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SPECIES DIVERSITY AND COMMUNITY ORGANIZATION IN DESERT SEED-EATING ANTS[1]

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Abstract. Patterns of species diversity and community organization in desert seed-eating ants were studied in 10 habitats on a longitudinal gradient of increasing rainfall extending from southeastern California, through southern Arizona, and into southwestern New Mexico. Local communities of harvester ants include 2–7 common species, and at least 15 species from five genera of Myrmecines compose the total species pool in these deserts. Ant species diversity is highly correlated with mean annual precipitation, an index of productivity in arid regions. Communities are structured on the basis of competition for food, and interspecific differences in worker body sizes and colony foraging strategies represent important mechanisms of resource allocation. Seed size preferences, measured for native seeds and in food choice experiments with seeds of different size but uniform nutritional quality, are highly correlated with worker body sizes. Species of similar body size can coexist within local habitats if they differ in foraging strategy. Interspecific aggression and territorial defense and microhabitat partitioning all appear to be relatively unimportant in these ant communities.

Patterns of species diversity and community organization in harvester ants are strikingly similar to those reported for communities of seed-eating rodents that occupy many of the same desert habitats. Separate regressions of within-habitat species diversity against the precipitation index of productivity for the two groups correspond closely in slope, intercept, and proportion of explained variation. Resource allocation on the basis of seed size characterizes local communities of both ants and rodents. Parallels between these two groups suggest that limits to specialization and overlap may be specified by parameters such as resource abundance and predictability that affect unrelated taxa similarly.

Key words: Ants; Arizona; California; communities; competition; desert granivores; diversity; insects; New Mexico; Novomessor; Pheidole; Pogonomyrmex; *resource allocation;* Veromessor.

INTRODUCTION

The southwestern deserts of the USA are inhabited by a remarkably diverse group of consumer species which have specialized to use the relatively nutritious and dependable seeds of desert plants. In an otherwise harsh and uncertain environment, a substantial proportion of the primary production exists as a persistent seed reserve in the soil. Numerous species of granivorous rodents, birds, ants, and other insects often coexist within local desert habitats, presenting a bewildering array of possibilities for competition and resource allocation. Here I analyze geographic patterns in the species diversity and coexistence of desert seed-eating ants in order to assess the interactions which determine the structural and functional organization of these communities. In this and a companion paper (Davidson 1977*a*), I present experimental and observational evidence bearing on mechanisms of resource allocation and consider the generality and significance of such mechanisms.

Desert ants have characteristics that facilitate the study of resource utilization and community organization. They are easily observed in their native habitats and manipulated in experiments, because of their relative insensitivity to the presence of observers. Unlike some other arthropods and many vertebrates, in which juveniles search for their own food and often utilize different resources than adults, ants have relatively fixed ecological roles based upon behavioral and morphological specializations of the adult workers. Workers are specialized food harvesters, and their behavior is not complicated by conflicting demands such as those related to courtship and mating. It is likely that natural selection on worker phenotypes operates at the level of the colony in these social insects, rather than individually on the sterile workers (Wilson 1971).

In the absence of recent perturbations, community diversity and organization should be determined by ecological interactions and reflect approximate equilibria between origination and extinction (Rosenzweig 1975). A total of at least 15 granivorous ant species inhabit the deserts studied here, and for any single habitat, the pool of potential colonists typically includes 5–7 species in addition to those coexisting in the habitat. The vagility of the winged reproductive forms should make ants excellent colonists, and if speciation rates have been broadly similar across these deserts, community diversity and structure should be determined primarily on the basis of extinction probabilities.

The distribution of diverse faunas of granivorous ants and rodents over the North American deserts presents a unique opportunity to compare geographic patterns of species diversity and community organization in unrelated taxa that exploit similar resources. Brown (1973, 1975) has analyzed rodent species diversity and community structure in relationship to both

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latitudinal and longitudinal gradients of precipitation, an estimate of seed production in these deserts. My study locations parallel one of Brown's (1975) transects from the extremely arid winter rain deserts of southern California to the more mesic regions of southeastern Arizona and southwestern New Mexico, which receive both summer and winter rains (Bryson 1957). I have compared ant communities over this geographic gradient in order to answer the following questions: (1) What determines species diversity in these ant communities? (2) How are communities organized and resources partitioned to permit coexistence of similar species? and (3) How do patterns of species diversity and community structure in desert harvester ants compare with those described for granivorous desert rodents?

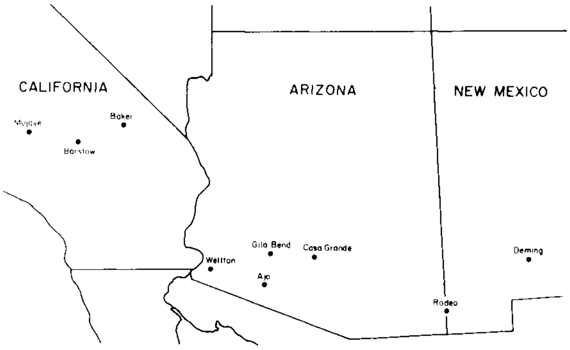

FIG. 1. Map of the study locations.

METHODS

Census techniques and calculations

Ten desert study sites were selected on the basis of precipitation records from U.S. Weather Bureau stations. A broad spectrum of rainfall regimes was chosen, but habitat features such as slope and soil characteristics were deliberately held as constant as possible. Once weather stations had been selected, exact study locations were determined on the basis of their proximity in distance (within 20 km) and elevation to weather stations and the presence of uniformly sandy soils, not dissected by washes or disturbed by human activity. Extremely rocky or sand dune substrates were avoided. Seven desert habitats were censused in spring (late April and early May) and summer (late July and early August) of 1974. Ants were substantially more active in the summer, and the remaining three habitats were censused only once, in August of 1975. Study sites are mapped in Fig. 1 and described in greater detail in Table 1.

Standard census procedures were used at all study sites and involved attraction of ants to seed baits. (Colony counts were attempted but found to be less reliable because of the difficulty of detecting cryptic nests.) At each locality 80 shallow glass ashtrays were placed in an 8 × 10 bait grid with approximately 5-m

TABLE 1. Descriptions of the study locations and characteristics of their ant faunas: mean annual precipitation ($\bar{x}$ ppt, mm), mean July temperature, species diversity of perennials (PSD), numbers of common and rare species of ants; ant species diversity (*H*) and mean distance from colony entrance to census bait ($\bar{D}$). See text for further explanation of these measurements

Location	$\bar{x}$ annual precipitation (mm)	$\bar{x}$ July temp. (°C)	PSD	Ant species: Common	Rare	Diversity (*H*)	$\bar{D}$
California							
1) San Bernardino County, 8.5 km SE Baker, 287 m	76	33.9	0.53	2	0	0.59	8.3
2) San Bernadino County, 11 km NNE Barstow, 659 m	88	29.6	1.57	2	1	0.78	6.7
3) Kern County, 1 km SE Mojave, 834 m	121	28.6	0.60	2	1	0.14	7.4
Arizona							
4) Yuma County, 15 km E Wellton (Tacna), 219 m	91	32.6	0.73	4	2	1.04	4.8
5) Maricopa County, 5 km SW Gila Bend, 225 m	142	34.4	0.00	3	0	1.08	2.9
6) Pima County, 8 km N Ajo, 537 m	216	32.9	0.33	6	1	1.43	5.0
7) Pinal County, 8 km SSW Casa Grande, 425 m	215	33.1	0.30	5	0	1.12	2.3
8) Cochise County, 10 km NNW Rodeo, New Mexico, 1,225 m (Rodeo A)	276	25.8	0.43	7	1	1.67	3.4
9) Cochise County, 9 km NW Rodeo, New Mexico, 1,225 m (Rodeo B)	276	25.8	0.59	7	1	1.77	2.4
10) New Mexico, Luna County, 9.4 km SE Deming, 1,320 m	224	27.0	1.29	5	2	1.54	4.1

spacing paced off among bait stations. The edges of the trays were flush with the surrounding soil surface. As in Brown et al. (1975), strips of masking tape were affixed to the trays to facilitate entrance and exit of ants, and one quarter-inch hardwarecloth was secured across the trays to prevent access by rodents; the screen did not interfere with the movements of ants. Baits consisted of barley seeds, ground in a grain mill to produce a variety of particle sizes ranging from entire seeds and large fragments to fine powder, and these were replenished continuously as foraging ants depleted them. Seed-eating ants were censused by direct observation of the numbers of individuals of each species removing seeds from each bait tray during a 60-s observation period, once every 2 h for a full cycle of diurnal and nocturnal surface temperatures. Bernstein (1974) and Whitford and Ettershank (1975) have demonstrated the importance of substrate temperatures in regulating activity patterns of the desert ants. Both air and soil temperatures were measured with a YSI telethermometer immediately before and after each census of the 80 baits.

Species diversity was calculated in two different ways. Shannon-Wiener diversities ($H = -\Sigma p_i \ln p_i$), incorporating a measure of species evenness as well as number, were computed on the basis of census data from seed baits. Because the values of p_i correspond to the proportion of the total seeds removed during the census that were taken by the ith species, this index measures diversity on the basis of resource exploitation rather than the relative abundances of colonies or workers of each species. In addition, the number of common species in each local habitat, a measure of species richness, was determined on the basis of criteria established prior to any of the censuses. Because seeds were supplied only in dense clumps, but interspecific differences in average colony size and foraging behavior were anticipated to influence the use of seeds in different patterns of dispersion (Davidson 1977*a*), common species were defined on the basis of both the numbers of baits which a species visited and its proportional contribution to seed removal. Common species are those which removed at least 10% of the total seeds taken during the combined observation periods and visited a minimum of 5% of the 80 baits, or those which took at least 5% of the seeds and visited at least 10% of the baits. For twice-censused habitats, species were designated as common if they met these requirements in either census, and diversity indices calculated for the two separate censuses were averaged.

For each species detected in a census, I recorded the distances from baits visited by workers to the entrances of their colonies. Mean distances were computed for each species, and these means, weighted by species abundances, were combined to calculate a community average foraging distance to baits. In this distance index,

$$D = \sum_i d_i S_i / S_T,$$

d_i corresponds to the mean foraging distance of the ith species, and S_i/S_T is the proportion of the censused seed removals that were attributable to species i. This estimate of mean foraging distance is analogous to that calculated by Bernstein (1975) for ants foraging on native seeds. For twice-censused sites, distance indices were averaged.

Several additional types of data were collected at each census location or compiled for each neighboring weather station. Seed harvesting ants of each species were collected and preserved in 70% ethanol and returned to the laboratory for measurement with a Wild M-5 binocular microscope and occular micrometer. The abundances of perennial plants were measured by the line intercept method, using ten 25-m transects at each census site. Species diversity indices ($H = -\Sigma p_i \ln p_i$) were calculated from these data on abundances. No attempt was made to quantify the abundance or diversity of annual plants, since these vary greatly over seasons and among years. Mean annual precipitation and mean July temperature were calculated from 20 yr of weather data (U.S. Climatological Data 1955 through 1974).

Ant species were categorized as either group or individual foragers based on their behaviors at baits and on numerous observations of ants collecting native seeds over a range of seasons and levels of resource abundance (Davidson 1977*a*). Individual foragers are those which were never noted to form distinct columns while gathering native seeds, although certain of these appeared to forage in groups while dismantling large insects or when seed baits chanced to be located very near their nest entrances. Species which form distinct columns to feed from seed baits and from reservoirs of native seeds in the soils are classified as group foragers, though certain of these may modify their behaviors somewhat seasonally (Whitford 1976; Davidson 1977*a*).

Overlaps between pairs of species on census baits were calculated and compared with values of overlap expected if species occurred on baits independently of one another's presence. The expected overlaps were generated as:

$$b_i \cdot b_j \cdot 80$$

where b_i and b_j are the proportions of baits used by species i and j respectively, and 80 baits were censused at each location. Overlaps were analyzed in this manner only for 51 pairs of species whose expected overlaps exceeded 5% of the census stations. Attractive seed baits may lure species from their normal foraging ranges and mask any existing interspecific microhabitat segregation. In order to test for these effects, a second census technique was employed in a 12-h census at Rodeo, New Mexico (site A). At 60 stations, separated from one another by distances of 5 m and not baited, ants were censused with a square-meter frame once every 2 h. Observed and expected overlaps were analyzed in the same manner as above. Finally, colonies on a 10,000-m^2 plot in this same habitat were accurately mapped in August of 1974 and compared with Poisson distributions for random spacing with respect to one another. Two distinct quadrat sizes (large = 100 m^2, $n = 25$; small = 25 m^2, $n = 100$) were employed to generate the Poisson distributions, because species differed considerably in their foraging ranges. For some ants, foraging was confined to within 3 m of the colony, whereas for others, workers frequently traveled up to 25 m, although the greatest densities of workers usually occurred near the colony entrances. Six of the seven species common to this site were sufficiently active to be mapped in August of 1974. Colonies of *Solenopsis xyloni* were not mapped, because they were only sporadically active during this period, and their use of multiple nest entrances made identification of individual colonies very difficult. *Novomessor cockerelli* also tended to forage from 2–3 nest entrances simultaneously, but colony boundaries were readily distinguished on the basis of the short (4–5 m) distances between related entrances of a single colony in contrast to the much more extensive spaces (approximately 20 m) between sets of nest mounds. In addition, I frequently observed workers commuting among associated nest entrances.

Relationship between worker body size and seed size

Both preliminary observations of body size patterns within communities and characteristics of the seed resources suggested that resources might be allocated in part on the basis of worker body size. Experimental and observational techniques were employed to test this hypothesis. Pearl barley seeds were ground in a grain mill and sieved in Tyler soil screens representing a geometric series of pore diameters. Four distinct size classes of seeds (size 1 median = 0.9 mm; size 2 = 1.5 mm; size 3 = 2.2 mm; and size 4 = 3.1 mm) were combined in equal quantities by weight (2.5 g of each size class), and presented in bait trays very near the nest entrances of seed-eating ants in habitats near Rodeo, New Mexico. For each of eight species, the sizes of the first 10 seeds removed by each of three colonies were noted and used to calculate a seed size index. This index was computed as

$$\sum_{i=1}^{4} p_i d_i,$$

where p_i is the proportion of seed choices of size i, and d_i equals the median diameter of seeds in the ith size class.

In order to test the relationship between seed size and body size for ants gathering native seeds, returning workers of six species of seed-eating ants at Rodeo, New Mexico (site A) were robbed of their prey items in September of 1974. The number of colonies sampled per species depended on the total number of colonies of that species present on the 10,000-m^2 study plot. The large and aggressive colonies of *Pogonomyrmex rugosus* have extensive foraging areas, and only three colonies actually occupied the study plot. To increase sample sizes, seeds were also collected from four additional colonies immediately adjacent to the study area. Thirty forage items were sampled from each colony except that, where colonies of *P. rugosus* had multiple foraging columns oriented in different directions, samples of 30 items were removed from each column and treated as measurements from independent colonies. The body size measurements of ants used in these comparisons are based on mean worker body lengths of ants sampled during the census of the Rodeo (A) study site.

RESULTS AND DISCUSSION

Species diversity and related patterns

The species diversity of granivorous ants in the southwestern deserts is strongly correlated with an estimate of seed production based on mean annual precipitation. Primary productivity is closely correlated with precipitation in arid regions (Rosenzweig 1968), and both seed production and germination in desert plants are known to depend on rainfall (Went and Westergaard 1949; Went 1955; Juhren et al. 1956; Tevis 1958*a*, *b*; Beatley 1967, 1974). Figure 2 illustrates the highly significant positive correlation between H, the index of ant species diversity calculated on the basis of exploitation of census baits, and the mean annual precipitation measured at nearby weather stations ($r = .83$; $P < .01$) for the 10 desert study localities. Any census procedure which measures the impact of species on baits risks overestimating those species which are most successful in exploiting high density resource patches. Measurements of the numbers of common species are less subject to this criticism, and this variable is even more strongly correlated with the estimate of productivity ($r = .94$; $P < .01$) than is the species diversity index. Table 2 gives the species compositions of the local ant communities.

At Mojave, California (mean annual precipitation equal to 121 mm), ant diversity falls considerably below the regression line. Strong winds prevailed during both censuses at this site, so that ants risked being carried away while foraging. If species differ in their degree of susceptibility to disruption of foraging by wind, the low measurement of exploitation diversity at this locality may simply be an artifact of censusing on windy days. Alternatively, if strong winds characterize Mojave, California, over much of the foraging season, seed production actually available to these ants may be significantly less than the precipitation value indicates.

The exploitation index of ant diversity (H) is poorly

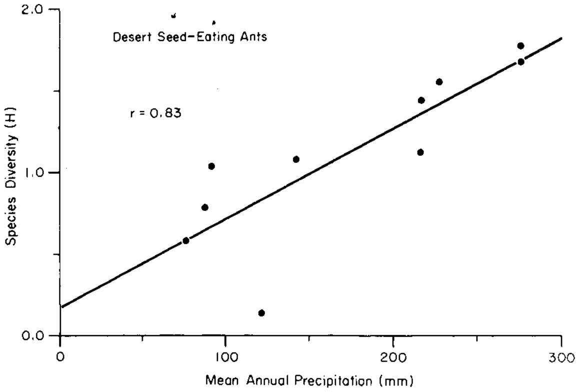

FIG. 2. Species diversity of seed-eating ants plotted against precipitation (index of seed productivity) for 10 census sites in the southwestern deserts. $H = -\Sigma p_i \ln p_i$ where p_i are the proportions of the total seeds removed by the ith ant species from seed baits.

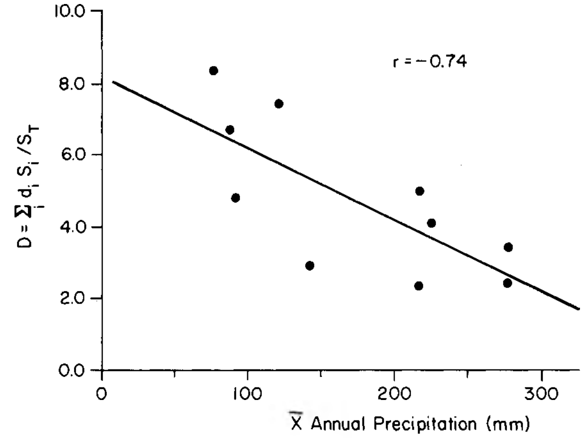

FIG. 3. The regression of mean foraging distance to baits (D) against mean annual precipitation. Here, d_i corresponds to the mean foraging distance (in meters) of the ith species, and S_i/S_T is the proportion of the censused seed removals attributable to species i.

correlated with both the diversity of perennial plants ($r = -.06$) and with mean July temperature ($r = -.40$), which varies with elevation along this latitudinal transect and may be an estimate of the length of the seed production period (Went 1948). Neither of these parameters contributes importantly as second variables to explaining the residual variance of the regression of H on the precipitation index of seed production.

The strong correlation between ant diversity and the estimate of productivity suggests that populations of desert granivorous ants are food-limited, and this interpretation is reinforced by the tendency for colonies to be more widely spaced in more arid habitats. The measure of mean foraging distance from colony entrances to census baits is significantly and inversely related to the mean annual precipitation in the habitat (Fig. 3). Bernstein (1975) noted that foraging distances for ants gathering naturally available seeds in the Mojave Desert decreased similarly with increasing elevation, which she assumed to be correlated with enhanced seed production. The greater colony density in more mesic habitats is striking and is primarily attributable to an increase in abundances of species characterized by small body sizes (*see* Fig. 4 *and below*). Such species typically are absent from the most xeric habitats and occur with increasing frequency in the more productive deserts and arid grasslands. Bernstein's data on the abundances of *Pheidole xerophila* and *Pheidole gilvescens* in the Mojave Desert reveal a similar increase in the proportion of these

TABLE 2. Species composition of ant faunas at 10 study locations in the Mojave and Sonoran deserts. BL = mean worker body length; FB = foraging behavior (group or individual); c = common species; r = rare species. Locations are labelled as in Table 1

			Locations of census sites									
Species	BL	FB	1	2	3	4	5	6	7	8	9	10
Novomessor cockerelli	9.8	I			c			c		c	c	c
Veromessor pergandei	5.5	G	c	c		c	c	c	c			
Solenopsis xyloni	3.1	G			r	c		c	c	c	c	c
Pogonomyrmex rugosus	9.2	G						c		c		c
P. barbatus	9.1	G									c	
P. maricopa	7.6**	I					c*				r	
P. desertorum	7.0	I								c	c	c
P. californicus	6.8	I		c	c	c		r	c			
P. magnacanthus	5.8	I	c									
P. pima	4.5	I						c		r		
Pheidole militicida	3.8	G										r*
Ph. desertorum	3.4	I				r				c	c	c
Ph. xerophila	2.3	G							c*	c*	c	
Ph. gilvescens	2.2	G				r*			c*			
Ph. sitarches	1.8	G				c	c	c*		c*	c	r
Ph. sp.			r	r								

* Species determinations by Roy R. Snelling.

** *P. maricopa* averaged 6.1 mm in body length at location 5.

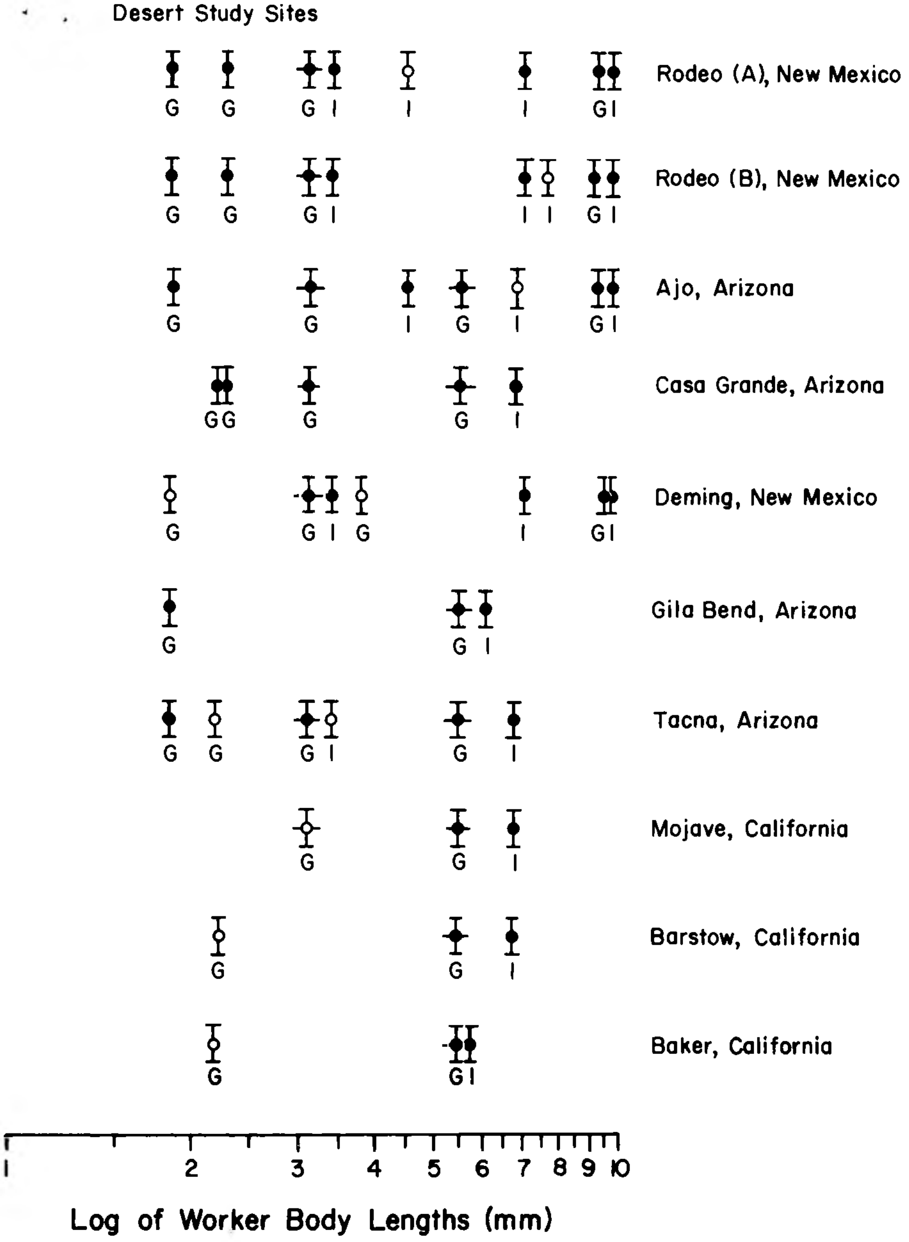

FIG. 4. Mean worker body lengths (vertical bars) of ant granivores censused in 10 southwestern desert habitats. Closed circles depict common species and open circles represent those which are rare. (Criteria for commonness and rarity are specified in the text.) Horizontal bars denote worker size polymorphism, and methods of foraging (G = group and I = individual) are indicated beneath the vertical bars.

small species (worker body length ≈ 2.5 mm) with increasing elevation. Colonies of smaller species tend to have more limited foraging ranges and may, thus, have access to fewer resources. Among the ants encountered in this study, those with body lengths <3 mm typically forage no farther than 3–4 m from their nest entrances. This contrasts sharply with the distances of 40 m or more traversed by large (>9.0 mm) workers of *Pogonomyrmex rugosus* and *P. barbatus* (Hölldobler 1974) and of the size-polymorphic *Veromessor pergandei* (3.0–8.5 mm).

Analyses of colony spacing and microhabitat overlap

If populations of desert seed-eating ants are food-limited, communities of these granivores should contain species that differ sufficiently in their resource

TABLE 3. Comparison of expected[a] and observed overlaps for species pairs in habitats censused by baiting (Rodeo B) and unbaited quadrat techniques (Rodeo A)

Species 1	Species 2	Bait census Expected	Bait census Observed	Quadrat census Expected	Quadrat census Observed
Novomessor cockerelli	*Pogonomyrmex barbatus* (or *rugosus*)	21.0	16	15.8	18
Novomessor cockerelli	*Pogonomyrmex desertorum*	19.4	22	32.1	31
Novomessor cockerelli	*Solenopsis xyloni*	24.7	23	10.5	10
Novomessor cockerelli	*Pheidole xerophila*	11.4	8	13.4	11
Pogonomyrmex rugosus (or *barbatus*)	*Pogonomyrmex desertorum*	18.5	6***	24.8	22
Pogonomyrmex rugosus (or *barbatus*)	*Solenopsis xyloni*	23.5	27	8.1	5
Pogonomyrmex rugosus (or *barbatus*)	*Pheidole xerophila*	11.0	10	11.0	8
Pogonomyrmex desertorum	*Solenopsis xyloni*	21.8	23	16.5	17
Pogonomyrmex desertorum	*Pheidole xerophila*	10.2	10	23.8	22
Solenopsis xyloni	*Pheidole xerophila*	12.9	10	6.9	6

[a] Overlaps were determined as $b_i \cdot b_j \cdot s$, where b_i and b_j are the proportions of baits or unbaited quadrats used by species i and j, and s equals the total number of stations.

*** This difference is significant at the .0001 level of probability.

requirements to permit coexistence. One potential mechanism of resource allocation is microhabitat partitioning, but competition between species of the granivorous ants studied here appears not to have been resolved primarily by interspecific territoriality or local differences in habitat preference. The results of the Poisson analysis of the spatial distribution of ant colonies at Rodeo, New Mexico (site A) are the first line of evidence supporting this conclusion. Colonies of only one pair of species, *Pogonomyrmex rugosus* and *P. desertorum*, were interspecifically spaced ($t = 3.8$; $P < .005$ with 25-m^2 quadrat size). Several more qualitative observations suggest interspecific territorial defense by *P. rugosus* against *P. desertorum*. In the fall of 1974, the former species ceased foraging somewhat earlier than did the latter. During late October, I observed *P. desertorum* workers attempting to establish colony entrances near *P. rugosus* mounds. Though not actively foraging, *P. rugosus* workers defended their territories against the intruders. However, by November *P. rugosus* was completely inactive and some *P. desertorum* colonies had successfully settled very near the nest mounds of their larger competitors (D. Hobbs, personal communication).

Demonstration of random interspecific colony spacing does not exclude the possibility that species feed in distinctly nonoverlapping foraging territories. Hölldobler (1974) reports that, within populations of *Pogonomyrmex barbatus*, foraging territories tend to be nonoverlapping, though regular spacing among nest mounds is not detected (but see Whitford et al. 1976). Analysis of interspecific overlaps of ants foraging on baits and in unbaited square-meter quadrats reveals little evidence for interspecific microhabitat partitioning of foraging grounds. Comparisons of observed and expected overlaps for 51 pairs yield only two significant chi-square values. (Because of the large number of relationships tested and the consequent possibility of Type I error, the .001 probability level was required for statistical significance. Two other comparisons approached significance at probability levels of .05 and .01 respectively. A replicate test of spatial interactions between the latter pair in another habitat indicated random interspecific spacing.) Only two pairs of species apparently subdivide microhabitats. *Pogonomyrmex rugosus* and *P. desertorum* at Deming, New Mexico ($P < .001$) and *P. barbatus* and *P. desertorum* at Rodeo B ($P < .0001$) represent spatially segregating pairs.

The considerable interspecific spatial overlap detected during baiting censuses does not appear to be merely an artifact of luring species away from their normal foraging areas to artifically high accumulations of resource. In Table 3, expected and observed overlaps are compared for similar ant faunas censused by baiting (Rodeo B) and quadrat (Rodeo A) techniques. (Data from the bait census at Rodeo A could not be used because many of the expected overlaps fell short of the 5% requirement.) These ant communities are identical in species composition with one exception: *Pogonomyrmex rugosus* is abundant at the Rodeo A area, while *P. barbatus* occurs instead of *P. rugosus* at Rodeo B. These congeners do not usually coexist within local habitats and appear to act as ecological replacements for one another in many respects (Whitford et al. 1976). Both census techniques reveal extensive interspecific overlap in foraging ranges. The single instance in which baited and unbaited censuses gave significantly different overlaps involved the interactions between *Pogonomyrmex desertorum*, an individually foraging species of approximately 7.0 mm worker body length and either *P. rugosus* or *P. barbatus*. In the unbaited quadrats, overlaps were significantly greater between *P. desertorum* and *P. rugosus* than they were between *P. desertorum* and *P. barbatus* on census baits. This result is the reverse of the expectation, were species being lured from their normal foraging areas by artificially large accumulations of seeds. Together the data on foraging overlaps in baited and unbaited quadrats, and those on colony spacing imply that microhabitat partitioning is not a major mechanism by which coexisting species of desert seed-eating ants avoid competition for food resources.

Body size and seed size selection

Resource partitioning on the basis of seed size plays a much more pronounced role in the organization of communities of desert seed-eating ants. This is strongly implied by the combination of patterns of worker body sizes among coexisting species and data on the seed size preferences of these species. For each of the 10 ant communities censused, mean worker body lengths of constituent species are plotted on a logarithmic scale in Fig. 4 (vertical bars). Several interesting patterns emerge from this graph. Coexisting species with similar worker body sizes tend to differ in their foraging behaviors. Within some communities, such as Tacna, Deming, and Ajo, group and individual foragers actually alternate along the body size gradient. Each of the three Mojave Desert habitats censused in southern California contains only two common species, and in each case the two species employ different foraging strategies. Certain combinations of species of similar size and foraging behavior never occur. For example, the five relatively productive communities which contain group foragers whose workers exceed 9 mm in body length contain either *Pogonomyrmex rugosus* or *P. barbatus* but never both. Where Hölldobler (1974) studied *P. rugosus* and *P. barbatus* in a zone of overlap in southeastern Arizona, foraging territories were defended interspecifically, and aggressive encounters between species were as intense as intraspecific aggressive encounters. In the 5.8–7.0-mm body length range of individual foragers, local habitats characteristically contain only one of four possible species (*Pogonomyrmex californicus*, *P. maricopa*, *P. magnacanthus*, and *P. desertorum*) in sufficient abundances to be categorized as common.

Finally, Fig. 4 illustrates that all species whose workers average less than 3.4 mm in length are group foragers. This foraging method may facilitate navigation and extend the feeding areas of these small workers. Bernstein (1971) has shown that, for desert seed-eating ants of a given body length, the maximum foraging distance of trail-forming ants exceeds that of individually foraging species of similar body size. Like trends are apparent in the present investigation.

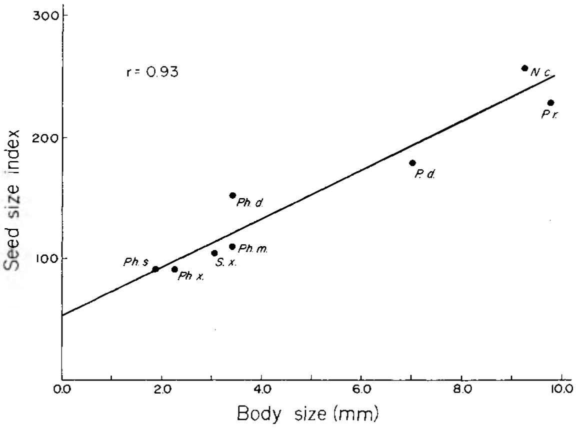

FIG. 5. The relationship between worker body length and seed size index for experiments with 8 species of seed-eating ants near Rodeo, N. Mex. Seed size indices were calculated as $\Sigma p_i d_i$, where p_i is the proportion of the seeds chosen from the ith size class of barley particles and d_i is the median diameter of seeds in that size class. Species designations are as follows: *Ph. x.* = *Pheidole xerophila; S. x.* = *Solenopsis xyloni; Ph. m.* = *Pheidole militicida; Ph. d.* = *Pheidole desertorum; P. d.* = *Pogonomyrmex desertorum; P. r.* = *Pogonomyrmex rugosus*; and *N. c.* = *Novomessor cockerelli*. All species except *Ph. m.* coexist at Rodeo, N. Mex. (Site A).

The patterns of worker body sizes among coexisting species are associated with resource subdivision on the basis of seed size. In food choice experiments with barley seeds and particles of several sizes, size indices of seeds foraged are highly correlated with worker body lengths (Fig. 5: $r = .93$, $P < .01$). For native seeds collected by ants in September of 1974 at Rodeo (A), New Mexico, an increase in average seed size with worker body length gradually levels off at the larger body sizes, presumably because large seeds are more rare than small and medium-sized seeds. The regression of the seed size index against the logarithm of worker body size for these data is highly significant (Fig. 6: $r = .76$, $P < .01$). On the average, larger workers take larger seeds, and this relationship is consistent even within colonies of the size polymorphic *Veromessor pergandei* (Davidson 1977*b*). The correlation between body size and prey size may arise in part from purely mechanical limitations of "fit" between seeds and ant mandibles, and in part from a reduced capacity of small ants to locate large seeds. Species with smaller workers forage over much shorter distances than larger species and may have fewer large seeds available to them.

Foraging behavior and resource allocation

Although worker body sizes and seed sizes are significantly correlated, coexisting species of similar body length overlap considerably in the ranges of seed sizes that they utilize (Fig. 6). Resource allocation on the basis of seed size alone appears insufficient to ac-

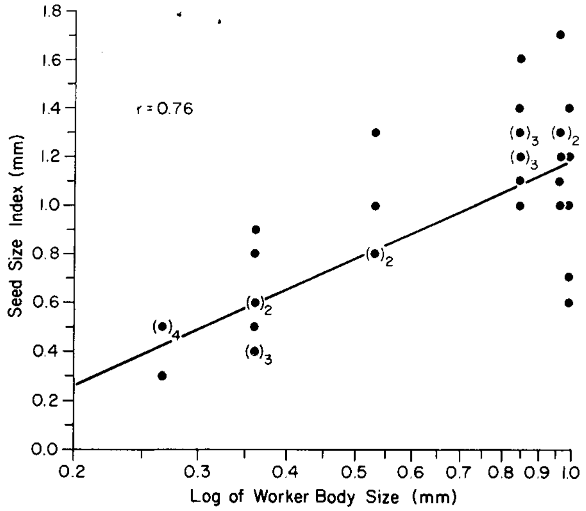

FIG. 6. Size index of native seeds foraged by 6 common species at Rodeo, N. Mex. (Site A) as a function of the logarithm of worker body length. Each point on the graph includes data from the seed component of 30 forage samples collected at one colony. Seeds were sized in a series of Tyler screen sieves. Indices were calculated as mean seed sizes, weighted by the abundances of seeds in each size class.

count for coexistence. The possibility that differences in foraging behavior may play a role in resource partitioning is suggested by the tendency for coexisting species of similar body size to forage in different ways (Fig. 4). In a companion paper (Davidson 1977*a*), I consider group and individual foraging techniques as specializations for exploiting seeds of different density or dispersion.

GENERAL DISCUSSION

Diversity and structure of ant communities

Differences in the species diversity of granivorous ants among 10 study sites in the southwestern deserts appear to be determined primarily by variability in the average productivity of the habitat. MacArthur (1972) hypothesized that, if the diversity of resources remains the same, consumer diversity should increase as productivity increases; previously scarce resources become sufficiently abundant to support new species, and greater specialization in the utilization of resources is also possible. Brown's (1973) studies of rodent communities in sand dune habitats of the Mojave and Great Basin deserts provided support for MacArthur's hypothesis, and Brown (1975) later confirmed this result independently for rodents in flatland sandy soil habitats of the Sonoran Desert. The demonstration of similar patterns for desert seed-eating ants attests to the generality of this relationship, at least for this relatively uncomplicated system in which groups of generalist consumer species utilize similar food resources in habitats that differ very little in structure, and where recent historical perturbations appear not to have played a significant role.

Although investigations of very different ant communities have shown species diversity to be ecologically determined, none have explicitly related diversity to resource productivity. Levins et al. (1973) note the excellent colonizing abilities of ants and present evidence that distributions of ants on islands in the Puerto Rican bank are dynamically determined by migration and extinction events accompanied by high species turnover. Culver (1974) censused ants in a grassy field in West Virginia over two summers and found 6–7 species coexisting at any one time, although species composition was temporally variable, and as many as 10 species actually inhabited the field during some portion of his investigation. He postulated that this numerical constancy might reflect an equilibrium between migration and extinction. In comparing ant communities in a variety of habitat types in Puerto Rico, St. John (Virgin Islands), and West Virginia, Culver (1974) noted a positive correlation between ant species diversity and the structural complexity of the habitat but made no attempt to quantify the availability of food resources. Comparisons of species diversity in habitats of similar structure in Puerto Rico and West Virginia gave mixed results: second-growth forests in both regions supported approximately the same number of species, while grassy fields in West Virginia included more coexisting species than similar habitats in Puerto Rico (6–7 vs. 3). Because Culver's studies included predominantly omnivorous species, even qualitative estimation of differences in the resource regimes of the various habitats is difficult.

Bernstein (1971) found an increase in the species diversity of the total ant community (primarily insectivores and granivores with a few omnivores) with increasing elevation in the Mojave Desert, but both precipitation and temperature vary simultaneously over this gradient, and their effects are not easily distinguished. Increased precipitation at higher elevations should be correlated with greater production of both seeds and insects, and generally lower temperatures may both prolong the length of the seed production period (Went 1948) and curtail the foraging season for these ectothermic invertebrates. Although Bernstein interpreted the greater colony density at higher elevations as a response to the greater resource productivity, she attributed the accompanying enhancement of species diversity to the lengthening of the period over which food resources were produced. By comparison, in the present investigation, mean annual precipitation accounts for considerably more of the variation in species diversity than does mean July temperature.

The species diversity of consumers should depend to some degree upon the diversity as well as the productivity of resources. Although it would be difficult to quantify seed diversity with certainty for so many sites in which rainfall and seed production fluctuate dramatically over seasons and years, it is unlikely that the habitats studied here differ drastically in overall seed diversity. Ant species diversity is unrelated to the diversity of perennials, and various of the sites contain many of the same or closely related species of annuals and perennials. If the sizes of ants present at a given locality are indicative of the sizes of seeds produced there, the range of seed sizes may be similar across these deserts. The presence of the continuously size polymorphic *Veromessor pergandei* in habitats where species of relatively large and small body size are absent and the tendency for colonies of this species to be more polymorphic in habitats where interspecific competition is less intense (Davidson 1977*b*) results in the presence of a relatively similar range of worker body sizes within each of the study localities. Workers of this species ranged in body size from 3.5 to 8.4 mm, while the span of mean body sizes for all species encountered in this study is 1.8 to 9.8 mm.

Has competition played a major role in the organization of communities of seed-eating ants? Various criteria have been used as indirect evidence for competition. Schoener (1974) discussed two patterns that frequently characterize competitively structured communities: overdispersion of species in niche space and complementarity of niche dimensions. In communities of desert harvester ants, resource allocation is related to interspecific differences in both worker body sizes (associated with differential exploitation of different size classes of seeds) and in colony foraging behaviors (correlated with different efficiencies in gathering seeds from various density distributions [Davidson 1977*b*]). Figure 4 provides some suggestion that niche separation based on worker body sizes and colony foraging strategies of coexisting species is greater than would be predicted if combinations of coexisting species occurred at random with respect to these characteristics. However, without a more precise knowledge of seed abundance in each resource state, this interpretation remains relatively subjective. Stronger evidence for the role of competition in structuring these communities derives from other observations. The two dimensions of resource allocation considered here are consistently complementary: species of similar body size tend to coexist only if they differ in foraging behavior. A corollary is that species of similar body size and foraging behavior behave as ecological replacements for one another, never demonstrating local coexistence. Diamond (1975) has observed such replacement patterns among ecologically similar bird species on islands of the coast of Central America and interpreted these "checkerboard" distribution patterns as evidence for competition. Finally, character shifts, such as that occurring in *Veromessor pergandei* in response to changes in the competitive environment (Davidson 1977*b*), constitute some of the most powerful evidence for competition. The within-colony worker size polymorphism in this species is reduced as the intensity of interspecific competition increases, with an accompanying reduction in the variance of resource types utilized.

The presence of numerous seeds in desert soils after extensive periods of drought (Tevis 1958*c*) does not contradict the argument for food limitation of granivore populations. Food may be present without being available in sufficiently large packages or dense associations to be profitably harvested. Clearly the most desirable seeds will be depleted first, and, as this happens, species will be forced to expand their diets and patch utilization to encompass less rewarding prey. Tevis (1958*c*) has observed such changes in the diet of *Veromessor pergandei*. Among desert seed-eating ants, diet breadth is positively correlated with resource abundance both for experiments with "seeds" of identical quality but different sizes and for native seeds as their abundances change seasonally (D. W. Davidson, personal observation). Species that have high maintenance costs or that derive their resources predominantly from unproductive regions of the resource spectrum (e.g., very large seeds on the dimension of seed size) should be particularly sensitive to changes in resource density. Reichman (1974), working on an extensive plot in the Sonoran Desert, has demonstrated an approximately 40-fold change in average seed densities over only 2 yr. Fluctuations of so great a magnitude must dramatically alter granivore foraging efficiencies.

How do strategies of resource allocation in desert harvester ants compare with those for ants as a whole? Culver (1974) postulated that, in general, ants tend to be less constrained by their morphologies than are many other kinds of organisms (for example, birds), and that their interspecific interactions are frequently behaviorally based. Sociality may well increase the potential for such behavioral adaptations, and, in desert harvester ants, niche separation on the basis of foraging strategy is representative of such a behavioral solution to interspecific interactions. In contrast, resource partitioning on the basis of food particle size may be exceptional among ants. Culver (1972) anticipated this somewhat atypical form of niche separation in granivorous ants after calculating low microhabitat niche breadths and high microhabitat overlaps for granivorous Colorado species reported on by Gregg (1963).

What factors have caused the seed-eating ants to depart from the broad microhabitat niches and narrow microhabitat overlaps that characterize many other ant species (Culver 1972, 1974; Levins et al. 1973)? Mechanisms of resource subdivision should reflect the absolute heterogeneity of resources as well as the capacity of organisms to respond to this heterogeneity. Habitat structure is relatively simple in the 10 desert study sites, and while local variability in seed density may be associated with microtopographic features of the substrate (Reichman 1976), the pattern of this local

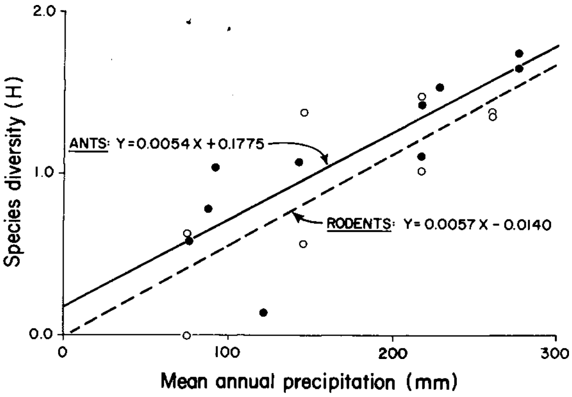

FIG. 7. Species diversities of seed-eating ants and rodents shown independently as functions of the precipitation index of productivity. Closed circles designate ant censuses, and open circles correspond to rodent censuses. Species diversities were calculated as $H = -\Sigma p_i \ln p_i$, where the p_i are the proportions of each species in the census or in the sample.

heterogeneity is probably not temporally stable. Culver (1974) noted a tendency for the frequency of aggression to be inversely related to habitat complexity and attributed this pattern to the greater ease of defending structurally simple habitats. Though living in relatively simple habitats, desert harvester ants may tend to use interspecific territorial defense and aggression very infrequently because of the high costs associated with defending so dispersed a resource as seeds. This generally low level of interspecific aggression may partially account for the high species diversity of granivorous ants in the southwestern deserts. MacArthur (1969) has pointed out that interference competition can reduce species packing of consumers that utilize noninteracting resources.

Parallels between communities of ants and rodents

Geographic patterns of species diversity and community organization in desert seed-eating ants may be compared in greater detail with the results of similar studies of desert rodent communities. Both the objectives and the methodologies of the present study closely resemble those of investigations by Brown (1973, 1975) and Brown and Lieberman (1973). Brown (1973, 1975) has described patterns of rodent species diversity along both latitudinal and longitudinal productivity gradients in the southwestern deserts. Over the longitudinal gradient, which parallels my own, Brown (1975) studied rodents in flatlands characterized by sandy soils and relatively uniform habitat structure. He demonstrated a significant positive correlation between rodent species diversity and an estimate of primary productivity by plotting the numbers of common species per habitat against the mean minus the standard deviation of the annual precipitation at nearby weather stations. Brown used this precipitation statistic as an estimate of the amount of productivity that is predictable in 5 of every 6 yr. I have computed species diversity indices from Brown's rodent data and plotted them as functions of mean annual precipitation, with which they are equally well correlated, to make his data comparable to my own.

The relationships of ant and rodent species diversity to the precipitation index of productivity are illustrated in Fig. 7. Several attributes of the fitted regressions are strikingly similar: (1) the proportions of explained variation, (2) the slopes, and (3) the intercept values. Mean annual precipitation accounts for approximately 69% of the variation in species diversity among ant communities ($P < .01$) and 64% of this variation among communities of rodents ($P < .05$). The slopes of the two regressions are statistically indistinguishable, and their intercepts differ by less than 2%, but are slightly higher than expected considering that zero diversity values correspond to single-species communities (although the density of individuals may be very low). The precise translation of rainfall into seed productivity is not known. Seed transport by wind and water may import seeds into unproductive habitats from more productive areas nearby. Alternatively, the relationship between granivore diversity and precipitation may become nonlinear where precipitation levels are extremely low.

Mechanisms of resource partitioning that permit coexistence of potentially competing species should depend in part on the nature of the resources and might also be expected to show similar patterns in unrelated organisms. The extent of resource subdivision on various dimensions should reflect the absolute heterogeneity of resources as well as the capacities of the two groups to respond to this heterogeneity. For particulate food items composed of diverse size classes, subdivision by size is a common pattern. Coexisting species of both ants and rodents (Brown 1973, 1975; Brown and Lieberman 1973) characteristically differ in body sizes and utilize different sizes of seeds. In Fig. 8, seed size data are compared for ants (this study) and rodents (Brown 1975) feeding on native seeds in the vicinity of Rodeo, New Mexico. (Although *Dipodomys deserti* does not coexist in this habitat with *D. spectabilis,* the former species is included for comparison.) Within each category of granivores, species allocate seeds on the basis of size, but the two groups overlap broadly with one another in seed size utilization. The overall positive correlations between body size and seed size may depend on a number of different factors, including species' efficiencies at transporting or cracking seeds and the distances over which species of various sizes can travel in search of food. In this regard, it is interesting to note yet another similarity in patterns of community organization in ants and rodents (Brown 1973, 1975 for rodents). In neither taxon are species of small body size represented in the least productive of these sandy

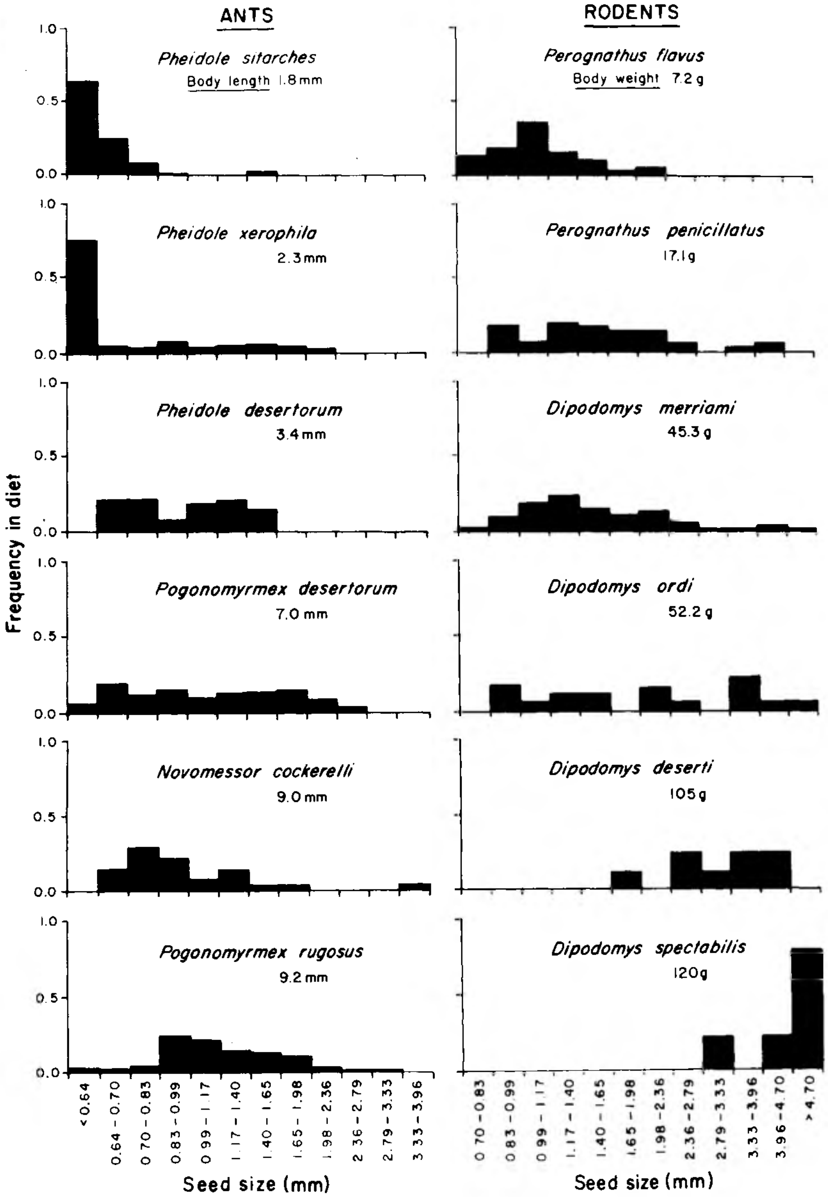

FIG. 8. Size frequency distributions for native seeds foraged by 6 species of harvester ants coexisting at Rodeo, N. Mex. and by 6 species of seed-eating rodents, 5 of which inhabit deserts near Rodeo, N. Mex. (*Dipodomys deserti* does not cooccur in the same habitats with *D. spectabilis*.) Data are not available for the cricetid rodents which lack cheek pouches. Seed size categories correspond to the geometric series of pore diameters in Tyler soil sieves which were used to classify seed sizes. Seeds from ants and rodents were sieved for different intervals of time, so that precise comparisons between taxa are not possible. Measurements correspond approximately to seed widths for ant seeds and to some value intermediate between width and length for rodent seeds. Rodent data are modified from Brown (1975).

soil habitats. The absence of small species from these communities may reflect their inability to harvest sufficient seeds because of limited mobility.

In both groups of granivores, resources also are subdivided on other dimensions as well, and two of these additional dimensions apparently reflect unique aspects of the biology of each taxon. Coexisting species of rodents that utilize similar size distributions of seeds tend to forage in microhabitats that provide different amounts of cover (Rosenzweig and Winakur 1969; Rosenzweig 1973; Brown 1975), a factor likely to be correlated with exposure to avian predation. The failure of ants to distinguish microhabitats on the basis of cover is not surprising, as their risk of being eaten by such predators as *Phyrnosoma* species and spiders is less likely to vary with proximity to shrubs. In contrast, the behavioral plasticity conferred by sociality in ants permits resource allocation on the basis of seed density, or differential use of the same microhabitat because of differences in colony foraging behavior (Davidson 1977*a*).

The similarities observed between ant and rodent communities appear to require that precipitation affect the abundance and heterogeneity of seeds available to each taxon in approximately the same way. Although direct data bearing on this point are difficult to obtain, those that do exist suggest that this is likely (Pulliam and Brand 1975, Brown et al. 1975), because the two taxa overlap considerably in all parameters that have been studied except for temperature and season of foraging. These two factors do not appear to be important in climatic gradients such as the present one, where latitude and altitude are held relatively constant. However, along a latitudinal gradient in the Mojave and Great Basin deserts, where mean temperature declines significantly as precipitation increases, the diversity of seed-eating ants does not increase (Brown and Davidson 1977). Brown (1973, 1975) noted a more rapid increase in rodent species diversity with productivity over this same latitudinal gradient than in the transect across southern California and southern Arizona. In Brown's regressions, numbers of common species were plotted against the mean minus the standard deviation of annual precipitation. If species diversities ($H = -\Sigma p_i \ln p_i$) are regressed against mean annual precipitation as above, the slope of this relationship is .014, slightly over twice the slope calculated for the east–west transect. One explanation for the greater increase in rodent species diversity over the latitudinal gradient is that rodents are able to exploit a larger percentage of the enhanced production in areas where communities of ants are relatively impoverished. Brown and Davidson (1977) have evidence for reciprocal density compensations between Sonoran Desert faunas of ants and rodents in response to experimental exclusions of one or the other of the two taxa. These results imply that competition among distantly related taxa, although often overlooked in ecological studies, may be very important to the structuring of communities of consumers.

The strikingly similar patterns of species diversity in granivorous ants and rodents imply that resource limitations may determine the structure of communities even more precisely than would have been anticipated from existing theory. Several investigators (Thorson 1958; Cody 1968, 1975; Karr and James 1975; Brown 1975; Pianka 1975) have described parallels in structural and functional organization among geographically isolated communities of different but taxonomically related groups of species that are exposed to similar selective pressures. Comparable geographic gradients in species diversity in relation to latitude, altitude, and ocean depth (MacArthur 1972; Sanders 1968) characterize many unrelated groups of organisms and imply the operation of common mechanisms. The nearly exact correspondence of the slopes of the two regressions of granivore diversity is particularly noteworthy, because ants and rodents differ enormously in their morphological, physiological, ecological, and behavioral attributes. Although species in unrelated taxa partition resources in somewhat different ways, limits to specialization and overlap may be specified by general parameters such as resource distribution in space and time that affect unrelated taxa similarly. In this regard, one of the major problems confronting desert granivores is that seeds are produced in pulses of uncertain magnitude and frequency. It is probably not coincidental that both ants and rodents employ similar strategies of food storage, hibernation, and estivation to minimize the impact of environmental fluctuations.

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