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EFFECTS OF PREDATION AND COMPETITION ON SURVIVORSHIP, FECUNDITY, AND COMMUNITY STRUCTURE OF DESERT ANNUALS¹

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Abstract. Effects of rodent and ant granivores, watering, and thinning were studied in a diverse community of winter annuals in the Sonoran Desert. Seed predation considerably reduced plant densities, but ants and rodents had qualitatively different effects on the plant community. Ants increased species diversity of annuals by differentially harvesting the numerically dominant species, while rodents preyed selectively on species which dominated the community in terms of biomass. Competition among annual plants reduced growth rate, biomass, and fecundity, but had no significant effect on mortality. One species, *Euphorbia polycarpa*, apparently increased in density when the density of competing *Erodium* species was reduced by rodent predation.

Key words: annual plant; community; competition; desert; fecundity; granivory; predation; species diversity; survivorship.

INTRODUCTION

Studies of factors influencing the abundance and spatial distribution of desert plants traditionally have emphasized the roles of water, soil, and temperature as they interact directly with morphological and physiological adaptations (cf. Shreve 1964, Hastings and Turner 1965, Mulroy and Rundel 1977, Ehleringer et al. 1979). Undeniably these abiotic influences are important in limiting the occurrence of particular taxa and life-forms over broad geographic areas and, where topography is varied, in determining the composition of local plant associations. Perennial plants, in particular, have been successfully studied from this viewpoint (Shreve 1964, and included references, Steenbergh and Lowe 1977).

In desert habitats where aboveground cover is typically well under 50%, biotic interactions among plants might seem to be relatively unimportant. However, several studies have suggested that seed dispersal (Campbell 1929), herbivory (Campbell 1929, Clements 1934, Glendening 1952), and competition (Yeaton and Cody 1976, Fonteyn and Mahall 1978, Inouye *in press*) influence the abundance and distribution of desert perennials.

Winter annuals, an important vegetational component in most North American deserts, often do not show as clear distributional patterns as perennials. This is apparently due to the particular life history features of these plants (Shreve 1964). They spend unfavorable periods, usually most of their lives, as seeds. They germinate, grow, and reproduce in the few months when soil moisture is available following notoriously variable winter rains (Went 1948, Went

and Westergaard 1949, Tevis 1958a, Beatley 1967). These annuals typically exhibit great phenotypic plasticity, and particular species often are distributed throughout desert regions that receive winter rains. On a local scale, distribution of annuals appears to be influenced by soil surface characteristics, which affect seed accumulation and water retention, and by perennials, which create distinct microhabitats.

While adaptations of desert annuals to harsh and unpredictable physical environments have been recognized, there have been few experimental studies of the effects of biotic interactions on the abundance and distribution of these plants (but see Klikoff 1966). The effects of predators on desert annuals have not been carefully studied, although their seeds are known to support large populations of granivorous ants and rodents (e.g., Brown et al. 1979a, and included references; see Borchert and Jain 1978 for California grassland community). In addition, the extent and consequences of inter- and intraspecific competition among annuals have not been closely examined, although conflicting viewpoints have been expressed (Shreve 1964, Went 1973). Since competition and predation have been suggested to play major roles in structuring communities (Mac Arthur 1972, Cody and Diamond 1975) we decided to assess their importance in a natural community of desert annuals.

METHODS

This study was conducted during the late winter and spring of 1977 at the Silverbell Validation Site of the United States/International Biological Program Desert Biome, located ≈60 km northwest of Tucson, Arizona. The study area, in the northeast corner of the Validation Site, was situated in a typical Sonoran lower bajada habitat where the dominant perennial shrubs

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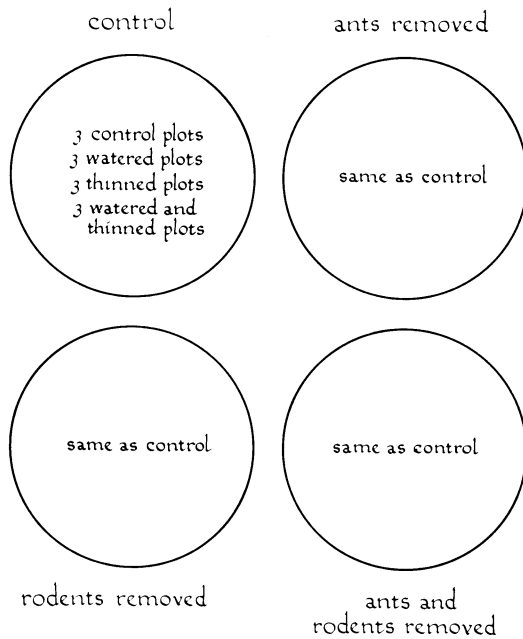


FIG. 1. Diagram of the experimental design showing the four granivore treatments (circular arenas) and four watering and thinning treatments in each arena. Each granivore treatment was replicated twice, giving a total of 12 plots in each of eight arenas, or 96 plots.

Larrea tridentata and *Ambrosia deltoidea* together accounted for $\approx 30\%$ cover.

Although the area was quite level and uniform topographically, distribution and density of annuals was highly heterogeneous, presumably largely as a result of microspatial heterogeneity of surface soil characteristics.

To detect patterns of biotic interaction which might easily be obscured by this heterogeneity we sampled replicated 1-m² quadrats. We reasoned that larger quadrats would obscure patterns resulting from competition among neighboring individuals, whereas smaller quadrats would emphasize the effects of microspatial soil heterogeneity. In addition we tried to maximize replication to overcome uncontrolled sources of variation and facilitate statistical analysis. We chose a 4 × 4 factorial design suitable for Analysis of Variance (ANOVA) in which presence or absence of rodents and ants was combined with watering and thinning treatments (Fig. 1). Eight circular arenas (36-m diameter, 0.1-ha area), established in 1973 to investigate competition for seeds between rodents and ants, were used to evaluate effects of these seed predators (see Brown et al. 1979b for details). The eight arenas consisted of two replicates of four treatments: ants excluded, rodents excluded, both ants and rodents excluded, and neither ants nor rodents excluded. Rodents were excluded by quarter-inch (6.5-mm) mesh hardware cloth fences buried to a depth of 20

cm and exposed to a height of 60 cm. The few rodents which crossed these fences were removed by periodic trapping. Ant colonies were eliminated by localized treatment with insecticide.

On 29 January 1977 we established 12 quadrats for sampling annuals within each of these arenas. Three replicates each of four treatments were represented in each arena: watered, thinned, both watered and thinned, and neither watered nor thinned. Quadrats were laid out in an arbitrary unbiased manner, except that proximity to perennial shrubs was avoided. Diagonal corners of quadrats were marked with metal tags. We watered appropriate quadrats with a watering can on three dates, supplying 11.6 mm on 18 February and 6 March, and 5.8 mm on 1 March 1977, for a total of 29 mm H₂O. Hand thinning, performed in as nearly random fashion as possible on 29 January 1977, reduced plant density on thinned quadrats to approximately one-third that on unthinned quadrats. Thus a total of 96 1-m² quadrats was established, consisting of 16 combinations of four factors (rodents, ants, watered, thinned), and each combination of factors was replicated six times, three in each of two arenas (Fig. 1).

Quadrats were censused initially on 29 January and recensused and harvested on 2–3 April 1977. In order to follow growth and survivorship of individual plants we mapped their location and size on transparent 6-mil (150 μ m) polyethylene sheets stapled to wooden frames, which were positioned precisely over quadrats using the metal corner tags. On the first census we used a black felt marker to trace the outline of every established plant and large seedling (diameter ≥ 1 cm) within each quadrat, and to mark the location of all small seedlings (diameter < 1 cm) in two 4-dm² subquadrats in opposite corners. On the second census we used a red marker to trace the new outlines of surviving plants on the same plastic sheets. At this time we also recorded the number of flowers and fruits for each individual of *Erodium cicutarium* and *Erodium texanum*. All annuals were counted by species, collected (with roots intact, whenever possible), and placed in paper bags for subsequent determination of biomass. These samples were cleaned of soil and detritus, oven dried, and weighed on an analytical balance. The two *Erodium* species were collected and weighed separately. Growth between censuses of individual *Erodiums* was measured by calculating change in area from average diameters of traced outlines on the plastic sheets. This provided a conservative estimate since some growth is vertical. The remaining species were weighed collectively.

The data were analysed with SPSS ANOVA and APL ANOVA 4. When assumptions of ANOVA were violated (e.g., heteroscedasticity) we used Wilcoxon matched-pairs signed-ranks tests. Least squares regression and correlation analyses were used where appropriate. Log-transformed variables were used for some anal-

TABLE 1. Means and standard deviations for certain parameters of control plots (unthinned, unwatered) with neither ants nor rodents removed. For the first 10 entries N represents the number of plots; values less than six are due to loss of one biomass sample and the absence of *Erodiums* on one plot. For the last four entries N represents the number of individuals.

	\bar{x}	SD	N
Final number of species	9.2	3.1	6
Final species diversity (H')	2.3	0.5	6
Initial number of plants	358.3	357.5	6
Initial number of small plants	322.5	341.8	6
Final number of plants	181.8	116.2	6
Final number of <i>Erodiums</i>	7.0	6.9	6
Total biomass (g dry mass)	5.8	5.2	5
Biomass of <i>Erodiums</i> (g dry mass)	2.4	2.0	5
Percent survivorship: large plants	71.0	38.7	6
Percent survivorship: small plants	41.5	34.2	6
Fruits per plant: <i>Erodium cicutarium</i>	25.1	16.5	62
Fruits per plant: <i>E. texanum</i>	17.4	26.1	60
Area per plant: <i>E. cicutarium</i> (cm ²)	31.5	9.8	62
Area per plant: <i>E. texanum</i> (cm ²)	31.9	7.4	60

yses. The biological significance of these transformations is not always apparent. However, many biological relationships reflect allometric changes because they involve interacting dimensions. Although the mechanisms remain obscure, it seems likely that biotic interactions of our annuals are reflected in allometric relationships, which can be linearized by logarithmic transformations.

RESULTS

The winter rains of 1976–1977 induced germination of a diverse community of annuals. Bimodal distribution of this rainfall (22.6 mm between 21 October and 26 November, 32.5 mm between 31 December and 22 January) produced two peaks of germination which in turn resulted in two cohorts of annuals. The first cohort, consisting primarily of *Erodium cicutarium*, *E. texanum*, and *Euphorbia polycarpa*, was represented by established individuals when first censused. These plants germinated and grew initially in response to the first rains, survived until the second rains as quiescent rosettes, and then reinitiated growth. The first cohort was dominated by the two *Erodiums*, which comprised >40% of the total annual biomass.

The second cohort consisted of seedlings when first censused because they had germinated after the later heavier rains of midwinter. These plants matured rapidly and individuals of both cohorts flowered and set seed in near synchrony in response to declining soil moisture and increasing temperature. All species encountered were represented in the second cohort, but different species were numerically dominant. The most abundant species, *Filago californica* and *Eriophyllum lanosum*, which accounted for 64 and 8% of the individuals at the final census, respectively, were members of the second cohort. Other species included, in decreasing order of abundance, *Monoptilon bellidiforme*, *Cryptantha barbiger*, *Lappula Redowskii*, *Pectocarya recurvata*, *Draba cuneifolia*, *Nemacladus glanduliferus*, *Tillaea erecta*, *Astragalus didymocarpus*, *A. Nuttallianus*, *Oenothera primaverus*, *Plantago insularis*, *Linanthus aureus*, *Calandrinia ciliata*, and *Daucus pusillus* (nomenclature from Kearney and Peebles 1951).

Erodium cicutarium is native to Europe and probably was introduced to the southwest at an early date by the Spaniards (Kearney and Peebles 1951). *Euphorbia polycarpa* is a root perennial which grows and blooms on the study site in response to rains. Judging by stem scars, a significant proportion of the individuals censused were in their first season. All other species are believed to be winter annuals native to the Sonoran Desert.

The composition of the winter annual community in 1977 is summarized in Table 1, which quantifies several characteristics of untreated control quadrats. In general variances were high. Heterogeneity in microtopography and soil characteristics probably contributed to significant variability in life history characteristics and community structure at all levels of sampling: within quadrats, between quadrats in the same arena, and between arenas across the study site.

Exclusion of granivores increased density and changed species composition of germinating annuals. Table 2 indicates that in 1975, one season after establishment of the arenas, there were no significant differences in densities of winter annuals among the arenas (Brown and Davidson 1976). Two years later densities were significantly higher in arenas where rodents, ants, or both had been removed. Removal of

TABLE 2. Ratios of final densities of annuals relative to control plots (mean density on control plots in parentheses) in 1975 and 1977. The 1975 data show no effect of removals; in fact, plant densities were highest on control plots. The 1977 data show significant increases in annual densities on removal plots. Differences in absolute density between 1975 and 1977 are due to differences in rainfall between years. Densities are individuals per square metre.

		1975 Rodents		1977 Rodents	
		present	absent	present	absent
Ants	present	1.0 (26.7)	0.8	1.0 (224.1)	1.4
	absent	0.7	0.9	1.7	2.3

TABLE 3. Effects of removal of ants, rodents, or both on densities of certain annual plant species, all plants, plant biomass, and two measures of species diversity. Values given are ratios of treatment to control (+Rodents +Ants) means. Numbers in parentheses are mean values for unthinned plots except for plant biomass and the two measures of diversity, which are for control plots. Statistical analysis was by ANOVA; NS = not significant.

	+Rodents +Ants	+Rodents -Ants	-Rodents +Ants	-Rodents -Ants	Effect of removal of	
					Rodents	Ants
Initial census						
29 January 1977						
1. Large plants	1.00 (35.8)	0.98	2.08	2.35	increase $P < .01$	NS
2. Small plants	1.00 (292.5)	3.30	3.32	3.17	NS	increase $P < .01$
Final census						
2 April 1977						
3. <i>Erodium cicutarium</i> (seed mass = 1.6 mg)	1.00 (1.8)	1.83	7.03	16.11	increase $P < .01$	NS
4. <i>E. texanum</i> (seed mass = 1.6 mg)	1.00 (0.6)	0.88	2.07	0.78	increase $P < .05$	NS
5. <i>Euphorbia polycarpa</i> (seed mass = 0.2 mg)	1.00 (0.6)	2.00	0.14	0.29	decrease $P < .02$	NS
6. <i>Filago californica</i> (seed mass = 0.04 mg)	1.00 (142.1)	1.90	1.43	2.59	NS	increase $P < .05$
7. <i>Lotus humistratus</i> (seed mass = 1.5 mg)	1.00 (11.4)	1.14	2.43	5.22	increase $P < .01$	NS
8. All plants	1.00 (209.6)	1.35	1.34	1.94	increase $P < .05$	increase $P < .01$
9. Dry mass (all species)	1.00 (5.8)	1.07	2.09	2.17	increase $P < .01$	NS
10. Species diversity (H')	1.00 (2.78)	0.73	0.99	0.89	NS	decrease $P < .05$
11. Species evenness (E)	1.00 (0.53)	0.77	1.99	1.04	NS	decrease $P < .05$

rodents resulted in increased density of "large" plants (rosette diameter at first census ≥ 1 cm) (Table 3, line 1). Most of these plants were members of the first cohort or large-seeded species of the second cohort which had produced large seedlings by the first census. In particular, relative density of the three species with the largest seeds, *Erodium cicutarium*, *E. texanum*, and *Lotus humistratus*, increased when rodents were excluded. The density of small plants (diameter at first census < 1 cm; all members of the second cohort) increased where ants had been eliminated (Table 3, line 2); ant-rodent interaction was not significant.

Two measures of species diversity, H' ($H' = 1/\sum p_i^2$) and E ($E = H/H_{\max}$, $H = \sum p_i \ln p_i$) were significantly lower in ant removal arenas than in those where ants were present (Table 3, lines 10 and 11). This was due primarily to the increased densities of *Filago californica* where ants were removed (Table 3, line 6). By decreasing the relative density of the two *Erodium* species, rodents increased the evenness with which biomass was distributed among species (Table 3, lines 3, 4, and 9; ant-rodent interaction was not significant). Where rodents were excluded the *Erodium* spp. accounted for $>60\%$ of the total biomass; this decreased to $<30\%$ when rodents were present.

The only species for which we had adequate sample sizes to show any trend and which showed patterns different from those outlined above were *Euphorbia polycarpa* and *Eriophylum lanosum*. *Euphorbia polycarpa* decreased in density in the absence of rodents (Table 3, line 5). This interesting result will be discussed in more detail in the next section. *Eriophylum lanosum* showed no significant effects of either rodent or ant predation.

We detected no effects of herbivory on either survivorship or fecundity of germinated plants. Survival from the first census to maturity was high for established plants and moderate even for recently germinated seedlings (Table 2). There were no significant differences between quadrats in fenced and unfenced arenas which could be attributed to mammalian folivores excluded by the fencing. The fences, designed to exclude granivorous rodents, also kept out herbivorous ground squirrels and probably cottontails and jackrabbits. None of our experimental treatments were designed to test directly for effects of large grazers (deer) or herbivorous arthropods. However, the generally high survivorship of plants suggests these predators did not cause significant mortality.

The thinning and watering treatments were designed

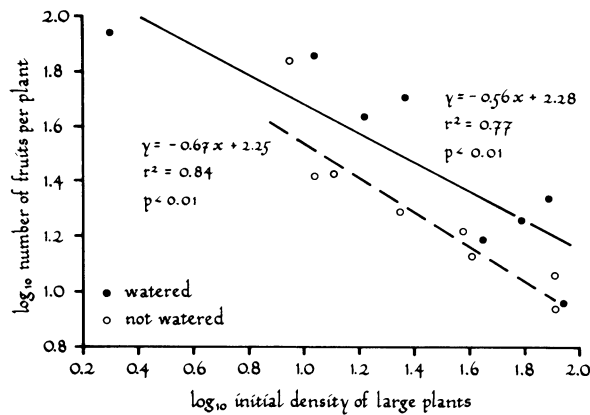


FIG. 2. Relationship between fecundity (fruits per plant) of *Erodium cicutarium* and initial density (plants per square metre) of large plants, indicating significantly greater seed production with reduced competition. The points represent average values for each treatment. The two regressions shown here are significantly different ($F = 14.6$, $P < .01$). Regressions calculated for individual plants rather than treatment averages had considerably greater variances, but were also significant ($r = .66$, $P < .01$ for watered plots; $r = .34$, $P < .05$ for unwatered plots).

to test effects of competition and water stress on survival and fecundity. Survivorship was unaffected by thinning and increased by watering only for small plants (Wilcoxon, $P < .02$). In contrast to survivorship, growth rates and fecundity were strongly influenced by both thinning and watering treatments. The most complete data are for *Erodium cicutarium*, in which the number of fruits, growth rate, and biomass all increased in response to both thinning and watering (Wilcoxon, all $P < .05$). A second way to test for competition is to examine the relationship between fecundity and initial density (Fig. 2). The significant negative correlation shows that fecundity increased in response to reduced density regardless of whether low

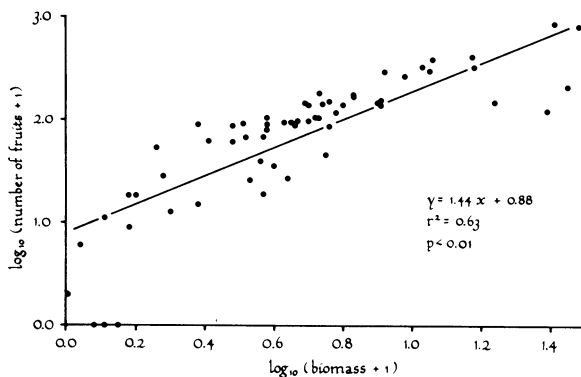


FIG. 3. Relationship between fecundity (number of fruits) and biomass (grams dry mass) for individual mature plants of *Erodium cicutarium*. Points represent average values for plants on watered and unwatered plots.

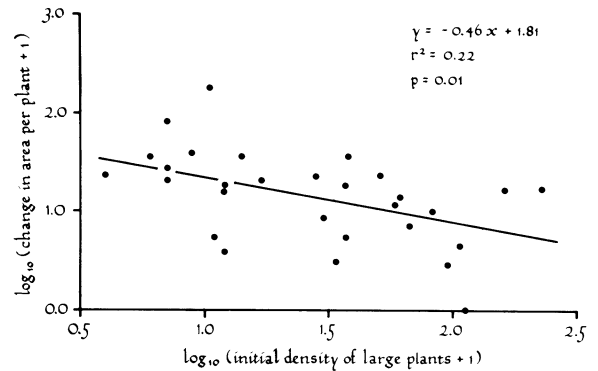


FIG. 4. Growth rate (change in square centimetres per plant) as a function of initial density (plants per square metre) of large plants, for *Erodium texanum* on unwatered plots only. Points are average values for individual plots. The significant negative slope of the regression is evidence that competition affects growth rates of *E. texanum*. Watered plots also gave a significant regression with a greater intercept ($y = -0.42(x) + 1.95$, $r^2 = 6.19$, $P < .05$).

densities resulted from artificial thinning, rodent seed predation, or edaphic factors. Watering consistently increased seed production (Fig. 2). For individual plants of *E. cicutarium*, fecundity was highly correlated with growth rate (change in area between censuses) and biomass at maturity (Fig. 3).

In the related species, *E. texanum*, change in area between censuses was negatively correlated with the initial density of large plants (Fig. 4). As in *E. cicutarium*, both change in area between censuses ($r = .64$, $P < .01$, $N = 65$) and the number of fruits per plant ($r = .64$, $P < .01$, $N = 65$) were highly correlated with biomass at the final census. However, neither number of fruits per plant nor final plant biomass showed a significant regression on initial density of large plants.

The only data relating to growth rate, biomass, or fecundity of species other than the *Erodiums* are for total biomass of all other species. Growth rates of these small plants were inhibited by high densities of other plants and stimulated by watering. Average biomass of these plants was negatively correlated with initial density of all plants ($r = .32$, $P < .05$, $N = 45$ unwatered plots; three samples were lost) and was increased by watering (Wilcoxon, $P < .02$).

DISCUSSION

By using experimental manipulations and intensive sampling we have demonstrated significant effects of predation and competition on survival and reproduction in a community of desert annuals. The increase in density of all plants in arenas where rodents, ants, or both were excluded indicates that both classes of seed predators had significant impact on populations of mature annual plants. Rodents appeared to prey selectively on large seeds because the larger seeded

species, *Erodium cicutarium*, *E. texanum*, and *Lotus humistratus*, all increased in density when rodents were excluded. Ants increased species diversity by differentially harvesting the small seeds of *Filago californica*, the most abundant species. The response of plants to reduced densities, whether these densities resulted from artificial thinning, seed predation, or other causes, clearly indicates the importance of competition. Effects of competition were manifested largely in reduced growth rates and fecundity, rather than increased mortality.

In fact, it is likely that we have underestimated the effects of these biotic interactions. Measured effects of seed predation probably are conservative, both because granivore removal was not completely successful (Brown et al. 1979a) and because seed dispersal by wind and water may diminish the effectiveness of granivore exclosures. In addition, Table 3 indicates that densities of winter annuals in the exclosures may still be increasing in response to removal of granivores. Effects of competition may be underestimated because we sampled 1-m² plots, but interactions between individual plants probably occurred on a much smaller scale. In addition, much of the large variability among replicates can probably be attributed to spatial heterogeneity within the study site. The fact that we observed significant effects of competition and predation despite high variances among replicates underscores the importance of these biotic interactions.

Although many studies of desert annuals have not emphasized the influences of predation and competition, our results are consistent with much of what is known about the foraging behavior of desert granivores and the growth of desert ephemerals. The different effects of rodent and ant predation fit well with reports that rodents forage selectively for large, energetically rewarding seeds (Soholt 1973, Reichman 1977), and that ants often specialize on certain abundant species (Tevis 1958b, Davidson 1977, Whitford 1978).

Our data indicating that competitors primarily reduce growth rate and fecundity rather than survivorship are consistent with reports of the extreme phenotypic plasticity shown by many plants, particularly desert annuals, in response to environmental variability (Tevis 1958a, Bradshaw 1965, Harper 1977). In particular, our observations agree with those of Went (1949) who found no significant effect of plant density on survivorship of Mojave Desert annuals. Although Went noted reduced growth and fecundity at high density he failed to appreciate their significance as consequences of competitive interactions. Several studies have indicated that survival of germinating desert annuals to maturity is often high. Our survival values for small seedlings of the second cohort ($\bar{x} = 41.5\%$ on unwatered quadrats) are remarkably similar to those reported by Juhren et al. (1956): 46%, Tevis (1958a): 50%, and Beatley (1967): 38%.

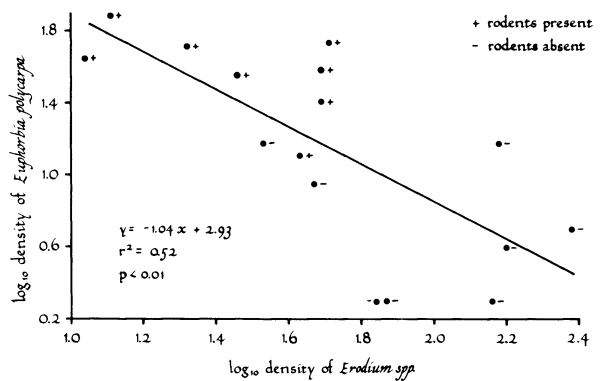


FIG. 5. A plot of final density (plants/6 m²) of *Euphorbia polycarpa* with final density of *Erodium cicutarium* and *E. texanum*. The significant negative slope of the regression can be interpreted as evidence of interspecific competition between the two *Erodium* species and *E. polycarpa*. A + or - sign indicates presence or absence of rodents. Points are sums of six replicates for each of 16 treatments. See text for further discussion.

Much of the current literature of community ecology discusses the relative importance of physical factors, competition, and predation in structuring natural communities. All of these appear to play important roles, both alone and in concert, in structuring communities of desert annual plants. The increased diversity resulting from ant predation is superficially similar to effects of predation on some other communities, including sessile organisms in the rocky intertidal (e.g., Paine 1966, Lubchenco 1978) and in grasslands (e.g., Harper 1977, and included references). Though authors do not always use the language of succession, it is generally held that the effect of predation in these communities is to increase diversity by disturbing the process of successional advance, either by creating a microspatial mosaic of seral stages or by preventing competitive domination by a few climax species. It is difficult and perhaps unnecessary to invoke these mechanisms to account for the influence of predation on desert annual communities. We have no evidence that those species which produce the largest seed crops (e.g., *F. californica*) are the best competitors for limited resources. Instead, ants may increase diversity much as switching prey-vertebrate predators with search images are thought to influence densities of alternative prey (Murdoch et al. 1975; for ants see Whitford 1978).

In contrast to ant predation, rodent predation did not affect species diversity measured in terms of proportions of individuals, but it interacted with interspecific competition among plants to influence community structure. Apparently by preying selectively on large seeds, rodents maintained lower relative densities of *Erodium* species and *Lotus humistratus*. When rodents were removed the two *Erodiums* increased in density to dominate the total plant biomass. Early ger-

mination and large seed size probably both contribute to rapid growth and competitive domination by *Erodiums*. We might expect that this growth response occurred at the expense of interspecific competitors. The decrease in *Euphorbia polycarpa* when rodents were excluded (Table 3, line 5) may have resulted from such competitive domination by *Erodiums*. This interpretation is strengthened by the significant inverse correlation between the densities of *E. polycarpa* and *Erodium* spp. (Fig. 5). Note that low densities of *E. polycarpa* were consistently associated with absence of rodents, suggesting that this relationship results from competition rather than differential response of the two genera to some edaphic factor.

Because of variation in abundance and diversity of desert annuals from year to year and place to place it may be hazardous to generalize from our results, but they clearly suggest that competition and predation play potentially important roles in structuring communities of these plants. Since granivore removal and plant thinning treatments were in effect for different lengths of time our evaluations of effects of competition and predation are not comparable. It might be interesting to assess the impact on the annual plant community of both species-specific and nonselective thinning experiments lasting for several generations so that such treatments would be comparable to our granivore exclusion treatments. This might indicate how the effects of competition vary between years depending on conditions for germination and growth. We hypothesize that competition might be particularly important in good years when density, biomass, and seed production are high. In such years we would expect density-dependent inhibition among large, closely spaced plants to influence seed production, thereby affecting the composition of future annual plant communities.

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