Competition and the Structure of Granivore Communities

Diane W. Davidson, James H. Brown, and Richard S. Inouye

Historically, studies of competitive interactions in ecosystems have been based on one of two approaches. A comparative approach has dominated investigations of competition between taxonomically related species that share similar morphological, physiological, and behavioral traits. Notwithstanding their general likenesses, these species often differ from each other in one or a few characteristics that reduce overlap in the use of resources. Ecologists have interpreted the differences in the body sizes, feeding structures, microhabitat specializations, and foraging behaviors of related and coexisting species as evidence for the importance of competition in structuring natural communities. The theoretical underpinnings of this comparative approach to the study of competition predict "limiting similarities" in characteristics relevant to allocation of scarce resources (May and MacArthur 1972, and reviewed in Schoener 1974).

A second approach to studying competition employs experimental manipulations of resources and/or competitive regimes. Because experimental methods do not depend on similarities of form and function between presumed competitors, this approach is more general and has proven especially useful in analyzing interactions between phylogenetically unrelated species. Such interactions are particularly common in space-limited systems; for example, organisms as distant taxonomically as plants and sessile animals compete for space on rocky ocean shores (Lubchenko and Menge 1978). Like competition for space, competition for food resources is not limited to closely related species. As investigations have expanded to include distantly related taxa, the inadequacies of the comparative approach have become increasingly apparent, and experimentation has gradually assumed a more prominent role in community-ecological research.

Here we trace the development of our investigations of granivory in desert ecosystems, illustrating the synthesis of the comparative and experimental approaches and noting the essential contributions of both. In the process, we also call attention to several major difficulties inherent to experimentation on this scale and describe some relatively unconventional experiments designed to circumvent some of these problems.

DESERT GRANIVORES AND THEIR RESOURCES

Associations of seed consumers in arid habitats of the southwestern United States have proven very useful systems for analyzing competitive interactions in ecosystems. Local granivore assemblages frequently contain representatives of several kinds of specialized seed-eaters, including birds, rodents, ants, and other insects. Our studies have emphasized ants and rodents, two groups of seed harvesters that are abundant and permanent residents of local habitats and have relatively generalized diets. As many as 14 common species of seed-eating ants and rodents may coexist and share seed resources in local habitats (see Figure 1).

Seeds of both annual and perennial plants are consumed by desert granivores, but those of annuals predominate in the diets of ants and rodents. The seeds of annuals may regularly constitute more than 95% of the total standing crop of seeds by number and more than 80% by biomass (Nelson and Chew 1977). Rapid, facultative development of annuals in response to available moisture effectively couples production of green vegetation and seeds to the infrequent and unpredictable precipitation that limits productivity in arid regions. Geographic gradients in the magnitude and predictability of precipitation are reflected in patterns of seed production. Eastward and northward from the Mojave Desert of southern California, both the mean annual precipitation and the mean amount of predictable precipitation increase, and there are corresponding increases in the productivity and standing crop biomass of both vegetation and seeds.

THE COMPARATIVE APPROACH

The distribution and coexistence of ants and rodents over the southwestern deserts afforded an excellent opportunity to gain rapid insight into processes determining the diversity and structure of granivore communities. We began by censusing rodents (Brown 1973, 1975) and ants (Davidson 1977a, b, Brown and Davidson 1977) over a gradient of precipitation and seed productivity.

Along a transect eastward from southern California into southern Arizona and southwestern New Mexico, patterns in the species diversity of ants and rodents are strikingly alike. Within each fauna, species richness increases along the gradient of resource productivity. The most diverse local assemblages of granivores occupy the extreme southeastern corner of Arizona, where rainfall and seed production are most bountiful and predictable. Estimates of ant and rodent numbers and biomass also vary directly with productivity. Within each of the two major taxa, the number of common species that occur together in a local habitat is significantly fewer (by approximately five species for both rodents and ants) than the number of species whose geographic distributions make them potential colonists of these sites. These patterns constituted our first indirect evidence that coexistence of granivores might be limited by competition for food.

Further indication of the importance of resource competition emerged from

---

Davidson is an assistant professor of biology, University of Utah, Salt Lake City, UT 84112; Brown is a professor and Inouye is a graduate student, both in the Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721.

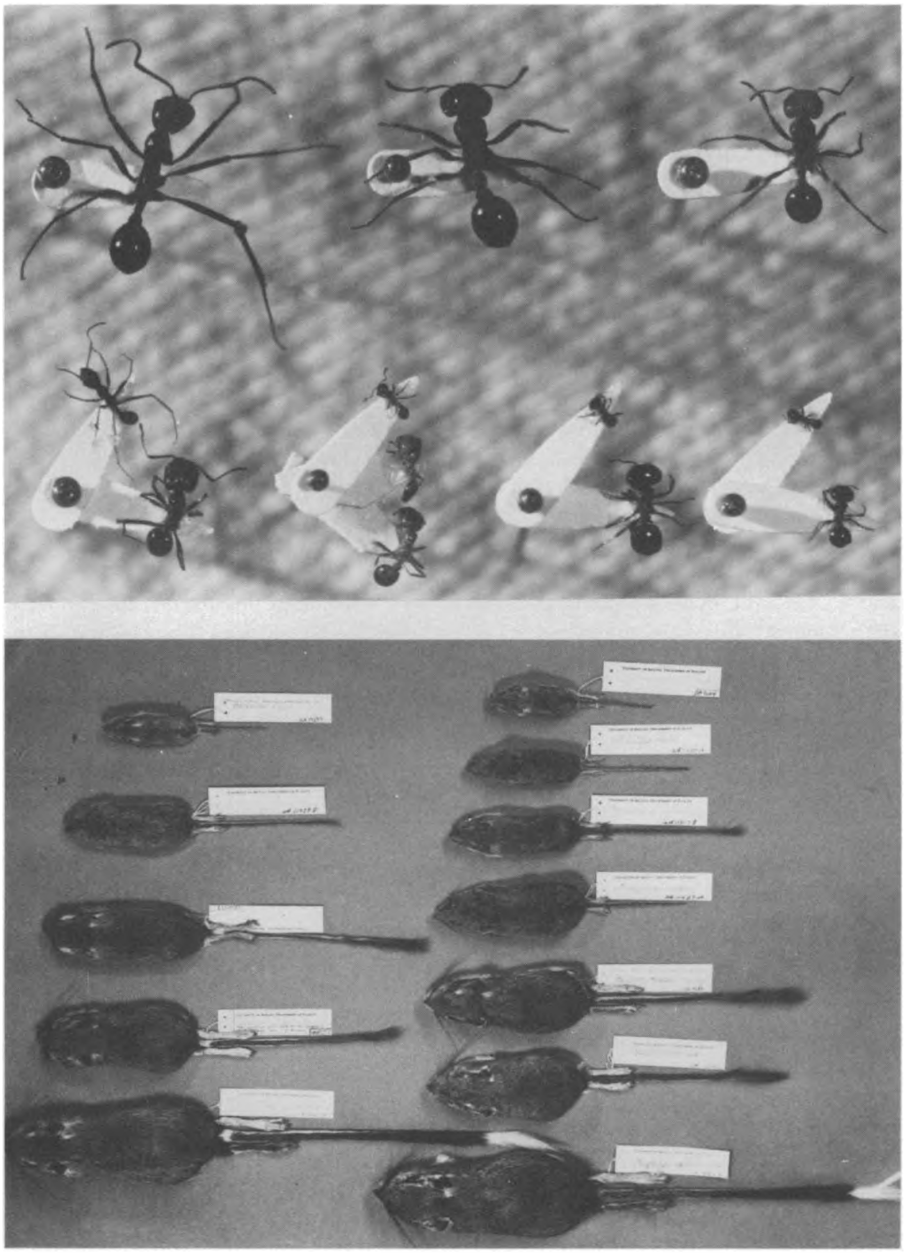

Fig. 1. Seed-eating ants and rodents inhabiting the Chiricahua Bajada study site near Portal, Arizona. Within each group note the obvious body size differences among coexisting species. From left to right, the ants are (top row): *Aphaenogaster (Novomessor) cockerelli* (I = individual forager); *Pogonomyrmex rugosus* (C = column forager); *P. desertorum* (I); and (bottom row): *Pheidole desertorum* (I, worker and soldier castes); *Solenopsis xyloni* (C, minor media, and major); *Ph. xerophila* (C, worker and soldier) and *Ph. sitarches* (C, worker and soldier). Rodents in the lefthand column include only specialized seed-eaters. From top to bottom, these are *Perognathus flavus, P. penicillatus, Dipodomys merriami, D. ordi,* and *D. spectabilis*. In the righthand column are included two additional species whose more generalized diets also contain many seeds. From top to bottom, these are *Perognathus flavus, Reithrodontomys megalotus, P. penicillatus, Peromyscus maniculatus, Dipodomys merriami, D. ordi,* and *D. spectabilis*.

analyses of spatial pattern in granivore communities over the same environmental gradient. Ant species characterized by small foraging territories and limited worker mobility decrease in abundance as mean annual precipitation and productivity decline (Davidson 1977a). For these stationary, ground-nesting species, availability of seed resources depends on access to space. Colonies with limited foraging areas are probably unable to acquire sufficient food for maintenance and reproduction where seed densities are very low. Within individual localities, uniform intraspecific spacing of ant colonies (Bernstein 1975, Hölldobler 1976) and of mounded burrow systems of some rodents (Schroder and Geluso 1975) reflect the desirability of excluding conspecifics from the feeding grounds.

Indirect evidence for resource competition also comes from the composition of local granivore associations. Where food resources limit consumer populations, differential use of resources should be a requirement for coexistence. Interspecific morphological and behavioral specializations characterize co-occurring species of both ants and rodents. The most striking patterns involve interspecific differences in body sizes (see Figure 1). Coexisting associations of harvester ants often differ conspicuously in worker body size, although species of similar body size can coexist if they differ in colony foraging mode (Davidson 1977a). Experiments and observations suggest that column-foraging ants have relatively populous colonies that specialize temporally and spatially on energetically rich concentrations of seed, whereas species whose workers forage solitarily gather primarily dispersed seeds (Davidson 1977b).

Harvester species that are alike in both worker body size and colony foraging behavior tend not to coexist locally within homogeneous habitats, even at localities that fall within the distributional ranges of both species. The interspecific territorial defense that occurs between some such species pairs (Hölldobler 1974, Whitford et al. 1976) suggests that these species are strong competitors and serve as ecological replacements for one another (Davidson 1977a).

The importance of worker body size to coexistence of harvester ants is perhaps best exemplified by the pattern of size specialization in relationship to faunistic diversity (Davidson 1978a). Dominating the depauperate communities of the relatively arid and unproductive Mojave and Colorado deserts is *Veromessor pergandei*, whose colonies display a continuous polymorphism in worker body size. Where this species is the only common harvester ant, the polymorphism is most extreme, and workers range from 3.5 to 8.5 mm in body length. The pattern of worker-size polymorphism in *V. pergandei* responds in a remarkedly precise way to changes in the competitive environment (Davidson 1978a). In more productive habitats at the eastern edge of its distribution, this ant occurs with larger and smaller ant species, and its colonies have relatively monomorphic workers of an intermediate body size. In the still more diverse and species-rich Chihuahuan Desert of southeastern Arizona, *V. pergandei* is replaced by more specialized monomorphic species.

Patterns in the organization of communities of harvester ants suggest that differences in worker body sizes functionally differentiate the ecological roles of coexisting species. Two kinds of empirical data support this interpretation (Davidson 1977a, 1978a). In experiments where ants were permitted to select from four sizes of quality-standardized seeds, worker size was strongly and positively correlated with an index of seed size both in interspecific comparisons and within colonies of *V. pergandei*. Similar relationships hold for ants collecting native seeds.

Mechanistic upper limits and energetic lower limits appear to determine the sizes of seeds that can be exploited profitably by worker ants of a given body size (Davidson 1978b). However, body size is a complex character and may influence ecological function in many ways. Recent multivariate analyses relating harvester ant diets to the pattern of resource availability suggest (though do not prove) that large body size also enhances both worker mobility and the capacity for ants to feed selectively on rare and patchily distributed but energetically superior resources (Davidson, unpublished analysis).

Similarly, body size patterns provide circumstantial evidence for competitive organization of rodent communities. In sand dune habitats spanning a latitudinal gradient of increasing precipitation, productivity, and species richness, the body sizes of coexisting rodents differ more than would be anticipated on the basis of random co-occurrence of those species whose geographic ranges allow them potential access to these sites (Brown 1973). Structurally and functionally convergent rodent communities characterize geographically distinct deserts of similar productivity (Brown 1975). Different species with similar body size and locomotory specialization represent ecological counterparts inhabiting geographically disjunct deserts.

Because rodents are much larger in relationship to their resources than are ants, simple differences in the sizes of seeds foraged are less likely to provide a functional basis for body size displacement. For seed types differing in size and dispersion, the foraging efficiencies of rodents are apt to be determined by a number of morphological and behavioral characteristics that correlate with body size. For example, the greater energetic expenditures of larger bipedal rodents such as kangaroo rats (genus *Dipodomys*) may constrain them to forage on large seeds or clumps of smaller seeds, whereas smaller scansorial rodents can profitably use small scattered seeds (Brown 1975, Brown and Lieberman 1973, Hutto 1978, Price 1978a, Reichman and Oberstein 1977).

Tendencies for ecological separation in foraging microhabitats are correlated with locomotor specializations in desert rodents. While quadrupedal pocket mice (genus *Perognathus*) tend to feed predominantly in or under vegetation, bipedal kangaroo rats (genus *Dipodomys*) and kangaroo mice (*Microdipodops*) are well adapted to locate seeds in the open. Their saltatorial locomotion permits rapid coverage of the territory separating resource patches and may also facilitate escape from predators (Brown 1975, Brown and Lieberman 1973, Lemen and Rosenzweig 1978, Price 1978b, Rosenzweig 1973, Wondolleck 1978).

That such microhabitat separation may be maintained in part by interspecific competition is evidenced by shifts in resource utilization accompanying changes in the competitive environment. On isolated sand dune habitats in the eastern Great Basin, where *Dipodomys ordi* occurs with a few other rodent species, this species forages in a wider range of microhabitats,[1] broadens the seed diet, and attains greater population densities (Brown 1973) than where it coexists with diverse species of rodents on less isolated dunes.

Thus, studies based on the comparative approach have revealed remarkably similar patterns of community diversity and structure in two major taxa of generalist granivores. We can infer that competition has played a prominent role in the assembly of local communities of both harvester ants and seed-eating rodents. Although circumstantial, the evidence for competition is strong because it has been derived from several independent lines of argument. Patterns of ecological separation within the two groups have probably arisen by distinctive routes that reflect basic biological differences between the two taxa. Despite such differences, the form of resource allocation is similar within ant and rodent communities, probably because of the similarities in the availability of seed resources to both groups.

Extensive biological differences between ants and rodents do not exclude the potential for competitive interactions between them, but they do preclude our use of the comparative approach to seek indirect evidence of such competition. Broad overlap in the sizes (Brown and Davidson 1977) and species (Table 1) of seeds used by the two taxa suggests the potential for competition. But though dietary overlap is a necessary condition for competition, it is not a sufficient criterion.

Tentative biogeographic evidence also hints at the possibility of competition between harvester ants and seed-eating rodents (Brown and Davidson 1977). Whereas both faunas become increasingly abundant and species-rich along a longitudinal gradient of enhanced precipitation and production, harvester ants decline in diversity and biomass over a similar but latitudinal gradient. Cooler mean temperatures at high latitudes in the Great Basin Desert may confront ectothermic ants with abbreviated foraging seasons and actually reduce the level of seed productivity effectively harvestable by them. Rodents appear to compensate for the missing ants by becoming even more populous and diverse (Brown and Davidson 1977). But the possibility of niche expansion and density compensation in the rodent fauna must be viewed cautiously, since translation of precipitation to productivity need not be identical along the two environmental gradients where the seasonality of precipitation is notably different. Cross-community comparisons fail to provide really convincing data on the extent and consequences of competition between ants and rodents.

EXPERIMENTAL APPROACHES

An early experiment was designed as a simple and direct test of the hypothesis that desert ants and rodents compete for limiting seed resources. To confirm this hypothesis, it was necessary to demonstrate that each major taxon grows more abundant when the other group is removed. Choosing a broad area of homogeneous Sonoran Desert scrub habitat, we established two replicates each of four experimental treatments (Brown and Davidson 1977). From two circular plots 18 m in radius, we excluded rodents alone with hardwarecloth fencing, partially buried to discourage tunneling from outside. By poisoning, we eliminated ants from two similar but unfenced plots. We removed both ants and rodents from a third set of exclosures, and left one final pair of plots unmanipulated as controls.

After only two years, we observed reciprocal density compensations in the

---

[1] Unpublished data from J. H. Brown, coauthor, and Eric Larsen, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson.

TABLE 1. Items composing ≥ 5% of the diets of ant and rodent granivores at the Chiricahua Bajada study site.*

	Rodents†				Ants†					
Seeds	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Amaranthus palmeri				+					+	
Astragalus sp.	+							+		
Boerhaavia coulteri		+				+	+			
Bouteloua sp.							+		+	
Chorizanthe sp.					+					
Cryptantha sp.		+		+		+				
Descurainia pinnata						+			+	+
Ephedra trifurca	+									
Eriogonum abertianum					+					
Eriogonum trichopes									+	+
Euphorbia micromera				+	+		+	+	+	
Euphorbia serpyllifolia								+		
Kallstroemia grandiflora								+		
Larrea tridentata	+	+	+	+						
Lepidium medium	+									
Panicum arizonicum				+	+	+		+		
Prosopis juliflora		+								
Tidestromia lanuginosa							+	+		
Unidentified grass		+			+		+		+	
Unidentified seed X	+									

*Based on seeds robbed from laden ants or found in rodent cheek pouches (or *D.s.* mounds) during spring, fall, and summer over the years 1972-73 for rodents and 1974-78 for ants. Because ant and rodent diets were sampled under different resource regimes, the overlap in 25% of resource categories used by the two groups probably represents an underestimate of actual overlap.

†KEY: Rodents: 1 = *Dipodomys spectabilis*, 2 = *Dipodomys merriami*, 3 = *Perognathus pennicillatus*, 4 = *Perognathus flavus*. Ants: 5 = *Aphaenogaster cockerelli*, 6 = *Pogonomyrmex rugosus*, 7 = *Pogonomyrmex desertorum*, 8 = *Pheidole desertorum*, 9 = *Pheidole xerophila*, 10 = *Pheidole sitarches*.

two faunas. In comparision with control plots, ant colonies reached 71% higher densities on plots from which rodents had been excluded. Rodent populations increased 20% numerically and 29% in biomass in the absence of ants. Simultaneous monitoring of seed levels on one of the replicated sets of treatments (Reichman 1980, Brown et al. 1979) suggested that these population responses were mediated through exploitative resource competition. Seed abundance, as measured either by numbers or biomass, was reduced to approximately the same level on plots where either ants or rodents or both were present, while seeds accumulated to approximately four times this level on the plot from which both faunas had been removed.

Recent analyses of plant responses on these experimental plots (Inouye et al. 1980) have documented competition within the producer trophic level as well, and underscore the potential complexity of interactions in this sytem. Density-dependent germination and/or mortality among annual plants is suggested by the fact that, while seed densities quadrupled in the absence of ant and rodent predation, plant densities merely doubled (Brown et al. 1979). Watering and thinning experiments undertaken on the same plots revealed significant competitive inhibition of germination, growth rates, biomass, and fecundity in annual plants (Inouye et al. 1980).

Seed predation by ants and rodents had qualitatively different effects on the plant community (Inouye et al. 1980). The predominant ants on the plots were small column-foraging species of *Pheidole* that specialized on the tiny but numerically dominant seeds of *Filago californicus* (Family Compositae). Predation by the ant community as a whole may commonly fall most heavily on abundant seed types (Davidson 1980), promoting diversity within the surviving seed pool.

In contrast, the rodents (principally *Dipodomys merriami, Perognathus amplus,* and *P. penicillatus*) foraged selectively on large-seeded species such as *Erodium cicutarium, E. texanum,* and *Lotus humistratus,* that tend to dominate annual plant biomass. With their greater starting reserves, these species may grow rapidly to outcompete smaller seeded plants. On plots containing rodents, differential harvesting of *Erodium* and *Lotus* species permitted *Euphorbia polycarpa* to reach significantly higher densities. Presumably, the smaller seeds of this species (approximately .18 mg in contrast to 1.5 mg for the larger-seeded species) were less attractive to rodent granivores.

Competition among producers greatly enhances the potential complexity of interactions between ants and rodents. Not only may these groups compete for shared resources, but they may interact indirectly through their use of non-overlapping but competing resources. For example, rodent predation on large-seeded species may indirectly benefit ants by facilitating growth and seed production by small-seeded plants. The reciprocal density compensations suggest that, at least in the short term, competition for shared resources is the dominant interaction. Even if resources do not interact, the potential importance of indirect pathways can complicate studies of competition in communities of three or more competitors (Levine 1976). Circumstantial evidence (Davidson 1980) indicates that *Pogonomyrmex rugosus,* a large and aggressive harvester ant, may indirectly facilitate coexisting ant species by differentially interfering with foraging and nest-founding by *P. desertorum,* an intermediate-sized ant whose resource requirements strongly overlap those of both larger and smaller species.

To decipher further the mechanisms of interaction among granivores and their resources, we have repeated and expanded our experiments in southeastern Arizona on the eastern bajada of the Chiricahua Mountains. Here, an exceptionally rich association of granivores includes seven common harvester ants and five-to-seven relatively abundant species of seed-eating rodents (see Figure 1). In so diverse an assemblage of species, the number of potential direct and indirect interactions is very great, and firm hypotheses about particular interspecific interactions are difficult to pose and test.

Our strategy has been instead to manipulate broad parameters which preliminary observations and experiments suggest may have demonstrable effects on community organization. In a number of treatments, we are supplementing natural resources with milo seeds, applied either continuously ($^1/_{12}$ of the total annual subsidy supplied each month) or in a single annual pulse coincident with summer seed set by ephemeral plants. Early observations indicate interspecific differences within each of the two major taxa in the proficiencies with which species use aggregated and dispersed resources, and preliminary experiments (Brown et al. 1975) suggest that ants and rodents differ functionally with respect to this same trait. Greater mobility and a capacity to gather large quantities of seed into external, fur-lined cheek pouches enable heteromyid rodents to be far more successful than ants at depleting dense concentrations of experimentally supplied seed. Rodents tend to ignore low-density seed subsidies, perhaps because the higher metabolic costs of endothermy prevent them from foraging profitably at low seed densities. Ants are apparently equally adept at using low- and high-density seed supplements. Both enhanced searching efficiencies and reduced foraging costs, associated with eusociality and ectothermy, respectively, probably contribute to the ability of ants to feed economically from dispersed seed distributions.

The demonstrated importance of size differentiation in coexisting granivores suggests the possibility of perturbing community organization by altering the spectrum of seed sizes. Among the newly established continuous seed addition plots, treatments are differentiated with respect to the particle sizes (small, large, and heterogeneous) of experimentally supplied milo.

In addition to repeating our whole faunal removal experiments, we have established replicated plots from which individual dominant ant or rodent species have been eliminated. These latter experiments should contribute to our understanding of ecosystem structure. Recently, ecologists have hypothesized that high diversity may be maintained in complex ecosystems if interactions center in small associations of closely interacting species that interact relatively weakly with other such groups. Provided such substructure exists in our system of granivores and resources, we might anticipate *a priori* that organization should follow taxonomic lines. Single-species removal experiments should lend insight to the problem of whether or not interactions are significantly stronger within than between major taxa.

Biogeographic comparisons of granivore communities hint at the possible role that "guild structure" may play in the maintenance of diversity. Over a latitudinal transect where precipitation increases but temperatures change very little, greater diversity is achieved by almost parallel increases in species richness in ant and rodent faunas, rather than by adding members of only one taxonomic association or the other (Brown and Davidson 1977). Above a certain threshold of seed productivity, diversity is enhanced by addition of a third (avian) guild of granivores. The finding that dietary similarity among coexisting rodent species exceeds that between cooccurring rodents and ants (Davidson, unpublished data) also lends support to the suggestion of taxonomically based guild structure.

Two years following initiation of these experiments, our results are still preliminary; only qualitative statements are justified at this time. First, granivore populations have responded more gradually to our perturbations than in past experiments. At this time, we do not know whether the system's resistance to change represents enhanced stability associated with a more complex and/or coevolved interaction structure or simply the obviation of competitive stress by the recent bounty of natural seed production. Competition need act only intermittently to be instrumental in regulating community structure, and prolonged maintenance of experimental treatments may be necessary to demonstrate its effects.

Considerable time may also be required before we can distinguish temporary from equilibrial responses to our manipulations. The most immediate responses to seed additions and species removals may occur in species that are opportunists rather than in the specialized species that eventually will prove to be the superior competitors for available resources. Opportunism is promoted by the ability to colonize through immigration and/or reproduction. Where kangaroo rat species (genus *Dipodomys*) have been excluded from experimental plots, pocket mice (genus *Perognathus*) have quickly immigrated to take advantage of surplus resources. Although harvester ants (*Pogonomyrmex rugosus*) have been observed to capitalize on *Erodium* seeds accumulating on rodent-free plots, this expansion in resource use has not yet been translated through reproduction into higher colony densities.

On Chiricahua Bajada plots where ant densities have risen, *Pheidole desertorum* has contributed most significantly to the increase. This true opportunist can colonize by overground colony movement and grow from small single-colony units to fill expansive nests with many disjunct units. Newly established queens of the species are similarly well-suited for taking advantage of underutilized foraging territory; their first worker broods are larger than those of coexisting ant species, and worker development is significantly more rapid.

Finally, short-term and long-term responses may differ for yet another reason. Responses involving very indirect routes of interaction may be expressed much later than those mediated through relatively short and direct pathways.

CONCLUSIONS

Two fundamentally different methodologies have made unique and often complementary contributions to our understanding of granivory in desert ecosystems. Biogeographic comparisons of species numbers and characteristics in independently assembled communities quickly provided an overview of the ecological processes underlying community organization. While lending useful perspective on interactions between closely related groups of competitors, cross-community comparisons have proven less fruitful in identifying patterns of association between taxonomically distant competitors. Experiments provide an alternative approach that we have employed successfully to demonstrate competitive interactions between ants and rodents as well as among primary producers.

At least two factors complicate the designing of additional experiments to phrase and test explicit hypotheses about interactions among these distantly related taxa. It is unclear which of the many differences between ant and rodent granivores favor their coexistence in desert ecosystems. Functional differentiation of the two groups may well depend on numerous minor distinctions in the use of seed resources. Secondly, potential interactions among granivores through distinct but competing resources, as well as through those that are shared, not only complicate hypothesis-formulation but may prolong the time period over which the system responds to a given perturbation.

Our ongoing experiments are unconventional in the sense that their immediate goal is description rather than hypothesis testing. By manipulating resource parameters whose natural variation figures prominently in resource subdivision among closely related competitors, we hope to alter community structure to a degree that will enable us to recognize major patterns in the organization of consumer-resource interactions.

ACKNOWLEDGMENTS

We thank the many colleagues, students, and assistants who have contributed in major ways to our research on granivores. Special thanks go to A. Brown, G. Byers, J. Munger, and K. Zemanek. D. Alstad provided helpful criticism of an early draft of the manuscript. The investigations summarized here have been supported by the Desert Biome, US/IBP, and by grants from the National Science Foundation.

REFERENCES CITED

Bernstein, R. A. 1975. Foraging strategies of ants in response to variable food density. *Ecology* 56: 213–219.

Brown, J. H. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. *Ecology* 54: 775–787.

———. 1975. Geographical ecology of desert rodents. Pages 315-341 in M. L. Cody and J. M. Diamond, eds. *Ecology and Evolution of Communities*. Harvard University Press, Cambridge.

Brown, J. H. and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. *Science* 196: 880–882.

Brown, J. H., D. W. Davidson, and O. J. Reichman. 1979. An experimental study of competition between seed-eating desert rodents and ants. *Am. Zool.* 19: 1129–1143.

Brown, J. H., J. J. Grover, D. W. Davidson, and G. A. Lieberman. 1975. A preliminary study of seed predation in desert and montane habitats. *Ecology* 56: 987–992.

Brown, J. H., and G. A. Lieberman. 1973. Resource utilization and coexistence of seed-eating rodents in sand dune habitats. *Ecology* 54: 788–797.

Davidson, D. W. 1977a. Species diversity and community organization in desert seed-eating ants. *Ecology* 58: 711–724.

———. 1977b. Foraging ecology and community organization in desert seed-eating ants. *Ecology* 58: 725–737.

———. 1978a. Size variability in the worker caste of a social insect (*Veromessor pergandi* Mayr) as a function of the competitive environment. *Am. Nat.* 112: 523–532.

———. 1978b. Experimental tests of the optimal diet in two social insects. *Behav. Ecol. Sociobiol.* 4: 35–41.

———. 1980. Some consequences of diffuse competition in a desert ant community. *Am. Nat.*, in press.

Hölldobler, B. 1974. Home range orientation and territoriality in harvester ants. *Proc. Natl. Acad. Sci. USA* 71(8): 3271–3277.

———. 1976. Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. *Behav. Ecol. Sociobiol.* 1: 3–44.

Hutto, R. 1978. A mechanism for resource allocation among sympatric heteromyid rodent species. *Oecologia* 33: 115-126.

Inouye R. S., G. Byers, and J. H. Brown. 1980. Effects of predation and competition on survivorship, fecundity and community structure of desert annuals. *Ecology*, in press.

Lemen, C. A., and M. L. Rosenzweig. 1978. Microhabitat selection in two species of heteromyid rodents. *Oecologia* 33: 127–135.

Levine, S. 1976. Competitive interactions in ecosystems. *Am. Nat.* 110: 903–910.

Lubchenko, J., and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.* 48: 67–94.

May, R. M., and R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. *Proc. Natl. Acad. Sci. USA* 69: 1109–1113.

Nelson, J. F., and R. M. Chew. 1977. Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. *Am. Mid. Nat.* 97: 300–320.

Price, M. V. 1978a. Seed dispersion preferences of coexisting desert rodent species. *J. Mammal.* 59: 624–626.

———. 1978b. The role of microhabitat in structuring desert rodent communities. *Ecology* 59: 910–921.

Reichman, O. J. 1980. Desert granivore foraging and its impact on seed densities and distributions. *Ecology*, in press.

Reichman, O. J., and D. Oberstein. 1977. Selection of seed distribution types by *Dipodomys merriami* and *Perognathus amplus*. *Ecology* 58: 636–643.

Rosenzweig, M. L. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. *Ecology* 54: 111–117.

Schroder, G. D., and K. H. Geluso. 1975. Spatial distribution of *Dipodomys spectabilis* mounds. *J. Mammal.* 56: 363–368.

Schoener, T. 1974. Resource partitioning in ecological communities. *Science* 185: 27–38.

Whitford, W. G., P. Johnson, and J. Ramirez. 1976. Comparative ecology of the harvester ants *Pogonomyrmex barbatus* (F. Smith) and *Pogonomyrmex rugosus* (Emery). *Ins. Soc.* 23: 117–132.

Wondolleck, J. T. 1978. Forage-area separation and overlap in heteromyid rodents. *J. Mammal.* 59: 510–518.