

Overall, the data suggest a deficit in the density of the left hemisphere in young chronic alcoholics, while no deficit could be identified in the right hemisphere. The deficit seems to have reduced or eliminated the left hemisphere advantage in density seen in the control group.

Thus, the data suggest that the left hemisphere is more sensitive physiologically than the right to the effects of alcoholism. On the face of it, this seems to contradict traditional psychiatric and psychological assumptions that the right (or nonverbal) hemisphere is more involved because of losses on tests traditionally seen as nonverbal (4). However, the results of such tests can be explained in several ways by our data. First, as Luria (8) pointed out, the left hemisphere plays a strong role in so-called nonverbal functions, especially in the parietal and frontal areas. Thus, the findings may simply indicate that damage to the left hemisphere, from a slowly developing disorder like alcoholism, affects visually related functions rather than the more overlearned basic verbal functions (which have long been recognized as resistant to slow brain diseases). The long-term presence of the alcohol may also prevent the right hemisphere from taking over these functions.

Alternatively, the destruction of the left hemisphere may cause the right hemisphere to attempt to take over the functions of the left hemisphere. In such cases, some of the normal functions of the right hemisphere may be compromised in favor of the more important verbal skills. This alternative is not as likely as the first. In either case, these results should caution physicians and psychologists from making hasty assumptions relating alcoholics to brain-damaged patients in general.

It is possible to attempt to explain these results by pointing out that alcoholics have larger ventricles than normal subjects. If enlarged ventricles were the major cause of the lower density, however, we would expect both hemispheres to show decreases, as such ventricular enlargement has never been found to be unilateral. In addition, such an explanation would not account for the observed changes in hemispheric relations. The left ventricle could be predicted to be sufficiently larger than the right (by at least 20 percent in this experiment). However, this was not the case in our films, nor has such a phenomenon ever been reported in alcoholics. (It should be noted that such a finding, if true, would be significant in itself.)

Each of these questions, as well as

questions regarding more precise areas of reduced density within the hemisphere, needs to be evaluated in future, larger studies. This study, however, has demonstrated both important findings about alcoholism and the utility of density analysis in studying alcoholics.

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References

1. J. O. Haug, *Acta Psychiat. Scand.* **203**, 135 (1968).
2. L. A. Cala et al., *Aust. N. Z. J. Med.* **8**, 147 (1978).
3. D. A. Wilkinson and P. L. Carlen, *J. Stud. Alcohol*, in press.
4. C. J. Golden, *Diagnosis and Rehabilitation in Clinical Neuropsychology* (Thomas, Springfield, Ill., 1978).
5. W. Meese, W. Lanksch, S. Wende, in *Cranial Computerized Tomography*, W. Lanksch and E. Kazner, Eds. (Springer, New York, 1976).
6. *Diagnostic and Statistical Manual* (American Psychiatric Association, Washington, D.C., 1980).
7. N. Nie et al., *Statistical Package for the Social Sciences* (McGraw-Hill, New York, 1976).
8. A. R. Luria, *The Working Brain* (Basic Books, New York, 1973).

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Competition in Desert Rodents:

An Experiment with Semipermeable Enclosures

Abstract. *Larger species of seed-eating desert rodents were excluded from experimental plots while smaller, potentially competing species were allowed to enter. Density of small granivores on these plots increased to nearly 3.5 times that on control plots but only after 8 months. These results indicate that interspecific competition affects the abundance of desert rodents; they also support indirect evidence that competition for seeds influences the organization of desert rodent communities.*

Although numerous studies suggest that interspecific competition plays a major role in structuring communities of terrestrial vertebrates, few experiments have demonstrated that the presence of one species affects the abundance, distribution, and resource utilization of coexisting species in nature (1-3). In part for this reason, the importance of competition in community ecology has been questioned with increasing frequency (4-6). Some experimental studies have assessed indirect, short-term consequences of competition, such as shifts in resource utilization after removal of coexisting species (1, 7-9); others measured numerical responses of artificially confined populations (2, 10). But long-term experiments on unconfined populations, which are most likely to demonstrate realistic community responses to competition (11, 12), often are impractical because of the difficulty in maintaining reduced population densities in the face of continual immigration (8, 12, 13).

We selectively excluded some species without restricting dispersal of others by taking advantage of size differences among seed-eating desert rodent species. In July 1977 we established eight square plots (50 by 50 m) on a 20-ha site in an area of superficially homogeneous Chihuahuan Desert shrub vegetation. The site is 6.5 km east of Portal, Arizona (14). The plots were fenced with 0.64-cm wire mesh, which was buried to a depth of 0.2 m and topped with aluminum flashing.

We assigned treatments to plots at random: two replicates of each of four treatments in a 2 by 2 factorial design.

The factor of primary concern in this report is the presence or absence of large rodents of the genus *Dipodomys*. Access of rodents to each plot was controlled by 16 holes of appropriate size cut at equal distances at ground level. Small holes (1.9 cm in diameter) in the fences of four plots excluded the three largest species of granivorous rodents (*Dipodomys spectabilis*, body weight, 120 g; *D. ordi*, 52 g; *D. merriami*, 45 g) but permitted free passage of the four smallest granivorous rodent species (*Perognathus penicillatus*, 17 g; *P. flavus*, 7 g; *Peromyscus maniculatus*, 24 g; *Reithrodontomys megalotis*, 11 g) as well as three species of small omnivorous rodents (*Onychomys leucogaster*, 39 g; *O. torridus*, 29 g; *Peromyscus eremicus*, 25 g) (15, 16). Larger holes (6.5 cm) in the fences of the other four plots allowed access to all rodent species. The other factor in this experiment was the presence or absence of large harvester ants, *Pogonomyrmex rugosus*, which forage in columns and were removed by poisoning colonies on two of the four plots subjected to each rodent treatment (17).

Our experiment was designed to determine whether the presence of large granivorous rodents limits the abundance of small rodents. Furthermore, if this effect is due to competition for food, we predict that the small granivores should

show greater increases in density in response to removal of *Dipodomys* than should the small omnivores. If, however, an increased density of small granivores is an artifact resulting from some effect of the different sizes of holes in the fences (such as differential exclusion of predators), then the density of small omnivores should also increase (18).

We sampled the rodent populations for a 3-month period (July through September 1977) during which large holes in all fences permitted free movement of all rodents. In September we reduced the size of holes in the fences of four plots and began removing *Dipodomys* from them. Censusing continued at approximately monthly intervals through June 1980. We trapped each plot for one night with live traps placed in a 7 by 7 grid. Holes in the fences were closed on the night of trapping.

Monthly records of captures by species and by plot were kept (Fig. 1 and Table 1).

Data for both small granivores and small omnivores were subjected to three kinds of statistical analysis. (i) We used the Wilcoxon matched-pairs signed-rank test to assess the effect of the exclusion of *Dipodomys* on the number of previously unmarked individuals captured; for each month, the sum of rodents captured on plots with *Dipodomys* removed was paired with the sum for plots with *Dipodomys* present. (ii) We used the Mann-Whitney *U* test to evaluate the significance of the difference between yearly totals of all rodents captured on

the four plots with *Dipodomys* present and the four plots with *Dipodomys* absent. (iii) With a repeated measures analysis of variance (19), we analyzed the effects of the main treatments (*Dipodomys* removal and *Pogonomyrmex* removal) and interactions between them (Table 1).

Densities of small rodents remained similar to those on control plots for 8 months (Fig. 1 and Table 1). Beginning on July 1978, however, small granivores reached and maintained densities that averaged 3.5 times higher on plots where *Dipodomys* were excluded than on controls, but the small omnivores never showed any significant response to removal of *Dipodomys* (Fig. 1 and Table 1).

Our results are consistent with studies that provide indirect, circumstantial evidence that populations of granivorous desert rodents are limited by availability of seeds and that the distribution, population density, and resource utilization of a particular species is determined in large part by competition for food with other species (20-22).

Two aspects of the increase of small granivores in the absence of *Dipodomys* are of particular interest. The first is the 8-month time lag, for which we can suggest two explanations. Since these rodent species reproduce primarily in the spring, dispersing juveniles would not have been available to colonize our plots until the summer after initiation of treatment. Also, because each species may have particular characteristics of seed

harvesting, food catching, scent marking, and burrow construction, it may take considerable time after the removal of *Dipodomys*, and perhaps the production of a new seed crop, before the area is perceived as favorable by small granivores.

The almost 350 percent increase in density of small seed-eating rodents on our experimental plots was not nearly sufficient to compensate for the densities and biomass of the excluded *Dipodomys*. After July 1978 we captured an average of 12.0 individuals and 837 g of *Dipodomys* per hectare per month on control plots, but only 4.2 individuals and 42.1 g of small granivores on experimental plots; this was a 26.5 and 6.2 percent compensation in density and consuming biomass, respectively (23). There are three likely explanations. (i) Increased densities of small granivores may result in increased intra- and interspecific aggression, which could prevent further increases. (ii) Each species may be so constrained by inflexible morphology, physiology, and behavior that it does not forage for particular foods or in certain microhabitats, thereby limiting its capacity to exploit food resources made available by removal of *Dipodomys* (7, 13, 15, 20, 24, 25). (iii) Perhaps most importantly granivores other than rodents, such as ants and birds, probably consume some of the seeds normally used by *Dipodomys* and make them unavailable to small granivorous rodents (26). Possible evidence for such an effect of ants comes from the analysis of variance

Table 1. Small rodents captured and analysis of the effects of the exclusion of *Dipodomys* on experimental plots. Years run from 1 July to 30 June. Numbers of small granivores in parentheses indicate the species in the following order: *Perognathus penicillatus*, *P. flavus*, *Peromyscus maniculatus*, and *Reithrodontomys megalotis*. Numbers of small omnivores in parentheses indicate the species in the following order: *Onychomys leucogaster*, *O. torridus*, and *Peromyscus eremicus*.

Year	Captures with <i>Dipodomys</i> present (N)				Captures with <i>Dipodomys</i> absent (N)				Statistical significance (P)			
	<i>Pogonomyrmex</i> present		<i>Pogonomyrmex</i> absent		<i>Pogonomyrmex</i> present		<i>Pogonomyrmex</i> absent		Mann-Whitney	Analysis of variance	Wilcoxon*	
	Plot 11	Plot 14	Plot 12	Plot 8	Plot 3	Plot 19	Plot 15	Plot 21				
<i>Small granivores</i>												
1977 to 1978	5 (4,1,0,0)	1 (0,1,0,0)	2 (0,2,0,0)	5 (0,5,0,0)	4 (1,3,0,0)	1 (0,0,0,1)	0 (0,0,0,0)	2 (0,2,0,0)	.171	> .25	< .005	
1978 to 1979	5 (4,1,0,0)	1 (1,0,0,0)	0 (0,0,0,0)	1 (0,1,0,0)	5 (1,4,0,0)	5 (0,2,2,1)	12 (8,2,2,0)	8 (2,5,0,1)	.029	< .025		
1979 to 1980	9 (3,4,0,2)	1 (0,0,0,1)	2 (0,0,0,2)	4 (1,3,0,0)	20 (0,12,0,8)	10 (0,0,0,10)	25 (9,12,0,4)	12 (1,8,0,3)	.014	~ .05		
<i>Small omnivores</i>												
1977 to 1978	1 (0,1,0)	2 (1,1,0)	7 (0,7,0)	3 (0,3,0)	8 (2,6,0)	1 (0,0,1)	0 (0,0,0)	17 (4,13,0)	> .6	> .5	≥ .05	
1978 to 1979	8 (4,4,0)	0 (0,0,0)	7 (0,7,0)	4 (2,2,0)	7 (0,7,0)	4 (0,2,2)	3 (0,3,0)	4 (1,3,0)	> .6	> .75		
1979 to 1980	8 (4,4,0)	5 (2,3,0)	8 (0,8,0)	6 (5,1,0)	11 (6,3,2)	7 (1,0,6)	10 (2,8,0)	7 (0,6,1)	.171	> .10		

*Performed on newly marked individuals from March 1978, when marking began, to June 1980.

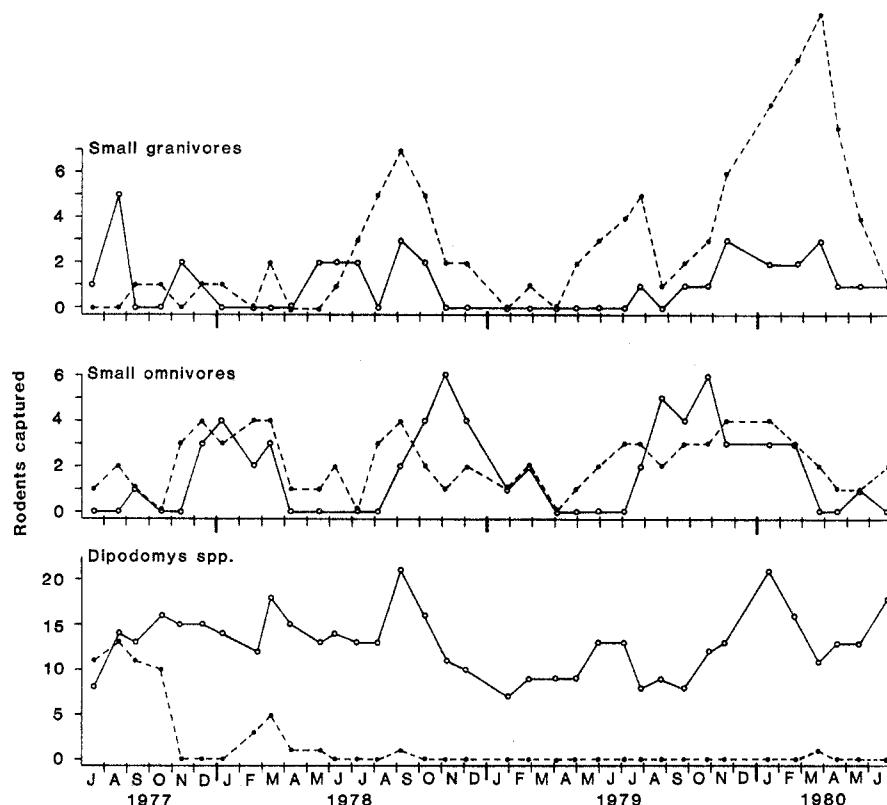


Fig. 1. Monthly sums of rodents captured on the four plots with *Dipodomys* excluded (dashed lines) and the four plots with *Dipodomys* present (solid lines). After 8 months, the density of small granivores on plots with *Dipodomys* excluded consistently exceeded that on plots where *Dipodomys* was still present. The omnivores showed no such response.

we performed. There is a significant interaction between treatments to remove *Dipodomys* and *Pogonomys* in the second year of the study [$F(1, 4) = 8.25$, $P < .05$]. During that time small granivorous rodents showed a greater increase in response to exclusion of *Dipodomys* on plots where *Pogonomys* was also absent.

This study provides direct evidence that interspecific competition plays a major role in structuring a community of terrestrial vertebrates. Because deserts are often thought to require extreme adaptations to the rigorous physical environment, our results show that biotic interactions among coexisting species are relatively unimportant in structuring communities (27). Furthermore, the food supply for many desert animals fluctuates widely because it depends on scanty, unpredictable precipitation, and it has been suggested that in such circumstances food scarcity and competition

occur only sporadically (4, 5). However, our study, together with earlier experiments demonstrating competition between seed-eating rodents and ants (26), indicate that interspecific competition for food plays a sustained role in determining the abundance of granivore species and the organization of desert communities.

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References and Notes

1. R. Colwell and E. Fuentes, *Annu. Rev. Ecol. Syst.* **6**, 281 (1975).
2. P. Grant, *ibid.* **3**, 79 (1972).
3. R. Miller, *Adv. Ecol. Res.* **4**, 1 (1967); R. MacArthur, *Geographical Ecology* (Harper & Row, New York, 1972); M. Cody, *Competition and the Structure of Bird Communities* (Princeton Univ. Press, Princeton, N.J., 1974); T. W. Schoener, *Science* **185**, 27 (1974); M. Cody and J. Diamond, Eds., *Ecology and Evolution of Communities* (Belknap, Cambridge, Mass., 1975).

4. J. Connell, in *Ecology and Evolution of Communities*, M. Cody and J. Diamond, Eds. (Belknap, Cambridge, Mass., 1975), pp. 460-490.
5. J. Wiens, *Am. Sci.* **65**, 590 (1977).
6. D. Strong, L. Szyska, D. Simberloff, *Evolution* **33**, 897 (1979); E. Connor and D. Simberloff, *Ecology*, in press; D. Simberloff and W. Boecklen, *Am. Nat.*, in press.
7. M. Price, *Ecology* **59**, 910 (1978); J. Wondolleck, *J. Mammal.* **59**, 510 (1978).
8. J. Davis, *Ecology* **54**, 174 (1973).
9. W. Sheppe, *Can. Field Nat.* **81**, 81 (1967); J. Koplin and R. Hoffman, *Am. Midl. Nat.* **80**, 494 (1968); S. Holbrook, *Ecology* **60**, 758 (1979).
10. P. Grant, *Can. J. Zool.* **47**, 1059 (1969); *J. Ani. Ecol.* **40**, 323 (1971).
11. K. Crowell, *Am. Nat.* **107**, 535 (1973); J. Redfield, C. Krebs, M. Taitt, *J. Anim. Ecol.* **46**, 607 (1977); N. Hairston, *Ecology*, in press; G. Camaron, *J. Mammal.* **58**, 488 (1977).
12. Z. Abramsky, M. Dyer, P. Harrison, *Ecology* **60**, 530 (1979).
13. G. Schroeder and M. Rosenzweig, *Oecologia (Berlin)* **19**, 9 (1975).
14. This experiment is part of a larger project designed and supervised by D. W. Davidson of the University of Utah and O. J. Reichman of the Museum of Northern Arizona in collaboration with J. H. Brown. The entire project involves 24 experimental plots.
15. Designation of granivorous species follows J. Brown [in *Ecology and Evolution of Communities*, M. Cody and J. Diamond, Eds. (Belknap, Cambridge, Mass., 1975), pp. 315-341].
16. We placed baffles (15 by 15 cm), made of 0.64-cm mesh and extending inward and outward from the fence, at half of the holes of each plot. These baffles serve to direct the rodents to the holes.
17. Because one of the plots originally assigned for *Pogonomys rugosus* removal was found to contain no colonies of this species, in August 1979 this treatment was assigned to another plot where *P. rugosus* could be removed. Although we present data for the new plot after that date, our results would have been slightly more significant had we continued to use the data for the original plot.
18. Our design does not control for differential access to experimental plots by herbivorous mammals, which might by their foraging affect the seeds available to granivores. In a similar experiment (R. Inouye, G. Byers, J. Brown, *Ecology*, in press), exclusion of herbivores by fencing had no detectable effect on survivorship or seed production of desert annuals, which produce the vast majority of seed consumed by granivores.
19. B. Winer, *Statistical Principles in Experimental Design* (McGraw-Hill, New York, 1971), pp. 559-563.
20. J. Brown, O. Reichman, D. Davidson, *Annu. Rev. Ecol. Syst.* **10**, 201 (1979), and references therein.
21. E. Larsen, thesis, Utah State University (1978).
22. M. Bowers and J. Brown, in preparation.
23. Compensation = $(x - y)/z$, where x = density (or consuming biomass) of small granivores on experimental plots, y = density (or consuming biomass) of small granivores on control plots, and z = density (or consuming biomass) of *Dipodomys* spp. on control plots. Consuming biomass = $\Sigma[(\text{weight of individual})^{.75}]$.
24. J. Brown and G. Lieberman, *Ecology* **54**, 788 (1973).
25. M. Rosenzweig, *ibid.*, p. 111; C. Lemen and M. Rosenzweig, *Oecologia (Berlin)* **33**, 13 (1978).
26. J. H. Brown, and D. W. Davidson, *Science* **196**, 880 (1977); O. Reichman, *Am. Zool.* **19**, 1129 (1979).
27. J. Diamond, *Am. Sci.* **66**, 322 (1978).
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