Ecology (1977) **58**: pp. 725–737

FORAGING ECOLOGY AND COMMUNITY ORGANIZATION IN DESERT SEED-EATING ANTS[1]

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Abstract. Granivorous ants in the southwestern deserts of the United States are characterized by species-specific colony foraging behaviors that determine their efficiencies at utilizing seeds from different density distributions. Workers search for food either in groups or as individuals, and these feeding strategies represent specializations for high and low density resources respectively. While gathering experimental seeds, simultaneously supplied in clumped and dispersed distributions, feeding by group foragers focused on the high density resource patches, while individual foragers harvested seeds predominantly from the dispersed distribution, which required that prey be independently discovered. Collecting native seeds from unmanipulated environments, individual foragers tended to spend proportionately more time searching and experience lower foraging success than did group foragers in the same local habitat. During a period of high seed abundance, group foragers collected a much narrower range of prey types than did individual foragers. Colonies of *Pogonomyrmex rugosus* exhibited a mixed foraging strategy, with the most distinct feeding columns occurring during a period of peak seed abundance. Among group foragers, greatest activity coincided with periods of relatively high seed densities and low climatic stress, and these species utilized tactics such as seed storage, hibernation, and estivation to weather less favorable periods in a resting state. Individual foragers were active at intermediate levels during less favorable periods.

Although high and low density seed resources are not renewed independently of one another, density specialization appears to promote coexistence between group and individual foragers. Their capacity to stably partition resources in this way should depend on (1) the degree of difference in their efficiencies at exploiting different density distributions of seeds and (2) the availability of seeds in the habitat as a function of seed density. In more mesic habitats, where seeds are renewed more frequently and probably also in larger pulses, group foraging species are proportionately more abundant.

Key words: Ants; Arizona; California; coexistence; communities; density specialization; desert granivores; foraging strategies; insects; New Mexico; resource partitioning.

INTRODUCTION

The southwestern deserts of the United States support a remarkably diverse fauna of seed-eating ants, with as many as seven common species coexisting in the same local habitat. In a companion paper (Davidson 1977*a*), I show that ant species diversity in these deserts is highly correlated with an estimate of habitat productivity and argue that ant populations are structured on the basis of competition for food. Coexisting species of granivorous ants subdivide resources in part on the basis of seed size, with larger workers collecting larger seeds, but some pairs of species coexist despite similar worker body sizes and substantial overlap in the sizes of seeds utilized. Analyses of nest dispersion and spatial utilization of the foraging grounds reveal considerable interspecific overlap in both of these parameters as well for all but two species pairs (Davidson 1977*a*).

Notably different species-specific colony foraging behaviors characterize these eusocial granivores: species may be categorized as either group or individual foragers. In colonies of individual foragers, workers search for and collect seeds independently of one another, and as a result, all of the area surrounding the colony is continuously and simultaneously searched. In contrast, workers of group foraging species tend to move together in well-defined columns, so that at any one time, most of the searching and feeding take place in a restricted portion of the area surrounding the nest. Foraging behavior in highly sedentary, central-place foragers such as ants should be subject to strong selection, and foraging success in these social insects should be determined at the level of the colony rather than the individual worker ant (Carroll and Janzen 1973).

Regularities in the organization of communities of desert harvester ants suggest that interspecific differences in colony foraging behavior are associated with resource allocation. Analysis of the species composition of 10 local ant communities (Davidson 1977*a*) revealed that species with similar worker body sizes could coexist if they employed different foraging strategies, while species that were alike in both body size and foraging behavior never coexisted, but acted as ecological replacements for one another. In addition, both foraging strategies were represented in all two-species communities. The purpose of this investigation is to determine how foraging behavior may be related to resource allocation in communities of desert seed-eating ants and to understand the implications of this form of resource subdivision for community organization.

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METHODS

Community censuses

Some of the data presented below are based on community censuses described in detail elsewhere (Davidson 1977*a*), and I will outline the census procedures only briefly here. Ten local desert habitats representing a broad range of rainfall regimes were censused for granivorous ants during the spring and summer of 1973 and the summer of 1974. Although drawn from three distinct provinces of the southwestern deserts, the Mojave, Sonoran, and Chihuahuan vegetation types (Schreve 1942), these habitats were similar in such features as slope, soil characteristics, and vegetation structure. A companion paper (Davidson 1977*a*) gives the locations and descriptions of the study sites and the taxonomic compositions of their granivorous ant faunas. I censused ants at seed baits, continuously supplied with barley seeds and particles in a broad range of sizes. Each of 80 bait stations in an 8 × 10 bait grid in each local habitat was observed for ants removing seeds over 60-s intervals, once every 2 h for a full cycle of diurnal and nocturnal surface temperatures.

For each common species detected in the first year's censuses (including 7 of the 10 sites eventually censused) I calculated the ratio of

$$\frac{s_i}{b_i},$$

where s_i is the number of seeds removed by the ith species during the census, and b_i represents the number of baits this species utilized. In a two-tailed, nonparametric Wilcoxan Matched-Pairs Signed Rank Test, I compared the s_i/b_i ratios of pairs of similar-sized species composed of one group forager and one individual forager from the same local habitat.

Experiments with supplemental seeds

Because group and individually foraging colonies deploy their workers in different spatial patterns, experiments were performed to determine whether the two foraging methods might represent strategies for using resources from different density distributions or dispersion patterns. Each of 10 colonies of *Pogonomyrmex barbatus* (a group forager averaging 9.2 mm in body length) and 10 of *Novomessor cockerelli* (an individual forager, mean body length equal to 9.8 mm) inhabiting a two-species community on an alkaline playa near Rodeo (Hidalgo County), New Mexico, was exposed to the distribution of millet seeds depicted in Fig. 1. Seeds colored with vegetable dyes have proven valuable for tracing foraging patterns of ants (Willard and Crowell 1965; Bernstein 1975; Whitford 1976) and are used here to distinguish exploitation of high density (colored millet) and low density (white millet) patches of seeds and the degree to which foraging is directionally restricted. Appropriate experiments had demonstrated no color preferences among these ants. Clumps of millet seeds (≈550 seeds/clump) were located at random with respect to preexisting feeding columns by positioning them before the initiation of morning or afternoon foraging activity. Approximately the same number of white millet seeds were distributed as uniformly as possible over a much larger area along arcs connecting the four clumps. At each ant colony, I noted the colors of the first 200 millet seeds returned to each nest from the experimental distribution.

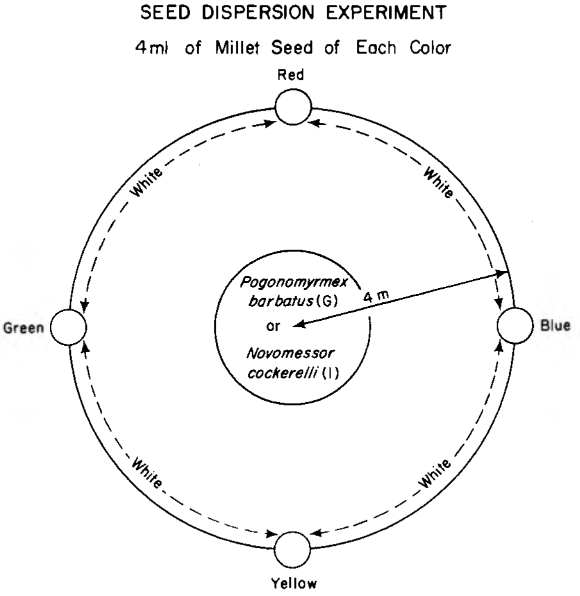

FIG. 1. Diagram of seed density experiment. Small circles denote 4-ml clumps of colored millet. A total of 4 ml of white millet (dotted line) was dispersed among clumps 4 m from the nest mound. G indicates group forager and I, individual forager.

Ants feeding on native seeds

The proportion of time spent searching for native seeds was compared for two group foragers and three individual foragers in a more diverse ant fauna inhabiting a region of bajada near Rodeo, New Mexico. This site, referred to hereafter as Rodeo (A), is described in more detail in Davidson (1977*a*). I defined search time as the amount of time required for workers to locate food after leaving the nest, and handling time as the period between location of an acceptable food item and return of the worker to the nest, usually by the most direct route (Bernstein 1975). Workers were individually marked with fluorescent "Hot Color" TM paints, and a number of feeding bouts (18–26) were timed for each species, with approximately equal numbers of observations drawn from each of two colonies.

Seasonal changes in foraging patterns were studied for colonies of *Pogonomyrmex rugosus*. In this species, the integrity of feeding columns occasionally

TABLE 1. Ratio of s_i/b_i for group and individual foragers*

Census locality	Group forager and seed/bait ratio		Individual forager and seed/bait ratio	
Baker, California	*Veromessor pergandei*	17.64	*Pogonomyrmex magnacanthus*	3.09
Barstow, California	*V. pergandei*	7.71	*P. californicus*	5.77
Mojave, California	*V. pergandei*	9.63	*P. californicus*	2.50
Tacna, Arizona	*V. pergandei*	17.74	*P. californicus*	2.84
Deming, New Mexico	*Pogonomyrmex rugosus*	4.75	*Novomessor cockerelli*	5.83
Deming, New Mexico	*Solenopsis xyloni*	6.67	*Pheidole desertorum*	4.68
Ajo, Arizona	*P. rugosus*	1.46	*N. cockerelli*	1.33
Ajo, Arizona	*V. pergandei*	10.17	*Pogonomyrmex pima*	1.50
Rodeo, New Mexico (A)	*P. rugosus*	6.67	*N. cockerelli*	3.72

* The s_i/b_i ratio differs significantly between group and individual foragers in a Wilcoxan Match-Pairs Signed-Rank Test ($P < .01$).

breaks down, as workers adopt increasingly independent search paths (Whitford 1976), and a marked decline in the numbers of active workers typically accompanies the disintegration of columns. I compared measurements of both the directionality of foraging and the activity levels of six *P. rugosus* colonies at the Rodeo (A), New Mexico study site for periods of high (September 1974) and low (July 1975) resource abundance. Directionality was quantified by counting the numbers of workers per 3-min interval returning to the nest entrance through each of six equal sectors radiating out from the nest mound. Observations were repeated four times during the morning activity period as soil temperatures and, consequently, activity levels changed. For each of the four sets of values, the numbers counted in all six sectors were summed.

Finally, seasonal changes in activity levels of six species of granivorous ants at Rodeo (A), New Mexico were monitored once each month for 6 mo that spanned a period of declining seed abundance. Activity levels were determined by recording the numbers of ants entering and leaving colonies within specified time intervals, and were repeated four times during the morning activity periods of each species as described above. From the four sets of values, the maximum activity level was selected for each colony, and these maxima were averaged to give a mean monthly maximum activity for each species.

TABLE 2. Responses of group and individual foragers to high and low seed densities

a. Number of seeds foraged from low density distribution ($N = 10$)

$\bar{x}$	*Pogonomyrmex barbatus* (G)	*Novomessor cockerelli* (I)	t	$P <$
1st 100 seeds	31.6	67.7	5.08	.0001
2nd 100 seeds	23.1	61.6	7.51	.00001

b. Maximum number of seeds foraged from a single clump ($N = 10$)

$\bar{x}$	G	I	t	$P <$
1st 100 seeds	48.4	19.4	4.36	.001
2nd 100 seeds	54.1	22.7	5.79	.0001

c. Evenness of clump utilization ($N = 10$) $H = -\Sigma p_i \ln p_i$

$\bar{x}$	G	I	t	$P <$
1st 100 seeds	0.71	0.93	1.86	.05
2nd 100 seeds	0.74	0.99	2.15	.025

RESULTS AND DISCUSSION

Census data

In the 1974 census, group foragers consistently had higher s_i/b_i ratios than did individual foragers of similar worker body size (Table 1; $P < .01$). Several different mechanisms, alone or in combination, could have produced this result. Group foragers may simply have found proportionately fewer baits than individual foragers, while taking approximately the same number of seeds from the baits they discovered. Alternatively, they may have used the same number of baits as individual foragers (or an even greater number) but depleted these artificially clumped resources more rapidly as a result of larger average colony size, use of recruitment chemicals, or some other adaptation for reducing worker travel times to the baits. Although the census results do not confirm the specific mechanisms of difference between group and individual foragers, they are valuable in suggesting that the two foraging behaviors may represent spatially different patterns of resource exploitation. They also provide some justification for extending the results of more detailed observations and experiments with a few species to other group and individually foraging granivorous ants as well.

Foraging experiments

The seed dispersion experiment (Fig. 1 and Table 2) provides more information on the mechanisms of difference between group and individual foragers. *Pogonomyrmex barbatus*, a group forager, tended to specialize on high density seed patches, taking proportionately fewer of the dispersed white millet seeds than did *Novomessor cockerelli*, an individual forager (Table 1a). Workers of the latter species took the greatest proportion of their seeds from the dispersed distribution, which required that seeds be independently discovered. *Pogonomyrmex barbatus* also tended to feed primarily from a single clump and thus used high density patches less evenly than did *N. cockerelli* (Table 2, b and c). The significance levels of the comparisons shown in Table 2 are consistently higher for the second than for the first 100 seeds taken from the experimental distribution, indicating that experience with the distribution may reinforce differences between the two species.

Differences were also apparent in the numbers of workers of *P. barbatus* and *N. cockerelli* responding to the experimentally supplied seeds. Colonies of *P. barbatus* collected 200 seeds within 5–10 min, while those of *N. cockerelli* commonly required 60–90 min. Workers of the latter species almost certainly spent more time locating millet seeds because they did not follow trails to high density seed patches. In comparison with the frenzied running of the group foraging *P. rugosus* workers, *N. cockerelli* workers used a slower, stalking gait. Prior to these manipulations (performed in June 1975), *P. barbatus* colonies were inactive except that several workers—perhaps scouts—emerged for brief periods on occasional mornings. *Novomessor* colonies foraged primarily at night but were active to a lesser extent each morning at soil surface temperatures lower than approximately 26°C. That colonies of both species responded to the presence of millet seeds by increasing their activity levels concurs with the observation of Whitford and Ettershank (1975) that the foraging activities of desert ants tend to be complex responses to the integrated costs and profits of foraging. The numerical response to the experimentally augmented seed supplies was dramatically greater in the group foraging *P. barbatus* than in *N. cockerelli*, but comparisons of numbers of foraging workers as proportions of total colony biomass cannot be made. During these manipulations, both species gathered millet seeds to the exclusion of all other prey, indicating that both found the seeds attractive.

In order to relate the experimentally observed differences in group and individual foragers to resource allocation in natural communities, it is necessary that native seeds have patchy distributions. Reichman (1976) has confirmed that seeds become aggregated in depressions and near obstructions in desert soils as a result of physical forces such as wind and rain. H. R. Pulliam (personal communication) has found that seeds are patchily distributed in arid grassland habitats of the Southwest and that the degree of patchiness (as measured by the variance:mean ratio of seeds in a number of surface samples) is positively correlated with seed abundance. Both seed production and germination in desert plants depend to a large extent on precipitation (Went and Westergaard 1949; Went 1955; Juhren et al. 1956; Tevis 1958*a*, *b*; Beatley 1967, 1974; Bamberg et al. 1976), and the sporadic nature of rainfall in these deserts must result in temporal as well as spatial patchiness in seed availability. The responses of group and individual foragers to temporal variability in the resource environment are considered below.

Experiments used to study foraging behavior may give conflicting or artifactual results that depend specifically on experimental design. Based on manipulations with *Veromessor pergandei*, Bernstein (1975) reached the contradictory conclusion that group foraging is adaptive for feeding on low density resources. She distributed rye grass seed in circles of 3-m radius from nest entrances and found that *V. pergandei* feeding columns broke down, and that workers began to forage independently. A more detailed understanding of the two foraging behaviors is useful in reconciling these discordant conclusions. Bernstein (1975) observed that in colonies whose workers forage independently, individuals have specific paths that they retrace on successive foraging bouts. After first returning to the point at which food was previously located, workers begin to search for additional seeds. I followed marked workers over successive foraging bouts and verified this general behavior pattern for both individual and group foragers. Group foraging workers of *Pogonomyrmex barbatus, P. rugosus, Pheidole xerophila*, and *V. pergandei* fan out on individual search paths at the distal ends of foraging columns and retrace these paths on successive excursions. Small proportions of workers digress laterally from columns near their origins, and the proportions of workers leaving the established trail increase with distance from the colony until all workers are foraging independently. This observation suggests that individual and group foragers behave similarly after they reach their respective foraging areas. *Veromessor pergandei* may travel over distances as great as 40 m in search of food. With resources augmented only 3 m from the nest mound in Bernstein's experiment, workers of this species may have responded to this "high density patch" as they would normally react to regions of relatively dense resources at the distal ends of foraging columns. Bernstein notes that *V. pergandei* workers forage independently for approximately 1 wk out of the year and that this week coincides with the period of seed production. At the time of seed set, prey should be available near the nest without the higher energy costs of foraging in columns at greater distances.

In some respects, *V. pergandei* appears to be intermediate between the more typical group and individual foragers. Although this species exploits high density resources very efficiently, as demonstrated by trail foraging to census baits (Table 1), it is also adapted to glean dispersed low density resources by rotating the foraging column at a rate which declines as resources become less abundant (Went et al. 1972; Bernstein 1975). None of the other group foragers encountered in this study appear to share this behavior. Regular and unidirectional column rotation suggests that the groups of workers discriminate levels of resource abundance and migrate in the direction of increasing

TABLE 3. Mean search time as a percentage of the total foraging bout ($\bar{x}_s$), compared for ants of similar body size collecting native seeds

Group forager	$\bar{x}_s$		Individual forager	$\bar{x}_s$	$P <$
Pogonomyrmex rugosus	76.43	<	*Novomessor cockerelli*	91.67	0.005
Pogonomyrmex rugosus	76.43	<	*Pogonomyrmex maricopa*	85.35	0.025
Pogonomyrmex rugosus	76.43	<	*Pogonomyrmex desertorum*	90.45	0.001
Pheidole xerophila	57.02	<	*Pheidole desertorum*	87.37	0.001
Individual forager	$\bar{x}_s$		Individual forager	$\bar{x}_s$	$P <$
Novomessor cockerelli	91.67	>	*Pogonomyrmex maricopa*	85.35	0.05
Novomessor cockerelli	91.67	≈	*Pogonomyrmex desertorum*	90.45	NS
Pogonomyrmex maricopa	85.35	≈	*Pogonomyrmex desertorum*	90.45	NS

seed density. Bernstein (1975) has pointed out that this behavior should maximize the time between successive visits to a given area and may be adaptive for foraging at low levels of seed abundance. *Veromessor* may employ an intermediate strategy, using group foraging techniques to reduce search times to high density patches of seeds when they are available, but employing column rotation during periods when seeds are less abundant. *Veromessor* frequently occurs in local habitats with few competitors (Davidson 1977*b*). Group foragers such as *Pogonomyrmex rugosus* and *P. barbatus* are typically associated with more diverse and abundant ant faunas, in which a strategy of regular column rotation might necessitate relinquishing valuable resources to competitors.

Foraging behavior in unmanipulated environments

Do the experimentally observed differences in density specialization result in resource allocation in the natural environment? As an indirect measure of species' encounter rates with native seeds, I have compared the search components of foraging bouts and the foraging successes of group and individual foragers feeding in an unmanipulated resource environment. These encounter rates should depend on both the absolute seed densities in the feeding grounds and the efficiencies with which ants locate seeds. Species that exploit high density resource patches or that are more efficient at finding seeds should spend a smaller proportion of the total foraging bout searching and a greater proportion travelling to and from the feeding grounds. Search components of foraging, expressed as percentages of the total foraging bouts, are contrasted in Table 3 for group and individual foragers of similar body size. Species are paired for body size in order to insure that comparisons are made only between ants with similar energetic costs that are likely to be using similar size distributions of seeds (Davidson 1977*a*). Individually foraging species had significantly greater search components to their foraging bouts in each of four possible comparisons (one-tailed *t*-tests). Table 3 also compares search components of foraging within pairs of individually foraging species of similar body size, and only one of these three comparisons yields a significant difference. For this set of species, *Novomessor cockerelli* and *Pogonomyrmex desertorum*, the difference is marginally significant ($P < .05$) in contrast to the highly significant differences between foraging types. The two group foragers differ in size by a factor of four and take very different size distributions of seeds (Davidson 1977*a*), so that comparisons between them would not be meaningful. The same may be said for comparisons between *Pheidole desertorum* (mean body length 3.4 mm) and other individual foragers (mean body lengths 7.0–9.8 mm).

In addition to spending proportionately less time searching, group foragers were somewhat more successful than individual foragers in locating food. By definition, a feeding bout was considered successful if the worker returned some item of food to the nest. Unsuccessful workers were readily apparent on the basis of their behavior as well as their empty mandibles, for they continued to search all the way back to the nest entrance. Successful workers moved swiftly and directly to the nest. Table 4 compares foraging success for four sets of species, again paired for different foraging behaviors but similar body sizes. In the two sets of species for which success differs significantly, group foragers experienced greater success than did individual foragers ($P < .05$ in both cases).

TABLE 4. Comparison of foraging success for group and individual foragers of similar body size gathering native seeds

Group forager	Foraging success (%)		Individual forager	Foraging success (%)	χ^2	$P <$
Pogonomyrmex rugosus	85.0	>	*Novomessor cockerelli*	35.0	8.44	.005
Pogonomyrmex rugosus	85.0	≥	*Pogonomyrmex desertorum*	55.6	2.69	NS
Pogonomyrmex rugosus	85.0	≈	*Pogonomyrmex maricopa*	96.1	0.65	NS
Pheidole xerophila	100.0	>	*Pheidole desertorum*	60.0	8.04	.005

TABLE 5. Comparisons of mean diet breadth ($\bar{H}$) for group and individual foragers feeding at Rodeo, New Mexico (Site A) in mid-September 1974

Group forager	$\bar{H}$[a]		Individual forager	$\bar{H}$	$P <$
Pogonomyrmex rugosus	0.31	<	*Novomessor cockerelli*	0.47	NS[b]*
Pogonomyrmex rugosus	0.31	<	*Pogonomyrmex desertorum*	0.73	.001*
Pogonomyrmex rugosus	0.31	<	*Pheidole desertorum*	0.93	.001*
Pheidole xerophila	0.37	<	*Novomessor cockerelli*	0.47	NS
Pheidole xerophila	0.37	<	*Pogonomyrmex desertorum*	0.73	.001
Pheidole xerophila	0.37	<	*Pheidole desertorum*	0.93	.001*
Pheidole sitarches	0.38	<	*Novomessor cockerelli*	0.47	NS
Pheidole sitarches	0.38	<	*Pogonomyrmex desertorum*	0.73	.001
Pheidole sitarches	0.38	<	*Pheidole desertorum*	0.93	.001*

[a] $H = -\Sigma\, p_i \ln p_i$, where the p_i are proportions of each food type in the diet, and each index is calculated from 30 food samples.

[b] The diet of *N. cockerelli* was relatively specialized during this sampling period, consisting largely of termite larvae rather than seeds.

* Pairs of species characterized by similar worker body sizes.

The proportionately high success rates and low search components that characterize foraging bouts of group foragers may be a consequence of higher encounter rates with seeds or may simply indicate that these species are less selective in making dietary choices. The latter explanation is unlikely, because the diets of group foragers tend to be considerably more specialized than those of individual foragers (Table 5). Following Colwell and Futuyma (1971), I have used the information theory index, H, to describe the equitability with which various food items are represented in the diet. (For the constant sample sizes used here, $H_{\max}$ is constant.) The data in Table 5 are based on food samples collected in September of 1974, a period of peak seed production by summer annuals at Rodeo (A), New Mexico and one of the few months during this study when almost all species were active. During this period, *Pogonomyrmex rugosus* collected predominantly the relative massive grass seeds of *Panicum arizonicum*, and the two other group foragers, species of *Pheidole*, specialized almost entirely on seeds of the annual forb, *Euphorbia serpyllifolia*. In sharp contrast, the individually foraging *Pogonomyrmex desertorum* and *Pheidole desertorum* collected seeds of diverse taxa (eight and six species, respectively) more equitably and some insects and vegetative material as well. MacArthur and Pianka (1966) and Emlen (1966) predicted an inverse relationship between a species' diet breadth and the overall level of productivity, provided that the relative proportions of the food items remain the same and that maximization of energetic efficiency is the primary goal of foraging. Smigel and Rosenzweig (1974) and D. W. Davidson (personal observation) have shown experimentally for granivorous rodents and ants respectively that selectivity increases with total resource abundance when the relative proportions of food types are held constant. These findings refer to intraspecific changes in diet breadth, and interspecific comparisons are more difficult to interpret, because species may differ in their energy budgets. However, it seems unlikely that the group foragers could afford to specialize to such a degree if they were not feeding in relatively productive habitats. Formation of trails to high density patches may increase encounter rates with seeds and make it energetically feasible to specialize on seeds offering a high net reward.

The foraging behavior of *P. rugosus* changes seasonally as shown in Fig. 2. Lengths of the arrows in this diagram express the percentage of workers foraging in each of six equal sectors radiating from the nest entrance of colony R at Rodeo (A), New Mexico. The strong directionality of foraging during the peak seed production period of September 1974 contrasts sharply with the much more uniform distribution of foragers in July of 1975—a full 8 mo after the most recent seed crop had matured. The transition from group to individual foraging was accompanied by a greater than twofold decline in the number of actively foraging workers in spite of the recent rainfall that had enhanced activities during the July measurements (see below). Similar patterns were observed in the other five colonies for which directionality was quantified. Table 6 shows that the equitability of utilization of six

TABLE 6. Seasonal change in the directionality of foraging in *Pogonomyrmex rugosus* at Rodeo, New Mexico (Site A)

Colony	September 1974[a] H[b]		July 1974 H
P	0.92	<	1.53
G	0.59	<	1.67
R	0.68	<	1.69
OS	0.81	<	1.41
ON	1.21	<	1.46

[a] In September 1974, a large crop of summer annuals was maturing, and seeds were very abundant. Ten months later in July 1975, no intervening seed set had occurred, and seed reserves in the soil had been substantially depleted.

[b] $H = -\Sigma\, p_i \ln p_i$ represents the evenness of utilization of 6 equal sectors around the nest ($H_{\max} = 1.79$).

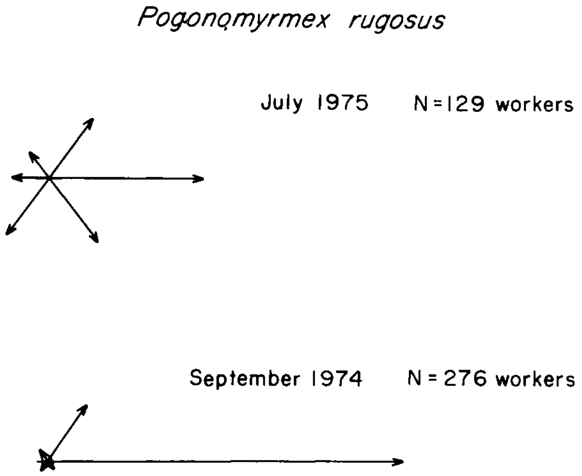

FIG. 2. Directionality of foraging during periods of high (September 1974) and low (July 1975) seed abundances for *Pogonomyrmex rugosus* (colony R) foraging at Rodeo, N. Mex. Lengths of the lines are proportional to the numbers of workers using each of six equal sectors radiating from the nest entrance.

sectors ($H = -\Sigma p_i$) ln p_i is greater at low than at high levels of available seeds for all six colonies sampled. In late summer of 1974, trunk trails were observed to form gradually over approximately 1 mo at colonies of *P. rugosus*. The few workers that remain active during periods of reduced resource abundance may fulfill the role of scouts, dispersing and alerting their nestmates to any sudden increase in available forage. If a net energy loss is accrued as a result of this behavior, it may be balanced by occasional discoveries of dead or dying insects or other such unpredictable rewards that provide protein or other important nutrients.

Activity patterns of group and individual foragers

Interspecific differences in the activity schedules of desert seed-eating ants may represent mechanisms of resource allocation over an annual or seasonal time scale. The pattern of seed renewal (one or two pulses of seeds annually) would seem to preclude temporal partitioning of resources over a 24-h cycle of temperature change. In an extensive and thorough investigation of the factors affecting the foraging activities of four species of harvester ants in the Chihuahuan Desert, Whitford and Ettershank (1975) found very similar temperature tolerances among species whose seasonal and diurnal foraging patterns were often very different. They noted that activity schedules are not predictable on the basis of any single variable but are integrated responses to complex physical and biotic factors that interact to specify the costs and profits of foraging. These parameters include food availability, the capacity for food storage, and the degree of colony satiation as well as surface temperatures and vapor pressure deficits (Whitford and Ettershank 1975; Kay and Whitford 1975; Ettershank and Whitford 1973). The variability introduced by all of these contributing factors complicates any search for patterns.

I hypothesized that group and individual foragers should differ in their seasonal activity schedules as a result of their specializations for exploiting different seed densities. During the period in which activities were measured for common species at Rodeo (A), New Mexico, the only significant seed set occurred in September of 1974. Winter rains were not substantial, and those few plants that germinated in the spring persisted as rosettes until the onset of summer rains. Summer seed set was somewhat delayed in 1975, beginning in mid-September. If activity levels are plotted as percentages of the maximum activity measured for the species during the 6 mo of observations, the curves are strikingly consistent for species with similar foraging behaviors (Fig. 3). Group foraging species, to the left of the figure, were entirely inactive during several of the censuses, and their activities peaked just after seed set, in fall 1974. The second peak, of smaller amplitude, in July 1975 represents the immediate response to a rainstorm the previous night. On the day prior to this census, and again 3 days after the storm, colonies of *Pogonomyrmex rugosus* were completely inactive, and those of the two *Pheidole* species were active at approximately the same levels as in July and September 1975. The response to rainfall may be indicative of a decline in the costs of foraging because of higher humidities or of an increase in the profitability of foraging based on the concentration of surface seeds by rainwater (Reichman 1976). For all three group foragers, activities during the remainder of the sampling periods averaged less than 5% of the maximum activity measured during the six periods of data collection. Foraging of *Solenopsis xyloni* was not monitored regularly, but the general activity schedule resembles those of other group foragers. Colonies of *S. xyloni* were difficult to locate throughout much of the year, except in the presence of seed baits. During peak seed abundance in late summer of 1974, colonies of this species became very conspicuous and harvested large numbers of native seeds.

Among individual foragers (right side of the figure), foraging was less an "all or none" phenomenon. Intermediate levels of activity occurred during most months and appear to be generally correlated with temperature and moisture conditions. The particularly low activities of *Novomessor cockerelli* and *Pheidole desertorum* in April may reflect the marginally suitable temperatures in early spring. Humidities were very low in June, another period of little activity among all ant species. The timing of peak activity in *N. cockerelli* is probably associated with the rainstorm in mid-July. Workers of this species collected many termites during this period, and these greatly increased in availability following the precipitation.

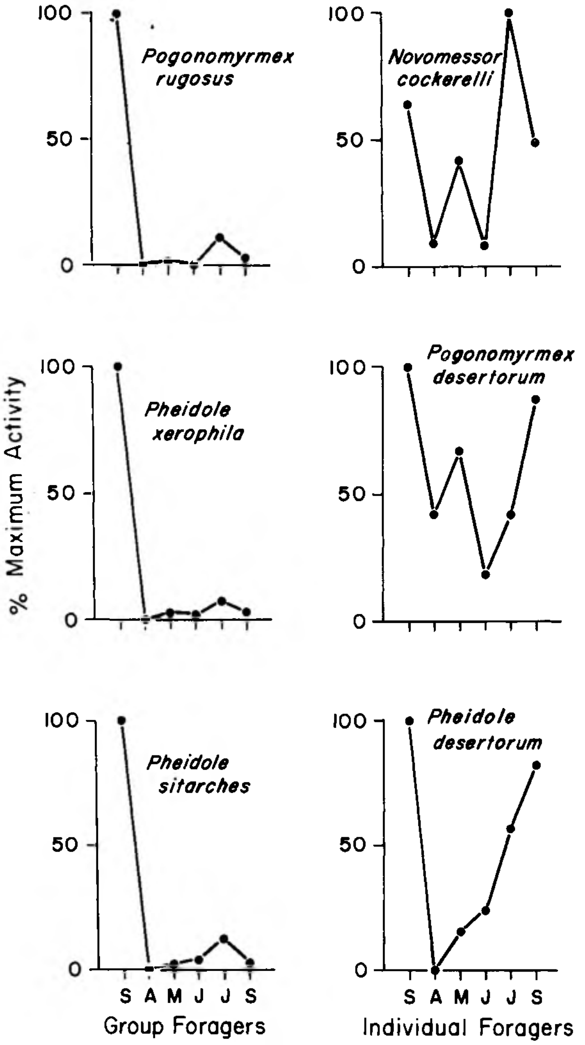

FIG. 3. Activity levels measured during the morning foraging periods for six species of seed-eating ants at Rodeo, N. Mex. In the order recorded on the abscissa, the months are: September 1974 and April, May, June, July, and September 1975. Maximum activity is defined as the greatest activity level measured during any of these six observation periods. Those species whose colonies had generally lower activity levels were observed for longer time periods. Numbers of colonies observed and lengths of observations (in parentheses) are: *P. r.*—6 (3 min); *N. c.*—6 (10 min); *P. x.*—6 (1 min); *P. d.*—6 (10 min); *P. s.*—6 (1 min); and *Ph. d.*—4 (10 min).

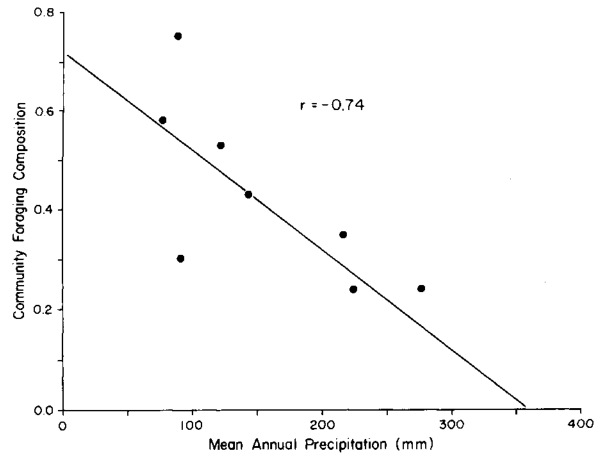

FIG. 4. Composition of the granivorous ant communities relative to the foraging methods used by component species as a function of the precipitation index of productivity ($P < .05$). Higher foraging scores indicate a greater proportion of low density specialists. See text for details of computing these indices.

Community composition relative to foraging behavior

If foraging behaviors represent specializations for resources of different density, the abundance and predictability of seed resources should influence the proportions of group and individual foragers within ant communities. High density specialists should predominate where seed crops are relatively frequent and abundant and low density specialists where they are not. The more productive census localities studied here, those in southeastern Arizona and southwestern New Mexico, are characterized by two annual rainfall peaks (Bryson 1957), each associated with a distinctive annual flora (spring and summer annuals). In contrast, the relatively xeric habitats in southeastern California and southwestern Arizona typically experience only winter rains that give rise to spring annuals. Although rainfall is sporadic over all of the deserts, the census localities span a gradient of precipitation and, consequently, of production.

It is possible to assign a "foraging score" to each ant community based on the number of species using each foraging behavior and weighted by their relative abundances as determined from the census data. Because seasonality may differentially influence the activity schedules of group and individual foragers, only the August census data are used. Group foragers other than *V. pergandei* were scored as zero, and individual foragers as one. *Veromessor pergandei* received a score of 0.5, because this species employs specializations for gathering seeds from both high and low density distributions. Figure 4 illustrates the significant inverse relationship between community foraging score and mean annual precipitation at the census locality ($r = -.74$; $P < .05$). Group foragers comprise a significantly greater proportion of the total granivorous ant community in more productive habitats. In two even more mesic arid grassland habitats in southern Arizona, I have observed that the relative abundance of individual foragers is still further reduced.

GENERAL DISCUSSION

In eusocial insects, competition may constrain not only a species' distribution, ecology, and morphology, but potentially its social characteristics as well. For example, Wilson (1971) hypothesized that ant species confined by competition to particularly small nest sites might undergo evolutionary reduction in colony size and that, in the event of severe reductions, they might also lose their capacities to communicate by odor trails. Elsewhere (Davidson 1977*b*), I have suggested that, in at least one species, *Veromessor pergandei*, caste ratios respond to changes in the competitive environment. Interspecific differences in colony foraging behaviors have been described and implicitly or explicitly related to competition for a number of species of social insects (Dobrzańska 1966; Bryan 1965; Yasuno 1965; Wilson 1971; Levins et al. 1973; Johnson and Hubbell 1975). Although differences in foraging behavior and related variation in aggressiveness and territoriality have sometimes been interpreted in the context of evolutionary progression in colony sophistication (Hölldobler 1971; Wilson 1971), others (Carroll and Janzen 1973) have cautioned that such adaptations are likely to appear and disappear repeatedly during the evolutionary histories of particular taxa in response to changing environmental selection pressures.

Among the desert seed-eating ants studied here, species-specific differences in colony foraging behaviors are associated with resource subdivision on the basis of seed density and dispersion and appear to promote coexistence between species with similar food requirements. Evidence that coexisting species of these ants compete for food and that competition affects the organization of ant communities with respect to the worker body sizes and colony foraging strategies of component species is given in a companion work (Davidson 1977*a*). The foraging behaviors of these ants appear to represent evolutionary responses to resource dispersion and are not simply maintained by high density specialists aggressively excluding other species from richer resource patches (Davidson 1977*a*). Although one individual forager, *Pogonomyrmex desertorum*, is aggressively excluded from the core feeding grounds of the group foragers, *P. rugosus* and *P. barbatus*, in habitats where these group foragers are absent or seasonally inactive, *P. desertorum* continues to employ individual foraging. This behavioral consistency characterizes other individual foragers as well.

I have argued that group foraging is primarily a specialization for exploiting high density resources efficiently. Although other effects may be associated with this behavior, it is likely that these represent secondary consequences of group foraging rather than ultimate explanations for its existence. Hölldobler (1974, 1976) suggested that, once formed, the trunk trail systems of *Pogonomyrmex rugosus* and *P. barbatus* function in reducing intraspecific aggression, but proposed that the paths originate from recruitment trails, presumably to some relatively productive resource patch. Group foraging may also facilitate travel by workers through dense vegetation during seasons of abundant plant cover, but it is frequently observed in cleared areas as well (Hölldobler 1976; Whitford 1976 and the censuses and experiments discussed here).

The foraging methods of ants may be differentiated more finely than I have distinguished them here on the basis of such characteristics as recruitment chemistry, orientational cues, and the relative permanence of feeding columns (Wilson 1971; Carroll and Janzen 1973; Bernstein 1975; Hölldobler 1976). In her studies of seed-eating ants in the Mojave Desert, Bernstein (1975) distinguished group foragers (species in which individual workers collect food independently of one another but move in columns or over trails) from recruit foragers (in which independently searching "scout" workers recruit nestmates for a highly coordinated group effort at collecting food) and classified *Veromessor pergandei* as the former. Although this classification scheme has been widely used (Wilson 1971; Carroll and Janzen 1973), it is probably an oversimplification. Because the values of foraging methods may vary with the pattern of resource renewal, mixed strategies are frequently employed, and combinations of cues may be used for orientation (Hölldobler and Wilson 1970; Hölldobler 1971, 1976). This may be especially true for desert granivores, since the availability of seed reserves in these habitats is extremely variable in both space and time (Reichman 1974, 1976).

The difficulties associated with attempting a more detailed classification of foraging behavior in desert harvester ants on the basis of simple field observations may be illustrated by examples. At some of the 10 desert locations censused in this study (for example, Tacna, Arizona and Barstow, California), colonies of *Veromessor pergandei* appeared to recruit to bait stations that were not in direct line with their preexisting feeding columns, and foraging proceeded uninterrupted during the nocturnal hours. Both of these observations suggest some chemical means of orientation (though they do not require such an explanation). Colonies of *V. pergandei* at other sites removed seeds primarily from baits that lay in close proximity to preexisting columns and curtailed their activity immediately upon the advent of darkness. Differences in the recent feeding histories of colonies may have produced these discrepancies. An additional example of the practical difficulties of categorizing species as group or recruit foragers concerns what Hölldobler terms "mass foraging" in *Pogonomyrmex rugosus* and *P. barbatus*. Hölldobler (1976) argues that the trunk trails of these species originate from recruitment trails, but after their formation, the feeding columns strongly resemble those of *Veromessor pergandei*, except that they do not show the same pattern of regular rotation. In her Mojave Desert study plots, Bernstein (1975) found that *P. rugosus* used the individual foraging method; but this difference may have constituted a response to some ecological variable such as resource availability or recent feeding history of the colonies rather than representing any evolutionary difference.

Because of complications such as these, I made no attempt to distinguish group foraging from recruit foraging, and the experiments and observations undertaken here were designed only to point out the general consequences of group (or recruit) foraging versus individual foraging. As defined here, individual foragers are those species never noted to form distinct columns while gathering native seeds, although certain of these appeared to forage in a coordinated fashion while dismantling large insects or when seed baits chanced to be located very near the nest entrances during a census. Species that formed distinct columns to feed from soil reservoirs of native seeds as well as from seed baits are classified as group foragers. Categorizations are based on numerous observations of ants collecting native seeds over a range of seasons and levels of resource abundance. Although *Pogonomyrmex rugosus* employed individual foraging when seeds were relatively rare, this species was classified as a group forager, because activity levels were substantially higher (Figs. 2 and 3) and significantly more seeds were collected by group foraging colonies during peak seed production periods.

Density specialization and resource allocation

The results of this study are markedly similar to those of Johnson and Hubbell (1975), who analyzed coexistence of group and individually foraging bees on nectar resources of the shrub *Cassia biflora* in a tropical dry forest habitat of Costa Rica. These authors demonstrated that the group foraging bee, *Trigonia fuscipennis*, specialized on clumps of *Cassia* flowers, while an individual forager, *T. fulviventris*, exploited primarily spatially dispersed flowers of the same shrub species. They suggested that the separation of feeding grounds is maintained in part by *T. fuscipennis* actively excluding *T. fulviventris* from the densest flower patches and in part by evolved differences in density specialization between group and individual foragers. To account for local coexistence of these nectar-feeding bees, Johnson and Hubbell (1975) proposed a hypothetical cost-benefit relationship similar to that shown in Fig. 5. Their hypothesis is consistent in several ways with what is known of group and individual foraging in granivorous ants and is useful in identifying the kinds of measurements that may eventually prove necessary to explain coexistence based on density specialization.

In Fig. 5, B_G and B_I are benefit functions of food density for high (G) and low (I) density specialists exploiting a single resource. Benefits may be conceptualized as species-specific, per colony rates of resource intake. Both species profit as resource density increases until a saturation density is reached, but benefits are assumed to accrue more rapidly and to reach a higher maximum for the group forager (species G). In order for the resource in Fig. 5 to be stably partitioned, there must exist resource densities at which the low density specialist alone can forage. The Johnson and Hubbell hypothesis incorporates a refugium for individual foragers by assuming higher maintenance costs for group foragers ($C_G > C_I$ for all d, where d is actual seed density) based on larger mean colony size and some unspecified "adaptive syndrome" of high density specialization. The graph shows that, as encounter rates with resource increase, the energetic costs of feeding diminish for both group (C_G) and individual (C_I) foragers (though a decline in the cost functions is not essential to their argument). Species are assumed to feed profitably only in regions of the graph, lined for species I and shaded for species G, where benefits exceed costs ($d > d_I$ and $d > d_G$ respectively). When $d_I < d < d_G$, only individual foragers can feed with a net profit. Although both species can harvest the resource where $d > d_G$, the high density specialist feeds with greater efficiency (B-C) over much of this region.

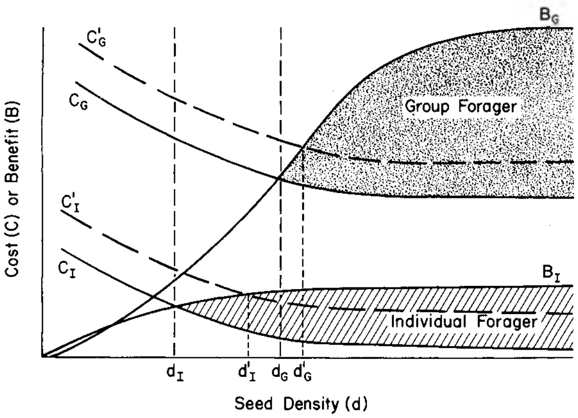

FIG. 5. Hypothetical cost-benefit analysis of high and low density specialists using a common resource. See text for details. (Modified from Johnson and Hubble 1975).

The data are not available to uniquely specify the cost and benefit curves of group and individually foraging ants, but some evidence exists in support of certain qualitative features of the above hypothesis. As illustrated by the foraging experiments, when resources are patchily distributed, group foragers have specializations that enable them to concentrate their foraging in regions of high seed density. Even in uniformly productive habitats with no patchiness, colonies of group foragers should have greater feeding rates if, on the average, they tend to be more populous than those of individual foragers. The strong subjective impression that this is so is difficult to verify, as commonly used mark-recapture studies assess only populations of active workers and will underestimate the sizes of colonies that are not foraging at or near maximum capacity. With respect to the cost curves, the activity schedules of group and individually foraging ants are consistent with the interpretation that specializations for exploiting high density resources may entail expensive adaptations that make foraging energetically unprofitable under other resource regimes. While my observations and those of Whitford and Ettershank (1975) indicate that resource availability and climatic factors influence the activities of both group and individual foragers, Fig. 3 demonstrates that fluctuations in levels of foraging activity are more extreme in group than in individual foragers.

Disparities in the maintenance and foraging costs of granivorous ants specializing on high and low density resources may be related to several factors in addition to average colony size. First, group and individual foragers probably invest differentially in recruitment chemicals. Hölldobler (1974) reported that the individually foraging workers of *Pogonomyrmex maricopa* rely primarily on visual orientation, although they sometimes used short-lived chemicals to recruit over short distances. In *P. rugosus*, a group forager, Hölldobler found that chemical orientation was considerably more important, especially during nocturnal feeding activity. The only five species that never foraged at night in the presence of census baits (*P. maricopa, P. californicus, P. pima, P. desertorum,* and *P. magnacanthus*) are individual foragers, and this may in part reflect a reduced capacity on the part of these species to navigate chemically. Although production of costly chemicals may not be energetically justified for species feeding on dispersed resources, the potential for extending activity into nocturnal periods should be an important asset to species that depend on gathering food when it is very abundant. This is especially true, because ants may be competing with unrelated desert granivores such as rodents (Brown and Davidson 1977) that may also forage selectively on high density distributions of seeds (Brown et al. 1975; Reichman and Oberstein 1977).

Other factors may effect disparities in the foraging costs of group and individual foragers. For example, high and low density specialists may differ in the extent to which they build and maintain granaries for seed storage. The nests of group foragers such as *Pogonomyrmex rugosus, P. barbatus*, and *V. pergandei* contain extensive granaries, but Whitford and Ettershank (1975) report that *P. californicus* and *P. desertorum* (both individual foragers) do not appear to store seeds. Predator pressure may differ to some extent on group and individual foragers. Though many organisms occasionally utilize desert ants as food, the most important and consistent predators of these ants may be lizards of the genus *Phrynosoma*. These lizards tend to feed at nest entrances and, when choosing among ants of similar worker body size, may prefer group foragers when active, because workers of these species tend to enter and leave the nest at the most rapid rate (D. W. Davidson, personal observation).

Clumped and dispersed distributions of seeds in deserts are probably not independently renewing food types. Physical mixing of seeds from various density distributions should occur when wind and rain disperse existing clumps and form new ones, and seed density generally declines between seed production periods as seeds become buried or are harvested by granivores. In the hypothetical consideration of density specialization depicted in Fig. 5, changes in climatic variables such as temperature and vapor pressure deficit may alter the cost functions uniformly over all densities (C_G' and C_I'), moving the critical intersections of cost and benefit functions to higher or lower seed densities (d_G' and d_I'). Granivorous desert ants also subdivide seeds on the basis of particle size (Davidson 1977*a*), but group and individual foragers of similar body size probably share the same resource pool to some degree.

Can the number of coexisting species exceed the number of resources? Several recent theoretical works have affirmed this possibility (Haigh and Maynard Smith 1972; Stewart and Levin 1973; Koch 1974*a*, *b*; Armstrong and McGehee 1976). Stewart and Levin (1973) demonstrated that stable coexistence of two species on a single resource is mathematically possible for periodic environments of alternately high and low resource levels, in which interactions between competing populations are determined entirely by the efficiencies with which individuals of each species acquire and convert resources at different resource concentrations. Utida (1957) experimentally obtained coexistence of two species of predatory wasps on a single prey population of beetles and showed that one species was the more effective predator at high prey densities and the other at low densities. Whereas the model of Stewart and Levin presumes that resources renew with regular magnitude and periodicity, Utida's beetle populations (and populations of their predators as well) fluctuated erratically over 4 yr and more than 70 generations without any of the three species going extinct.

Although the pattern of seed renewal in deserts is much less regular than the resource renewal assumed by Stewart and Levin (1973), long-term profiles of resource availability in different density distributions may predictably include sufficient seeds in high and low density distributions to support both group and individual foragers. Adaptations such as hibernation, estivation, and seed storage should help to moderate the environmental uncertainty encountered by these desert granivores and reduce the likelihood that either high or low density specialists will be eliminated. In part as a result of such evolutionary responses (frequently neglected in models that analyze coexistence in ecological time), community composition may reflect long-term profiles of resource availability in the habitat. In the relatively mesic deserts of southeastern Arizona and southwestern New Mexico, seed production should be more frequent and copious on the average than in the more xeric regions of southeastern California and southwestern Arizona, and it is here that group foragers reach their greatest relative abundance. The tendency for community composition to reflect the production spectrum of resources suggests that studies of resource allocation on the basis of density specialization might profit from an approach commonly applied to studies of resource subdivision on other dimensions. Rather than asking whether or not species can coexist on the basis of density specialization, we might ask how similar these species might be in their use of different density distributions and yet coexist.

Finally, precipitation in deserts is often patchy in space as well as time. Local extinctions undoubtedly occur, but rapid recolonization by vagile winged reproductive forms from spatial refugia may enhance the predictability of community organization and species diversity even within local habitats.

ACKNOWLEDGMENTS

I am grateful for the assistance of many people during the course of these investigations. James H. Brown generously provided helpful counsel and stimulating discussion throughout the study and read earlier drafts of the manuscript. Karen Zamanek and Sanuel Davidson assisted in the field under very trying and uncomfortable conditions. Logistic assistance was given by H. Bond, and E. Roos, and G. and A. Miller furnished shelter near the Rodeo, New Mexico study area. Conversations with T. C. Gibson and K. Zamanek were particularly helpful. I thank Roy R. Snelling for identifying some of the ants and H. R. Pulliam for permitting me to cite his unpublished data. This research was supported by the Desert Biome of the International Biological Program (Grant No. 556 to James H. Brown) and two grants to the author from the Society of the Sigma Xi and was submitted in partial fulfillment of requirements for the doctoral degree at the University of Utah. The University of Utah provided a graduate research stipend for 1 yr.

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