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Quantification of Competition among Coexisting Heteromyids in the Southwest

Cliff A. Lemen
University of Nebraska-Lincoln, clemen2@unl.edu

Patricia W. Freeman
University of Nebraska-Lincoln, pfreeman1@unl.edu

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QUANTIFICATION OF COMPETITION AMONG COEXISTING HETEROMYIDS IN THE SOUTHWEST

CLIFF LEMEN AND PATRICIA WARING FREEMAN

ABSTRACT.—Three trapping grids, 225 m on a side, where established in the desert of southern New Mexico. On grid 1 all *Dipodomys* (Heteromyidae, Rodentia) were removed; on grid 2 all *Perognathus* (Heteromyidae, Rodentia) were removed; and on grid 3 no rodents were removed. All grids were censused at two-week intervals for six weeks. When the larger *Dipodomys* (40g) were removed, the *Perognathus* (15g) population increased 2.56-fold (from 27 to 69 individuals) in two weeks. Removal of *Perognathus* had no effect on numbers of *Dipodomys*. Our data allow us to estimate the magnitude of the competition between *Dipodomys* and *Perognathus*.

About 45 species of heteromyid rodents inhabit the southwestern deserts of North America. Most of these taxa belong to the genera *Dipodomys* (kangaroo rats) and *Perognathus* (pocket mice). All are nocturnal, burrowing, largely granivorous rodents with cheek pouches. At localities of greatest diversity, four or five species live syntopically (Brown, 1975).

Coexistence in these ecologically similar rodents offers the opportunity to test a basic tenet of competition theory: to what extent can competing species coexist (Volterra, 1928; Gause, 1934; Levins, 1968; MacArthur and Levins, 1968; May, 1973)? In response to this question, much of the research on heteromyids has centered on quantification of methods of niche separation among syntopic species (Brown, 1975; Lemen and Rosenzweig, 1978; Wondolleck, 1978; Price, 1978).

Relatively few studies (Munger and Brown, 1981; Schroder and Rosenzwig, 1975) actually try to measure competition directly. Schroder and Rosenzweig (1975) removed rodents from large study plots with the surprising result that little competition exists between two coexisting species of similar size. They concluded that competition had been important in the past, but is not presently affecting interspecific interactions. Munger and Brown (1981) demonstrated the existence of competition in coexisting desert rodents by documenting an increase in the density of small rodents, *Perognathus* (7-17g), *Reithrodontomys* (11g) and *Peromyscus* (17g), in response to the removal of *Dipodomys* (40g). However, this increase in the density of *Perognathus* took place only after *Dipodomys* has been kept off experimental plots for 8 months.

We have concentrated on short-term effects of density perturbations. Schroder and Rosenzweig (1975) found it difficult to lower a species' density because after removing most individuals from an experimental grid other individuals of that same species took their places, often within two weeks. This might indicate an intraspecific mechanism for adjusting local population density that worked very quickly. Our goal was to determine if there is a corresponding short-term mechanism acting intergenerically as well. Here we report an additional experiment to determine the effects of removal on population densities of coexisting heteromyids.

METHODS.—The study area was located about 4 km west of El Paso, Texas in New Mexico, and was trapped during June, July, and August of 1979. Mesquite hummocks dominated the region, and three plots, all of a similar vegetation type, were set out about 1.5 km apart. Each plot consisted of a 16 x 16 grid of trap stations at 15 m intervals (5.1 ha with 256 traps). Sherman folding live traps (7.5 x 23 cm) were used.

The species of heteromyids trapped included *Dipodomys ordii*, *D. merriami*, *Perognathus penicillatus*, and *P. flavescens*. *Perognathus flavescens* represented only 2% of all *Perognathus* caught. Numbers of the two *Dipodomys* were nearly equal. We pooled species into *Dipodomys* or *Perognathus* corresponding to medium and small heteromyids. Other rodents trapped included *Neotoma albigula* and *Onychomys leucogaster*, but together they made up only 4% of the total trap success. Neither of these cricetids responded to the removal experiments.

Each study plot was censused every two weeks with two nights of trapping. The traps were baited with wild bird seed, and the same amout of seed was placed at the trap stations of the control grid. All heteromyids trapped were weighed, sexed, and individually ear-tagged or toe-clipped. After each census a Lincoln index was used to estimate rodent densities. The average trap success for all census preiods was 24%, indicating that trap competition was minimal. The difference between the Lincoln index density estimate for a plot and the total number of different individuals trapped was small, averaging 2.1 animals per species. These two facts indicated that our techniques provided reasonable estimates of rodent densities.

One grid served as a control (no removals), another as a *Dipodomys* removal, and the third, a *Perognathus* removal. Rodents were removed during the first two weeks of the study. The two removal grids were trapped approximately every 3 days during this two-week period using a grid of one-half normal trap density. After the first two weeks no more animals were removed and all plots were censused at two-week intervals to study the changes in the rodent populations.

Census periods for the control grid were as follows: census period 1 = July 9-10; period 2 = July 27-28; period 3 = August 8-9; and period 4 = August 26-27. On the *Perognathus* removal grid the census peirods were: period 1 = July 6-7; period 2 = July 25-26; period 3 = August 12-13; and period 4 = August 24-25. The census periods for the *Dipodomys* removal plot were: period 1 = July 4-5; period 2 = July 23-24; period 3 = August 10-11; and period 4 = August 22-24.

RESULTS.—Estimates of the number of rodents on our grids are shown in Fig. 1. Confidence limits on estimates (Table 1) were calculated following Pielou (1974, p. 124-5). Our removal technique significantly lowered rodent densities on the experimental plots. On the *Dipodomys* removal plot numbers of *Dipodomys* were decreased by 51%, while only a 27% decrease in *Perognathus* occurred on the *Perognathus* removal plot. In both cases these new densitiies were significanlty lower than initial densities ($P < 0.05$; for *Dipodomys* removals t = 3.58; for *Perognathus* removals t = 2.34; using confidence limits discussed above).

To test the effect of rodent removals, we compared rodent numbers on the control plot with those on the experimental plots. Numbers of both *Dipodomys* and *Perognathus* increased on the control plot in the first two weeks of the experiment. Chi-square tests were performed for both experimental plots using the change in rodent numbers on the control plot as a standard for the numbers on the experimental plots. On the *Perognathus* removal plot there was no difference in the number of *Dipodomys* as compared to the control plot ($\chi^2 = 0.003$, df = 1, $P < 0.05$). In fact, there is a remarkable similarity in the number of *Dipodomys* on the control and *Perognathus* removal grids througout the experiment (Fig. 1).

The census data from the *Dipodomys* removal plot show a different pattern. There is a significant increase in the number of *Perognathus* as compared to the control plot ($\chi^2 = 4.05$, df = 1, $P < 0.05$). The number of *Perognathus* on this grid increased by a factor of 2.56 in two weeks (Table 1).
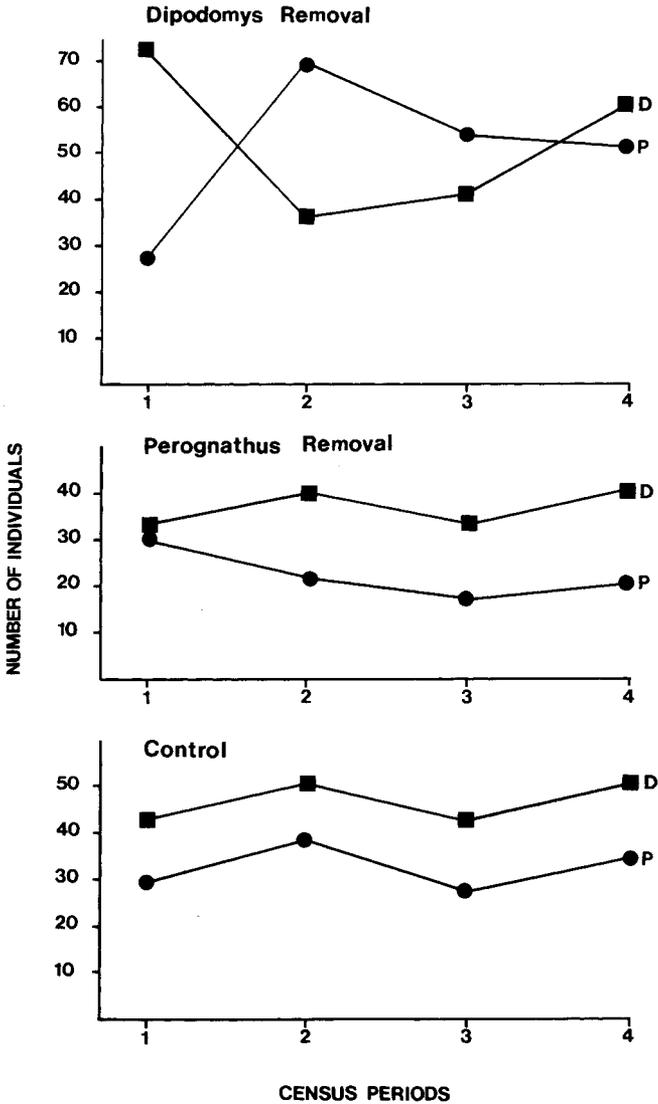
FIG. 1.—Estimated numbers of *Dipodomys* (D) and *Perognathus* (P) on the three trapping grids. Refer to Methods for exact dates of census periods.

From census period 2 to 4 on the *Dipodomys* removal plot, the recovery of *Dipodomys* toward their original number was matched with a similar decrease in the number of *Perognathus*. The general inverse relationship between *Dipodomys* numbers and *Perognathus* numbers on this plot is shown in Fig. 2. The regression is significant ($P < 0.05$) with a negative slope of -0.93. This slope is an estimate of the short-term competitive effect of *Dipodomys* on *Perognathus*. For every one *Dipodomys* removed their are

TABLE 1.—*Estimates of rodent population sizes (± 2 standard deviations) in the first two census periods on the three study plots.*

	CENSUS #1		CENSUS #2	
	Perognathus	Dipodomys	Perognathus	Dipodomys
Control plot	29.3 ± 5.1	42.9 ± 8.9	38.5 ± 1.5	50.7 ± 3.1
Perognathus removal plot	30.0 ± 3.6	33.3 ± 2.8	21.8 ± 3.4	40.1 ± 0.7
Dipodomys removal plot	27.1 ± 2.8	60.5 ± 4.3	66.7 ± 4.0	36.0 ± 9.4

0.93 more *Perognathus* expected on the grid. This estimate is possible because we altered the number of *Dipodomys* and measured the response in the number of the *Perognathus*. We are assuming all other factors that might also change the density of *Perognathus*, such as food resource levels or habitat structure, were constant through the two weeks of the removal. Therefore, any change in the number of *Perognathus* is attributable to the removal of *Dipodomys*. The stability of the number of *Perognathus* on the control grid supports our assumption that without *Dipodomys* removal, the number of *Perognathus* on the grids would have remained nearly constant. On the *Perognathus* removal plot there was no significant relationship between number of *Perognathus* and *Dipodomys*, indicating that the removal of *Perognathus* had no effect on the number of *Dipodomys*.

On the *Dipodomys* removal plot, where large numbers of both *D. ordii* and *D. merriami* were removed, the ratio of the number of these two species
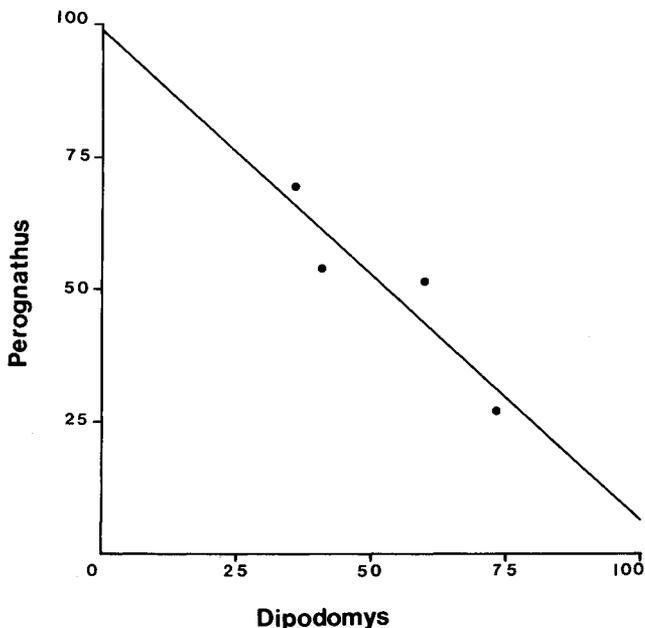

FIG. 2.—The regression of the number of *Perognathus* (Y) on the number of *Dipodomys* (X) on the *Dipodomys* removal plot for all 4 census periods, y = 98.9 - 0.93x, P slope is zero < 0.05. Exact dates of census periods are in the Methods section.
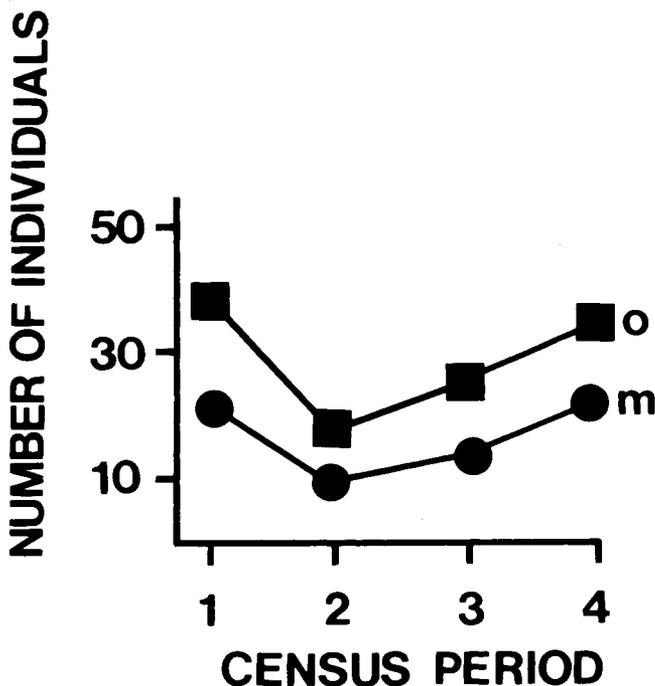
FIG. 3.—Estimated densities of *D. ordii* (o) and *D. merriami* (m) on the *Dipodomys* removal plot for all 4 census periods. Exact dates of census periods are in the Methods section.

remained nearly constant throughout the recovery phase of the experiment (Fig. 3).

DISCUSSION.—Our findings offer evidence that these heteromyids are competing. The competitive nature of the interaction was suggested by increase in the number of *Perognathus* in response to removal of *Dipodomys*. This result is contrary to that found by Schroder and Rosenzweig (1975) who found no density response between two species of *Dipodomys* of very similar size. In addition, the quick increase of the number of *Perognathus* to the removal of *Dipodomys* differs from the findings of Munger and Brown (1981) were it took 8 months for the small rodents to increase in number in response to the removal of *Dipodomys*.

One point not yet considered is the mechanism of the competition between *Dipodomys* and *Perognathus*. The 8-month lag found by Munger and Brown (1981) might indicate resource-mediated competition. It may have taken that long for the resource levels to come to a new equilibrium in response to removal of *Dipodomys*. Conversely, direct interference may also be important in competition among heteromyids (O'Farrell, 1980) as has been shown in other rodent assemblages (Grant, 1972). Our results are consistent with the hypothesis of interference competition through aggressive interactions for two reasons. First, the density adjustment of *Perognathus* was too quick for food resource levels to change. Second, the number of

Perognathus was effected by removal of large rodents, but not vice versa. This is consistent with the speculation that large body size would be an advantage if aggressive interactions are mediating this interaction.

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Address of authors: *Dept. of Zoology, Field Museum of Natural History, Chicago, IL 60605* Current addresses: CL, *School of Life Sciences,* PFW, *Univ. of Nebraska State Museum, Univ. of Nebraska, Lincoln, NE 68588*)