1976

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Recommended Citation

Reichman, O.J. 1976. Effects of Rodents on Germination of Desert Annuals. U.S. International Biological Program, Desert Biome, Utah State University, Logan, Utah. Reports of 1975 Progress, Volume 3: Process Studies, RM 76-20.

FINAL REPORT

EFFECTS OF RODENTS ON GERMINATION OF DESERT ANNUALS

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Museum of Northern Arizona

US/IBP DESERT BIOME
RESEARCH MEMORANDUM 77-13

in

FINAL PROGRESS REPORTS
Process Studies, pp. 57-72

1976 Proposal No. 2.3.2.2

Printed 1979

Citation format: Author(s). 1979. Title.
US/IBP Desert Biome Res. Memo. 77-13.
Utah State Univ., Logan. 16 pp.

Ecology Center, Utah State University, Logan, Utah 84322

ABSTRACT

This process study deals with a wide range of topics centered around granivorous desert rodents and ants, and their resources. The report details the impact of seed caching by rodents on the germination of the seeds, the microhabitat distribution of seeds in the soil and the microhabitats from which both ants and rodents garner seeds. The study took place at the Silverbell site and involved primarily large numbers of soil samples from various microhabitats, as well as several laboratory experiments in which natural seed distributions were mimicked and their use was determined for rodents. Field experiments in microhabitat seed distribution use were also carried out for ants and rodents.

Rodent caches which were screened from use by the rodents had approximately twice as many seedlings germinating from them as adjacent controls. It was found that seeds are distributed in a number of microhabitats in a wide array of densities. Different species of rodents were found to gather seeds from different density distributions; ants and rodents were found to divide the resource on the basis of seed density as well as of vertical distribution in the soil. These aspects appear to be very important to the coexistence of the desert granivores and to the granivore community structure.

INTRODUCTION

The seeds of plants in the Sonoran Desert appear to be very important as a driving biotic force. Not only do the seeds germinate and reproduce parent plants, but they also serve as food for a number of animals in the desert. Thus, this project was funded to investigate the distribution of seeds in the soil and the relationships between the seed distributions and seed consumption by granivorous ants and rodents.

The distribution of seeds in the soil is important to both the plants themselves and to the consumers. Very little is known about the distribution of native seeds in soils, as access to the seeds by researchers involves considerable time and effort. As Emlen (1973) has noted, much is known about what animals eat, but very little is known about where they get their food. In this study, the microgeographic areas of seed distribution were determined, and field and laboratory experiments were conducted to determine where rodents and ants collect seeds. The objectives of the study, as proposed in 1975, included only rodents in the investigations. Under original funding in 1974, ants were also to be included, but difficulties with using ants in the laboratory caused that portion of the proposed work to be terminated. Subsequently, field techniques were developed which allowed the inclusion of ants, along with rodents, in field experiments on foraging microhabitats. Thus, the ants have been added to the data in this final report.

A major development that allowed the field studies on foraging areas for ants and rodents was the construction of exclosures which excluded ants, rodents or both from experimental areas. Controls with both types of granivores present were also available on the Silverbell site. These exclosures were constructed under the grant to Dr. James H. Brown and have been extremely helpful for investigating foraging propensities of granivores in the field. In addition, they have allowed me to determine the impact of either granivore group to compare that impact to the presence or absence of either group.

Knowing more about the distribution and use of seed resources by granivores has allowed a closer look at the factors promoting coexistence between species members of rodents or ants and between groups of ants and rodents. These two widely diverse and divergent groups of granivores appear to be foraging on the same kinds of seeds and, in some cases, to be getting them from the same general habitats. The studies presented herein elucidate newly observed ways in which these granivores are dividing the resources.

OBJECTIVES

1. To observe marked surface seed caches made by rodents to determine the influence of caching on seed germination.
2. To sample soil microhabitats to determine the distribution of seeds in the soil and to determine the relative impact of ants and rodents on the seed reserves in the soil. (This second part of Objective 2 developed with the availability of ant and rodent exclosures. Soil samples for seed analysis were taken in areas with ants, with rodents, with both and with neither.)
3. To periodically resample microhabitats to determine the renewal rates of seed reserves in the soil.
4. To determine from which spatial distributions different species of rodents gather seeds and how this promotes coexistence. (This objective was added as an addendum to the 1975-76 proposal.)
5. To determine from which spatial distributions ants gather seeds. (This added objective was originally proposed in the 1974 proposal and at that time was found to be too difficult to complete under that proposal. Subsequently, in conjunction with Objective 4, field techniques were developed which allowed the inclusion of ants in the field experiments on microhabitat utilization by the two groups of granivores.)

METHODS

To determine the impact of seed caching by rodents on subsequent seed germination, 25 surface seed caches made by rodents were covered with small plastic cages, which were secured to the soil. These cages prevented the rodents from returning to the caches after having made them. Control cages were set up next to each of the 25 experimental cages in areas which were not disturbed by rodent digging activity. Plastic cages were used to prevent active elements, such as iron, from entering the soil and affecting the germination responses of the seeds. The cages were sufficiently open to allow in sunlight. The cages were sampled in September and December 1974 and March, June, September and December 1975. (Fifteen additional cages were established in September 1975, but no seedlings germinated from either experimental cages or controls, and these data are not included in this report.) During each sampling period the numbers of seedlings germinating from experimental and control cages were recorded (DSCODE A3URC01).

To understand the microhabitat distribution of seeds, small (37 mm x 20 mm deep), circular soil samples were taken from September 1974 through December 1976 in a number of microhabitats, including the following (A3URC02): 1) NW and SE sides of large ($<$ 2-m diameter) *Larrea* bushes and small ($<$.75-m diameter) *Ambrosia* bushes, and obstructions (no larger than 25 x 100 mm); these directions represent the prevailing wind directions; 2) washes; and 3) areas where ants, rodents and ants and rodents were absent, as well as control areas where both were present.

Ants were excluded by periodically poisoning colonies in the experimental areas and colonies which were within foraging distance of the experimental plots. Rodents were excluded by trapping and removing in rodent-proof hardware cloth pens.

To determine the density of seed in surface caches, the contents of 50 surface seed caches were spooned out and the soil was analyzed for seed content (A3URC04).

To determine the propensity for seeds to clump in small depressions, 30-cc plastic medicine cups were buried level with the soil in an area contiguous to an area which was sampled with the 37 x 20 mm sample method. This allowed comparisons between random surface samples and small depressions in the soil. In addition, 32 medicine cups were placed in four directions (NW, NE, SE, SW) around eight *Larrea* bushes which were at least 2 m in diameter. This provided information on seed accumulations in relation to prevailing winds and, when compared to data from the medicine cups in the open areas, information on relative clumping under bushes and out in the open (A3URC03). Indices of aggregation were calculated for the seed data using the following formula (MacArthur and Connell 1966): $V/M - 1$, where V = variance and M = mean number of seeds per sample.

Seeds were extracted from the soil using the following techniques:

1. The soil samples are stored in small coin envelopes. The samples are weighed to the nearest tenth gram and the weights are recorded.
2. Each sample is run through a #12 sieve to catch sticks and large pieces of gravel. This size sieve is large enough to allow seeds to pass through. The sample is shaken through a piece of organza cloth to remove silt and clay particles which clog the filter paper, removing about 40% of the sample weight. The more efficient the job done with the organza, the faster the filtering is. The organza cloth is used for only five samples and is then discarded, because it stretches easily and the mesh dimensions become unreliable.
3. To float the seeds, a saturated solution of K_2CO_3 (density 1.56) is made by adding 113 g K_2CO_3 per 100 ml distilled water. This density is sufficient to float off most of the organic material in the sample. A layer of K_2CO_3 is left on the bottom of the container to maintain a density of 1.56 as the solution is reused. The sample is poured into a beaker which is filled to 175 ml with the K_2CO_3 solution. It is stirred thoroughly and the dirt is allowed to settle to the bottom. The filtrate is poured through a 7-cm Buchner funnel connected to an aspirator. This is repeated once to catch any particles that cling to the side of the beaker the first time and those that were trapped by the dirt particles. When the filtrate is gone, the funnel is moved to another suction flask and washed twice with water to remove any K_2CO_3 from the seeds so that identification can be easily made. The washing is done by pouring the water into the original beaker so that even more organic material can be washed out of the dirt. When the sample is dry enough so that the filter paper can be removed from the funnel, it is set aside to dry for about 30 min. The flask containing the K_2CO_3 solution is kept separate from the wash flask so that the solution can be reused without dilution. At the end of a floating session the K_2CO_3 solution is poured through a filter to remove the dust particles that did get through the filter, and the solution is made back up to a density of 1.56.
4. If there is much dust left in the sample, it should be run through the organza cloth again so that the seeds are not hidden. The sample is put under a microscope (power less than 10X), and the seeds are picked out and put back in the original envelopes.

The cost of preparing soil samples of the size used in this study, including labor and materials, is approximately $800 per 1000 samples.

A series of laboratory and field experiments was designed to determine from which microhabitats and seed distributions rodents and ants gather seeds. The first group of experiments was carried out in the laboratory using pocket mice and kangaroo rats (A3URC05-7).

The first experiment (A3URC05) was designed to take advantage of the fact that small heteromyid rodents readily enter torpor under conditions of low ambient temperature and limited quantities of food (Brown and Bartholomew 1969; Howard 1951; Tucker 1962, 1966). These studies indicate that desert rodents use torpor to reduce energy expenditure and to maintain homeostasis of body weight and physiological condition in response to these environmental conditions. Since the temperature in our study was constant (9 C), torpor thus can be used as an indicator of the availability and use of food, which was varied by providing different seed distributions rather than different quantities of food as in the previous studies (Fig. 1). Only the pocket mice could be used in this experiment as kangaroo rats do not normally go torpid under similar conditions. Individual *Perognathus amplus* were provided with various combinations of seed distributions and depths (scattered, four equal-size clumps and one clump of 10 g mixed bird seed, at depths of 0, 1, 2, 8 and 12 cm, yielding 15 combinations) in a 15-gal aquarium within an environmental chamber. Records were kept of the number of times during a 4-day run the animals were observed to be in torpor, as determined by the inability of the animals to right themselves when turned upside down. There were three observation periods per day: one hour after darkness, one hour prior to daylight and "midday." It was assumed that those seed distribution/depth combinations that result in the greatest use of torpor by the pocket mice were the distributions which were least available (yielded the lowest net return) to the mice. Two controls provided with ad lib seeds on the surface and with no seeds were also monitored.

At any one time half (10) of the experimental animals were participating in an experimental run, while the other half were kept at room temperature and provided with ad lib seed and lettuce. Individual animals were rotated through each distribution, and all distributions were tested simultaneously during any one 4-day run. The experiment was continued until 10 replicates of each distribution/depth combination were obtained. The animals were kept on a daylight:darkness ratio of 10:14 to simulate winter light, as it is this time of year when mice in the field are most often torpid. To further facilitate the use of torpor the experiments were carried out on recently captured rodents during the late fall and winter of 1974-75, the season of greatest torpor (A3URC05).

A second experiment (A3URC06) involved providing both kangaroo rats and pocket mice with 0.8-g packets of seeds at various depths (2.5 to 20 cm, at 2.5-cm intervals) in a uniform distribution (see Fig. 2; this figure relates specifically to experiment #3 below, but the spatial distribution of the seed packets in the arena is the same in this experiment). The rodents were not fed for 24 hr prior to their introduction into the experimental arena (1.2 x 0.8 m), which occurred at dusk each evening. The arenas were divided into a Cartesian coordinate system so that the locations of all digging attempts could be recorded each morning after the animals had been foraging all night, and these coordinates were compared to the location of the seed packets. Each seed packet was covered with hardware cloth to prevent the rodents from actually securing the seeds. After each run, the sand was mixed and planed smooth for the next night's run.

In a third experiment (A3URC06) the same arenas were used, but the maximum depth used was halved (to 10 cm). In additiion, the weight of the seed packet was varied, and included 0.4, 0.6, 1.0 and 1.2 g (Fig. 2). Again, the locations of the diggings were recorded and compared to the seed packet distribution. In both experiments two arenas were used, and the depth/size combination was placed randomly on a uniform grid. All experimental animals were run through both pens, yielding 18 replicates for the kangaroo rats and 14 for the pocket mice.

In a final experiment, the distributions most frequently used by the rodents (as determined from the previous experiments) were tested in conjunction with the presence or absence of surface cues (small rocks and/or depressions) to ascertain if the rodents use such cues for directing foraging efforts. It has been observed in the field that these microtopographic features provide areas where seeds are likely to

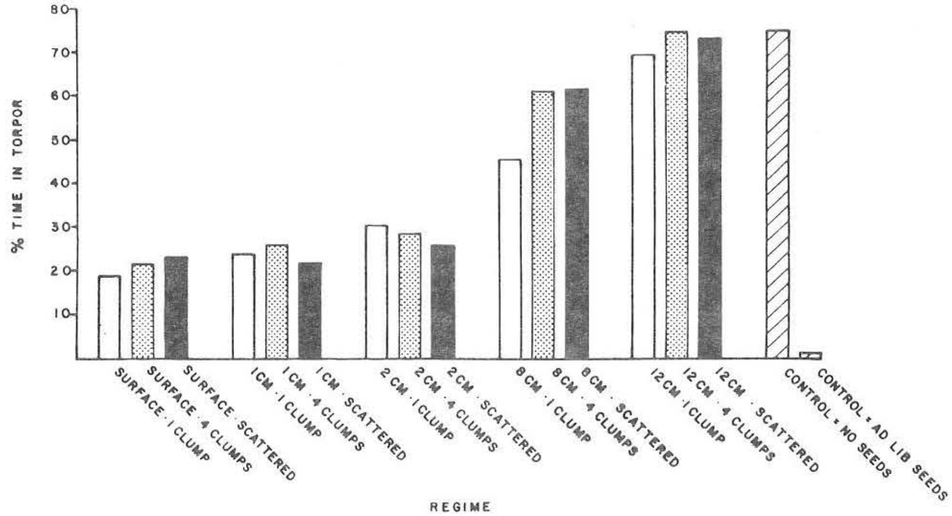

Figure 1. Histogram relating the percent time spent in torpor by *Perognathus amplus* and the depth/distribution regime presented to the rodents. There were 10 replicates of all regimes, except the two controls which were represented by 20 replicates. Note that the bars of similar stippling represent similar distributions, whereas the groups of three bars are similar depths.

accumulate, and this experiment was designed to determine if the rodents cue directly on these objects. The rodents, however, completely neglected the surface cues, and foraged only where there were packets of seeds.

A series of replicated circular plots (36 m in diameter) in which either ants or rodents were excluded were used to ascertain the microhabitats from which these granivores gathered seeds in the field (A3URC07). Ants were excluded by poisoning colonies within foraging distance of the experimental area, and rodents were excluded by the presence of a hardware cloth fence. When the experimental areas were established in 1973, the ants were poisoned and the rodents were trapped and removed from the pens; periodic efforts maintained the animals' absence. The experiments were run in mid-September 1976 on the US/IBP Desert Biome Silverbell site, 30 km northwest of Tucson, Arizona.

Initially, six distributions were presented to the animals; clumped and dispersed distributions below the surface, on the surface and above the surface (in bushes). Initial observations indicated that none of the animals foraged in the bushes, and this portion of the experiment was terminated, leaving four distribution types. One-gram packets of pearled barley seeds, ground to three different size categories (U.S. Standard sieves no. 10, 12 and 14; equal proportions by weight), were presented to the animals in the experimental areas. It was determined from recent field studies that a 1-g clump of seed is approximately the maximum clump size the animals would be likely to encounter, and that same quantity spread in the dispersed distributions used approximated an average dispersed seed density in the area (Reichman 1976; Reichman and Oberstein, in press).

In each of the four plots (two each without ants or rodents) 24 Styrofoam plates (20-cm diameter) were arrayed in a uniform pattern, each approximately equidistant from adjacent plates. The plates were buried level with the surface, and the seeds were placed either on or below the surface (1.5 cm) and either clumped or dispersed over the area of the plates (approximately 315 cm²). The seeds were distributed early in the morning and allowed to remain for 24 hr, at which time they were retrieved and stored in paper sacks for later analysis. In order to account for the fact that rodents are attracted to surface disturbances in their foraging areas, plates were set out the first day without distributing seeds, to preclude the rodents from associating seeds with the plates. During the second day only one-half of the plates had seeds in them, and all plates contained seeds the third and fourth days, yielding a total of 30 plates for each of the four seed distribution types (except in a few cases in the experimental area which supposedly excluded rodents; several *Perognathus amplus* were trapped in this exclosure after having foraged in 15 of the plates). Considerably fewer plates were foraged when there were no seeds present than when there were seeds present (Table 1). A previous attempt at this experiment was foiled by foraging birds, so the plates were covered with 1½-inch poultry wire cages, which allowed the ants and rodents to forage, but deterred the birds.

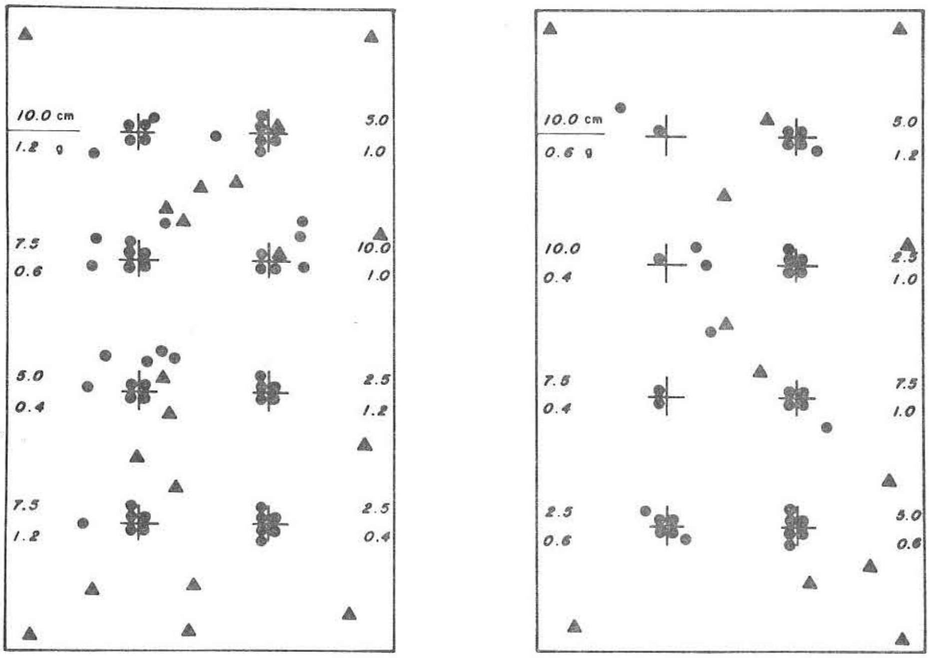

Figure 2. Arena arrangement of seed packets for experiment #3. Numbers adjacent to crosses indicate seed packet depth (top number) and size (g). Symbols represent digging efforts by kangaroo rats (circles) and pocket mice (triangles). Symbols contiguous to crosses indicate digging efforts directly over the seed packet.

Table 1. The number and percentage (in parentheses) of the plates foraged exploratorily by the rodents during each day of the experiment. On day 1, none of the plates contained seeds; on day 2, only one-half of the plates had seeds; on days 3 and 4 all plates had seeds in them

Day	Replicate A	Replicate B
1 (none with seeds)	5 (21)	8 (33)
2 (one-half with seeds)	12 (50)	12 (50)
3 (all with seeds)	24 (100)	24 (100)
4 (all with seeds)	24 (100)	24 (100)

Soil samples were returned to the laboratory for seed extraction, using a flotation method described earlier. The weight of the remaining seeds was subtracted from the initial 1 g distributed in the experiment, and the average quantity and percentage used were calculated. Seeds from a number of samples in which there had been no foraging were also extracted; it was determined that approximately 0.05 g of the samples was lost during the extraction process, and this figure was taken into account when calculating the amount of seed gathered by the granivores. Because each sample was small (1 g), the samples for each distribution for each taxa had to be combined for sieving to calculate the quantity of each size category used by the animals (A3URC07).

The ant species known to be foraging in the experimental area include *Pogonomyrmex rugosus*, *P. pima*, *Novomessor cockerelli*, *Veromessor pergandei*, *Solenopsis xyloni*, *Pheidole xerophila*, *Ph. sitarches* and *Ph. gilvescens*, producing a total of 59 colonies in one rodent exclosure and 41 colonies in the other. The rodents foraging in the area include several *Dipodomys merriami*, *Perognathus amplus*, *P. Penicillatus* and possibly one *P. baileyi*.

RESULTS

SEED DISTRIBUTION, GERMINATION AND DENSITY

Significantly more seeds germinate from areas showing no surface rodent caching activity (Table 2; A3URC01). The caches and controls were observed three times after their establishment in September 1974, and during each of these observation periods there were almost twice as many seedlings in the caches as in the control areas (Table 2; A3URC01).

Data for the microhabitat distribution of seeds (A3URC02), for the occurrence of seeds in medicine cups (artificial depressions, A3URC03) and for the occurrence of seeds in natural depressions (A3URC04) will be presented together, as they all relate directly to seed distribution.

Figure 3 presents data on the densities of seeds in various microhabitats. Some data (such as those for artificial depressions) are averaged over a number of sampling periods, while others (e.g., seeds from the wash) represent data from 50 samples in one sampling period. The data indicate that there is a wide array of seed densities, ranging from a low of 5,894/m^2 in depressions under bushes to over 80,000/m^2 near obstructions in the interspaces between bushes. The highest densities occur in several areas between bushes, and there is a considerable decrease in seed densities under bushes. A similar figure presenting clumping indices for most of the same microhabitats (Fig. 4) shows a similar pattern, with high values occurring in the open areas. It is interesting to note that although an area apparently worked by kangaroo rats (numbers in quotation marks) had seed densities only slightly higher than areas under bushes, the clumping value for the area was relatively high.

Figure 5 illustrates the data for seeds occurring under bushes and in the open in artificial depressions at 3-mo intervals for over 1 yr. Several points are evident. The depressions in the open areas maintain much larger densities than equivalent depressions under bushes. In addition, the two directions which receive the greatest wind (SE in summer and NW in winter) have the highest average seed densities. Seasonally this holds true as well. Values after the summer storms (September 1975) are highest for the SE, and values after the winter storms (March 1975) are highest for the NW (Fig. 5).

There is no correlation between the size of the *Larrea* and *Ambrosia* shrubs under which samples were taken and the densities of seeds from those locations (Table 3). It appears that all of the *Larrea* and *Ambrosia* shrubs were essentially the "same size" in terms of the wind shadows they produced and the subsequent seed densities. Nevertheless, the smaller *Ambrosia* shrubs have slightly higher densities than the *Larrea* shrubs, and the small "obstructions" have considerably higher densities than either of the shrub species (Fig. 3).

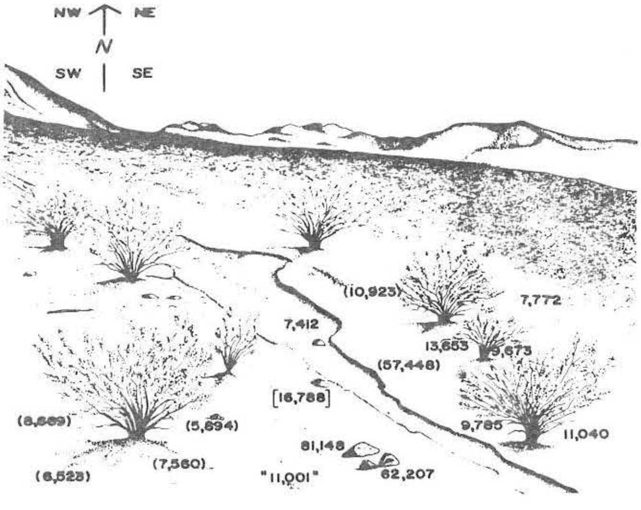

Figure 3. Densities of seeds (no./m^2) in a number of microhabitats in the Sonoran Desert. Numbers in parentheses are samples from artificial depressions (see Methods). Number in brackets represents data from natural depressions, and number in quotation marks is for soil samples taken in an area of concentrated rodent foraging. The small rocks in the foreground represent "obstructions" (<25 x 100 mm). The placement of the numbers is accurate in terms of compass direction; prevailing winds are from the SE in the summer and NW in the winter; large shrubs represent *Larrea* and small shrubs, *Ambrosia*.

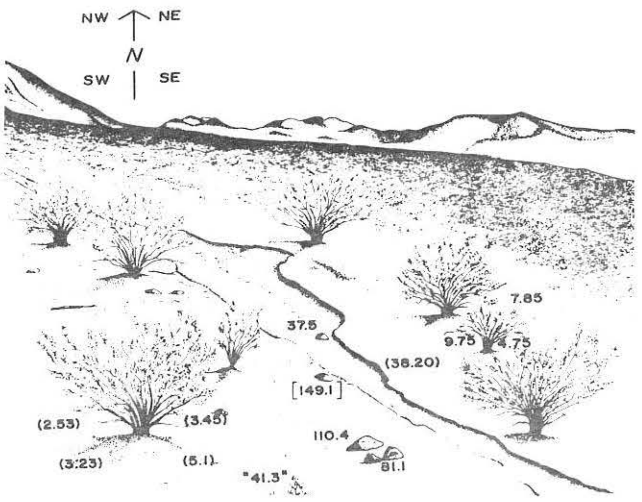

Figure 4. Clumping indices for seeds in a number of microhabitats, as explained in Figure 3.

Table 2. Total number and average number of seedlings germinating from surface areas disturbed by rodent digging and from adjacent control areas showing no digging activity by rodents. Seedlings were not extracted after counting each sampling period, so totals indicate accumulated totals. There were 25 caches and controls, and the differences in the means of the two each month are statistically significant at the 0.01 level (DSCODE A3URC01)

Month	Caches		Controls	
	Average	Total	Average	Total
October 1974	4.12	103	1.88	47
December 1974	7.84	196	4.16	104
March 1975	3.96	99	2.16	54

Table 3. Correlations between the volumes of *Larrea* and *Ambrosia* shrubs, and the seed densities under the shrubs. Seed densities were obtained from two compass directions, and volumes were calculated with two formulas. Numbers in parentheses = standard error

	Larrea	*Ambrosia*
$\bar{x}$ Seeds/Sample-NW	12.74 (2.84)	14.68 (2.51)
$\bar{x}$ Seeds/Sample-SE	9.40 (1.89)	7.74 (1.55)
$\bar{x}$ Seeds/Sample-Total	22.16 (3.32)	25.08 (3.08)
$\bar{x}$ Volume I (4/3 W^3)	5.88 (1.53)	1.28 (0.27)
$\bar{x}$ Volume II (1 x w x h)	9.82 (2.12)	0.24 (0.04)
r (Volume I/NW)	.16	.13
r (Volume I/SE)	.07	.22
r (Volume I/Total)	.17	.22
r (Volume II/NW)	.16	.02
r (Volume II/SE)	.04	.22
r (Volume II/Total)	.14	.13

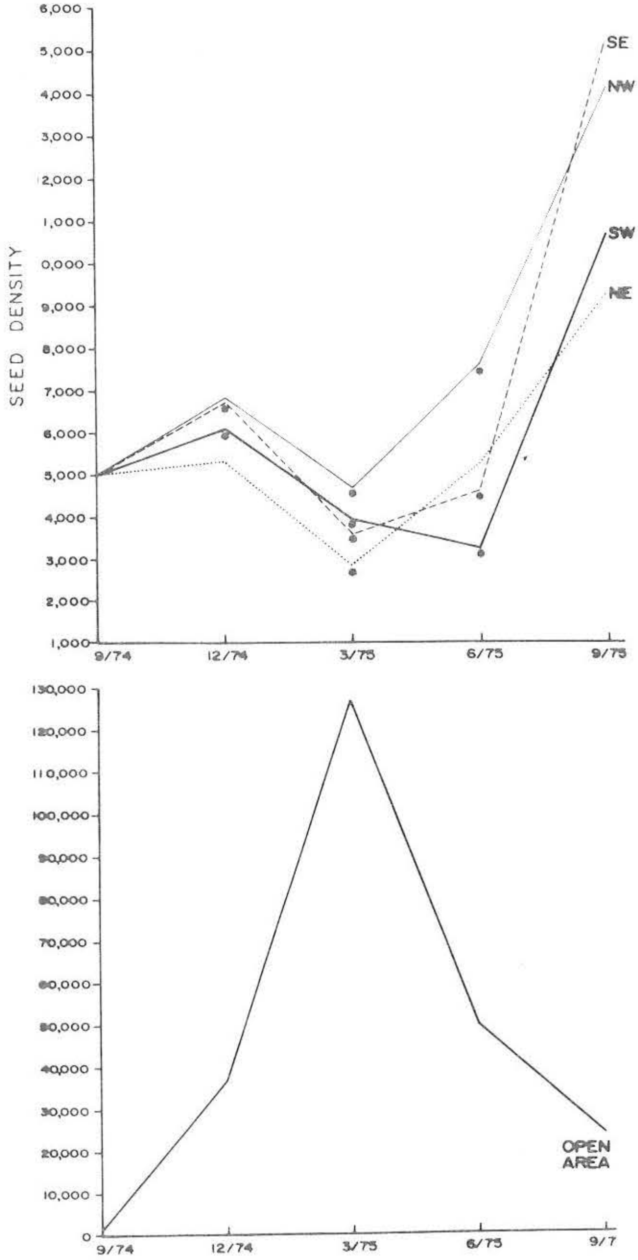

Figure 5. Densities of seeds in artificial depressions in the interspaces between bushes and in four directions around bushes. Note the tremendous differences between the values obtained under the bushes and those in the open areas. There are no significant differences for values under bushes, but all of these values are statistically different from values for the open areas after December 1974.

IMPACT OF GRANIVORES ON SEED DENSITY AND DISTRIBUTION

A major aspect of the experiments reported herein is the investigation of the impact of granivores on seed densities and distributions. Where neither ants nor rodents were present, seed densities originally were relatively low but rapidly climbed, reaching densities over twice as high as areas inhabited by either or both major groups of granivores; these relatively high densities were maintained throughout the period of investigation (Fig. 6). There appears to be some granivore density compensation, as the seed density figures for pens in which either or both of the granivore groups were present were statistically similar, and these were significantly different after June 1975 from the densities in the pens which contained neither group (Fig. 6). Figures comparing clump indices for the various exclosures (Table 4) indicate that rodents maintain the lowest clump values for seeds in their area, although there is considerable seasonal variation.

Data from the experiment dealing with torpor use by the pocket mice indicate that there is a strong, significant rank correlation (Spearmann Rank Correlation, $r_S = 0.93$, $p < .05$) between the degree of access difficulty (seed depth/seed packet size, where size of one clump = 10 g, four clumps = 2.5 g and scattered = 0.1 g) and the percent time spent in torpor, although the correlation is almost entirely due to the depth factor (Figs. 1 and 7, A3URC05).

In using torpor as a bioassay for seed availability (or net return on foraging effort), two points are evident and important. First, there is a significant positive correlation ($r = 0.99$, $p < .05$) between the depth of a seed pack and the percent time spent in torpor (Fig. 7). Thus, to the pocket mouse, depth is an important criterion for choosing seeds. Second, the pocket mouse does not differentially use scattered and clumped distributions of seeds. There is no significant difference between the amount of time spent in torpor by the pocket mice provided with scattered distributions of seeds, four small clumps of seeds and one large clump of seeds (Fig. 7). When comparisons between distributions within depth categories are made, the only occurrence of statistical differences in the use of torpor is between the scattered distribution and one clumped distribution at 8 cm, with no differences between distributions at any other depth (A3URC05).

The second laboratory experiment further illustrates the ineffective use of clumps by *Perognathus amplus* and the diminishing ability of the pocket mouse to detect seeds at increasing depths. It also points out the facility with which kangaroo rats detect and dig for clumps of seeds. In this experiment, seed clumps of the same size (0.8 g) were buried at depths from 2.5 to 20.0 cm. A greater proportion of *Dipodomys* dug for the seeds at the 2.5- and 5.0-cm depths than did pocket mice (Table 5). In addition, 11% of the *Dipodomys* dug at 7.5 cm, whereas none of the pocket mice did so (Table 5). None of the animals of either species pursued seeds at depths greater than 7.5 cm in this experiment (A3URC06).

In the third experiment, the maximum depth of the seeds

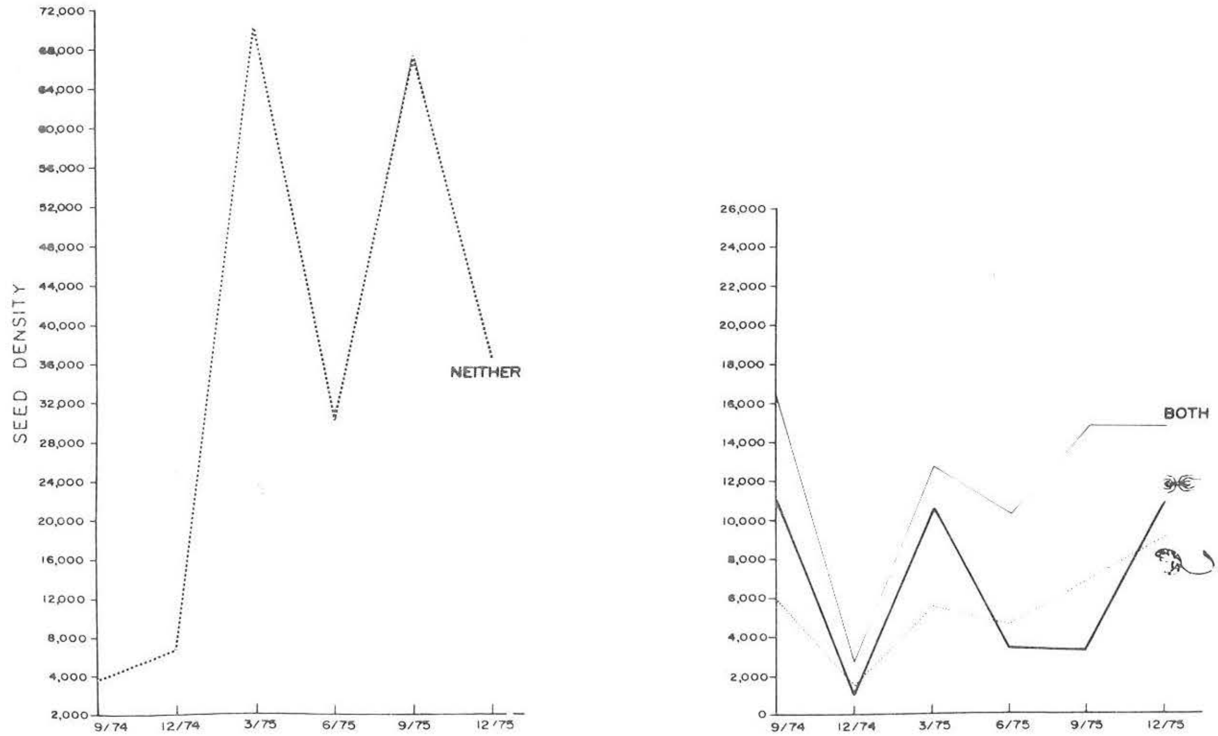

Figure 6. Seed densities in experimental areas containing ants, rodents, neither and both (control area). Note the high seed densities in the areas without either granivore taxa and the similarity of values for areas with either or both of the taxa. Asterisks indicate values that are statistically different from values in the area without either taxa.

Table 4. Clumping indices for areas with ants, with rodents, with both (control area) and with neither

	Sep 1974	Dec 1974	Mar 1975	Jun 1975	Sep 1975	Dec 1975	Mar 1976
ANTS	92.3	3.1	26.0	6.4	4.8	20.8	
RODENTS	7.8	6.8	5.5	6.5		22.3	7.2
BOTH	22.8	66.7	71.0	19.3	24.0		
NEITHER	10.2	19.3	32.1	9.9	57.0	17.2	

was halved (to 10 cm) and the seed packet sizes were varied (0.4, 0.6, 1.0 and 1.2 g), providing the rodents with various depth/size combinations. To determine the fidelity of either species to clumps, the average distance from a dig to the nearest clump of seeds was determined (Table 6). There is a significant difference between the kangaroo rats and the pocket mice in the average distance of their digs from a clump of seeds; indeed, the kangaroo rats accurately located and dug to the clumps. There was no statistical difference, however, between the diggings of the pocket mice and randomly generated points within the area (Table 6). Only 9% of the digging efforts made by the pocket mice were directly over a packet of seeds. By contrast, over 71% of the foraging efforts made by the kangaroo rats were over a seed packet. The "workings" of the two species differed sharply; whereas the diggings of the kangaroo rats were discrete and prominent, the efforts of the pocket mice were frequently difficult to determine. Direct observations of the animals revealed that *Dipodomys* proceeded directly to the location of a clump of seeds and began digging. *Perognathus* meandered about the arena, occasionally attempting to dig but more often simply nosing about, sifting the sand as if filter feeding.

As an adjunct to this experiment, a determination was made of the relationship between the depth:size ratios and the rodent's ability to detect and/or pursue clumps of seeds. Only data from the kangaroo rats could be used, as too few pocket mice dug for clumps of seeds. The data (Fig. 8) indicate that there is a significant negative relationship between the depth:size ratios and the probability of a kangaroo rat digging for the seeds. As the seed packets get smaller and deeper, the probability of a digging effort declines. Seed packet depth and size appear to contribute approximately equally to the probability of a digging effort by the kangaroo rat, as there is a perfect negative rank correlation between packet depth and number of digging efforts and a perfect positive rank correlation between packet size and digging effort (Fig. 2).

Data presented earlier in this report suggest that seeds accumulate in desert soils in specific locations within various sizes of "wind shadows" (Fig. 3, A3URC02-4). The data indicate that there is an array of seed densities ranging from 5,894/m^2 in the interspaces between bushes to 81,148/m^2 around small obstructions in open areas. Small depressions and obstructions, the lee sides of which produce effective wind shadows, are particularly effective at clumping seeds. Thus a fourth experiment was attempted to determine if the rodents use visual or tactile cues, such as depressions and small rocks, as indicators of potential seed clumps. None of the results suggested that the animals responded directly to these microtopographic features; the rodents merely wandered about, paying no attention to the surface cues and stopping only to dig over a seed packet. Previous field manipulations, and reports of dragging a boot heel in the soil to attract heteromyids to traps (Hall 1946), indicate that the rodents are very aware of their environment and that few disturbances go unnoticed. I speculate that the rodents learn the locations of surface irregularities in their foraging ranges which are likely to accumulate seeds and visit these periodically during their foraging excursions. Recent preliminary field observations with a night viewing device support this suggestion.

Data from the field experiments on ant and rodent foraging suggest some pertinent points concerning within-phyla comparisons of seed distribution use by the experimental animals, and these will be presented first. Subsequently, comparisons will be made between ants and rodents.

A major point concerning the ants is that they foraged only on the surface distributions of seeds (Fig. 9). The seeds buried at 1.5 cm were apparently unavailable to the ants at this depth, as has been noted by other authors (Bernstein 1974; Tevis 1958).

The ants took a significantly greater percentage ($t = 2.1$, $df = 50$, $p < .025$) of the seeds from the dispersed/surface distribution than from the clumped/surface distribution (Fig. 9). Figures 9 and 10 show that the ants find more of the dispersed than of the clumped distributions, but even considering only those specific plates that were foraged, the ants still took more from the dispersed rather than from the clumped distribution. The column foraging habit used by 75% of the species in the area (see Davidson, in press a) was well illustrated by one *Veromessor pergandei* colony which was less than 0.5 m from a clumped/surface distribution. The ants got all of the seeds the second day of the experiment, but got none of the seeds on the remaining days as the column foraged in a different direction.

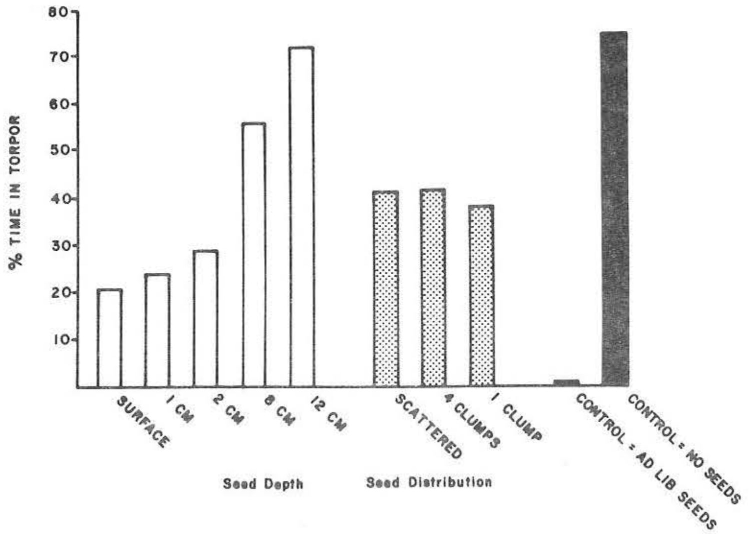

Figure 7. Histogram relating the percent time spent in torpor by *Perognathus amplus* with data combined by depth and distribution. There is a 0.99 correlation between the percent time spent in torpor and depth ($p < .05$). Statistically there is no difference in the time spent in torpor (used as an indicator of access difficulty or net return on foraging).

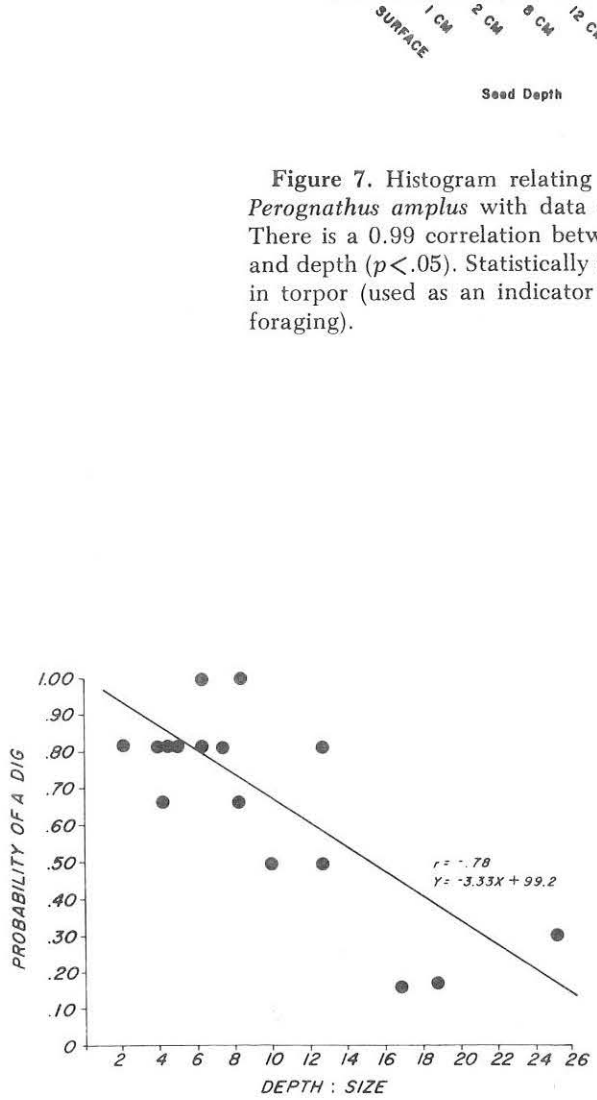

Figure 8. Relationship between the percentage of the kangaroo rats which dug for various depth/seed packet size combinations (= probability of a digging effort) and a ratio determined by dividing the depth of a packet by its size in grams (D:S). Line represents least square regression line of probability of a digging effort on D:S. There is a significant ($p < .01$) negative correlation between the probability of a digging effort and D:S.

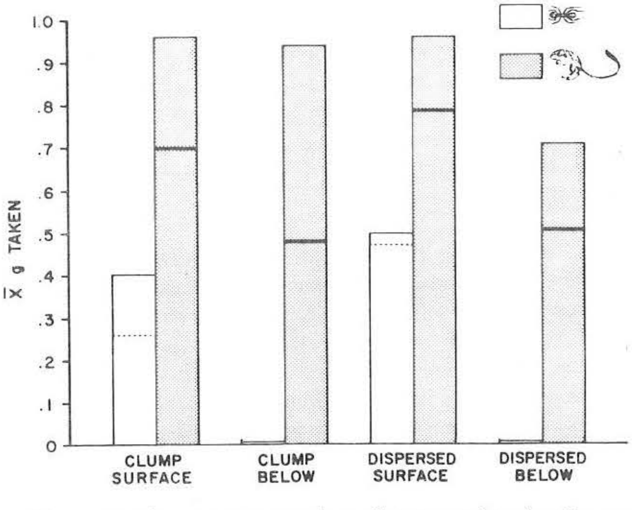

Figure 9. The average number of grams taken by the ants and the rodents in the four distribution types offered to the animals. The dotted line in the ant histogram bars represents the average grams taken when all samples are considered, while the solid line represents the averages only for those distributions in which at least some of the seed was removed. The solid line in the rodent histogram bars represents the average grams of seeds removed by several *Perognathus amplus* that foraged in the exclosures which were supposed to contain only ants; see text for further details.

Table 5. The percentage of the rodents which dug at the various depths of seeds provided in experiment #2. Numbers in parentheses indicate sample sizes

Depth (cm)	*Dipodomys merriami* (18)	*Perognathus amplus* (14)
2.5	72.2	28.6
5.0	44.4	21.4
7.5	11.1	0.0
10.0 - 20.00	0.0	0.0

In both of the distributions used by the ants (clumped and dispersed surface) they tended to select the smallest seed sizes (Fig. 11). In the clumped/surface distribution there was a statistically significant difference between all three size categories. In the dispersed/surface distribution the ants took equal portions of the small and medium seed sizes, but significantly fewer large-size seeds (Fig. 11).

The rodents were very effective at locating the seeds (100% of the plates were foraged; Fig. 10); they garnered almost 100% of the seeds in each distribution except dispersed/below, where they recovered approximately 75% of the seeds (Fig. 9). In addition to the data from the rodent exclosures, important information is available about one species of rodent from the pen where only ants were supposed to be present. Several *Perognathus amplus* made their way into the ant pens and made obvious foraging efforts in 15 of the seed distributions. This species recovered significantly fewer seeds from the below-ground distributions than from the above-ground distributions, but showed differences in its use of clumped vs. dispersed distributions (Fig. 9). This last point bolsters, in the field, previous laboratory experiments comparing the use of different densities of resources by kangaroo rats and pocket mice (Reichman and Oberstein, in press).

There were no size use differences in the data from the rodent pens (Fig. 10). When the data from the *Perognathus amplus* in the ant pens were analyzed, however, they showed that the small rodent tended to use the smallest seeds the least, but the differences were not statistically significant.

Comparisons of the foraging efforts between the ants and the rodents show that the rodents find considerably more of the experimental distributions than the ants and that they secure twice as many seeds as the ants once the seeds are detected (Fig. 9; Brown et al. 1975). One striking qualitative difference is that the rodents detected and garnered seeds from below-ground distributions, while the ants apparently lacked the ability to detect these seeds or interest in the seeds if they are detected.

Table 6. Average distances (cm) from the digs of the rodents to the nearest clump of seeds. Numbers in parentheses indicate sample sizes; SD = standard deviation

Dipodomys merriami (92)		*Perognathus amplus* (22)		Random (40)
2.97; SD = 5.53		11.09; SD = 6.16		13.55: SD = 6.57
	$t = 6.06$ $df = 110$ $p < .001$		$t = -1.25$ $df = 40$ $p > .05$	

There are also general gross differences in the sizes of seeds taken by the granivores. The ants tend to gather small seeds, whereas the rodents take all sizes of seeds. It should be noted that since there is a fourfold weight difference between the smallest and largest rodent species, they might be expected to take the entire array of seed sizes, while the size variation in the ants is considerably less.

DISCUSSION

SEED GERMINATION

The data indicate that there are approximately twice as many seedlings germinating out of areas of surface digging activity by rodents as in adjacent control areas (Table 2). These depressions made by the rodents contain more seeds (approximately twice as many: 7,772 to 17,788; Fig. 3) than nearby unworked areas, thus providing a larger base number of seeds for germination. It is also possible that the small depressions provide a more favorable microclimate for germination than the nearby control areas. Other authors (Reynolds 1958; Tappe 1941) have also noted increased germination from old rodent caches.

SEED DISTRIBUTION AND DENSITY

The data presented in this report concerning the microhabitat distribution of seeds is important both to the seeds and their subsequent generations and to the animals that forage on the seeds. Perhaps the most salient point in relation to the seed distributions is that the seeds are distributed by wind and water in the desert, and these forces in combination with the physical structure of the desert determine the distribution types produced. In the case of the this study, a series of microhabitats (washes, depressions, bushes, obstructions, etc.) provided statistically different densities and degrees of clumping by the seeds.

Just as pebbles in a stream, the seeds are sorted by environmental forces and are laid down in wind shadows which serve to trap the seeds by decreasing wind velocities. Thus, an array of sizes of *Larrea* and *Ambrosia* bushes are all too large to sort out seeds in terms of wind shadow. There is considerable difference, however, between *Larrea* and *Ambrosia* bushes and the small wind shadows produced by depressions (both artificial and natural) and obstructions (Fig. 3). Not only are seed densities in these areas high, but values of clumping indices are particularly high in these microhabitats. Thus, it appears that small, effective wind shadows accumulate the highest densities of seeds. It seems reasonable to suggest that as we learn more about the physical forces and structure of deserts, with additional information on their productivity, we should be able to predict with some certainty the densities and distributions of seeds occurring there. As will be seen in a later section of the discussion, it appears that the granivores can do just that.

Further studies will be necessary to relate the known seed distributions in the desert to the pattern of seedling germination and subsequent adult success. Previous studies (Franz et al. 1973) have shown that seedlings and adults tend to occur as a carpet over the desert floor, but the first experiment in this report (A3URC01) suggests that seeds can at least germinate from clumps. Subsequent seedling competition or predation may reduce the cluster of seedlings to a more dispersed adult population. In the first experiment rodents were precluded from foraging on the seeds in the small depressions but, as will be discussed later, rodents are very effective at harvesting clumps of seeds, even those that are buried, and they may harvest a great proportion of seeds in a clump before they can germinate.

Preliminary evidence from this study suggests that seeds of similar morphotypes tend to occur together in the soil and, if this is the case, it could have an important impact on the structure of the mature plant community. Certainly, this needs further study.

Relationships of Seed Density and Distribution to Granivores

There are two aspects to consider in relating seed densities and distributions to the consumers: impact of granivores on the seeds and impact of the seed distributions on the foraging animals. When both ants and rodents are absent from the experimental area, the seeds increase tremendously in number and are maintained at relatively high levels. Although this is not especially startling, an adjunct fact—that in the presence of either ants or rodents, or both, the seed densities stay relatively low and similar—is somewhat surprising. This alone would indicate that there is competition when both groups of granivores are present, and that in the absence of either, there is density and biomass compensation by the remaining taxa. Recent work by Brown and Davidson (1977) has shown this to be the case.

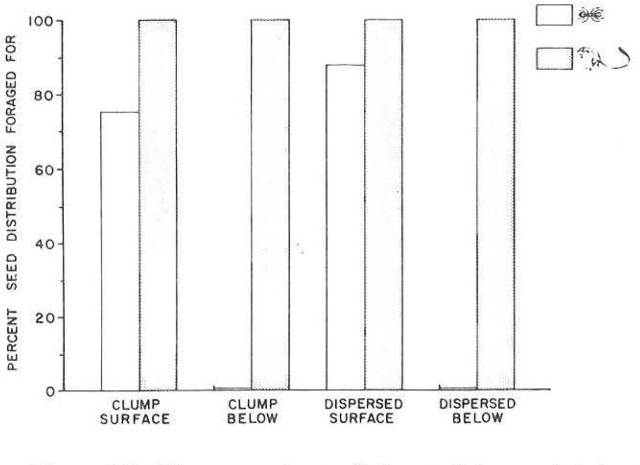

Figure 10. The percentage of those plates containing seeds that were foraged by the ants and the rodents. Note that none of the below-ground distributions was used by the ants.

The primary point dealing with the seed distributions and the consumers is that there is a broad array of seed densities available. As will be pointed out in following discussion sections, this appears to be of great importance to the animals in their resource allocation and coexistence. First, however, it is necessary to show that the animals involved do actually differentially use the array of distribution types.

A number of clues from past work on heteromyids indicate that the animals forage on different distributions of seeds. Evidence from this study suggests that small pocket mice effectively forage on a dispersed resource, even to the extent that they use clumps of seeds no more effectively than scattered distributions of seeds. Kangaroo rats, on the other hand, use large clumps of seeds much more effectively than dispersed distributions. The absence of differential use of scattered and clumped seeds by *Perognathus amplus* is puzzling. It is perhaps related to detection ability. Observations in this study and in the field indicate that small pocket mice move slowly while foraging and may not encounter the sharp odor gradient produced by a clump of seeds at a speed sufficient to detect the clump as a large seed source. Conversely, kangaroo rats move rapidly while foraging and could quickly move through the odor gradient and pinpoint a seed clump.

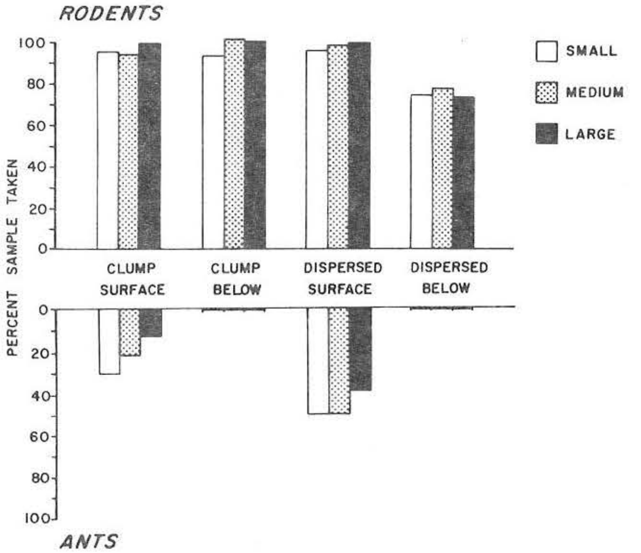

Figure 11. The proportion of each seed size category gathered by the ants and the rodents from each of the four distribution types offered the animals.

Coexistence of Heteromyid Rodent Species

Recent efforts to explain coexistence of heteromyid rodent species in southwestern deserts have implicated either habitat selection or seed size selection (see cited works of Brown, Rosenzweig and their colleagues). It is unlikely that either of these means is sufficient to account for coexistence in some cases. As many as seven species of granivorous species coexist in some productive desert habitats (Hoffmeister and Goodpaster 1954). It is difficult to imagine the number of discrete microhabitat types required for coexistence by means of microhabitat selection where this many species co-occur. The species involved must frequently travel through adjacent and complementary microhabitats during their foraging activities. Presumably the animals would use resources wherever they were sufficiently abundant and available, although Rosenzweig (1974) suggests that habitat specialists could not forage in alternative habitats. Brown (1975) obtained seed size-body size correlations in the Mohave and Sonoran deserts, but large overlaps in seed size used by the various sizes of rodents make it unlikely that this is a primary means of coexistence. Rosenzweig, Brown and their colleagues have shown the absence of seed size selection in several of their studies, although these usually involved two-species systems where habitat selection alone may be sufficient to permit coexistence. Data from Reichman (1975a, b) suggest that *Dipodomys merriami* (46 g) uses smaller seeds on the average than *Perognathus amplus* (13 g), although this again is a two-species system.

Authors of these previous studies have frequently mentioned these problems and have suggested other possibilities. Rosenzweig (1973) suggests that measures of vegetation may be a proximate factor to consider. Smigel and Rosenzweig (1974) mention that seeds vary in size, shape, distribution and other characteristics which might be important in heteromyid coexistence. Brown (1975) indicates that overlap measured in two dimensions (seed size use and habitat selection) is large for communities of several species and that there may be other important dimensions. He also mentions that important differences in foraging techniques remain to be elucidated. Brown, cited in Rosenzweig et al. (1975), state that mobility may be important and that the assumption that different seed sizes have similar distributions may be crucially wrong. Smigel and Rosenzweig (1974) discuss the possibility that large seeds clump more than small ones and that there may be a differential harvest of seed sizes. They suspect that larger animals are not more mobile and postulate instead that larger animals may be more aggressive, preventing smaller species from obtaining the large seed clumps. Hutto (1973) also suggests that aggression and mobility might be important. Brown et al. (1975) believe that the division of seed resources between phyla, such as granivorous ants and rodents, occurs along as yet unmeasured dimensions because the taxa overlap greatly in foraging microhabitat and in the sizes of seeds consumed.

I propose an alternative means of coexistence in seed-eating rodents, based on the information presented in this report; that this mechanism is operative in most desert habitats and may account for many of the reported habitat selection or seed size selection preferences. The experiments demonstrate great differences in the abilities of two coexisting rodent species to exploit different distributions of seeds. I suggest that the rodents (and other granivores) differentially use the array of seed distribution types available and that seed distribution selection is a major component of resource allocation among granivores. This has also recently been shown to occur in granivorous desert ants (Davidson, in press a and b), which share many of the problems of coexistence in deserts with rodents. Johnson and Hubbell (1975) also noted density selection in two bee species, and many of their ideas hold for desert rodents. In the case of desert rodents, however, the factors of aggression and group foraging present in eusocial bees are replaced by mobility and efficient high speed locomotion by kangaroo rats.

Selective foraging on the basis of seed distribution is an attractive hypothesis to account for coexistence among desert rodents. It is an ultimate factor which can reconcile the arguments about the relative importance of habitat selection and seed size selection, as both patterns may be consequences of seed distribution selection. Distribution selection can allow a number of species to forage in the same microhabitat, with the large species using greater mobility to efficiently harvest clumps and the smaller species collecting a more dispersed distribution of seeds. The fact that pocket mice tend to forage under bushes and kangaroo rats in the open interspaces may be explained by the distributions of seeds generally available in these areas. Recent work indicates that seeds may occur in clumps in the open, where kangaroo rats forage, in densities 10-15 times those under bushes (Fig. 3).

Distribution selection might also explain the apparent weak tendency for rodents to select seed sizes that correlate with their body sizes. Our data suggest that large rodents select larger clumps than smaller rodents. Depending on the microhabitat type, either large seeds or small seeds will form the largest and most widely dispersed clumps and hence become available to the largest rodent species. If large seeds clump to a greater degree than small seeds, or if there are large numbers of individual large seeds which the kangaroo rats could equate to large clumps of small seeds, a resultant pattern would be one of large seed size used by the kangaroo rats, as suggested by Brown (1975). In an area near Tucson, Arizona, Reichman (1975a, b) found that kangaroo rats used smaller seeds than pocket mice. Subsequent seed studies indicate that small seeds in this area tend to clump to a greater degree than large seeds, yielding the false impression that the kangaroo rats foraging on the clumps are choosing small seeds. In fact, they are choosing the largest collectable unit, a clump composed of small seeds. Pocket mice, on the other hand, use much smaller clumps, frequently using individually spaced seeds. There are relatively few large seeds in the Sonoran Desert (Reichman 1975 a, b); it would appear that the pocket mice are selecting small seeds (they would rarely encounter large seeds), when in fact they are selecting small "clumps" or dispersed individual small seeds.

MacArthur (1972) suggested that as resources become more clumped, species would respond to the perceived increases in resource density and specialize on clumps. Brown and Lieberman (1973) state that large home ranges would be of particular advantage to an animal which uses a resource that is scarce (widely spaced) and clumped. Both ideas suggest that mobility and foraging technique would be important to distribution selectors, especially clump users. Eisenberg (1975) and Bartholomew and Caswell (1951) argued that bipedal locomotion is less efficient than quadrupedal, and that bipedalism probably evolved in kangaroo rats for predator avoidance. Bartholomew and Carey (1954) later suggested, however, that bipedalism was associated with freeing of the forelimbs for foraging. Recent studies have shown that bipedalism is actually more efficient than quadrupedal locomotion at high speeds (Marlow 1969; Dawson 1976). The mobility and speed of the kangaroo rat (nightly movements of up to 190 m and running speeds of 32 km/hr for *Dipodomys merriami*; Kenagy 1973) are impressive and, when coupled with the efficiency of bipedalism, fit well with the idea of large kangaroo rats traveling long distances for large, widely spaced clumps of seeds. Although bipedalism may be effective for predator avoidance (pocket mice are "facultative bipedalists," Bartholomew and Carey 1954), it also seems to promote the efficiency of foraging for dispersed resources in open habitats. This study, and preliminary field observations, document the short-distance, meandering foraging style of the pocket mouse. Kangaroo rats appear to be coarse-grained foragers that use their mobility to specialize on clumped resources, whereas pocket mice are fine-grained foragers that systematically search areas and collect seeds as they encounter them. One might predict that the cheek pouch contents of pocket mice would more closely match the seeds in randomly taken soil samples than the cheek pouch contents of the kangaroo rats. In a previous study (Reichman 1975a) this was the case.

Comparison of Seed Foraging by Ants and Rodents

The final field experiment allows one to look for a pattern of seed use which might promote coexistence in deserts between the member species of two major taxa which are very similar in the foods they gather and in the areas where they forage. One obvious difference between the two phyla in the study is that ants tend to be diurnal and rodents nocturnal. Unless the seed resources are renewed at least twice a day (an unlikely occurrence), however, this factor would not be important. In addition, during the hottest times of the year, ants become increasingly crepuscular and eventually forage during the night, as do the rodents. None of the granivores foraged in shrubs, so this portion of the microhabitat spectrum can be dismissed.

The data presented in this paper suggest that the foraging niches of the ants are somewhat nested within those of the rodents. At least in the distribution available to the ants and rodents in this study, the rodents took everything the ants did and took more of it (Figs. 9 and 10). Additionally, the rodents were able to exploit seed distributions below the surface.

Granivorous ants forage either in columns, with many workers stretched out in a long column, effectively vacuuming the soil surface, or as individuals, with single workers foraging for single seeds (Davidson, in press a). The fact that the ants found fewer clumps than dispersed seeds (Fig. 10) can perhaps be explained by the target effect. Clumps present a smaller target for the column foragers than dispersed distributions. The individually foraging ants, which forage for individual seeds, would represent very fine-grained foragers poorly adapted to harvesting clumps of seeds (Davidson, in press a). Over 75% of the species found in the experimental area were column-foraging ants, and Davidson (in press a) and Whitford (1976) have noted the effectiveness of these types of foragers on high-density seed concentrations. Although fewer clumps than dispersed distributions were found by the ants in this study, once the clumps were found they were harvested in relatively high proportions (Figs. 9 and 10).

Davidson (in press a, b) has shown that granivorous ants subdivide the seed resource by specializing on different distributions of seeds, and Reichman and Oberstein (in press) have shown a similar phenomenon for rodents. This brings up the possibility of considerable competition between the ants and rodents, as has been demonstrated by Brown and Davidson (1977), with certain species of ants potentially being closer competitors with small rodent species (e.g., pocket mice) than would be larger rodent species (e.g., kangaroo rats). Both individual and group-foraging ants are probably capable of using the lower end of the resource density spectrum (and seed size spectrum), with individual foragers using the lowest densities (Davidson, in press a; Whitford 1976). Among the rodents, the small pocket mice use the lowest densities (although not as low as the low-density specialists among the ants), while the kangaroo rats specialize on dense seed clumps (Reichman and Oberstein, in press). Thus, there appears to be overlap between ants and rodents for seeds along a continuum of seed densities, as there is overlap in their diets. Resource density selection could produce a situation in which all of the granivores could eat the same species of seeds (yielding high overlap values for diets), but could get the seeds from different density distributions. Using primarily the mobility and seed-detection ability of the rodents, I believe the seed distribution uses of the taxa can be sorted out.

As Figure 12 suggests, the individually foraging ants use the least dense seed distributions (see also Brown et al. 1975; Davidson, in press a). Both the group-foraging ants and the small pocket mice should compete for seeds of low and intermediate density, but they are able to coexist because of the ability of the pocket mice to detect and gather seeds from below the soil surface. Recent studies by Reichman and Oberstein (in press) have shown that, statistically, pocket mice do not differentially use surface distributions of seeds over seeds which are 1 or 2 cm below the surface. This effective use of below-ground distributions is probably due to the greater detection ability of the rodents compared to the ants. Not only is the detection ability of the rodents greater, but because of their high mobility and speed compared to the ants, they are better able to "pursue" their prey. Although the group-foraging ants and the pocket mice are probably using similar seed distributions, the rodents are able to "beat" the ants to the most appropriate distributions and are able to use below-ground seeds. At least at the presumed granivore equilibrium densities in this study, the rodents were able to detect and harvest many more seeds than the ants (Figs. 9 and 10). While the pocket mice are detecting and pursuing their prey, however, the group-foraging ants will find some high-density patches of seeds and harvest them before the rodents can get to them. Implicit in these suggestions is that there is a certain minimum turnover rate of seeds in the soil, and recent work (Reichman, unpubl. data) indicates that it is the low and intermediate densities that are rapidly replenished and maintained. Because of its very high mobility and high speed locomotion, the kangaroo rat is the only forager which can afford to specialize on widely scattered, very dense seed clumps (Reichman and Oberstein, in press). Overlain on this system are the gross differences in seed size use between the two taxa, with ants being able to collect the smallest seeds (Davidson, in press a; Figs. 3 and 4). It is important to note, however, that seed size and distribution are probably not independent.

This is not to suggest that those animals which use the least dense resources do not also use high-density distributions (clumps) when they encounter them, but only that they cannot afford to specialize on them. Individually foraging ants, however, probably cannot effectively use clumps of seeds because these ants rely on individual workers foraging randomly for individual seeds (Whitford 1976). Column foragers can effectively use clumps when they encounter them (but they cannot afford to search for them) because of the large numbers of ants in the columns.

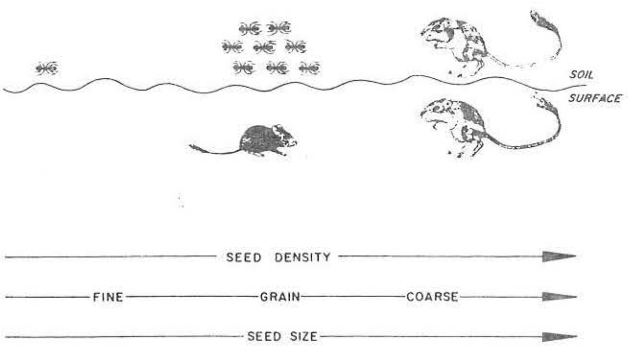

Figure 12. Diagram of potential means of coexistence of granivorous ants and rodents. It is proposed that seed density selection is a major vehicle of coexistence, with seed size selection having a minor role. The ability of the rodents to use underground distributions is the major distinction between ants and rodents.

Pocket mice can exploit clumps because the rodents have cheek pouches which they can fill and also have the ability to return to the clumps should one load not deplete it (Brown et al. 1975). Kangaroo rats are the only foragers which can specialize on clumps and, in fact, cannot afford to use a distribution of seeds below a certain threshold density (Reichman and Oberstein, in press).

When compared to the rodent species the ants are fine-grained foragers, taking seeds in the approximate proportions that they encounter them, with the two major types of ant foragers specializing on different densities of seeds. The rodents, on the other hand, are better able to "pursue" their prey, in terms of both mobility (speed) and detection ability. Comparisons between the pocket mice and kangaroo rats indicate that the small pocket mice are the more fine-grained foragers (Reichman 1975a, b; Reichman and Oberstein, in press), although less so than some of the ants. The same type of mobility and detection differences that allow the ants and the pocket mice to coexist also aid in the coexistence of the pocket mice and the kangaroo rats.

ACKNOWLEDGMENTS

A number of individuals assisted in various laboratory and field aspects of this project, and I especially thank David Daurelle, Jeff Hogue, David Oberstein and Linda Strnad. George Ruffner offered very able field assistance. Pam Lunge prepared the figures, and Jan Scott the manuscript. Terry Vaughan and C. N. Slobodchikoff provided important discussion, and James H. Brown and Diane Davidson were especially helpful in developing ideas related to the coexistence of granivores. Kim Marshall of the US/IBP Desert Biome data processing group was entirely responsible for the computer work, and it is a pleasure to thank him. Facilities were provided by the University of Utah and the Museum of Northern Arizona, with the support of the US/IBP Desert Biome.

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