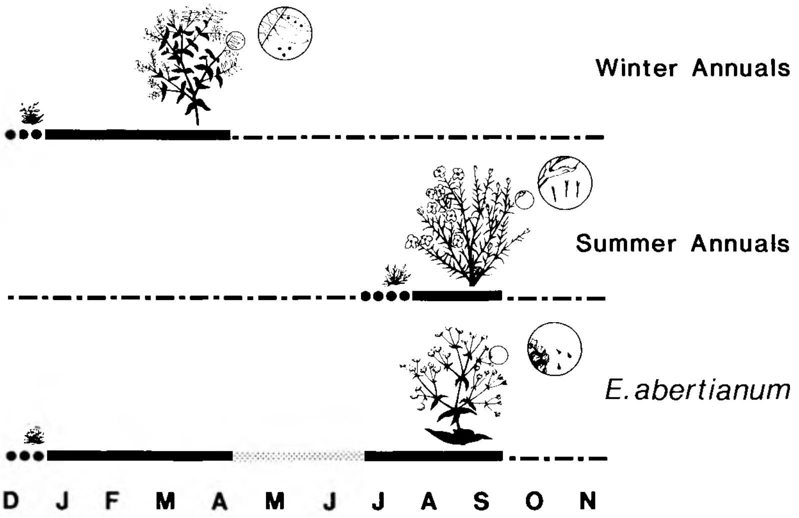

FIG. 2. Summary of vegetative and reproductive phenology of three groups of annuals on the Cave Creek Bajada study site. ● germination; ■ = periods of growth. Intervals of dormancy are depicted by -·-·- (seed dormancy) or □ (plant dormancy); episodes of flowering and fruiting are shown pictographically.

[Dixon and Brown 1977]; see also Myers 1979: Chapters 7 and 17) to calculate the probability that trends in plant population densities differed between control and treatment plots. With treatments 1–3 and 8 included in the analysis, ants and rodents represented the primary treatments for grouping variables of a nested ANOVA, and treatment replicates constituted trial factors. For this fully nested design, RMA output specified significance levels for the effects through time of ant removal, rodent removal, interactions between ant and rodent treatments, and differences between replicate plots within treatments. Analyses were repeated to discern the simple main effects of (1) ants with rodents present, (2) ants with rodents absent, (3) rodents with ants present, and (4) rodents with ants absent.

Because plots assigned to treatment CSL received only one-half the standard amounts of small and large seeds supplied to small- and large-seed addition plots, respectively, seed addition experiments CS, CL, CSL, and C did not conform to a completely nested design. Annual plant densities were compared separately against control plots for each seed-addition treatment. Thus, we have no measure of the interaction effect of small-seed and large-seed additions.

In all analyses, orthogonal decomposition of the repeated measures was used to indicate the kinds of trends (e.g., linear, quadratic, cubic, or quartic) accounting for differences between treatment and control plots. Intuitively, this means that we used plant densities through time on control plots as a baseline against which we compared patterns of change in plant densities on treatment plots. For example, if plant densities on plots from which all granivorous ants and rodents had been removed increased in relation to densities on control plots by a constant factor each year, this change could be detected as a significant linear trend. If the factor of increase gradually declined as plants became more and more crowded on granivore removal plots, a quadratic trend would be detected. More complex patterns of change were also possible. For example, removal of rodents could have led to an immediate increase in plant densities on treatment plots, but density compensation by ants could have caused plant populations to decline eventually in relation to those on control plots; this pattern of change would produce a significant cubic trend in comparisons of control and treatment plots.

Although RMA analysis identifies instances in which plant densities change differently through time on treatment and control plots, it does not directly specify the direction of these differences. Patterns of change were determined by plotting mean density of plants (summer annuals, winter annuals, or *E. abertianum*) through time. To simplify the presentation of results, we plotted only the means of the two replicates. In general, as evidenced by the highly significant differences between treatment and control plots, replicate treatment plots tended to exhibit similar changes in plant densities. Densities were graphed on a logarithmic scale to facilitate identification of trends despite marked fluctuations in plant densities in response to year-to-year variation in precipitation.

Two adjustments in our data were necessary to conform to the assumptions of RMA analysis. First, plant census data were normalized using a log transformation ($\log[D + 1]$, where D = measured density in a quadrat). Second, because winter quadrats censused in 1979 and 1980 were to be disturbed in manipulative studies of plant competition (Inouye 1980), we did not use the same quadrats monitored during the other winters of the study (1978 and 1981–1983). Therefore, data from the 1979 and 1980 winter censuses had to be dropped

TABLE 1. Species list of granivorous ants and rodents on the Cave Creek Bajada.

Ants	Rodents
*Novomessor cockerelli**	*Dipodomys merriami*
*Pheidole desertorum**	*Dipodomys ordi*
*Pheidole militicida**	*Dipodomys spectabilis*
Pheidole rugulosa†	*Perognathus flavus*
Pheidole xerophila	*Perognathus penicillatus*
*Pogonomyrmex barbatus**	*Peromyscus maniculatus*
Pogonomyrmex desertorum	*Reithrodontomys megalotis*
*Pogonomyrmex maricopa**	
Pogonomyrmex pima	
*Pogonomyrmex rugosus**	

* For species with relatively large colonies and few colonies per site, the total number of colonies in each plot was determined in each summer census, but all other ant species were sampled by censusing 49 permanent quadrats per treatment pen.

† Referred to as *Pheidole sitarches* in previous publications based on studies at this site.

from the analysis because RMA analysis requires repeated censuses of identical quadrats in successive years. Thus, although analyses of summer annuals span five consecutive years, those of winter annuals include only 4 yr, with a 2-yr omission early in the study.

Ant censuses

Colonies of all ant species were first enumerated on each plot in July 1977, prior to initiation of experimental treatments. These censuses were repeated annually during July and August, when summer rains stimulate high levels of ant activity, and nest excavation makes colonies most conspicuous. In addition to counting colonies of harvester ants, we censused ants of other trophic specializations and used these data as another form of control (e.g., for effects of differential predation under the various treatments).

We used different census techniques for species with high and low colony densities (Table 1). The small colonies of abundant species were sampled by systematically searching for nest entrances in 49 evenly spaced permanent circular census quadrats (2 m in radius) within each ¼-ha plot. Nest entrances within 0.5 m of one another were assumed to represent the same colony, and those separated by distances greater than this somewhat arbitrary threshold were scored as belonging to different colonies. Control and treatment plots were compared with respect to the number of entrances as well as the number of colonies of each species. For species with relatively large colony biomass and low colony density, the total number of colonies within each plot was assessed, and individually marked colonies were followed from year to year. During the summer rainy season, *Solenopsis xyloni* excavated so many nest entrances that it was difficult to assess which entrances belonged to the same colony. We scored this species simply as to whether workers were present or absent in each of the permanent census plots.

During the summers of 1980, 1981, and 1982, we censused harvester ants at bait stations to assess the effectiveness of our ant removal treatments and to detect differences in the activity levels of colonies on different treatment plots or in the mean number of workers per colony. Bait censuses were timed to coincide with a mean surface temperature of ≈32°C, as all of the common harvester ants on our study plots can show high levels of activity at this temperature.

TABLE 2. Numerical prominence of *E. abertianum* in communities of summer and winter annuals.

		Control plot A			Control plot B		
Year	Start date	Rank*	% of numbers	No./0.5 m²†	Rank*	% of numbers	No./0.5 m²†
Summer censuses							
1978	19 Aug	8	0.4	35.4	3	42.5	34.8
1979	15 Jul	1	86.6	25.4	1	76.0	38.0
1980	6 Sep	1	44.4	36.4	1	66.9	22.5
1981	31 Jul	1	28.6	92.8	1	45.1	48.3
1982	9 Sep	2	30.6	77.2	1	31.3	28.8
Winter censuses							
1978	11 Mar	1	83.5 (43.4)‡	206.8	1	88.4 (30.3)‡	143.3
1979§	5 Mar	1	34.0	197.4	1	43.4	134.6
1980§	8 Mar	ND‖	ND	533.3	ND	ND	331.8
1981	29 Mar	1	89.0	179.0	1	95.9	103.3
1982	17 Apr	1	69.7	529.5	1	77.5	200.5
1983	20 Apr	2	20.6	265.4	1	80.0	148.9

* Numerical ranking of *E. abertianum* relative to all other annual species.

† Mean density of individuals of all annual species, measured on eight quadrats per plot.

‡ % dry biomass.

§ Data for quadrats other than permanent census quadrats (see Habitat and Methods: Plant Phenology and Plant Censuses). In 1980, individuals were too small to be distinguished by species.

‖ ND = no data.

TABLE 3. Common species of winter and summer annuals other than *Eriogonum abertianum* on the Cave Creek Bajada.

Winter annuals	Summer annuals
Cryptantha micrantha (Boraginaceae)	*Boerhaavia spicata* (Nyctaginaceae)
Cryptantha crassisepala (Boraginaceae)	*Bouteloua aristidoides* (Poaceae)
Descurainia pinnata (Brassicaceae)	*Euphorbia fendleri* (Euphorbiaceae)
Descurainia sophia (Brassicaceae)	*Mollugo cerviana* (Aizoaceae)
Eriastrum diffusum (Polemoniaceae)	*Panicum arizonicum* (Poaceae)
Malacothrix fendleri (Asteraceae)	*Pectis papposa* (Asteraceae)
Phacelia popei (Hydrophyllaceae)	*Tidestroemia lanuginosa* (Amaranthaceae)

On all treatment plots, we placed small quantities of cracked millet at the bases of each of 25 permanent census stakes (alternate stakes in our 49-stake grid) and returned 30 min later to assess the numbers and identities of ants visiting these baits. Because of limited personnel and the necessity for censusing over a brief time interval with relatively constant surface temperatures, we censused one replicate of each treatment during each of two consecutive days.

Populations of seed-eating rodents (Table 1) were also censused on these plots. Methods and results are described in Brown and Munger (1985).

Short-term observations and experiments

As our long-term experiments progressed, it became increasingly apparent that the unusual phenology of *E. abertianum* might enable this abundant annual to interact with winter and summer annuals in ways that affect the abundances of these two groups of annuals, their interactions with one another, and the availability of their seeds to the two classes of granivores. In 1982 and 1983, we initiated new studies of this species' phenology and its intraspecific and interspecific competitive interactions. First, we estimated the percentage of *E. abertianum* seeds that germinate readily in the year of seed production. In late November 1982, the seeds of many individuals were collected and returned to the laboratory. Within 1 wk of collection, 50 seeds from each of 10 individual plants were placed in flats on a vermiculite-soil substrate and irrigated with distilled water. Flats were housed in an unheated greenhouse under natural photoperiod in Salt Lake City, Utah. Over a 15-d period, we recorded the number of seeds germinating daily. Second, to ascertain the contributions of intraspecific and interspecific competition to *E. abertianum* mortality between winter and summer censuses, we sampled plant densities in all 16 permanent census quadrats (summer and winter quadrats) in 1983.

Finally, we designed experiments to test directly for inhibition of summer annuals, germinating from seed, by previously established populations of *E. abertianum*. On 5 July 1983, prior to the advent of summer rains, we established four additional plots within our barbed-wire exclosure. On each 10 × 10 m plot, we imposed a square grid of 36 steel stakes (6 rows and 6 columns) spaced at 2-m intervals along north-south and east-west axes. Within each plot, each of the 16 central stakes served as the center of a 0.25-m^2 square quadrat; all 64 quadrats were censused for plants on 5 July 1983 and again in the following September. In two randomly chosen plots, we removed all identifiable individuals of *E. abertianum* from the entire area (100 m^2). By pulling on the aboveground plant parts, we also easily removed small taproots with little disturbance to the substrate. In order to equalize the impact of our presence over all four plots, we walked systematically over each control plot for 30 min, but took care not to break established *E. abertianum* individuals growing at low density.

RESULTS

Plant responses to long-term experiments

Composition and covariation of plant classes.—*Eriogonum abertianum* tends to be the numerical dominant in summer and winter censuses of annuals and can make up >80% of all annual plants during either season of plant production (Table 2). We have data only for one winter on this species' biomass in relation to that of other annuals (mean ≈37% in 1978; Table 2), but biomass is certain to be high on a regular basis. This is especially true in summer, for at the onset of summer rains individuals of *E. abertianum* are already established and can take immediate advantage of rainfall.

In RMA analyses, population densities of *E. abertianum* in winter censuses ($E.a._w$) covaried strongly and positively with those of other winter annuals (OA_w), both for the full nested design in granivore removal experiments ($P = .000$) and in seed addition experiments. This covariation, largely dependent on cubic trends in the data sets ($P = .005$ for nested design), probably reflects annual variability in rainfall and other conditions influencing germination, growth, and survivorship in similar ways for the two sets of plants. In all of the graphs showing serial changes in densities, effects of this positive covariation were removed by plotting adjusted cell means of log-transformed data. Densities of summer populations of *E. abertianum* ($E.a._s$) and other summer annual (OA_s) did not covary significantly, probably because these densities are dependent to a large extent on different seasonal rainfall events.

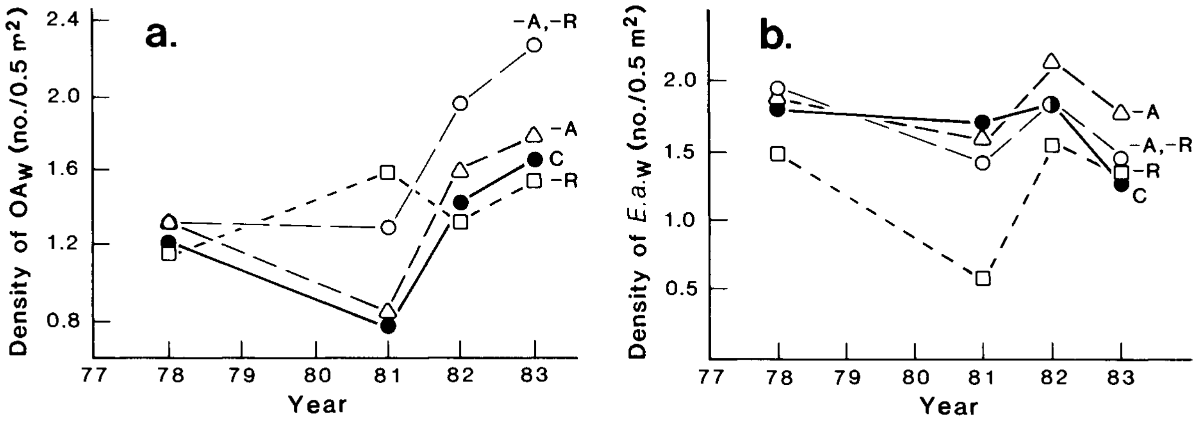

FIG. 3. Mean-log-transformed plant densities (number of plants/0.5 m^2) on two replicates each of four experimental treatments for four yearly winter censuses. (a) Other winter annuals. (b) Winter populations of *Eriogonum abertianum*. Treatments: −A = ant removal; −R = rodent removal; −A,−R = removal of both ants and rodents; C = unmanipulated control.

Aside from the presence of *E. abertianum*, communities of winter and summer annuals are floristically distinct (Table 3). Here we treat data in summary form for the three seasonal categories of annuals.

1. *Winter censuses, granivore removal.*—Despite a slight decline in 1981, OA$_w$ densities increased on both treatment and control plots (Fig. 3a; see also Seed Addition Experiments). This trend, effectively factored out of all comparisons in RMA analysis, was apparent whether or not the effects of positive covariation with *E.a.*$_w$ were removed. The most likely explanation for the increase is our exclusion of domestic grazing stock and/or *Lepus californicus*.

In granivore removal experiments, both ants (P = .000) and rodents (P = .000) had a significant impact on OA$_w$ densities, and there was a pronounced inter-

TABLE 4. Results of Repeated-Measures ANOVA (RMA) analyses comparing densities of winter annuals on control and treatment plots.

a. Full nested design:

Annual plants	CV (B)	Treatment effects (P =)*						
					Trends			
		A	R	AR	L	Qd	Cu	
OA$_w$	.000	.000	.000	.005	.001	.235	.024	(A)
	(+.350)				.534	.010	.000	(R)
					.014	.457	.013	(AR)
					.022	.255	.005	(CV)
					(+.277)	(+.555)	(+1.183)	(B)
E.a.$_w$		.612	.025	.006	.599	.653	.146	(A)
					.535	.018	.171	(R)
					.012	.104	.089	(AR)

b. Simple main effects:

Annual plants	Effect of:	Treatment effects (P =) for trends:			
		T	L	Qd	Cu
OA$_w$	+/−A within +R	.923	.410	.884	.741
	+/−A within −R	.000	.001	.328	.017
	+/−R within +A	.000	.197	.073	.000
	+/−R within −A	.010	.033	.095	.091
E.a.$_w$	+/−A within +R	.405	.106	.443	.723
	+/−A within −R	.085	.059	.227	.123
	+/−R within +A	.003	.031	.039	.061
	+/−R within −A	.319	.195	.301	.818

* Treatment effects of ants (A), rodents (R), or the interaction of ants and rodents (AR) for total pattern (T) and linear (L), quadratic (Qd) and cubic (Cu) trends in data sets through time. The effects of covariation between OA$_w$ and *E.a.*$_w$ have been removed. P = level of significance in RMA analysis. CV = probability that covariation in OA and *E.a.* densities is due to chance alone. B = coefficient of the covariate.

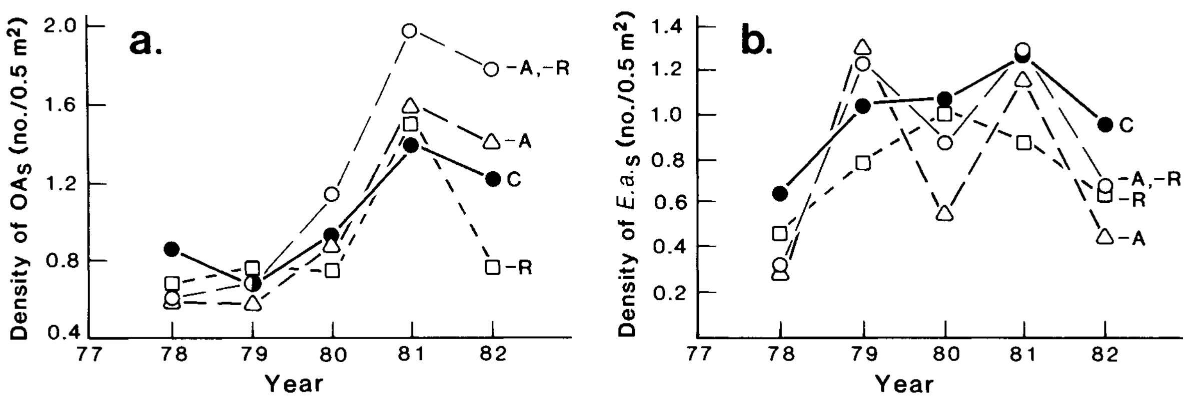

FIG. 4. Mean log-transformed plant densities (number of plants/0.5 m²) on two replicates each of four experimental treatments for five summer censuses. (a) Other summer annuals. (b) Summer populations of *Eriogonum abertianum*. Treatment codes as in Fig. 3.

action effect of the two granivore groups (P = .005; Table 4a). The significant linear increase and cubic trend associated with ant removal occurred only in the absence of rodents (Table 4b; comparison of −R with −A, −R plots in Fig. 3a). This suggests that when rodents were present without ants, they increased their use of OA_w resources. Thus, changes in OA_w populations on −A plots closely paralleled those on control plots.

In contrast, rodents influenced OA_w densities both in the presence and absence of ants, but the effects were different in nature (Table 4b, Fig. 3a). Where ants were absent, rodent removal contributed to a significant linear increase in OA_w densities (−A vs. −A, −R plots). However, in the presence of ants, where the effects of rodent removal were most highly significant, differences between experimental and control plots were more complex, and were attributable primarily to cubic trends in the data sets (−R vs. C plots). Between 1978 and 1981, OA_w densities on −R plots increased markedly relative to those on control plots, but this pattern then reversed. In 1983, as in 1978, OA_w densities were approximately the same on −R and C plots. Ants appear to have compensated for missing rodents in their use of OA_w resources, but only after an initial time delay. Unfortunately, we cannot assess the precise point at which OA_w densities on −R plots began to decline in relation to densities on C plots, because data for 1979 and 1980 are missing.

The effects of ants and rodents on winter populations of *E. abertianum* (Table 4, Fig. 3b) can best be understood in relation to changes in the densities of other competing winter annuals (see Short-term Observations and Experiments below). Although both rodents (P = .025) and the interaction of ants and rodents (P = .006) influenced $E.a._w$ densities, ants alone had no measurable impact (P = .612; Table 4a). The ant-rodent interaction may be interpreted as follows: in the presence of rodents, ant removal did not affect $E.a._w$ densities (P = .405; −A vs. C in Fig. 3b), but in their absence, ant removal contributed to an approximately significant linear decline in winter densities of this species (P = .059; −A, −R vs. −R in Fig. 3b). Probably, this decline occurred in response to the marked increase in OA_w densities on these same plots (Table 4, Fig. 3a).

Rodent removal did not affect $E.a._w$ densities in the absence of ants (Table 4b; −A vs. −A, −R in Fig. 3b). However, it had a highly significant (P = .003) and complex effect on $E.a._w$ populations where ants were present (−R vs. C in Fig. 4b). On the −R plots, $E.a._w$ densities declined while OA_w densities increased between 1978 and 1981; in the 1981–1982 period these trends were reversed (Fig. 3a, b). Eventually $E.a._w$ densities were slightly (but not significantly) higher on −R plots than on C plots. This complex pattern of change in $E.a._w$ densities accounts for the significant quadratic trend in the data set for this comparison and probably reflects the importance of competition from OA_w populations.

Finally, inverse patterns of change in OA_w and $E.a._w$ populations on −R plots were not simply statistical artifacts, emerging when positive covariation between the two sets of annuals was removed. When data were reanalyzed without taking this positive variation into account, identical trends were apparent at approximately the same levels of statistical significance for changes in the density of OA_w (P = .060 for quadratic, P = .001 for cubic trends) and $E.a._w$ (P = .031 for quadratic trends).

2. *Summer censuses, granivore removal.*—Like OA_w populations, those of summer annuals other than *E. abertianum* (OA_s) increased in density during the tenure of our study (Fig. 4a), probably because of relief from grazing. Although rodents alone did not measurably affect OA_s densities (P = .090; Table 5a), the influence of ants alone was highly significant (P = .000), and the interaction of ants and rodents bordered on significance (P = .062). The primary consequence of removing ants was a linear increase in OA_s densities,

TABLE 5. Results of Repeated-Measures ANOVA (RMA) analyses comparing densities of summer annuals on control and treatment plots.

a. Full nested design:

	Treatment effects (*P*=)*							
Annual plants				Trends				
	A	R	AR	L	Qd	Cu	Qt	
OA$_s$	.000	.090	.062	.000	.324	.822	.523	(A)
				.438	.034	.315	.043	(R)
				.070	.188	.788	.067	(AR)
E.a.$_s$	.000	.430	.366	.233	.148	.448	.000	(A)
				.783	.929	.791	.062	(R)
				.050	.576	.814	.959	(AR)

b. Simple main effects:

Annual plants	Effect of:	Treatment effects (*P* =) for trends:				
		T	L	Qd	Cu	Qt
OA$_s$	+/−A within +R	.115	.033	.829	.734	.416
	+/−A within −R	.000	.000	.076	.975	.072
	+/−R within +A	.032	.361	.048	.392	.019
	+/−R within −A	.188	.120	.437	.586	.869
E.a.$_s$	+/−A within +R	.005	.020	.481	.499	.008
	+/−A within −R	.028	.605	.201	.702	.028
	+/−R within +A	.341	.158	.603	.985	.148
	+/−R within −A	.470	.174	.766	.687	.231

* Qt = quartic trends in the data set through time. All other designations as in Table 4.

and this linear trend was greatly accentuated in the absence of rodents (−A, −R and −R, vs. −A and C in Fig. 4a; $P = .000$ and $P = .033$, respectively). Changes in OA$_s$ densities on −R plots closely paralleled those on −A plots until 1982, when OA$_s$ populations declined dramatically on −R plots. This decline, detectable as significant quadratic ($P = .048$) and quartic ($P = .019$) trends in the data (Table 5b, +/−R within +A), coincided with the decline in OA$_w$ densities on these same plots (Fig. 3a) and probably had the same cause, compensation for missing rodents by seed-harvesting ants.

Differences in *E.a.*$_s$ densities on control and granivore removal plots were highly complex and were significant primarily for quartic trends (Tables 5a, b, Fig. 4b). Fluctuations in the density of *E.a.*$_s$ were much greater on ant removal plots, where they resembled density-dependent cycles, than on control plots ($P = .000$ for quartic trends in full nested design). A weaker quartic trend ($P = .062$) occurred in response to rodent treatment. The major effects of rodent removal were: (1) continuation of the increase in *E.a.*$_s$ densities between 1979 and 1980, so that population decline was delayed until 1981, and (2) reduction of population fluctuations on −A, −R plots (in contrast with −A plots). Ant-rodent interaction effects were significant only for linear trends (Table 5a). Although rodent removal produced no significant linear trend in *E.a.*$_s$ densities in the presence or absence of ants, removal of ants led to a linear decline (relative to control plots) in *E.a.*$_s$ populations, but only where rodents were present ($P = .020$; Fig. 4b).

Summer populations of *E. abertianum* consist of individuals surviving from winter populations of this species. Our data demonstrate that the probability of survivorship is determined in part by both intraspecific and interspecific competition. In 1983, when *E.a.*$_w$ densities were relatively low (Table 2, Fig. 3b), short-term studies (see below) showed that density-dependent mortality was primarily or soley interspecific (from OA$_w$). However, intraspecific competition may prevail when and where these densities are high. For example, dense populations of *E. abertianum* on −A and −A, −R plots in the summers of 1979 and 1981 (Table 2, Fig. 4b) led to relatively dense winter populations that had suffered high mortality by the following summers (1980 and 1982). The ranking of *E.a.*$_w$ densities on the eight treatment plots included in the full nested design in 1982 is strongly and positively correlated with the ranking of the magnitude of population decline in *E.a.*$_s$ between 1981 and 1982 (Spearman Rank Correlation $r_s = 0.786$, one-tailed $P = .02$). Unfortunately, lacking data for *E.a.*$_w$ in 1980, we cannot examine similarly the cause of the decline in *E.a.*$_s$ populations between 1979 and 1980. Finally, low population densities of *E.a.*$_s$ tended to be succeeded by relatively low densities the next winter or spring and high densities during the following summer. High survivorship between winter and summer is likely to have been associated with a reduction in the intensity of interspecific competition when winter densities were low.

Seed addition experiments.—In general, seed addition experiments produced less dramatic responses in vegetation density than did granivore removal exper-

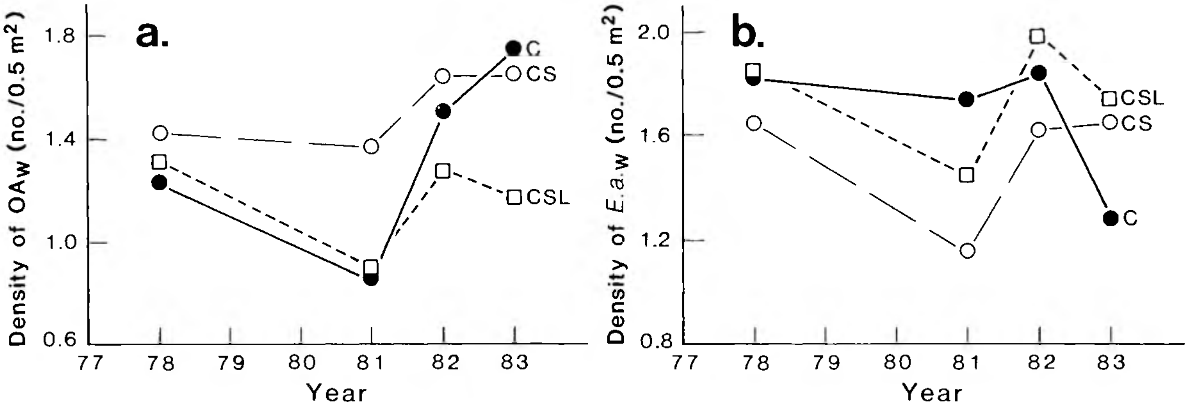

FIG. 5. Mean log-transformed plant densities (number of plants/0.5 m²) on two replicates each of control and two seed addition treatments for four yearly winter censuses. (a) Other winter annuals. (b) Winter populations of *Eriogonum abertianum*. Treatments: CS = continuous (monthly) addition of small seeds; CSL = continuous addition of both large and small seeds; C = unmanipulated control.

iments, and these responses were more pronounced in winter than in summer censuses. None of the seed addition treatments resulted in statistically significant changes in OA$_s$ ($P \geq .110$) or *E.a.*$_s$ ($P \geq .215$) populations.

Addition of large seeds (CL) produced no significant responses in winter annual populations, but responses were apparent for treatments in which all (CS) or half (CSL) of the seed supplements consisted of small seeds (Table 6). Patterns of vegetational change on CS and CSL plots qualitatively resembled changes on −R plots more closely than those on −A or −A, −R plots (Table 6 vs. Tables 4, 5; Fig. 5 vs. Figs. 3, 4). As on −R plots, OA$_w$ densities on CS plots remained high in relation to densities on control plots through 1981. Beginning in 1981–1982, increases in OA$_w$ densities on CS and CSL plots were less pronounced than on control plots. Again, these changes paralleled those on −R plots. Winter densities of *E. abertianum* on CS and CSL plots, like those on −R plots, showed the reverse pattern, first declining and then increasing relative to densities on control plots. Use of non-native seed supplements by rodents may have reduced their impact on OA$_w$ densities early in the study and allowed these plants to increase at the expense of *E. abertianum*. If, by 1981, ants had compensated by taking a greater fraction of OA$_w$ seeds on CS and CSL plots, this may explain the relatively small increases in OA$_w$ densities and large increases in *E.a.*$_w$ populations in the years that followed.

Granivore population responses

In aggregate, harvester ant populations sampled in permanent census quadrats showed no significant changes in response to rodent removal or seed addition treatments (RMA analyses of log-transformed densities of colonies or nest entrances, 1977–1983; replicate plots treated as independent trials). In similar analyses for individual species populations, only one comparison was significant: population densities of *Pogonomyrmex desertorum* declined slightly on −R plots in relation to control plots (Fig. 6). For species with large colony biomass and low colony densities, the total number of colonies per plot did not change significantly

TABLE 6. Results of Repeated-Measures ANOVA (RMA) analyses comparing densities of winter annuals on control and seed addition plots.

			Treatment effect ($P =$) for trends:†			
Annual plants	Treatment*	CV†	T	L	Qd	Cu
OA	CS	.001	.067	.250	.434	.105
	CL	.008	.201	.491	.119	.356
	CSL	.000	.000	.000	.282	.941
	PSL	.037	.131	.061	.986	.666
E.a.	CS		.004	.016	.015	.349
	CL		.596	.859	.393	.526
	CSL		.016	.289	.036	.172
	PSL		.454	.626	.201	.172

* Treatment designations: CS = continuous application of small seeds; CL = continuous application of large seeds; CSL = continuous application of small and large seeds; PSL = pulsed application of small and large seeds.

† Designations as in Table 4.

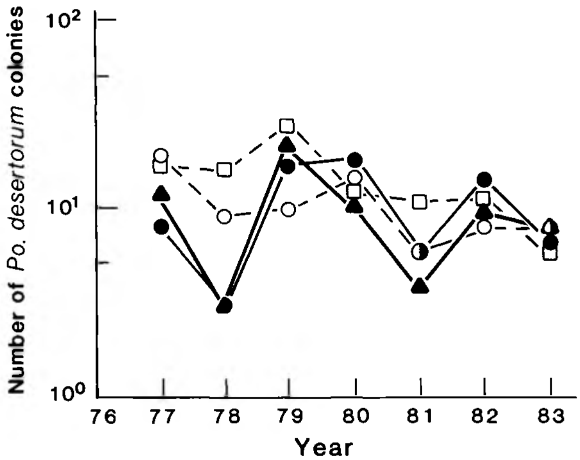

FIG. 6. Number of *Pogonomyrmex desertorum* colonies per 49 permanent census quadrats, 12.56 m^2 in area, in seven consecutive summer censuses. Numbers on rodent removal plots (– – –) declined significantly in relation to those on control plots (——) in RMA analysis (P = .032 for total pattern and .077 for linear trend).

in response to rodent removal or seed addition for any individual species or all species in aggregate.

Low sample sizes and high variability in worker visitations to census baits may have diminished our ability to detect ant responses to our experimental treatments. We observed no significant responses to seed addition experiments, and only *Pheidole xerophila* exhibited a measurable increase in worker population per colony and/or in activity level in response to rodent removal. Over the course of three bait censuses, control and experimental plots diverged progressively until, in 1982, workers were, on average, 10 times more numerous at occupied census baits on rodent plots (29.9 vs. 3.0; P = .001, Mann-Whitney U test). In this analysis, we lumped data from replicate treatment plots because the distributions of worker numbers at occupied census baits on these plots were statistically indistinguishable ($P > .12$, Mann-Whitney U tests).

Rodent responses to our experimental treatments have been reported in Brown and Munger (1985). Although the relative abundances of rodents changed markedly in response to seed addition experiments (regardless of seed size-class), removal of harvester ants produced no measurable responses in the density, body mass, or reproductive activity of any rodent species or any group of species analyzed collectively.

Short-term observations and experiments

In greenhouse trials, a majority of *E. abertianum* seeds germinated on days 4 and 5 after planting. Activity ceased by day 8, by which time 82% of the seeds had germinated ($\bar{X}$ = 41.0 of 50 seeds; SD = 5.2).

In 1983, survivorship of *E. abertianum* averaged 49.8% (SD = 29.0) between the April and July censuses of 32 quadrats on control plots. For granivore removal and control plots combined, survivorship was negatively correlated with OA_w densities in the April census, but this relationship was based largely on data from the two −A, −R plots, where OA_w densities were particularly high (Fig. 7). For quadrats on these two plots, we used stepwise multiple regression (statistical package BMDP2R, replicate plots treated as separate trial variables) to assess the relationship of *E. abertianum* survivorship to a combination of three log-transformed independent variables: density of OA_w, density of $E.a._w$, and the square of the density of $E.a._w$. A significant correlation of survivorship with the last of these three variables would indicate intraspecific density dependence (e.g., Inouye 1980). In this analysis, survivorship in *E. abertianum* was significantly correlated only with the log-transformed density of OA_w ($F_{1,30} = 14.2$, $P < .001$; $r^2 = 0.32$). In similar regression analyses for quadrats in each of the other three treatments (−A, C, and −R), OA_w density was the only independent variable to show a significant relationship to survivorship, and was inversely correlated with survivorship in each case. Thus, in this year of relatively low $E.a._w$ densities (Table 2, Fig. 3b), survivorship was reduced by interspecific but not by intraspecific competition.

Finally, in experiments conducted during the summer of 1983, densities of OA_s were markedly higher on *E. abertianum* removal plots than on control plots ($P < .001$ in ANOVA with replicate plots treated as separate trial variables). On average, each individual of this species appeared to reduce the number of other summer annuals by $\gtrsim$3 individuals (Table 7). *Bouteloua aristidoides* accounted for most of the increase in annuals on experimental plots, but all five of the most common species showed highly significant responses.

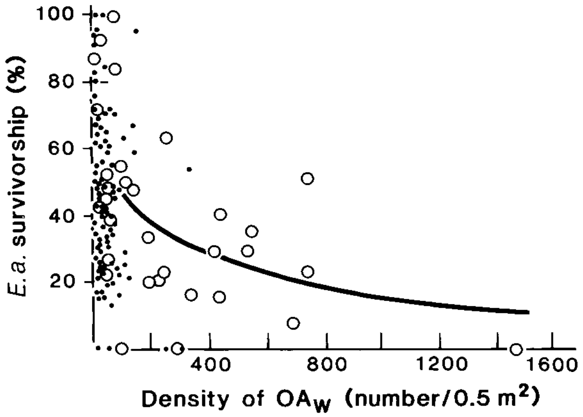

FIG. 7. Percentage survivorship in *E. abertianum* as a function of number of individuals of other winter annuals (OA_w) in each of 32 ½-m^2 quadrats in each of four experimental treatments (● C, −A, and −R plots; ○ −A, −R plots). For ○ only, $y = 1.03 - 0.29 (\log x)$, as depicted by ——. Statistics are presented in Results: Short-term Observations and Experiments.

DISCUSSION

Plant competition

Fig. 8 summarizes interactions among granivorous ants and rodents and the three seasonal resource classes on the Cave Creek Bajada. We begin by discussing interactions among the resources themselves, as these processes are crucial to understanding how ants and rodents affect populations of their resources and of one another.

The distinctive life history of *E. abertianum* gives this annual a unique set of intraspecific and interspecific competitive interactions. Unlike typical winter and summer annuals, this species grows in virtually monospecific stands during May and June and is, therefore, its own strongest competitor during the season when droughts are most predictable and pronounced (Figs. 1 and 2). Moreover, because *E. abertianum* is the most abundant annual in winter (Table 2), individuals of this species should frequently have conspecific neighbors that may inhibit them throughout the winter growing season. Not surprisingly, then, regular fluctuations in the density of *E. abertianum* resemble intraspecific density-dependent cycles with a periodicity of 2 yr. Cycles were demonstrated most convincingly by summer censuses (Fig. 4b) but, despite missing data points, there was tentative evidence from winter censuses as well (Fig. 3b).

We propose the following interpretation of the abundance cycles in *E. abertianum*. When *E.a.*$_s$ densities were low in relation to densities in other years, comparatively few seeds were produced. Consequently, population densities of *E.a.*$_w$ during the following winter were generally low and were positively correlated with the magnitude of seed crops produced on different treatment plots. Because ants are the major seed predators of this species, seed numbers and winter plant densities were highest on −A and −A, −R plots. Low density-dependent mortality during these population lows resulted in comparatively high *E.a.*$_s$ densities in the succeeding summers. In turn, prolific seed production in these dense stands gave rise to high *E.a.*$_w$ densities during the following winters. Consequently, intraspecific density-dependent mortality was high and most severe on −A and −A, −R plots, where fall seed and winter plant densities of this species were greatest. Where ants were present, removal of rodents appears

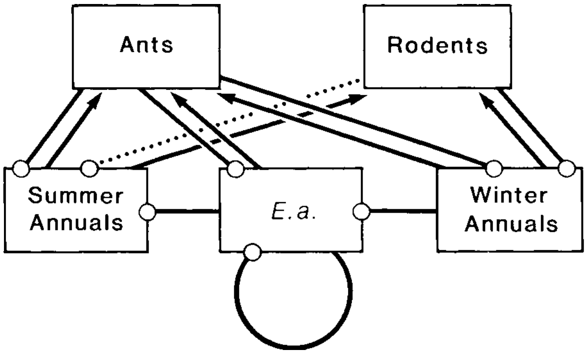

FIG. 8. Diagrammatic representation of interactions of the two major taxa of resident granivores and three seasonal resource classes on the Cave Creek Bajada. Population enhancement and damping of particular species groups are indicated by arrows and circles, respectively. Dotted lines represent interactions that have only weak effects on population dynamics.

TABLE 7. Densities of summer annuals on control and *E. abertianum* removal plots in September 1983.*

Species or species group	Mean density (no./0.25 m^2)					
	Control plot		Removal plot			
	R1	R2	R1	R2	P_R	P_T
Eriogonum abertianum	12.13	18.81	0.75	1.13	.202	.000 (.000)
OA$_s$ (all species)	1.31	5.06	58.00	45.00	.351	.000 (.000)
Bouteloua aristidoides	0.63	4.00	50.31	33.94	.128	.000 (.000)
Tidestroemia lanuginosa	0.50	0.69	6.38	7.81	.774	.000 (.000)
Euphorbia fendleri	0.06	0.00	0.69	1.19	.418	.001 (.000)
Boerhaavia spicata	0.13	0.31	0.50	1.25	.065	.006 (.008)
Pectis papposa	0.000	0.06	0.13	0.81	.007	.005 (.002)

* R1 and R2 = replicates 1 and 2, respectively. P_R = probability that density differences between treatment replicates are due to chance alone. P_T = probability that density differences between treatments are due to chance alone. Both P_R and P_T are for comparisons in analysis of variance (ANOVA). The assumption of normality holds only approximately, but for very low probability levels, exact correspondence to normality is not crucial (Sokal and Rohlf 1973). Densities were not log-transformed because many of the data points were zeros. P_T levels in parentheses are for Kruskal-Wallis Tests, which are not dependent on the assumption of normality.

to have lengthened the period of abundance cycles in *E. abertianum* (−R vs. C in Fig. 4b), probably because increases in the densities of competing winter annuals delayed the peaks and subsequent declines. Similarly, rodent removal reduced the magnitude of population cycles where ants, the major seed predators, were absent (−A vs. −A, −R in Fig. 4b).

As a possible consequence of its abundance cycles, *E. abertianum* may be subject to density regulation by intraspecific competition and interspecific competition in alternating years. In 1983, a year of comparatively low winter densities, we found no evidence for intraspecific density-dependence. However, interspecific competition clearly reduced survivorship of *E. abertianum* between winter and summer censuses, probably by causing a decline in the average sizes (resources) of individual plants. Awareness of the potentially key role of *E. abertianum* in plant population dynamics has led us to begin sampling all quadrats in both winter and summer. Additional years of sampling should enable us to detect whether or not the source of population regulation in *E. abertianum* cycles in the proposed manner. Whether or not it occurs cyclically, interspecific competition from other winter annuals has had the effect of limiting populations of *E. abertianum*. Over the 5-yr term of our study, gradual increases in OA_w densities on granivore removal plots have led to parallel declines in $E.a._w$ densities.

The results of *Eriogonum* removal experiments showed unambiguously that this species suppresses the population densities of other summer annuals. Competition from *E. abertianum* may help to account for the comparatively low densities of annuals in our summer censuses (on average about sixfold lower than in winter censuses; Table 2). However, at least one other factor may contribute to this trend. If warmer temperatures produce more rapid growth rates during summer rains than during winter rains, exclusion of competitively inferior species or genotypes (by germination suppression or resource competition) may occur more quickly and completely than in winter conditions of colder temperatures and slower growth rates (e.g., models of Tilman [1983]).

Competitive inhibition of other summer annuals by *E. abertianum* completes an indirect pathway by which we might expect winter annuals to have a positive effect on summer annuals by suppressing *E. abertianum*. To date, our annual censuses provide no evidence that the decline in this species' density on rodent removal plots has affected populations of summer annuals. However, *Pheidole xerophila* has increased on these plots and may be consuming any excess summer annual seeds that are produced in response to the reduction of *E. abertianum*. In addition, in any given summer, the variance in *E. abertianum* biomass may be much less than the variance in density over the moderate range of stand densities represented on our control and experimental plots. If this is so, OA_s populations may exhibit measurable release from competition only when $E.a._s$ densities are lower than they have been to date, low enough to prevent biomass compensation in the very lowest density stands.

Although we have not tested for competitive inhibition of other winter annuals by *E. abertianum*, or for suppression of this species by other summer annuals, we have nonetheless omitted representing these interactions in Fig. 8. Pairwise competition between major resource classes is likely to be highly asymmetric in each case. Competitive inferiority of *E. abertianum* in relation to other winter annuals is indicated by the delay of this species' growth and reproduction despite considerable risk of mortality during spring droughts. Similarly, the competitive superiority of this species over other summer annuals is strongly suggested by: (1) the much greater size of $E.a._s$ individuals in relation to other summer annuals germinating from seed at the advent of summer rains, and (2) the magnitude of the reduction in OA_s densities where *E. abertianum* is present.

Exploitative interactions of ants and rodents

Differential use of resource classes.—Plant responses summarized in Tables 4–6 yield two kinds of information. First, they specify which of the seasonal resource classes are used by each major taxon of granivores. Second, by indicating the extent to which each taxon compensates for the other's absence, they provide an estimate of the potential for resource competition between ants and rodents. We assess compensation strictly in terms of granivore effects on seasonal plant densities. On average, rodents tend to use larger seeds than do ants (Brown and Davidson 1977, Inouye et al. 1980), and compensation measured as seed biomass or densities of individual plant species is likely to reveal different patterns than those discussed here.

The three seasonal resource classes are affected differently by seed-eating ants and rodents (Tables 4 and 5, Figs. 3 and 4). Although harvester ants had strong direct effects on the densities of plants in all three classes, seed predation by rodents directly reduced only OA_w densities. Thus, winter annual densities showed significant linear increases in response to both ant removal where rodents were absent and rodent removal where ants were absent. In contrast, densities of summer annuals increased measurably in response to ant removal where rodents were excluded but not in response to rodent removal where ants were excluded. Finally, although direct predation by ants on the seeds of *E. abertianum* reduced the magnitude of population fluctuations in this species, rodents do not appear to use the seeds of this species. Rather, they facilitate *E. abertianum* indirectly by lowering populations of competing winter annuals.

To some extent, both ants and rodents compensate by using resources relinquished in one another's absence, but the extent and symmetry of compensation differ for summer and winter annuals. Both ants alone and rodents alone held densities of winter annuals to approximately the same levels evidenced on control plots. However, compensation by ants on rodent removal plots occurred only after a time delay of 2–3 yr. Although ants also appeared to use most of the OA_s resources made available by rodent removal (after a time delay), rodents did not compensate significantly for missing ants in their use of the seeds of summer annuals. Avian granivores are present in large numbers during the fall and early winter and may also be using summer-produced seeds in substantial quantity. We do not yet have data to evaluate the importance of avian granivores in reducing seeds on these plots.

Density specialization by ants and rodents.—At the moment, we are unable to identify precisely the reasons for the differential responses of winter and summer annuals to rodent removal, but a combination of factors is probably involved. First, especially during the annual resource peak in late summer, rodents may be more likely than ants to feed from areas of resource concentration. If so, they would be less likely to reduce soil seed reserves to below threshold levels at which competition limits plant densities. There are several reasons why we might expect this to be so. The relatively low mobility of ants should necessitate more intense use of resources in the immediate vicinity of the nest. High searching efficiencies and low foraging costs, associated with eusociality and ectothermy, respectively, should enable ants to feed economically from the resultant areas of resource depression. In contrast, the relatively high mobility of rodents and their capacity to gather large quantities of seed in a single foraging bout should facilitate location and use of especially dense resource patches or profitable resource types. In turn, the high metabolic demands of endothermy and long-distance foraging may force rodents to forage selectively for these valuable resources.

Considerable evidence supports this view. The most direct evidence comes from the experiments of Reichman (1979), who showed that rodents find and deplete a greater proportion of natural and supplemental resource clumps than do ants. Second, although ants as a group use seed species approximately in proportion to the availability of these seed types in the environment (Davidson 1980), rodents forage selectively on large-seeded or otherwise valuable species (Brown and Davidson 1977, Inouye et al. 1980, Hay and Fuller 1981). Direct and simultaneous sampling of ant and rodent diets at a variety of seasons, resource levels, and locations (including the Cave Creek Bajada) has shown that rodents consistently exhibit greater dietary specialization than do ants. This relationship holds for comparisons of individual species as well as for the two major taxonomic groups (D. W. Davidson and B. J. Cole, *personal observation*). In the present study, rodents had no measurable direct effect on density of *E. abertianum*. Seeds of this species are small (≈0.2 mg), packaged and dispersed individually at maturity, and available in quantity for only a brief time when alternative and more nutritious seed resources are abundant. Finally, rodents were the primary beneficiaries of our seed subsidies (see also Brown and Munger 1985). Preferential feeding by rodents on these relatively large (1 and 6 mg) non-native seeds appears to have reduced the impact of rodents on native species and caused plant population responses on seed addition plots to resemble those on rodent removal plots.

Seasonal periods of inactivity in rodents least proficient at exploiting clumped resources may also help to explain the differential effects of rodents on populations of summer and winter annuals. Although the most common rodent granivores, relatively large-bodied *Dipodomys* spp., tend to forage year-round on the Cave Creek Bajada, smaller species in the genera *Perognathus, Peromyscus,* and *Reithrodontomys* show reduced activity in the majority of winters (Munger and Brown 1981, Brown and Munger 1985). In relation to *Dipodomys* spp., these smaller rodents are less proficient at finding and depleting resource clumps (Price 1978, Reichman and Oberstein 1979, Bowers 1982). For this reason, the smaller rodents may be the species most likely to compete with ants for seeds in low-density distributions. However, the potential for resource competition through summer annuals may not be realized, because cold temperatures curtail foraging activities of both these groups before depletion of the prolific summer seed crop forces small rodents to feed from low-density distributions.

Granivore responses to manipulations

It is puzzling that rodent use of excess resources on ant removal plots produced no measurable change in rodent density, body mass, or reproductive activity. We can suggest several possible contributing factors. First, the resource gain to rodents on ant removal plots was limited to seeds produced in the smaller of the two annual resource peaks. When spread over all individuals of seven species of seed-eating rodents at our site, these additional winter-produced resources may have led to responses that were too small to be detected in rodent censuses. Because of the high probability of Type II error associated with rodent censuses, plant censuses were much more sensitive indicators of rodent compensation on ant removal plots. Second, especially if smaller rodents benefit disproportionately on ant removal plots, interference interactions with larger species may restrict population increases in these species (e.g., Price 1978*a*, Brown and Munger 1985). Third, much evidence suggests that desert rodents in general and smaller species of *Perognathus, Peromyscus,* and *Reithrodontomys* in particular may depend on shrub cover for protection from predation (e.g., Brown and Lieberman 1973, Price 1978*b*). If this is so, population increases on ant removal plots have been limited by the amount of cover available. Finally, intraspecific aggression, or territoriality, may restrict population responses.

Although we found no measurable increases in densities of ant colonies on rodent removal plots, workers of *Ph. xerophila* visited census baits in significantly greater numbers on rodent removal plots than on control plots. Unfortunately, without destructive sampling of these colonies, we were unable to judge whether the response reflected an increase in worker populations per colony, greater activity by individual workers, or some combination of these responses. Although the time delay suggests a change in worker numbers, one might also hypothesize that increases in ant activity are contingent on some threshold rise in seed density, and that this threshold was not reached until 1981. All or part of any surplus resources may be shunted to colony reproduction, but as yet we have no measure of colony reproductive output. Intense predation by ants and vertebrate predators on founding queens (D. W. Davidson, *personal observation*) may partially explain the failure of colony densities to increase. The total biomass of ants on rodent removal plots may have increased only slightly, if at all in relation to control plots, because colony densities of *Pogonomyrmex desertorum* actually declined in the absence of rodents.

Pheidole xerophila and *Po. desertorum* are the two species whose colony densities are greatest at our study area. Three major ecological differences between these species may be invoked to explain why *Ph. xerophila* exhibited increased activity (and/or increased worker numbers) on rodent removal plots, but densities of *Po. desertorum* colonies declined (Fig. 6). First, *Ph. xerophila* is active at colder substrate temperatures than *Po. desertorum* (16°–35° vs. 24°–46°C) and may be better adapted to take advantage of relatively high densities of winter-produced seeds on rodent removal plots in the cooler spring months. Second, worker populations of *Po. desertorum* are relatively small (on the order of hundreds per colony) and workers forage individually on dispersed as well as concentrated resources. In contrast, *Ph. xerophila* is characterized by relatively large worker populations (thousands per colony) and column foraging behavior, two attributes interpreted (Hölldobler 1976, Davidson 1977*b*) as specalizations for rapid and efficient exploitation of resources from high-density distributions. Third, on average, workers of *Ph. xerophila* are 2.5 times smaller than those of *Po. desertorum* and collect smaller seeds (Davidson 1977*a*). The seeds of *E. abertianum*, although small, are larger than the seeds of some common summer annuals, including the very abundant *Bouteloua aristidoides* (Table 7). As rodent removal caused *E. abertianum* populations to decline, and this annual competitively inhibits *B. aristidoides*, exclusion of rodents may have favored the smaller *Ph. xerophila* over its larger competitor, *Po. desertorum*. The diets of *Ph. xerophila* and *Po. desertorum* overlap considerably, and in pretreatment censuses of treatment and control plots, a negative correlation in the abundances of these species suggested resource competition between them (Davidson 1980). In experiments at this same study site, *Ph. xerophila* populations declined significantly in response to increases in *Po. desertorum* colonies on plots where a competitor with even larger worker body size had been removed (Davidson 1985). Together with responses of *Po. desertorum* on rodent removal plots, these results suggest that abundances of these two ant species are regulated by a combination of resource availability (as determined by both the seed production and the use of seeds by other granivores) and resource competition between the two species.

Contrasts with Sonoran Desert experiments

The absence (among rodents) or weakness (among ants) of density compensation contrasts sharply with the strong and reciprocal density compensation that occurred in earlier removal experiments on the Silverbell Bajada in the Sonoran Desert (Brown et al. 1979*a*). We consider three possible explanations for these differences.

First, granivore populations may not be regulated by food availability on the Cave Creek Bajada. Several lines of evidence contradict this hypothesis, however. Seed subsidies had major effects on the organization of the rodent community (Brown and Munger 1985), and the failure of ants to respond may have resulted simply from rapid depletion of these supplements by more mobile avian (D. Thompson and J. Brown, *personal communication*) and rodent granivores. In addition, experimental removal of individual rodent and ant species led to major changes in the densities of other species within the same higher taxon of granivores (Munger and Brown 1981, Brown and Munger 1985, Davidson 1985). Within both ant and rodent communities, competitive interactions proved to be strongest between granivores whose body size similarity or dietary overlaps suggested strong similarity in resource use. Finally, in contrast to the far-reaching effects of our experiments on granivorous ants and rodents, we observed no detectable effect on nongranivorous species in these groups (see also Munger and Brown 1981, Brown and Munger 1985). Despite the evidence for food limitation, it seems clear that factors such as interference competition and predation may interact with resource availability to regulate granivore populations on the Cave Creek Bajada.

Second, despite the time delay naturally encountered when responses radiate sequentially through populations of several species, we have found strong evidence for a number of indirect interspecific interactions over the relatively brief time span of 3–6 yr. Prominent indirect interactions occur within and between the major granivore taxa, between consumer and resource classes, and between major categories of resources (Fig. 8; see also Davidson et al. 1984, Davidson 1985). Some of these indirect effects appear to moderate exploitative competition between ants and rodents (Davidson et al. 1984). In this study, for example, rodents facilitate *Po. desertorum* indirectly by inhibiting *Ph. xerophila* and possibly by suppressing densities of winter annuals that compete intensely with *E. abertianum.* As a consequence of both the greater granivore diversity on the Cave Creek Bajada and the strength and rapid expression of indirect pathways mediated through these granivores and through *E. abertianum,* responses to our experimental manipulations have been spread over more species populations than were responses in the Sonoran Desert experiments. Such "diffuse compensation" should increase in proportion to both diversity and connectance and may make individual species populations on average more resistant to change.

Finally, if the extent of dietary overlap is positively correlated with the intensity of resource competition, ants and rodents should compete more strongly in the Sonoran Desert than in the Chihuahuan Desert. Significantly higher resource overlaps in the Sonoran Desert are partially a consequence of differences in the seasonality of resource production and use by the two taxa (D. W. Davidson and B. J. Cole, *personal observation*). The results of both experiments and studies of resource overlaps suggest that, in comparison to the situation in the Sonoran Desert, resource competition in the Chihuahuan Desert may be more intense within each of the two higher taxa and less intense between them.

CONCLUSIONS

Our experimental studies of granivory in desert ecosystems demonstrate remarkable complexity in the organization of consumer-resource interactions. These studies show that, despite the climatic variability and unpredictability of desert environments, populations respond to the steady deterministic processes of competition and predation. Phylogenetically related and unrelated consumers do interact through their resource species. However, an intricate array of factors, some of these idiosyncratic to the particular seasonal pattern of precipitation at our site, determines the extent and symmetry with which these consumers respond to one another's abundances. Strong competition among resource species influences the net interactions among consumer species. Predators of granivores and interference interactions among closely related competitors also appear to affect the extent and nature of density compensation by ants and rodents, though these effects are not well demonstrated in our study. Together, these observations point to the folly of assigning community organization to any single factor such as competition, predation, or the physical environment.

The importance of long-term experimental studies is underscored by the observations that population responses to our manipulations were sometimes periodic or time-delayed and were often indirect. Direct and variously indirect routes of interaction have different rate constants that cause these effects to be expressed on different time scales. For example, as in prior studies in the Sonoran Desert (Inouye 1982, Davidson et al. 1984), large-seeded annuals gradually increased at the expense of small-seeded annuals on rodent removal plots. In time, we may find that ants will decline in abundance on these plots, as they have on the Sonoran Desert because of the reduction of their small-seeded resource species. For the present, however, interactions between ants and rodents appear to be dominated by the more rapidly resolved pathways shown in Fig. 8. Interaction pathways that are expressed relatively quickly need not be the most important in determining the organization of biological communities. The extent to which granivore communities are molded by these processes in ecological and evolutionary time should depend on the relationships between the rate constants of the pathways and the natural disturbance cycles of the environment. Additional long-term monitoring of experiments may help to elucidate these relationships.

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