probably in the process of disappearing). It appears that low frequency reduces the rate at which females encounter conspecific males, thereby delaying female insemination, shifting the emergence curve to a later time, and lowering the effective growth rate of the population. Thus, the per capita impact of competitors is not linearly related to density, as the Lotka-Volterra competition equations assume.

OUTLOOK FOR PREDICTIONS

Our goal was to explore the potential power of the community reconstitution approach by synthesizing complex laboratory systems of *Drosophila* flies. We used these systems to study problems of multispecies competition. Our experience yields one type of bad news and two types of good news.

The bad news is that it is difficult to understand the structure even of laboratory communities in which one creates and controls a simple homogenous environment, chooses species, and adds those species singly, pairwise, or in higher combinations at will. After eight years of work we still have not established the relative importance of various proximate mechanisms of competition. We do not have detailed interpretations for why competitive rank shifts with food type. Our understanding of what produces the observed assembly rules is rudimentary. If these tasks are difficult in the laboratory, think how much more difficult they will be in the field, where there is an uncontrolled and heterogeneous environment, dozens or hundreds of relevant but little known species, and no opportunity for studying those species in isolation or in pairs.

One type of good news is that it has proved feasible and rewarding to study a complex laboratory system in steps. Life history parameters of single species can be measured as a function of environmental temperature and food supply; pairwise competition can be reconstructed from those single-species parameters; and the outcome of competition within sets of 10 species is illuminated by the outcome of the pairwise contests. This approach tests whether we really have identified the significant components of a higher system, just as does the approach of a biochemist attempting to reconstitute the mitochondrial electron-transfer system from its components.

The other type of good news is that the laboratory system succeeded in capturing the essence of many phenomena important in field ecology. We were able to confirm unequivocally the existence of assembly rules, competitive exclusion, species coexistence by niche partitioning, competitive transitivity, and one mechanism of competitive intransitivity (i.e., environmental heterogeneity). We were able to predict competitive rank and to interpret some shifts in rank with temperature and food thickness. The richness or multidimensionality of single-species behavior observed in the laboratory accords with *Drosophila* lore (cf. Ayala's [1969] article on the variability of intrinsic growth rate in different environments).

Of the three traditions of experimental ecology—natural, field, and laboratory experiments—the laboratory tradition is the one currently being least exploited. We hope that we have demonstrated the potential value of community reconstitution studies pursued in the laboratory.

ACKNOWLEDGMENTS

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chapter 3

Experimental Community Ecology: The Desert Granivore System

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

*I am tempted to give one more instance showing how plants and animals, remote in the scale of nature, are bound together by a web of complex relations. . . . I find from experiments that humble-bees are almost indispensable to the fertilisation of the heartsease (*Viola tricolor*), for other bees do not visit this flower. I have also found that the visits of bees are necessary for the fertilisation of some kinds of clover; . . . Hence we may infer as highly probable that, if the whole genus of humble-bees became extinct or very rare in England, the heartsease and red clover would become very rare, or wholly disappear. The number of humble-bees in any district depends in a great measure upon the number of field-mice, which destroy their combs and nests; and Col. Newman, who has long attended to the habits of humble-bees, believes that "more than two-thirds of them are thus destroyed all over England". Now the number of mice is largely dependent, as every one knows, on the number of cats; and Col. Newman says, "Near villages and small towns I have found the nests of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice." Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!*

Darwin, 1859

INTRODUCTION

Despite the recent emphasis on experimental approaches to ecology, there have been few long-term, intensive experimental studies of terrestrial communities. Such investigations are important because they can provide rigorous independent tests of the inferences obtained from the numerous comparative and observational studies that have produced most of the data and ideas on community structure and function. In addition, because experimental manipulations are perturbations of a kind and magnitude that are usually difficult or impossible to observe without human intervention, they may reveal important patterns and processes that have not been detected by other methods.

For more than a decade, we and our collaborators have been using controlled field experiments to analyze the interactions among desert seed-eating animals and between these granivores and their primary food resources, the seeds of desert annual plants. One purpose of the present paper is to summarize, synthesize, and discuss the current status of these continuing experiments. Many of the results have already been published or are now in press (Brown and Davidson 1977; Brown et al. 1979a, 1979b; Reichman 1979; Davidson et al. 1980, 1984, in press; Inouye 1980, 1981; Inouye et al. 1979; Munger and Brown 1982; Brown and Munger in press). We shall summarize and synthesize the results of these earlier studies in order to document the diverse effects of the different kinds of animals and plants on the organization of this important part of desert ecosystems.

The other goal of this paper is to consider the general implications of these results for contemporary ecological theory and practice. Although our results are generally consistent with both current community theory and with nonexperimental empirical studies of this and other systems, the kinds and magnitudes of the responses to our manipulations reveal a diversity of interactions and a complexity of community organization that is not easily characterized either theoretically or empirically. Long-term experimental studies provide a unique perspective on the organization of communities, because the sustained perturbations set in motion a complex sequence of dynamic behaviors as many different kinds of organisms are affected through both direct and indirect pathways. Perhaps most importantly, our experiments demonstrate several kinds of strong indirect interactions, in which species influence each other through intermediary species. The theoretical importance of such indirect interactions for community organization has been emphasized (e.g., Chapters 20, 26, and 32; Levins 1974, 1975; Levine 1976; Holt 1977; Lawlor 1979; Vandermeer 1980; Patten and Auble 1981; Schaffer 1981; Patten 1982; Bender et al. 1984), but there have been few rigorous field studies to show how these indirect pathways actually operate in natural ecosystems.

THE SYSTEM

The Organisms

The system of seeds and granivores is an important component of desert ecosystems. Primary production in deserts is limited by the availability of water, and the ephemeral or annual plants account for a large fraction of the productivity, because they are able to complete the entire vegetative part of their life cycles during the brief, unpredictable periods when sufficient soil moisture is available following precipitation. These plants produce large crops of seeds, some of which survive buried in the soil for the long intervals between rains. In most desert habitats annuals are taxonomically diverse and account for 85 to 95% of the total seed production. The various species differ in the timing of their life cycles and in the size, shape, and chemical composition of their seeds.

These seeds comprise the primary food resources of a major, taxonomically diverse group of consumers, the granivores. In the Chihuahuan and Sonoran deserts of southwestern North America where we have performed our experiments, three classes of animals have representatives that are specialized to varying degrees to feed on dry seeds.

The first of these classes is the rodents, which include highly granivorous kangaroo rats (*Dipodomys*) and pocket mice (*Perognathus*), as well as more omnivorous deer mice (*Peromyscus*) and harvest mice (*Reithrodontomys*). These small mammals are nocturnal and resident throughout the year (although most pocket mice hibernate during the coldest months). Most species collect large quantities of seeds when they are available and store them underground for use in times of food shortage.

The second major class of desert granivores is the harvester ants, which include the specialized seed-eaters in the genera *Pogonomyrmex*, *Veromessor*, and *Pheidole* as well as more omnivorous representatives of the genera *Novomessor* and *Solenopsis*. These ants live in colonies that may survive for many years and contain as many as tens to thousands of foraging workers. During limited periods of warm temperature, high humidity, and food availability these ants collect seeds and store them in granaries within their underground galleries.

The third important class of desert granivores is birds, in particular the sparrows that invade the desert in flocks in winter, and doves and quail that may be present, either singly or in flocks, throughout the year. These birds differ conspicuously from both rodents and ants in that they do not store seeds; instead they respond to variation in local food availability by traveling over large distances to exploit abundant seed crops.

This system of seeds and seed-eaters has several advantages for long-term experimental studies. First, the system is a fairly discrete part of relatively simple desert ecosystems. Thus, we can focus our investigations on one closely interacting group of organisms. Second, the system is an important part of the entire desert ecosystem. Annual plants and granivores account for a substantial proportion of the species diversity and biomass of primary producers and consumers, respectively, in deserts. Third, there is sufficient taxonomic and ecological diversity among both the seed-eaters and their food plants to make possible many kinds of interesting interactions. The diversity is sufficiently low, however, that it is possible to analyze experimentally the roles of either individual species or entire groups of species. Finally and perhaps most importantly, the system lends itself, perhaps more readily than most other terrestrial systems, to carefully controlled experimental manipulation. It is both possible and practical to set up numerous replicated plots of biologically realistic size, to remove selected kinds of granivores and plants with almost surgical precision, to manipulate the availability of food for granivores, to census most important species in the community with sufficient precision to quantify their responses to the manipulations, and to maintain the experiments for sufficiently long periods to record the dynamics of the diverse responses. Although major artificial manipulations can be performed on a sufficiently large scale to produce informative results, the effect on the local biota is sufficiently small so as to be politically feasible and morally justifiable.

The Experiments

The basic procedure is straightforward: Find an area of appropriate desert habitat that is as homogeneous as possible, establish replicated plots of adequate size, assign treatments at random, perform manipulations, and census the rodents, ants, birds, and plants at regular intervals to quantify their responses.

The present paper describes the results of two sets of experiments. The first was begun in the Sonoran Desert northwest of Tucson, Arizona, in 1973 and continued until 1977. There were eight circular plots, each 0.10 ha in area. Two replicates of each of the following manipulations were performed to test for the effects of competition between rodents and ants and for the influence of predation by these two classes of granivores on the annual plants: (1) rodents excluded by fencing, (2) ants removed by poisoning, (3) both rodents and ants removed by both fencing and poisoning, and (4) control (both rodents and ants present and neither fenced nor poisoned). It was usually possible to maintain virtually complete exclusion of the taxon designated for removal (see Fig. 3.1, for example). Standardized methods were used to census the rodents, ants, seeds in the soil, and annual plants. Additional, smaller-scale experiments were conducted on these plots in 1977 in order to assess the role of competition within and between species of annual plants as well as the interaction between such competition and seed predation by the granivores. Additional details of methodology are given in Brown et al. (1979a), Inouye et al. (1980), and Davidson et al. (1984).

A second, much more elaborate set of experiments was begun in 1977 and is still continuing. On a 20-ha study area in the Chihuahuan Desert of extreme southeastern Arizona, we set up 24 plots, each 0.25 ha in area. All of these are fenced similarly, except that some have gates (holes) of particular sizes in the fences to allow free passage of selected rodent species. The complex, partial factorial design is summarized in Table 3.1. Basically, there are three main classes of manipulations: (1) exclusion of some or all rodent species by means of different-sized gates in the fences, (2) exclusion of some or all ant

Table 3.1 OUTLINE OF THE 12 EXPERIMENTAL TREATMENTS, INCLUDING CONTROL, IN THE CHIHUAHUAN DESERT

Control		Seed addition		Rodent removal		Ant removal	
Plots 11, 14:	unmanipulated	Plots 6, 13:	large seeds, constant rate	Plots 5, 24:	*Dipodomys spectabilis*	Plots 8, 12:	*Pogonomyrmex rugosus*
		Plots 2, 22:	small seeds, constant rate	Plots 15, 21:	all *Dipodomys* species	Plots 3, 19:	*Pogonomyrmex rugosus* and all *Dipodomys* species
		Plots 9, 20:	mixed sizes, constant rate	Plots 3, 19:	all *Dipodomys* species and *Pogonomyrmex rugosus*	Plots 4, 17:	all seed-eating ants
		Plots 1, 18:	mixed sizes, temporal pulse	Plots 7, 16:	all seed-eating rodents	Plots 10, 23:	all seed-eating ants and rodents
				Plots 10, 23:	all seed-eating rodents and ants		

Note that some of the rodent and ant removal experiments have a factorial design, and duplicate treatments are listed under both headings.

species by means of poisoning the appropriate colonies, and (3) addition of 96 kg of millet seed per year in different-sized particles and in different temporal patterns. We use standardized techniques to census rodents, ants, birds, and annual plants on the plots at regular intervals. Additional methodological details are given by Davidson et al. (in press) and Brown and Munger (in press). In addition, supplemental experiments in which birds or certain plants are selectively excluded have been performed (Inouye 1980, 1981; Davidson et al. 1984) or are in progress.

The Questions

Collectively, these experiments are designed to assess the roles of interspecific interactions among granivores and between granivores and plants. We are especially concerned with the effects of competition within and among the three classes of seed-eaters, predation by granivores on the annual plants, competition among these plants, and indirect interactions that are the result of a series of two or more direct interactions involving intermediary species.

Even this relatively simple system is too complex and we already have too much data to attempt to summarize our current understanding in the limited space available here.* The present paper will focus on the interactions involving only the rodents, but these are sufficient to document a rich variety of direct and indirect effects, some of which profoundly influence the structure and function of the entire desert ecosystem. We shall concentrate on the answers that the experiments can provide to the following questions.

1. To what extent do different species of granivorous rodents compete with each other for limited food resources?
2. To what extent do these rodents also compete with the other major classes of seed-eating animals, especially ants?
3. What is the impact of these rodents as seed predators upon the desert plants, and how does this predation interact with competition among the plant species to affect the composition of the flora?
4. What are some of the important indirect effects of rodents on other organisms in the ecosystem, and through what pathways are these interactions effected?

Thus the approach will be to begin by considering direct competitive interactions between closely related, ecologically similar rodent species and then gradually to expand the perspective to include other kinds of organisms and interactions.

RESULTS OF THE EXPERIMENTS

Competition Among Rodent Species

The experiments at the Chihuahuan Desert site include treatments designed to test the hypothesis that seed-eating rodent species compete for limited food resources (see Munger and Brown 1981, Brown and Munger in press, for more details on methods and results). The most direct tests are provided by semipermeable exclosure experiments that use different-sized gates in the fences to exclude selected species. Small gates allow only species smaller than some threshold body size to enter experimental plots, whereas larger gates give all species free access to control plots. In the absence of complicating indirect effects, the competition hypothesis predicts that the smaller species should increase and maintain higher densities on the experimental plots from which larger rodents have been excluded than on control plots where larger species are present.

We have conducted two tests of this hypothesis. The first documents the response of five species of small granivorous rodents to the exclusior of three larger species of kangaroo rats (*Dipodomys*) on four experimental and four control plots (Fig. 3.1). After a lag of approximately nine months following initiation of the manipulation in October 1977, four of the five species of small rodents (*Perognathus flavus*, *Peromyscus maniculatus*, *Pm. eremicus*, and *Reithrodontomys megalotis*) increased dramatically on the plots where all *Dipodomys* species had been removed. The fifth species (*Pg. penicillatus*) has shown a tendency to increase as well, but the

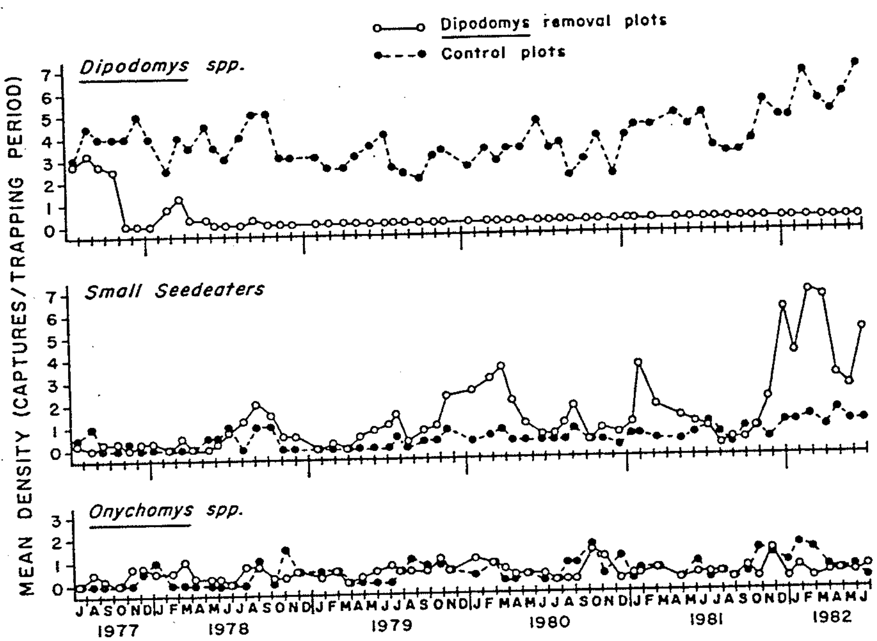

Fig. 3.1 Changes in the densities of three groups of rodents at the Chihuahuan Desert site on four experimental plots where all three *Dipodomys* species were removed beginning in October 1977 (solid lines) compared to the densities on four control plots (dashed lines). (Above) Effectiveness of removal of *Dipodomys*. (Middle) Compensatory increase in total densities of five species of small granivorous rodents. (Below) Lack of effect of *Dipodomys* on the combined densities of two species of insectivorous *Onychomys* species. (From Brown and Munger in press.)

response is not statistically significant. Collectively, the increase of the five small species is highly significant; their combined densities on the experimental plots average 2.2 times higher than on the control plots where *Dipodomys* are present. This result strongly supports the competition hypothesis. That this reflects the effects of competition for shared food resources is additionally indicated by the fact that two species of insectivorous rodents (grasshopper mice, *Onychomys* spp.) that could travel through the small gates showed absolutely no differences between experimental and control plots.

The second semipermeable exclosure experiment involves the removal of only the largest of the granivorous rodent species (*Dipodomys spectabilis*, body weight 120 g). This treatment, begun only in 1980 and consisting of just two replicates, has so far produced one striking result. In the absence of *D. spectabilis*, five of the seven granivorous rodent species shift their foraging behavior to use microhabitats different from the ones used on the control and most of the other experimental plots (Bowers et al. in preparation). *D. spectabilis* is aggressively dominant over smaller species. The patterns of habitat shifts suggest that this aggression is directed primarily toward *D. merriami* (body weight 45 g; see Frye 1983), the most abundant species and one of the next two largest after *D. spectabilis*.

D. spectabilis could affect the other rodent species either directly, by interfering with their foraging, or indirectly, through its effect on *D. merriami*. Surprisingly, despite the pronounced changes in microhabitat use, there are as yet no significant differences in population density of any of these rodents between *D. spectabilis* removal and control plots. Of course, the short duration of this experiment and the small number of replicates would contribute to the difficulty of detecting statistical differences. *D. merriami* and *D. ordii* have increased in the absence of *D. spectabilis*, but these two species also have increased and *D. spectabilis* has decreased on the control plots (Fig. 3.2).

These reciprocal density shifts between *D. spectabilis*, on the one hand, and *D. merriami* and *D. ordii*, on the other, provide additional evidence of competition between these species, especially when their responses to other treatments are also considered (Fig. 3.2). There is a strong tendency for *D. spectabilis* to increase and *D. merriami* and *D. ordii* to decrease on plots to which supplemental millet seeds are added. The reverse trend occurs on the other plots, including the controls, perhaps because the fences interfere with the foraging of *D. spectabilis*. These reciprocal density shifts induced by experimental perturbations provide evidence not only that the three kangaroo rat species compete for seeds, but also that the outcome of this competition is asymmetrical, with the interactions dominated by *D. spectabilis* whenever food resources are sufficiently abundant for it to maintain high densities.

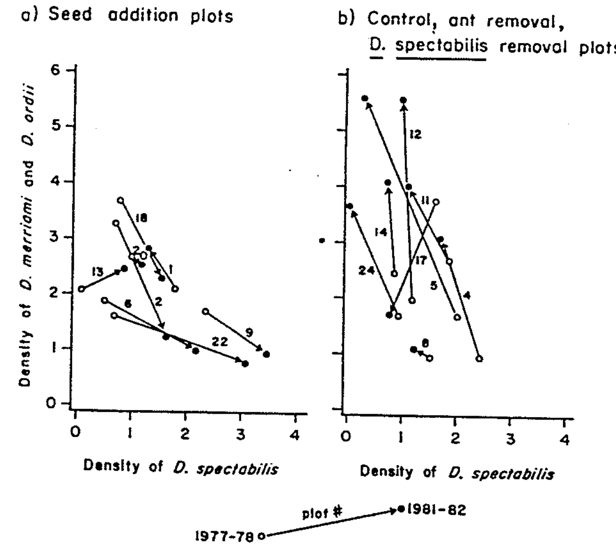

Fig. 3.2 Changes in the total mean density of *Dipodomys merriami* and *D. ordii* relative to changes in the density of *D. spectabilis* in response to various experimental manipulations at the Chihuahuan Desert site. Each line represents changes on one plot between the first year of the study (1977–1978) and the last two years (1980–1982). Note the pronounced reciprocal density shifts, with *D. spectabilis* increasing from 1977–1978 to 1980–1982 at the expense of its smaller congeners in response to seed addition and the reverse trend on other plots. The reciprocal pattern is highly significant (Fisher's exact test, $p = 0.0055$). (Data from Brown and Munger in press.)

This fits well with the biogeographical pattern that *D. spectabilis* is found only in the most productive desert habitats, and it usually occurs in the absence of other *Dipodomys* species in even more productive arid grasslands.

Three aspects of the response of desert rodents to experimentally induced changes in food supply and density of other rodent species warrant special comment. First, all of the changes in population density occurred long after the manipulations were initiated. As discussed in more detail in Brown and Munger (in press), the most likely explanation for these long time lags seems to be either the failure of the rodents to perceive a significant change in the availability of resources (perhaps because a new seed crop is required) or their inability to respond quickly to a detected change (perhaps because of the seasonality of reproduction and dispersal). Second, the magnitudes of the responses to our perturbations, while highly significant statistically, are nevertheless much less than would be expected if those food resources made available by our manipulations were completely utilized by those rodents that potentially had access to them. In fact, although population densities of particular species were greatly affected by our treatments, the almost negligible compensation in consuming biomass (Table 3.2) indicates that most of the seeds made available were not consumed by rodents. Explanations for this phenomenon (see also Brown and Munger in press) include the possibilities that intraspecific interactions, predators, or constraints on foraging behavior or habitat use precluded a more complete response by the rodents and that other classes of granivores consumed a large portion of the available seeds (see below). Third, the interactions among the rodent species appear to be highly asymmetrical, because aggressive domination of smaller species by larger ones is an important mechanism of competition. We have not tested directly for these asymmetries by removing small species and measuring the response of large ones. We predict that if we did these experiments, however, the magnitude of density compensation would often be statistically undetectable and would always be less than we observe in the reciprocal experiments, in which the larger species are removed.

The results of our experiments, then, strongly support the hypothesis that competition for limited food resources plays a major role in determining the absolute and relative abundances of the rodent species that comprise this community. However, the interactions among the rodents are not so simple as we had naively assumed when we began the manipulations. Indeed, the results reveal such interesting complications as long

Table 3.2 ENERGETIC COMPENSATION (MEASURED IN UNITS OF CONSUMING BIOMASS PER 0.25-HA PLOT) BY DESERT RODENTS TO SUPPLEMENTAL SEEDS AND TO REMOVAL OF SELECTED RODENT SPECIES

	Experimental treatment		
	Addition of metabolizable millet	Removal of *D. spectabilis*	Removal of all (3) *Dipodomys* species
Energy made available (KJ/day)	3060	201.4	439.7
Energetic response (KJ/day)	91	49.4	33.2
Response by what species	All 8 species of granivorous rodents	7 species of smaller granivorous rodents	5 species of small granivorous rodents
Percent compensation	2.9	33.8	9.5

Note that rodent compensation for the additional food made available by either adding seed or removing other rodent species was always low; never more than 33%.

Percent compensation is calculated as: [(1977–1978 consuming biomass minus 1978–1982 consuming biomass for the average of the removal plots) minus (1977–1978 consuming biomass minus 1978–1982 consuming biomass for the average of the control plots)] divided by metabolized energy of added seeds or consuming biomass of the rodents removed.

From Brown and Munger in press.

Table 3.3 SUMMARY OF THE RESULTS OF EXPERIMENTS AT THE SONORAN DESERT SITE IN WHICH ANTS OR RODENTS WERE ELIMINATED FROM PLOTS AND THE UNMANIPULATED TAXON WAS REPEATEDLY CENSUSED

	Rodents removed	Ants removed	Control	Percent increase relative to control	Fraction of comparisons, experimental > control
Ant colonies	543	—	318	70.8	9/10
Rodent individuals	—	151	126	19.8	17/27 (5 equal)
Rodent biomass (kg)	—	5.41	4.21	28.5	17/27 (3 equal)

Values in the first three columns are totals of all censuses. Ants were censused 5 times and there were 2 replicates of each treatment for a total of 10 comparisons. There were 27 comparisons for rodents, 14 censuses of the first replicate (established in August 1973) and 13 censuses of second set (established in December 1973).

Rodent biomass is based on average body weights on the study area of 41.1 g for *Dipodomys merriami*, 28.1 g for *Perognathus baileyi*, 16.9 g for *P. penicillatus*, and 11.4 g for *P. amplus*.

From Brown and Davidson 1977.

time delays, low biomass compensation, and asymmetrical interference interactions.

Competition Between Rodents and Other Classes of Granivores

The first experiments, begun in the Sonoran Desert site in 1973, were designed primarily to test the hypothesis that rodents and ants compete for limited seed supplies. The simple competition hypothesis predicts that each of these taxa should increase in overall population density in response to experimental exclusion of the other. The results support this prediction (see Brown and Davidson 1977, Brown et al. 1979a, for details). Compared to control plots, numbers of ant colonies almost doubled on plots where rodents had been removed, and rodent biomass and censused numbers of individual rodents increased respectively by about 29% and 20% where ants had been removed (Table 3.3).

The second set of experiments was designed in part to test for the repeatability of these reciprocal density changes at the Chihuahuan Desert site. The results, however, are not so distinct as those of the earlier experiment at the Sonoran Desert site. Only *Pheidole xerophila*, one of the smallest of the 10 granivorous ant species, increased in response to removal of rodents (see Davidson et al. in press, for details). Censuses of foraging workers of this species over three years, 1980 to 1982, documented a consistent increase, with densities attaining levels almost 10 times higher on rodent exclusion plots than on controls in the last year. The situation is further complicated, however, because *Pogonomyrmex desertorum*, a somewhat larger species, declined slightly on the rodent removal plots. Thus, it is questionable whether there was any significant compensation in total ant biomass for the missing rodents, despite the dramatic increase in *Pheidole*. We can detect no evidence of significant increases in rodent populations in response to exclusion of ants (Brown and Munger in press).

Clearly, either the results for the Sonoran Desert site are in error, or the competitive relationships between rodents and ants are quite different at the Chihuahuan Desert site. We favor the latter explanation for three reasons. First, Bryant et al. (1976) excluded rodents and ants in habitat similar in vegetation and productivity to the Sonoran Desert site (even though it was in the Chihuahuan Desert of New Mexico) and obtained similar results; the same ant species showed quantitatively similar increases in colony densities in response to removal of rodents. Second, overlap in the diets of the rodents and ants is much greater at the Sonoran than at the Chihuahuan site, indicating that the potential competition for seeds is much greater at the site where the largest and most consistent density compensation was observed (Davidson and Cole, unpublished data). Third, the Sonoran and Chihuahuan sites differ considerably in climate and productivity (especially in the seasonality of seed production in relation to the activity of the different classes of granivores), as well as in the composition of the rodent, ant, and plant species. Since the relationship between rodents and ants apparently is not just simple, direct competition, but is complicated by interactions between these granivores and other organisms (see below), it is not unreasonable to expect that the intensity of competition (at least as revealed by this kind of simple exclusion experiments) might differ between the two sites. A result common to the experiments at both the Sonoran and Chihuahuan Desert sites is that rodents had substantially greater effects on ants than the converse. This is not surprising, given the apparently greater ability of rodents to find and collect seeds (Brown et al. 1975) and the much greater effect of climate on ant than on rodent activity (Davidson et al. in press).

We also have some evidence that rodents compete for seeds with birds. Avian foraging at the Sonoran Desert site was much greater on plots where both rodents and ants had been excluded and large quantities of seeds had accumulated, than on plots where either rodents or ants or both were present and standing crops of seeds were much lower (Brown et al. 1979a). At the Chihuahuan Desert site avian foraging for seeds is significantly greater on plots where supplemental millet seeds have been added than on control plots. Since rodents also increase their foraging in response to seed addition, this suggests that rodents and birds compete for the supplemental millet and perhaps for native seeds as well. Unfortunately, we did not begin to census avian foraging intensively until 1982, about five years after the treatments were initiated. In data collected since then, it appears that birds actually forage less on plots where rodents have been removed than on control plots where rodents are present. We are not yet certain how to account for this result, but it may well represent the outcome of a long-term indirect mutualistic interaction mediated through the direct effects of rodents and birds as selective predators on different but competing species of annual plants. Such an interpretation does not by any means deny the possibility of substantial short-term competition between rodents and birds.

Thus, our experiments indicate that rodents compete for seeds, not only with other closely related rodent species, but also with other distantly related taxa of granivores such as ants and birds. These interactions among distantly related taxa must be considered when attempting to interpret the results of field experiments designed to test for competition between closely related species. When the effects of other organisms that might respond to the same manipulations are not controlled for, they potentially can have a profound influence on the results. For example, the fact that birds consume a significant proportion of the seeds presumably accounts at least in part for the failure of rodents to compensate completely in consuming biomass for the seeds made available by either removing certain rodent species or by adding supplemental seeds.

Predation by Rodents on Annual Plants

Granivores are predators. They kill and eat seeds, which are immature plants. This predation might be hypothesized to have two effects on the prey. First, it should tend to reduce the overall density, biomass, and productivity of plants. Second, to the extent that predation is selective on certain plant species, it should also affect the species composition and pattern of dominance in the plant community. Both of these hypotheses can be tested by comparing the abundances of the various plant species on control plots, where rodents are present, with those on experimental plots where some or all rodent species have been removed. We have such data for both the Sonoran and Chihuahuan sites. Here we shall focus primarily on the effects on annual plants of removing all rodents at the Sonoran Desert site.

Our experiments clearly demonstrate that the influence of rodents as predators on plants is at least as important as their effect as competitors on other seed-eating animals. Fig. 3.3 shows that the density and biomass of both seeds and adults of annual plants increase significantly when either rodents or ants are excluded and especially when both classes of granivores are removed (for additional details see Reichman 1979, Inouye et al. 1980). Shortly after the start of the manipulations there were no significant differences between experimental and control plots (upper half of Fig. 3.3), but after three years there were substantially more seeds and mature vegetative plants on the experimental plots where one or both taxa of granivores had been removed (lower half of Fig. 3.3). The patterns for seeds and mature plants are qualitatively similar; the apparently greater effect of granivores on the seeds than on vegetative plants can probably be attributed to density-dependent inhibition of germination (Inouye 1981).

Effects of rodent exclusion on composition of the annual flora are equally great. A consistent pattern is for those plant species with relatively large seeds (seed mass > 1 mg) to increase dramatically in density to dominate the annual plant community on plots where rodents have been removed (Fig. 3.4). Thus, individual large-seeded species were 1.5 to 8.2 times more dense on rodent removal plots than on controls. Two of these large-seeded species, *Erodium cicutarium* and *E. texanum*, accounted for over 60% of the annual plant biomass on rodent exclusion plots

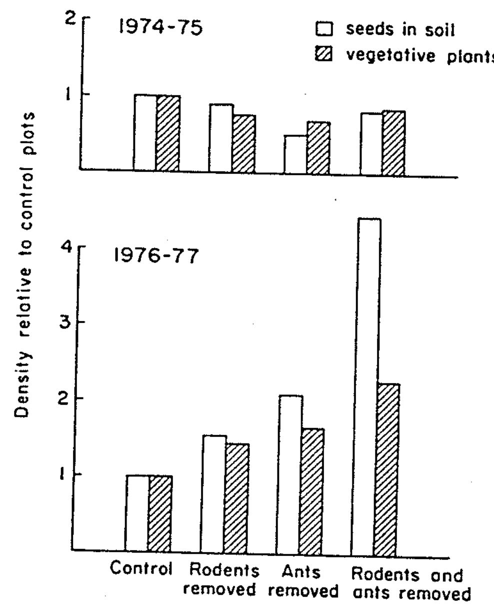

Fig. 3.3 Effects of experimental exclusion of rodents and ants on the densities of seeds in the soil and of vegetative annual plants at the Sonoran Desert site. In 1974–1975, approximately one year after initiation of the granivore removals, there were no significant differences among any of the treatments. Two years later there were significantly more seeds and plants on plots where rodents or ants or both had been removed.

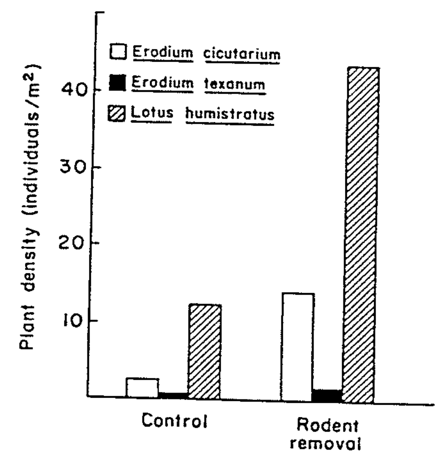

Fig. 3.4 Densities of the three most abundant species of large-seeded annual plants on rodent removal and control plots at the Sonoran Desert site.

compared to less than 30% on plots where rodents were present (see Inouye et al. 1980 for additional details).

The explanation for these results appears to be straightforward. Because of their large body size and the energetic costs of temperature regulation and year-round activity, rodents are constrained to forage selectively for large seeds. This is consistent with other data on the sizes of seeds in rodent diets (e.g. Brown and Davidson 1977, Brown et al. 1979b). The effects of this selectivity on the plant community are profound. Not only do rodents suppress populations of their preferred large-seeded prey, but this suppression is sufficient to prevent these large-seeded plants from completely dominating the annual plant community. Furthermore, this phenomenon appears to be very general, because we can document it at other sites where the habitat and flora are quite different. Thus, large-seeded species dominated the annual plant community in an 18-year-old rodent exclosure constructed by R. M. Turner in the Sonoran Desert east of Tucson, Arizona, but the dominant species in this rocky hillside habitat were completely different from those at our Sonoran Desert site a few kilometers away (Table 3.4). Similarly, preliminary analyses of the plant responses to the manipulations at our Chihuahuan Desert site indicate that large-seeded species are still changing in density to comprise an increasingly large share of the annual plant biomass on plots from which rodents have been excluded compared to plots where rodents are present (Table 3.4; see also Davidson et al. in press). Thus, all of these experiments indicate that rodent predation has a major consistent effect in preventing the domination of desert annual plant communities by a few large-seeded species.

Indirect Effects of Rodents on Other Species

From the magnitudes of the direct effects of rodents, especially as predators on selected plants, it is apparent that they can potentially have important indirect effects on other species that are mediated through these direct interactions. We have tested for only a few of the many possible kinds of such indirect effects, but we can show that some of these can easily be documented. Furthermore, these (and very likely others that we have not yet investigated) probably are extremely important in the organization of desert ecosystems. Here we shall focus on three of the best documented indirect effects of rodents, all of which are mediated through their direct effects as selective predators on large-seeded annual plants.

Table 3.4 RELATIVE INCREASE OF LARGE-SEEDED PLANTS ON PLOTS WHERE RODENTS HAVE BEEN EXCLUDED AT THREE DIFFERENT SITES IN SOUTHEASTERN ARIZONA

Site and species	Family	Seed mass (mg)	Relative increase (density on rodent removal/density on control)
Sonoran Desert			
Erodium cicutarium	Geraniaceae	1.62	9.2**
E. texanum	Geraniaceae	1.60	1.5*
Lotus humistratus	Fabaceae	1.50	3.57**
Saguaro National Monument			
Astragalus nuttallianus	Fabaceae	1.36	157.3***
Lupinus sparsiflorus	Fabaceae	1.51	8.2***
Chihuahuan Desert			
Erodium cicutarium	Geraniaceae	1.62	7,936.4*
E. texanum	Geraniaceae	1.60	1,000***
Lesquerella gordonii	Brassicaceae	0.94	9.7*
Astragalus nuttallianus	Fabaceae	1.36	4.3***

Asterisks denote significance levels: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.005$.
Note that different plant species and families increased at different sites, but that all had relatively large seeds (mass > 1 mg).
Data are from Inouye et al. (1980). Sonoran Desert; Kurzius and Brown (unpublished). Saguaro National Monument; and Samson, Thompson, Davidson, Kurzius, and Brown (unpublished). Chihuahuan Desert.

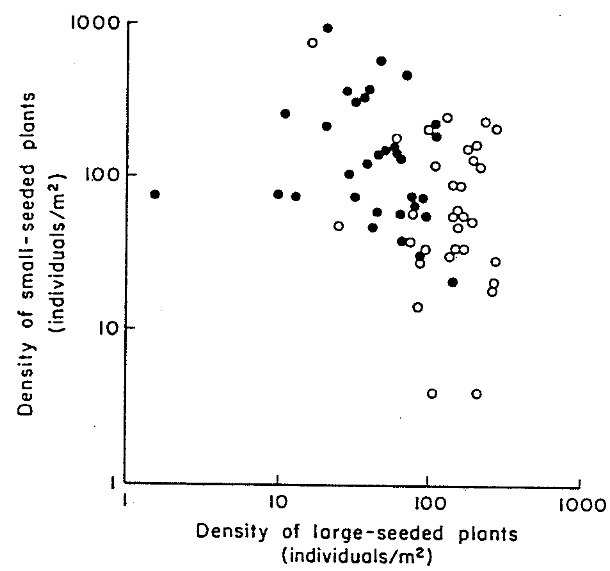

Fig. 3.5 Reciprocal density relationships between large- and small-seeded annual plants on rodent removal (unshaded circles) and control plots (shaded circles) at the Sonoran Desert site. When rodents were removed, large-seeded plants increased greatly in density; this was accompanied by a decrease in the density of small-seeded species as a result of competition.

The first indirect effect concerns the interaction between rodents and small-seeded plants. Because rodent predation suppresses populations of large-seeded plants, which increase to dominate the annual community when rodents are excluded, we hypothesize that rodents have an indirect beneficial effect on small-seeded plants, provided that small- and large-seeded species compete for limited resources. Experimental evidence strongly supports this hypothesis. The assumption that small- and large-seeded plants compete (in this case probably primarily for limited water, but perhaps also for nutrients) is confirmed by selective thinning experiments, which demonstrate a highly asymmetrical interaction: large-seeded species have a substantial negative effect on small-seeded ones, but any reciprocal effect is too small to detect (Davidson et al. 1984; see also Inouye et al. 1980). Presumably this asymmetry is owing to the fact that the large-seeded species, by virtue of their large seed reserves, have larger seedlings and never relinquish the competitive superiority conferred by this initial advantage.

Thus, when the effects of rodents are also considered, the result is an important interaction between competition and predation that affects the organization of the entire plant community and can clearly be seen in the results of our experiments. On the Sonoran Desert site on plots where rodents were excluded, large-seeded plants increased to dominate the community, and this was accompanied by a substantial decline in the density of small-seeded species, even though there was also a significant increase in total annual plant biomass (Fig. 3.5). On the Chihuahuan Desert site plants are still changing in response to the granivore removal experiments begun in 1977. Preliminary results suggest that the increase of large-seeded winter annuals on rodent removal plots has been accompanied by a decrease in the density of seedlings of the abundant small-seeded species, *Eriogonum abertianum*, but only on plots where ants have not also been removed (i.e., there is a significant rodent-ant interaction effect). This unusual species germinates in winter, but survives as a vegetative rosette until it is able to complete its life cycle with the moisture made available by the summer rains. Because *E. abertianum* begins the summer as an established vegetative plant, rather than as a seedling, it capitalizes on this initial size advantage to grow rapidly and competitively dominate the summer annual community. Its seeds are avidly consumed by ants, and it increases substantially on plots where ants have been removed. Thus rodents, even though their direct effects are primarily on the winter annuals, interact with ants to have an important influence on the summer annuals by limiting the density of the dominant species through a combination of indirect and direct pathways (see Davidson et al. in press).

We can also document an important indirect effect of rodents on the fungus *Synchytrium pallatum*, which is a specific pathogen that infects vegetative parts of the large-seeded plant *Erodium cicutarium* (see Inouye 1981 for details). Because its ability to infect host plants is highly density-dependent, *S. pallatum* in effect competes with seed-eating rodents, even though these competitors attack different life history stages of the plant. This is apparent from the results of our experiments. Exclusion of rodents resulted in a dramatic increase in the densities of both the large-seeded host plant and its fungal pathogen (Fig. 3.6). Although we have no experimental evidence to document it, the reciprocal effect of the fungus on the rodents almost certainly is significant. Because *E. cicutarium* is one of the dominant large-seeded annuals in many desert habitats and in some years infection by *S. pallatum* may cause sufficient mortality to drastically reduce seed production, the fungus probably has a substantial competitive effect on the rodents.

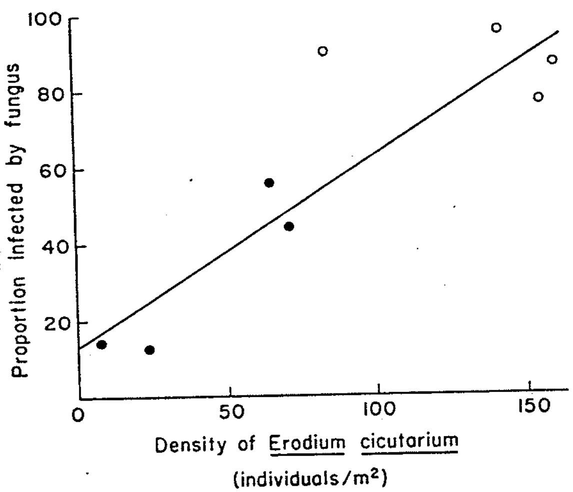

Fig. 3.6 Proportion of individual plants of *Erodium cicutarium* infected by the fungus *Synchytrium pallatum* as a function of both host plant density and rodent predation at the Sonoran Desert site. Note that on plots where seed-eating rodents were removed (unshaded circles), *E. cicutarium* attained a higher density of individuals which then suffered a higher incidence of fungal infection than plants on control plots (shaded circles). (Data from Inouye 1981.)

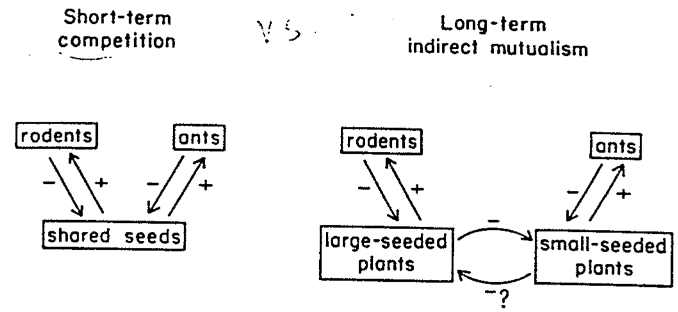

Fig. 3.7 Resource-mediated interactions between granivorous rodents and ants. In the short term the two taxa compete if they overlap in their feeding on limited seeds, but in the longer term the two taxa can have indirect mutualistic effects on each other if they feed differentially on different plant species that also compete with each other.

The third documented indirect effect of rodents is on ants. The short-term interaction between granivorous rodents and ants is, if anything, competitive. Presumably this competition results from overlap between the two taxa in the seed resources that they exploit. If, however, the overlap in the diets is not complete, then over the long term the interaction could actually be mutualistic because of the importance of indirect pathways. For such indirect mutualism to occur, it is necessary for the rodents and ants to prey selectively on seeds of different plant species, and for these plants to compete with each other for resources during the vegetative phase of their life cycle (Fig. 3.7). Our data not only show that these conditions are met, but also provide evidence of the expected long-term, indirect, beneficial effect of rodents on ants. Rodents and ants differ significantly in diet, with rodents specializing on larger seeds than most harvester ant species, especially the numerically dominant but tiny ants of the genus *Pheidole* (Brown and Davidson 1977, Brown et al. 1979a). Large- and small-seeded plant species compete for resources (see above and Inouye et al. 1980, Inouye 1982). If plant-mediated indirect interactions between the two taxa are important, we would expect the initial increase in ants in response to rodent exclusion to be followed by a decrease that coincides with appropriate compositional changes in the plant community. This hypothesized pattern is exactly what is observed at the Sonoran Desert site (Fig. 3.8; see Davidson et al. 1984). Note that the abundance of ants on plots where rodents were removed did not ever fall below the initial, premanipulation levels. However, such a result, indicative of a net positive indirect effect of rodents on ants, would not necessarily be expected as long as there is also some direct competition between the two taxa. The magnitude of the indirect effect should depend on such factors as the extent of overlap in the diets of the two taxa and the intensity and symmetry of competition between the two classes of plant species. Our failure to detect any reciprocal positive long-term effect of ants on rodents is probably due to the pronounced asymmetrical competition between small- and large-seeded plants (see above and Davidson et al. 1984).

IMPLICATIONS OF THE EXPERIMENTS

Interspecific Interactions and Community Organization

Recently there has been much discussion of the effect of interspecific interactions on the organization of communities. Some investigators have cast doubt on studies purporting to demonstrate the importance of these interactions (e.g., Connor and Simberloff 1979, Strong et al. 1979,

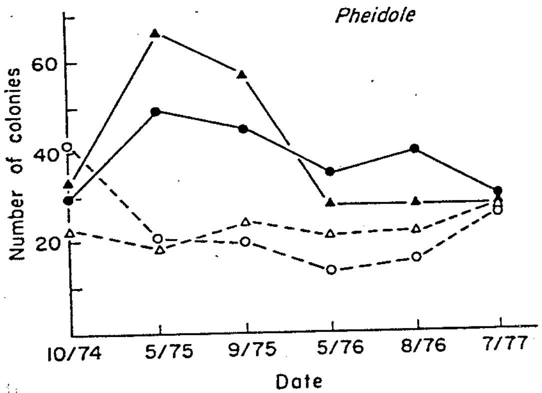

Fig. 3.8 Temporal trends in the densities of colonies of *Pheidole* ants, primarily *P. xerophila*, on rodent removal (shaded symbols) and control plots (unshaded symbols) at the Sonoran Desert site. Circles and triangles refer to different individual plots. In 1974, about a year after initiation of the treatments, there were no significant differences. Ant densities then increased on rodent removal plots (presumably as a result of release from competition) and then decreased again. We suggest that this last decrease is the result of indirect mutualism, mediated primarily through the effect of rodent predation on large-seeded plants that competitively dominate the small-seeded plants that produce the small seeds preferred by these small ants.

Simberloff and Boecklen 1981). Others have suggested that because the physical environment is so variable, the kind of resource limitation that would cause strong interactions rarely occurs in nature (e.g., Wiens 1977; Strong 1983, 1984b). Still others have searched for generalizations by trying to determine whether the organization of particular systems is determined primarily by competition, predation, mutualism, or temporal or spatial variation in the physical environment (e.g., Connell 1975, 1980).

The paucity of rigorous, long-term experimental studies in community ecology has contributed to the failure to resolve these issues. Although there has been an increasing number of experimental manipulations to test for the effects of particular kinds of interactions (e.g., Colwell and Fuentes 1975, Schoener 1983b, Connell 1983), there have been very few detailed, experimental investigations designed specifically to assess the diverse kinds of possible interactions among the species within a community and between the organisms and their nonliving environment (but see, for example, Connell 1961a, Lubchenco and Menge 1978, Paine 1980).

Although our experiments by no means constitute a complete investigation of the desert granivore system, they are sufficient to provide insights into the issues raised above. We can document the occurrence of: (1) competition among rodent species, (2) competition among ant species (not mentioned above, but see Davidson 1985), (3) competition among rodents, ants, and birds, (4) competition among annual plant species, (5) predation by rodents, ants, and fungus on plants, and (6) several indirect effects of rodents and ants on other species in the community that are mediated through their direct effects as predators on plants. Perhaps the most important thing about these interactions is not that they can be shown to occur within the same community, but that most of them are sufficiently strong to have major effects on community organization. Experimental exclusion of rodents, for example, results in substantial changes in the absolute and relative abundances of ants, birds, annual plants, and a fungus on our experimental plots.

We can test simultaneously for the effects of both competition and predation on the annual plants, and we find that they interact with each other in such a way that it would be misleading to suggest that either is more important than the other. Furthermore, other relationships that we have not emphasized in these experiments may be equally important. Thus, predation by carnivorous vertebrates may have as much impact on rodents as the rodents have on plants (e.g., see Kotler 1984). Fluctuations in the physical environment have important influences on all desert communities; in particular, variation in the quantity and timing of precipitation affects primary productivity, competitive relationships among plant species, seed production, and granivore

populations (e.g., Brown et al. 1979b, MacMahon 1979). The dramatic increase in small seed-eating rodents in the winter of 1981–1982 shown in Fig. 3.1 is probably a direct consequence of heavy precipitation and high seed production during the preceding months.

Thus, we conclude that it is hazardous to attribute the organization of any reasonably complex natural community to the overriding influence of any single kind of interaction, especially when other kinds of interactions and the relationships between them have not been studied by rigorous experimentation. Although we are cautious in generalizing from the granivore system to other communities, we suspect that similarly complex and interacting relationships among the species and between them and their physical environment will often be found. There is a precedent for this in careful experimental studies in other habitats, such as the intertidal (Connell 1961a, Lubchenco and Menge 1978, Paine 1980). In addition, this complexity is to be expected on conceptual grounds for several reasons.

1. Each species has the capacity to increase at an exponential rate, but continued population growth is eventually checked.
2. Competition occurs whenever different species overlap in their requirements for essential resources that are in short supply.
3. Predation is ubiquitous, because almost every species either eats or is fed upon by other organisms.
4. Mutualistic associations, in which species are dependent on each other for essential resources or other benefits, are common.
5. Each species potentially can limit many others through indirect, as well as direct pathways.
6. All species are limited by spatial and temporal variation in their abiotic environment as well as by intra- and interspecific interactions.

Thus, in order to understand the complex organization of natural communities, it seems necessary to adopt a pluralistic approach that can take into account the diverse, interacting influences of all of these processes.

Theoretical Implications

In a general way the results of our experiments are consistent with current theories that interspecific interactions have important influences on community organization. Our manipulations reveal effects of competition and predation on desert animals and plants that are reminiscent of those described by MacArthur (1958, 1972a), Brooks and Dodson (1965), Paine (1966, 1980), and Lubchenco and Menge (1978) for other systems. In many cases the mechanisms as well as the outcomes are similar: a combination of exploitative and interference competition, selective predation on competitively dominant consumer species, and so on.

We began our experimental research program in 1973, at a time when mathematical models of pairwise population interactions seemed to offer a simple and rigorous conceptual framework for interpreting the patterns of abundance and distribution of closely related species revealed by natural experiments (e.g., MacArthur and Levins 1965, Levins 1968, MacArthur 1972a, May 1973a, Cody and Diamond 1975, Roughgarden 1979). When we set out to test these ideas experimentally, we fully expected that the results would support both the theory and our interpretation of geographical patterns in desert granivore associations (e.g., Brown and Lieberman 1973, J. H. Brown 1975, Davidson 1977).

The experiments do confirm that interspecific competition plays a major role in the organization of the desert granivore system, but they have also revealed a degree of complexity that neither the simple pairwise models nor the geographical comparisons had prepared us to expect. We were surprised to observe the long time lags, highly asymmetrical relationships, slight compensation for absent species, and substantial competition between distantly related taxa that our manipulations have so clearly demonstrated. In retrospect, it is easy to come up with realistic hypotheses to explain these results, but these just emphasize how naive and unrealistic our initial ideas were.

Consider just two examples: the asymmetries and the slight compensation among rodent species. The Chihuahuan Desert study site was one of the localities used by J. H. Brown (1975) in his geographical comparisons of granivorous rodent guilds. Based on measurements of seed and microhabitat utilization at this and other sites, Brown calculated overlaps between species in overall resource utilization using standard techniques. Values of these overlaps, which are supposed to indicate the degree of interspecific competition (but see Case and Gilpin 1974), are uniformly high and symmetrical. Other slightly different methods could have been employed, but the results, while not necessarily exactly symmetrical, would have been similar. These large measured overlaps in resource utilization would lead to the following predictions: (1) the remaining rodent species should increase in density and biomass to compensate to a large extent for experimental removal of selected rodent species; (2) all species that can use millet seeds should increase in response to food addition treatments, and collectively the rodents should consume most of the supplemental food.

Clearly, the results of the experiments support neither of these predictions, and any good biologist who knows rodents and deserts should have no difficulty in coming up with reasonable explanations for the discrepancies. The calculations of overlap in resource utilization did not take into account: (1) pronounced differences between species in both body size and population density that influence resource requirements and habitat utilization; (2) morphological, physiological, and behavioral constraints that affect the interactions between species and their physical environment; (3) effects of interspecific aggressive interference; (4) mechanisms of intraspecific competition, such as territoriality, that could maintain population sizes below the limit set by the availability of food per se; (5) use of seed resources by other animals, such as birds and ants; (6) effects of predators on the resource utilization and population densities of the rodents; and (7) indirect interactions, through which a variety of other organisms could potentially have a wide range of effects. We now have evidence (much of it cited above) that all of these factors are important in determining the roles of different rodent species in the organization of desert communities.

A fundamental problem with much of traditional community theory is that it treats species as if they affect each other in a simple pairwise fashion within a closed system. It ignores the fact that species are imbedded in a complex biotic and physical environment that affects almost every aspect of their ecology, including their interspecific interactions. Although theoretical ecologists have recognized the importance of this imbedding problem (e.g., Levins 1974, 1975; Schaffer 1981; Bender et al. 1984), the additional complexity that it introduces seems to be as difficult to characterize mathematically as it is empirically.

Considerable progress has been made, however, in developing a body of theory that explores the consequences of possible kinds of indirect interactions among species (e.g., Levine 1976, Holt 1977, Lawlor 1979, Vandermeer 1980). Our experimental results show not only that these kinds of indirect interactions occur in natural systems, but also that relationships mediated through these indirect pathways have major effects on the organization of the entire desert community. A simple perturbation, such as the removal of rodents, sets in motion a complex series of changes that ripple through the community, affecting an increasing number of species. Eventually there must be a limit to these changes and the system should approach a new state, but it is a testimony to the importance of these indirect effects that we are still observing pronounced changes in plants and other organisms at least seven years after exclusion of rodents began.

Our experiments suggest a view of community organization in which virtually all species affect each other through a complex web of direct and indirect interactions (see concluding section of Chapter 20 for further discussion). These relationships are highly asymmetrical, nonlinear, and influenced importantly by the physical environment as well as by other species. They vary from site to site, even among superficially similar habitats, and their dynamics are sufficiently slow and complex that many years are required to observe their full effect.

We still have a long way to go, both empirically and theoretically, before we have a really satisfactory understanding of these structural and dynamic properties of communities. Eventually, it would be nice to know enough about the networks of interaction so that we could predict the diverse ramifications of experimental manipulations and identify the frequency-dependent negative feedback loops that must account for the resiliency of the system to natural and experimental perturbations. At present there have been so few comprehensive empirical studies of complex, multispecies systems that it is difficult to know what properties are specific to a particular system and what ones are of general importance. Without an adequate data base to reveal a clear phenomenology of patterns and processes, it is difficult for theoreticians to produce realistic models. Nevertheless, recent progress, such as that in the study of food webs (Cohen 1978, Yodzis 1982, Pimm 1982, DeAngelis et al. 1983), suggests that even the most complex communities may reluctantly reveal their secrets in the face of a combined theoretical and empirical assault.

Advantages and Limitations of Field Experiments

In recent years controlled, manipulative experiments conducted in the field have played an increasingly influential role in making contemporary ecology a rigorous, quantitative science. Several advantages of field experimental methods are frequently mentioned: (1) the precise control of variables that can be achieved by human intervention, (2) the statistical rigor that can be attained as a result of replication and use of powerful experimental designs, and (3) the strength of inference that can be achieved by applying the full logical force of the hypothetico-deductive method. The results of our experiments confirm the importance of all these advantages. For example, they provide evidence for the importance of competition among species of terrestrial vertebrates that not only is difficult to dispute, but also is consistent with the results of other manipulative studies (e.g., Hairston 1980, Pacala and Roughgarden 1982).

Our work emphasizes yet another advantage of field experimental methods, however, and one that is rarely mentioned. This is the ability to monitor the trajectories of the complex dynamic behaviors set in motion by a single controlled and sustained perturbation. Many features of community organization can be analyzed as the system adjusts to the altered state through interactions of varying length, strength, and time constants. Because indirect pathways are chains of direct interactions, the temporal sequence of events reveals a great deal about the processes by which species affect each other and about the patterns of connectance that link the fates of species in different taxonomic groups and trophic levels. Our experiments show that the exclusion of particular species or groups of species may have unanticipated effects on many other species that may take many years to be resolved. Although it may be better hypothetico-deductive science to perform perturbations to test specific hypotheses, rather than just to see what happens, nevertheless these kinds of unexpected results may tell us more about the organization of communities than those predicted by our naive and simplistic hypotheses.

These kinds of insights provided by field experimentation cannot usually be obtained by recording the results of "natural steady state experiments," as discussed in Chapter 1. Comparative observations of unmanipulated systems usually provide only a snapshot that records the more-or-less steady state response of the system to a particular set of environmental conditions. A controlled, replicated perturbation permits precise, quantitative documentation not only of final response of the community to the altered conditions, but also of the complex sequence of dynamic processes by which the changes take place. Terrestrial ecologists, in contrast to some of their colleagues working in the more controlled, replicated environment of lakes (e.g., Brooks and Dodson 1965 and many subsequent studies), have been slow to appreciate the importance of indirect interactions, through which many taxonomically unrelated species can have major effects on each other. We suspect that this is not because such indirect interactions are unimportant in most terrestrial habitats, but rather because the kinds of comparative, nonmanipulative studies that have traditionally been performed did not provide sufficiently precise data to document their effects. For example, imagine trying to convince anyone that the higher density of a fungal plant pathogen on an island, compared to a nearby mainland, was owing to the absence of seed-eating rodents from the island. But we can show experimentally that the density of *Synchytrium pallatum* increased on plots where nothing else was done except to remove rodents.

Although there are those zealous experimentalists who would imply that purely observational studies have no place in modern ecology, this extreme perspective is misguided and at variance with our own experience. Our earlier nonexperimental studies of desert granivores (e.g., Brown and Lieberman 1973, J. H. Brown 1975, Davidson 1977) not only suggested hypotheses about interspecific competition that called for rigorous experimental test, but they also revealed enough about probable mechanisms of interaction to design appropriate experiments and procedures for monitoring the results. Furthermore, although the manipulations have yielded some surprises, they have also confirmed many of the inferences drawn from purely observational studies. For example, comparisons of the abundance, distribution, diet, and foraging behavior of rodents within local habitats and among geographically separated sites clearly suggested important influences of limited food availability, body size differences, seed size selection, microhabitat selection, and competition with ants, and we have subsequently documented these phenomena experimentally. Our experimental program has required a major commitment of time, effort, and resources. To have attempted this project without the background provided by several years of nonexperimental studies would have been not only difficult to justify, but also inefficient, and even likely to fail because of poor design.

Despite the great advantages of the experimental method for dissecting ecological communities and revealing the complexities of their structure and function, we must recognize that many of the important questions cannot be answered by experimental manipulations alone. The experimental method has several limitations and disadvantages. First, the price of the human intervention necessary to manipulate and control variables is the creation of possible artifacts. Although we have tried to minimize the possibilities of such artifacts, it is important to emphasize that the fencing, trapping, poisoning, seed addition, and other manipulations may have unexpected and undetected effects on the community. For example, fencing might differentially exclude predators and folivores, and these could conceivably have caused some of the results we have attributed to granivores. Second, the spatial and temporal scale on which it is practical (and legally and morally permissible) to manipulate ecological systems is necessarily limited. As discussed in Chapter 8, there are good reasons to believe that interactions over geographical spatial scales and evolutionary time scales may affect the organization of local communities. That we might obtain very different results if we were able to perform our manipulations over thousands of square kilometers and maintain the treatments for thousands of years does not mean that the present results are any less important. However, it should encourage us to be cautious in generalizing from such experimental studies and to use "natural experiments" to provide the essential geographical and evolutionary perspectives.

Finally, experiments such as ours represent extreme examples of what we call the microscopic approach to community ecology. This approach has its own limitations. Although a detailed analysis of the interrelationships among species and between species and their abiotic environment within one local community can reveal the complexity of patterns and processes that characterize that particular system, it can provide little insight into which of these are specific to that system and which can be generalized to other communities. Furthermore, if there are general rules that govern the organization of communities, it may be impossible or impractical to adduce all of these from microscopic studies of the interactions of individual species (Brown 1981). For example, the statistical distributions of population densities, body sizes, rates of energy use, and areas of geographical ranges among the many species that comprise local communities may elucidate patterns and processes that cannot be discovered from microscopic experimental studies, which must for practical reasons be focused on only a small proportion of the species present. Large-scale geographical studies, especially comparisons of communities inhabiting similar physical environments in widely separated regions inhabited by different taxa of organisms, should continue to provide a valuable perspective.

The challenge of community ecology is to understand the structure and function of some of the most complex natural systems. Those who accept this challenge have no excuse for complaining about its difficulty, but they have every reason for keeping an open mind and encouraging different approaches by a diversity of ecologists.

SUMMARY

Experimental removal of species or groups of species of granivorous animals and experimental addition of seeds have profound effects on desert communities. In the present paper we focus on the response of seed-eating rodents to these manipulations and on the effect of manipulating rodents on other species. These results show that: (1) rodents compete for a limited food supply, not only with other seed-eating rodent species, but also with granivorous animals such as ants and birds; (2) rodents forage selectively for the seeds of certain large-seeded plant species, and as predators they have major impact on these plant species; and (3) as a consequence of their direct interactions with these large-seeded plants, rodents have important indirect effects on small-seeded plants, a parasitic fungus, and granivorous ants.

The diverse and often indirect interrelationships among the species within this relatively simple system have important implications for our understanding of community organization. For the most part, our results provide strong support for some of the conceptual generalizations of community ecology, such as the importance of competition, predation, abiotic factors, and indirect interactions. On the other hand, the specific, quantitative responses to our perturbations reveal a complexity of community organization that remains poorly understood, both empirically and theoretically. Species interact, not in isolated pairs as simple theories originally assumed, but within a complex matrix of other species and the abiotic environment. Species in different taxonomic groups and trophic levels affect each other directly and indirectly, through pathways of varying length, strength, and time constants. Long-term experimental studies have important advantages for investigating the organization of complex ecological systems, but a diversity of theoretical and empirical approaches focused on different spatial, temporal, and organizational scales will almost certainly be necessary to develop a viable general theory.

ACKNOWLEDGMENTS

So many people have helped with the research described here that it is impossible to thank them individually. However, this does not diminish our gratitude for their assistance; without it we could never have undertaken a project of this magnitude. This chapter has benefited enormously from the helpful comments of T. J. Case, J. M. Diamond, P. J. Grubb, and P. Yodzis. The National Science Foundation has generously supported the research from the outset, most recently with Grants BSR 80-21535 to J.H.B. and BSR 80-21537 to D.W.D.