

A PRELIMINARY STUDY OF SEED PREDATION IN DESERT AND MONTANE HABITATS¹

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Abstract. Multifactorial experiments in which domestic seeds in shallow glass containers were distributed in desert and montane habitats provided data on identity of seed predators (whether rodents or ants), spatial and temporal pattern of their foraging activities, and their preferences for sizes and species of seeds. The results indicate that in some desert ecosystems both rodents and ants are important and efficient collectors of seeds. These two taxa overlap greatly in several parameters of seed utilization, suggesting that they are potentially close competitors. Rodents removed much more seed than ants, perhaps because they are more efficient at locating and harvesting large clumps. This technique has considerable promise for assessing the significance of competitive interactions between distantly related taxa in natural ecosystems.

Key words: *Ant; competition; granivory; predators, seed; rodent; seed selection.*

INTRODUCTION

Competition between species for food and other limited resources plays a major role in determining patterns of distribution and composition of natural communities. Most work on competition has been concerned with interactions between closely related, often congeneric species (review articles by Miller 1967, Grant 1972). When closely related species coexist, they may differ conspicuously in a few characteristics that enable them to subdivide limiting resources and avoid competitive exclusion (e.g., Cody 1968, Brown and Lieberman 1973, Diamond 1973). However, very distantly related taxa frequently use the same kinds of resources. Competitive interactions among organisms belonging to different orders, classes, and even phyla are potentially of great significance in community ecology. Such competition is difficult to study because the organisms differ in so many respects that it is hard to know which are relevant to their ecological interactions.

Recently we have begun studying competition and community structure in desert granivores. Seeds are important food resources for at least three kinds of animals abundant in most xeric habitats—rodents, birds, and ants. We have developed a simple technique which yields a great deal of reproducible, quantitative data on foraging activities of various kinds of granivores. M. Mares and M. L. Rosenzweig (*pers. comm.*) independently had planned to

use similar experiments to study patterns of seed predation in the deserts of Argentina and Arizona. They modified their technique as much as possible to conform to ours.

METHODS

This work was done as projects in field ecology classes in southeastern Arizona in May of 1972 and 1973. In the 1st yr, experimental clumps of domestic seeds were exposed to seed predators in one montane and three desert habitats. Experiments were designed to identify seed predators and to provide data on sizes and species of seeds harvested and temporal and spatial distributions of foraging activities.

Habitats

Experimental procedures were repeated at four different localities as follows:

- 1) Mesquite scrub habitat, 2 km SE of Portal, Cochise County, Ariz., elevation, 1,350 m; 8-10 May 1972.
- 2) Mixed desert shrub habitat, 5 km SE of Portal, Cochise County, Ariz., elevation 1,250 m; 10-12 May 1972.
- 3) Mixed desert shrub habitat, 9 km S of Artesia, Graham County, Ariz., elevation 1,200 m; 13-15 May 1972.
- 4) Border between mixed coniferous forest and montane meadow habitats, 7 km S of Hanagan Meadow, Greenlee County, Ariz., elevation 2,750 m; 16-18 May 1972.

¹ Manuscript received 10 May 1974; accepted 7 January 1975.

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TABLE 1. Outline of multifactorial design for experimental analysis of seed predation

Seeds in container	Position relative to vegetation	Type of presentation	Time of presentation	First replication	Second replication
Experiments in 1972					
1) 10 g mixture of 4 sizes and 8 species	1) Center of shrub	1) Covered with hardware cloth screen	1) Day	10 replicates of each treatment	Repeated on second day
	2) Edge of shrub	2) Uncovered	2) Night		
	3) 1 m from shrub in open				
	4) > 2 m from shrub in open				
1 seed combination \times 4 positions \times 2 types \times 2 times \times 10 replicates \times 2 days = 320 experimental units/habitat (repeated in 4 habitats)					
Experiments in 1973					
1) 1 seed barley	1) Under shrub	1) Covered with hardware cloth screen	1) Day	6 replicates of each treatment	Repeated on second day
2) 5 seeds millet	2) > 1 m from shrub in open	2) Uncovered	2) Night		
3) 10 g barley					
4) 10 g millet					
4 seed combinations \times 2 positions \times 2 types \times 2 times \times 6 replicates \times 2 days = 384 experimental units					

Seeds and ashtrays

Four nonoverlapping size classes of seeds, each composed of two equally abundant species, were exposed to predators in shallow dishes (glass ashtrays). The following sizes and species of seeds were used: (1) 3.33–3.96 mm, mung peas and pearl barley; (2) 2.36–2.79 mm, wheat and brown rice; (3) 1.65–1.98 mm, millet and rape; and (4) 1.17–1.40 mm, alfalfa and red clover. All of these seeds are relatively spherical, and measurements of seed size are linear dimensions. We sorted seeds into size classes by passing them through a set of Tyler screen sieves. We weighed out 2.5 g of each size class and combined them to produce 10-g samples. A 10-g seed sample was placed in a round glass ashtray that had been embedded in the substrate. Ashtrays were colored green, weighed approximately 200 g, and measured 10 cm in diameter; their concavity was 2 cm deep. Two strips of masking tape were placed at right angles to each other across the bottom of each ashtray to provide footing for ants. Half of the ashtrays were covered with one-fourth in (6-mm) mesh hardware cloth to prevent rodents and birds (but not ants) from removing seeds.

Experimental design

The basic experimental unit consisted of an ashtray containing 10 g (composed of 4 sizes and 8 species) of seeds set out on the substrate for approximately 12 h. These units were presented in a highly replicated, multifactorial design (Table 1) to identify predators and indicate time and location of their foraging. Half the ashtrays were screened to prevent predation by rodents and birds, but to allow harvesting by ants. Two ashtrays, 1 screened and 1 unscreened, were placed at each of 4 positions relative to a perennial shrub: (1) in the center of the shrub; (2) at the edge of the shrub; (3) 1 m from the shrub on bare ground; and (4) > 2 m from the shrub on bare ground. Screened and unscreened ashtrays at each position were placed as far apart as the features of the habitat would permit. This procedure was replicated 10 times at shrubs 15–25 m apart. Thus 80 ashtray units were exposed to seed predators at any one time. The first 80 units were placed out at dawn and collected at dusk; at that time 80 more units were placed in the same positions and collected at dawn. The entire program was repeated during the next 24 h. The same pro-

TABLE 2. Quantitative measures of seed predation in desert and montane habitats. During the day almost as many seeds were removed from screened as from unscreened containers in the desert habitats; this indicates ant predation. Rodents removed many seeds from unscreened containers at night in the desert habitats and during the day in the montane habitats. Ants discovered a smaller proportion of the trays available and removed a smaller fraction of seeds from these trays than did rodents

Locality	Number of trays discovered ^a				Grams of seed removed ^a			
	Day		Night		Day		Night	
	Screened	Unscreened	Screened	Unscreened	Screened	Unscreened	Screened	Unscreened
Mesquite scrub (Cochise County)	19	16	15	16	8.2	17.0	6.9	45.3
Mixed desert shrub (Cochise County)	37	43	24	77	54.3	70.5	20.1	688.1
Mixed desert shrub (Graham County)	38	48	27	66	158.4	187.5	44.2	592.9
Forest-meadow boundary (Greenlee County)	1	71	0	9	0.3	653.7	0.0	42.6

^a Eighty tray units containing a total of 800 g of seed were available for each treatment (day or night, screened or unscreened) at each locality.

cedure was followed in all four habitats so that a total of 1,280 ashtray units were exposed to predators.

After each diurnal or nocturnal exposure period, seeds remaining in each ashtray were collected in an individually labeled plastic bag. These samples were returned to the laboratory, sieved to recover the original classes of seed sizes, and then weighed to determine how much had been removed by predators.

Experiments with different-sized clumps of seeds

In 1973 a set of experiments was performed to test the abilities of rodents and ants to locate and harvest clumps of seeds of different sizes. These experiments were carried out between 7 and 9 May 1973 in mixed desert shrub habitat 6.5 km east of Portal, Cochise County, Ariz. Two kinds of seeds, pearl barley and millet, were distributed in ashtrays in clumps of two sizes: 10 g and approximately 0.035 g (1 seed of barley or 5 of millet). These were placed in screened or unscreened ashtrays at two positions relative to vegetative cover and were collected and replaced at dawn and dusk (Table 1). With the exceptions noted above and in Table 1, these experiments were performed similarly to those of 1972.

RESULTS

In 1972 the experimental seeds were found and removed by both rodents and ants; we verified this by observing many ants and tracks of rodents at the ashtrays. There was no evidence that birds took any seeds; certainly they did not remove a significant number. We were able to distinguish between predation by rodents and ants, and we obtained considerable information on temporal and spatial patterns of foraging. The technique provided less satis-

factory data on selection of sizes and species of seeds.

General patterns of seed removal at the four localities are shown in Table 2. There was little seed predation in the mesquite scrub habitat. In the two mixed desert shrub habitats large numbers of seeds were taken during both day and night. In the daytime all or nearly all seeds removed were harvested by ants, and only slightly more seeds were taken from unscreened ashtrays than from screened ones. During the night there was some ant predation (indicated by seeds taken from screened ashtrays and by direct observation), but it was significantly less than during the day. Nocturnal predation by rodents was very intense, as demonstrated by the large number of seeds taken from the unscreened ashtrays. In the montane forest-meadow ecotone there was no significant seed removal by ants, and rodent predation was much more severe during the day when ground squirrels and chipmunks were active than at night when deer mice apparently were the major seed predators.

In habitats where they were abundant, nocturnal rodents were particularly effective at locating and removing the bait. In the two desert shrub habitats rodents removed approximately 70%–80% of the 800 g of seed available at night in unscreened containers. Similarly, diurnal montane rodents collected more than 80% of the available bait. Ants were much less efficient than rodents. Heaviest ant predation occurred in the two desert shrub communities where about 350 (20%) of the 1,600 g of seeds available in both screened and unscreened containers were taken during the daylight period. In these desert habitats ants found a smaller proportion of the trays available to them and removed a smaller fraction of the seeds than did rodents (Table 2).

Rodents tended to empty completely those con-

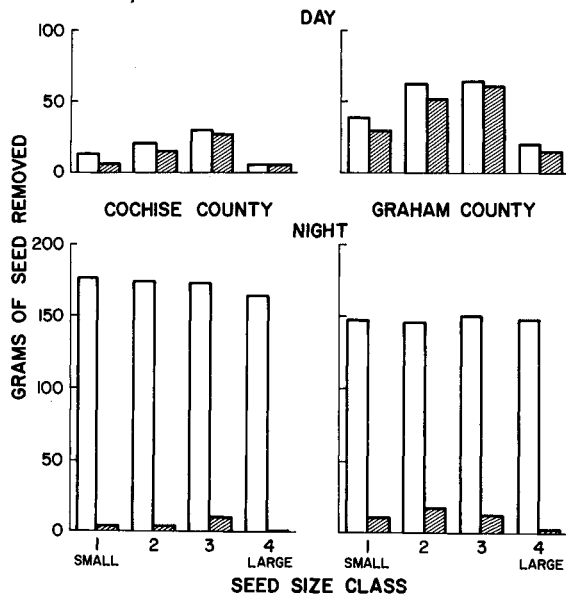


FIG. 1. Quantity of seeds of different sizes removed from screened (shaded bars) and unscreened (unshaded bars) containers in two desert shrub habitats. Sizes and species of seeds in each category are described in the text. Ants showed definite preference for certain sizes of seeds as indicated by those removed from both screened and unscreened containers during the day and from screened ones during the night. Rodents that removed seeds from unscreened containers at night were much less selective.

tainers which they discovered, and to find all four unscreened ashtrays near a given shrub. This all-or-nothing behavior provided little information on seed selection or the spatial distribution of foraging activities. For example, in the mixed desert shrub habitat in Graham County, of the 80 unscreened ashtrays distributed around 20 shrubs which were exposed at night, 62 (78%) were completely emptied and all 4 ashtrays were emptied at 13 shrub sites. There was a slight tendency for rodents to forage more in the open and to leave some of the smallest seeds unharvested (Fig. 1 and 2). In contrast to rodents, ants selected for both sizes and species of seed. They preferred seeds of the two intermediate size classes (Fig. 1), and in the two larger classes they clearly selected barley and rice in preference to mung peas and wheat. Frequently all of the two preferred species were removed, but more than a gram of the others was left. Although ants removed slightly fewer seeds from screened than from unscreened ashtrays, the screen mesh had no effect on the general pattern of seed size and species selection. Ants showed definite spatial patterns of foraging, but these differed even between the two mixed desert shrub localities (Fig. 2). In Cochise County they tended to forage under and adjacent to shrubs,

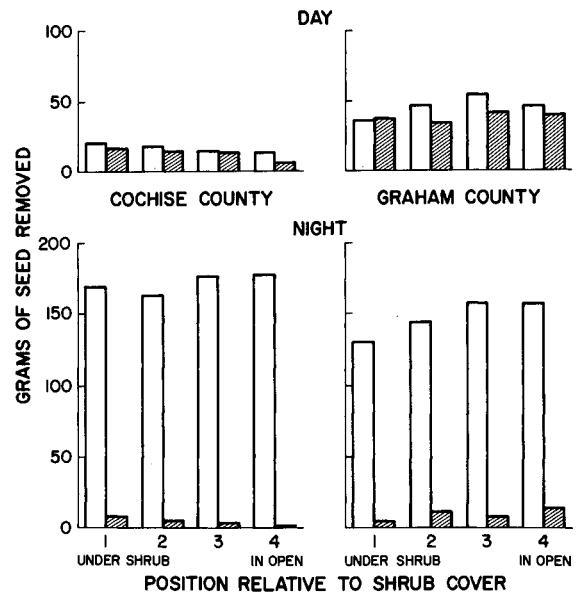


FIG. 2. Quantity of seeds removed from screened (shaded bars) and unscreened (unshaded bars) containers placed in different positions relative to shrub cover (details in text) in two desert shrub habitats. Both rodents and ants showed some preference for foraging areas but these differed between sites; in general both taxa were efficient at harvesting seeds from all positions.

whereas in Graham County more of their foraging was in the open.

Experiments performed in 1973 to measure ability of ants and rodents in locating different-sized clumps of seeds showed mixed success. Rodents were much more efficient at locating and exploiting large clumps than small clumps. They discovered and harvested seeds from 35 of the 48 uncovered containers with large (10-g) clumps that were available at night, but only 5 of the 48 containers with single (barley) or 5 (millet) seeds. These differences are highly significant ($\chi^2 = 37.5$; $p \leq 0.005$). Ants took very few seeds from any of the containers and there were no significant differences between their discovery of large and small clumps. The experiments were performed during a period following heavy winter rains when natural seeds were extremely abundant. The presence of alternative natural seeds probably accounts for the low level of predation on the artificial seeds.

Although our technique enables us to distinguish unequivocally between rodent and ant predation, it does not permit identification of the species that removed seeds from particular containers. The following nocturnal granivorous rodents were common at the desert localities: *Dipodomys spectabilis*, *D. merriami*, *Perognathus penicillatus*, *Perognathus baileyi*, *Perognathus flavus*, *Peromyscus eremicus*,

Peromyscus maniculatus, and *Reithrodontomys megalotis*. In the montane meadow-forest ecotone *Spermophilus lateralis* and *Eutamias cinereicollis* were active during the day and *P. maniculatus* was the only common nocturnal rodent. The common granivorous ants in the desert habitats were *Pogonomyrmex rugosus*, *P. desertorum*, *Novomessor cockerelli*, *Solenopsis xyloni*, and several species of *Pheidole*.

DISCUSSION

Our results indicate that within the limits tested by our experiments rodents and ants have extremely similar patterns of seed harvesting. The two taxa overlap broadly in spatial distribution of foraging activity and in sizes and species of seeds taken. The primary difference between the taxa is in their diel activity patterns, but this seems unlikely to be of major significance in resource partitioning because in deserts seeds are renewed at intervals of months or years. Although these experiments indicate that granivorous rodents and ants are likely to be close competitors, if seeds are a limited resource, our results are hardly sufficient to characterize the nature of competition between the two taxa or its role in the ecosystem. In fact, our data suggest that if coexistence of rodents and ants depends on their subdividing seeds, then subdivision is accomplished on the basis of parameters that we have not yet tested.

Several patterns of seed predation are indicated which appear to be of biological significance. Rodents are much more efficient than ants at harvesting large clumps of seeds. Apparently rodents locate these aggregates by olfaction. Once they find a clump they fill their cheek pouches with whatever sizes and species are available. The data suggest that they make repeated trips until they not only harvest an entire clump, but locate and exploit all clumps in the immediate area. Seeds are stored in burrows or shallow subsoil caches. Our experimental technique does not demonstrate the well-defined patterns of seed-size selection and spatial foraging activity that can be shown by trapping rodents and examining the natural seeds in their pouches (Brown and Lieberman 1973). Apparently, the large aggregates attract rodents from their usual foraging areas (Rosenzweig 1973), and the mixture of seed sizes makes it more efficient to fill the cheek pouches indiscriminately rather than select specific sizes of seeds.

Ants must harvest seeds one at a time. As a result, they demonstrate clear preferences for certain sizes and species. Ants definitely selected medium-sized seeds and tended to leave those in the largest and smallest size categories. Size selection seems to be based on energetic efficiency. Optimal

harvesting should maximize the nutritive value of food brought to the nest per unit time. Seeds of intermediate size should be harvested most efficiently. Small seeds are readily transported but low in energy; large ones contain much energy but are difficult and time consuming to transport. The basis for selectivity of species within a size category is not clear, but there is some indication it may be mechanical. In the largest size class barley is preferred over mung peas, and in the next largest size rice is preferred to wheat. Both of the preferred species have rough, textured surfaces in contrast to the smooth, hard surfaces of the other species. The ants may simply find the textured seeds easier to grasp and transport. R. Pulliam (*pers. comm.*) independently has concluded that ants have a relatively difficult time harvesting hard, smooth seeds.

The exclusively nocturnal predation by desert rodents and the tendency of ants to do most of their foraging during daylight hours reflect basic differences in physiology and behavior. These are most likely to affect competition between the taxa and ecosystem dynamics on a seasonal time scale rather than a daily one, because available seeds probably are renewed slowly. Problems of heat and water balance and predator avoidance cause most desert rodents to be nocturnal, but endothermy enables them to be active throughout the year, provided sufficient food (and in some cases, water) is available. In contrast, ants are ectothermic and cannot be active at extreme environmental temperatures (Bernstein 1971). During warm months high insolation and substrate temperatures may inhibit diurnal foraging in open areas away from the shade of shrubs. During cold months all activity may be drastically curtailed and the impact of ants as seed predators should be greatly reduced. These activity patterns may have important effects on the structure and function of the ecosystem; in part, these could be tested by repeating our experiments at different seasons. M. Mares and M. L. Rosenzweig (*pers. comm.*) are examining this question using similar techniques.

The great variation in patterns of seed predation among habitats seems to reflect underlying differences in the organization of granivore communities and ultimately in the climate and seed production of the habitats. In mesquite scrub habitat there was little seed predation by either rodents or ants. This habitat is virtually a monoculture of the perennial woody shrub *Prosopis juliflora*. Compared to the mixed desert shrub habitat only a few kilometers away, the abundance and diversity of seeds is probably very low. The two mixed desert shrub habitats showed encouragingly similar patterns of seed predation, especially since these localities are ap-

proximately 150 km apart. Both rodents and ants removed large numbers of seeds, and both are obviously important, potentially competitive granivores in this kind of habitat. In the montane-forest meadow habitat there was no significant predation by ants, and most of the seeds removed by rodents were harvested during the day. The relatively cold climate with its short summers and limited fruiting season precludes successful exploitation by granivorous ants. Chipmunks and ground squirrels, which harvested most of the seeds, forage during the long days of summer and hibernate during the winter.

Some of our results probably reflect artifacts of the experimental design. Rodents apparently were much more efficient than ants at harvesting seeds. Our technique of putting seeds in several large clumps distributed around a single shrub almost certainly biased the results to favor rodents with their great mobility and ability to harvest many seeds at a time. This bias could be corrected simply by using individual seeds (or smaller clumps) and spacing them farther apart. It is not clear how much artifact is produced by placing the seeds in ashtrays. Certainly the hardware cloth screens made it slightly more difficult for ants to remove seeds, but this did not change the qualitative pattern of size selection (Fig. 1). It should not be hard to modify the general method somewhat to avoid these problems and to examine patterns of predation on native species of seeds, seeds buried in the substrate, seeds mixed with inedible material, etc.

The important point is that this sort of simple, multivariate experimental design can provide a great

amount of data on patterns of foraging and interactions between unrelated taxa. Such information is difficult to obtain with more conventional observational or experimental methods. The data from such experiments are readily analyzed by analysis of variance or chi-squared techniques. Statistical analyses are not presented in this paper because the general patterns are clear and the results are admittedly preliminary.

ACKNOWLEDGMENTS

These experiments were performed in part as class projects in two field ecology courses. We thank the students in those classes and A. MacArthur and A. K. Brown for assistance. The technique has been discussed extensively with M. L. Rosenzweig and M. Mares, who kindly read an earlier version of the manuscript.

LITERATURE CITED

- Bernstein, R. A. 1971. The ecology of ants in the Mojave Desert: Their interspecific relationships, resource utilization and diversity. Ph.D. Thesis. Univ. California, Los Angeles.
- Brown, J. H., and G. A. Lieberman. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. *Ecology* **54**:788-797.
- Cody, M. L. 1968. On the methods of resource division in grassland bird communities. *Am. Nat.* **102**: 107-147.
- Diamond, J. M. 1973. Distributional ecology of New Guinea birds. *Science* **179**:759-769.
- Grant, P. R. 1972. Interspecific competition among rodents. *Annu. Rev. Ecol. Syst.* **3**:79-106.
- Miller, R. S. 1967. Pattern and process in competition. *Adv. Ecol. Res.* **4**:1-74.
- Rosenzweig, M. L. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. *Ecology* **54**:111-117.