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In the sage community of California, Oregon and Washington, the sympatric species Perognathus parvus and Peromyscus maniculatus are often the most common nocturnal rodents. The importance of interspecific competition between these similar sized granivores was studied on four grids and in a field enclosure (154 cm sq) in central Oregon. After collecting baseline population data for two months, removal experiments were initiated on three grids and one grid was designated a control. Perognathus numbers increased at a faster rate, resulting in a greater density, on the two grids from which Peromyscus was removed relative to the control. Female Perognathus increased their activity and were more reproductive in the absence of Peromyscus. Perognathus did not show any microhabitat preference nor shift in

~~shift in~~ microhabitat use due to the removals or season and rarely used arboreal traps ($\leq 3\%$). The reciprocal removal on the single grid resulted in a slower rate of increase and a smaller density of Peromyscus. Female Peromyscus showed a trend for reduced reproduction in the absence of Perognathus, but simultaneously increased their activity. Peromyscus frequently used arboreal traps ($\leq 39\%$) and showed a trend for decreased arboreality in the absence of Perognathus. No ground level microhabitat preference nor shift was shown by Peromyscus. I hypothesize that Peromyscus accrues a benefit from the presence of Perognathus by parasitizing its seed caches. Potential costs (if any) from increased arboreality and decreased female activity in the presence of Perognathus apparently are less than benefits gained from the association.

Observations on interspecific pairs in a field enclosure showed that nonaggressive acts accounted for 95% of behavior between the species. Of all the behavioral encounters retreat behavior was the most common. These data suggest that overt interspecific aggression is not common and consequently may not be important as a competitive mechanism.

Experimental Analysis of Competition
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Emile Schoffelen

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Redacted for privacy

Professor and Chairman, Department of Zoology

Redacted for privacy

Dean of Graduate School

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EXPERIMENTAL ANALYSIS OF COMPETITION
BETWEEN DESERT RODENTS IN OREGON

INTRODUCTION

To understand community structure it is necessary to elucidate the mechanisms promoting its organization. Theoretical studies (i.e. Lotka 1925, Gause 1934, Levins 1968, May 1973, Levine 1976, Tilman 1980) suggest that interspecific competition is important in limiting population growth and influencing community structure. Empirical evidence indicating the importance of competition as a community organizer has come from community perturbation experiments (i.e. Connell 1961, Davis 1973, Redfield et al 1977, Dhondt and Eyckerman 1980, Hairston 1980, Munger and Brown 1981) and from observations supportive of the competition hypothesis (see Pianka 1976, Schoener 1974 for reviews). Observation alone does not allow strong inferences to be made about the causal mechanisms underlying community structure (Platt 1964). Studies which document differential and non-random use of space, time, or resources between ecologically similar species (Schoener, 1974) often cannot infer whether these differences are due to interspecific competition acting at the time of the study or if other factors, either current or historical, are responsible for the patterns (Connell 1975, Wiens 1977, Holbrook 1979, Thomson 1980). However, observations provide data pertinent to the construction of experimentally testable hypotheses regarding the basis for community structure.

The experimental removal of presumed competitors provides the best method for determining the importance of competition because interpretation of results is not confounded by uncontrolled factors. In a well designed experiment the treatment(s) provide the basis for data interpretation. Removal treatments in which the density, demography and resource use of a population shift in a predicted manner and in contrast to an adequate control indicate a competitive interaction (Grant 1978).

Experimental study of competition between small mammals suggests that competition is an important determinant of community structure (Grant 1972, 1978 and Brown et al 1979 for reviews). Unfortunately, many experimental studies of small mammals used fenced populations (Grant 1972, 1978). Fencing may alter the demography of rodent populations (Krebs et al 1969, and Krebs and Myers 1974) and affect rodent predation (Holbrook 1979). Both population structure and predation may affect population growth and confound any interpretation of results stemming from enclosure experiments. Nonetheless, experimental studies conducted on unconfined small rodents and other terrestrial vertebrate populations indicate that interspecific competition can affect microhabitat and resource utilization (Davis 1973, Chappell 1978, Holbrook 1979, Abramsky et al 1979, Koplin and Hoffman 1968), demographic parameters (DeLong 1966, Redfield et al. 1977) and density (DeLong 1966, Redfield et al 1977, Munger and Brown 1981, Dhondt and Eyckerman 1980, Hairston 1980). Few experimental investigations on terrestrial vertebrate interspecific competition have simultaneously studied all 3 aspects (but see Petersen 1973). Concurrent observations on density, demographic structure and resource

use would provide a more thorough perspective from which to assess the role of competition in structuring communities.

It was the purpose of this study to experimentally analyze the role of competition in structuring a two species desert rodent guild in the sage habitat of central Oregon. Throughout many areas of the Great Basin sage community in California, Oregon, and Washington Perognathus parvus (Great Basin pocket mouse) and Peromyscus maniculatus (deer mouse) are the most common nocturnal rodents (Kirtzman 1974, Ambrose and Meehan 1977, O'Farrell et al 1975, personal observation). These species are sympatric (Hell and Kelson 1959), and both are granivorous (O'Farrell et al 1975, Kirtzman 1974, Meserve 1976, Flake 1973), similar in size (O'Farrell et al 1975, Redfield et al 1977). Furthermore, the two species appear to be agonistic towards each other, both in laboratory and natural encounters (Kirtzman 1974, Ambrose and Meehan 1977). The reported similarities in diet, size and habitat use and the reported interspecific aggressiveness suggested that the two species compete. The central hypothesis of this study was that P. parvus and P. maniculatus compete and consequently affect each others density, demography (the relative importance of the sex, age and reproductive classes in the population) and resource use.

Several demographic parameters and resources have previously been suggested to be affected by interspecific competition. Blaustein (1980) and Lidicker (1966) indicated that a superior competitor can depress the proportion of reproductive females in the inferior competitor's population. Redfield et al, (1977) showed that male P. maniculatus trappability was suppressed by the presence of a competitive superior

Microtus townsendi (Townsend's vole) in grasslands of Vancouver, Canada. Other studies have documented microhabitat preference (Rosenzweig and Winakur 1969, Brown and Lieberman 1973, Rosenzweig et al, 1975, Price 1978, Holbrook 1979 and Glass and Slade, 1980) and shifts in microhabitat preference and arboreality accompanying the addition or removal of competitors in rodent communities (Price 1978, Holbrook 1979). The results of these studies suggest that if P. parvus and P. maniculatus compete, they may affect each others reproductive condition, movement as measured by trappability, ground level microhabitat use and arboreality. Furthermore, they emphasize ecological pressures may affect individuals differentially depending on sex, age, and physiological condition. Thus, in this study it was hypothesized that shifts due to experimental manipulation may vary by sex, reproductive status and age.

An additional goal of this study was to investigate the role of aggressive interference as a competitive mechanism. The solitary and intraspecifically aggressive nature of P. parvus (Kritzman 1974) as compared to the relatively more gregarious P. maniculatus (McCabe and Blanchard 1950) suggests that P. parvus should be behaviorally dominant. Ambrose and Meehan (1977) observed behavioral interactions between the two species in the laboratory and described one natural field encounter. They concluded that P. parvus was socially dominant. Kritzman (1974) described encounters in which P. maniculatus was aggressively dominant. Ambrose and Meehan (1977) suggest that P. parvus will be dominant in unconfined areas and P. maniculatus in confined situations such as burrows. Their conclusion indicates that labeling a

species as dominant based on a single criterion in a single situation may be inappropriate. Consequently, alternate criteria for defining a dominant under a variety of situations may yield conflicting results. In this study two criteria were used to define and investigate the role of interspecific aggression.

METHODS

Study Area and Species

The study site was in the High Lava Plains physiographic province (Franklin and Dyrness 1973) 16 km due north of Fort Rock, Oregon (1370 m). The terrain was generally flat with slight depressions, rises and small ridges of volcanic exposure. The mean annual precipitation is about 300 mm. The July mean maximum temperature is 30°C and the January mean minimum temperature is -11°C (Franklin and Dyrness 1973). The dominant shrubs were big sagebrush (Artemisia tridentata) and green rabbitbrush (Chrysothamnus viscidiflorus). The common perennial grasses were bluebunch wheatgrass (Agropyron spicatum), Idaho fescue (Festuca idahoensis) and Thurber's needle grass (Stipa thurberiana). Characteristic herbs were blue-eyed Mary (Collinsia sparsiflora), hoary chaenactis (Chaenactis douglasii), pink microsteris (Microsteris gracilis), wooly groundsel (Senecio canus) and groundsmoke (Gayophytum sp.). P. maniculatus and P. parvus were the dominant nocturnal rodents on the study grids. Other small nocturnal rodents, rarely captured, were dark Kangaroo mice (Microdipodops megacephalus), Ord's kangaroo rats (Dipodomys ordii), sage voles (Lagurus curtatus) and northern grasshopper mice (Onychomys leucogaster).

Trapping Procedure and Design of Removal Experiments

From 17 May 1980 until 19 October 1980 animals were livetrapped on four grids separated by at least .8 km. The grids were located on flat areas that were similar in terrain and vegetation. Each grid consisted of an 8 x 10 trap station configuration with 15 m between each station (area trapped = 1.8 ha/grid). One large Sherman livetrapp baited with a mixture of rolled oats and bird seed was placed at each station. Nylon batting was provided to prevent death from hypothermia. To monitor climbing activity by the rodents, 30% of the traps in each grid were placed on wooden platforms, and affixed to a shrub approximately 40 cm above the ground. Forty cm represented the average mid height of the shrubs. Platform stations were randomly chosen and each platform was placed in the shrub nearest the stake marking the grid coordinates.

Baseline data were recorded throughout May and June, 1980. During this period all 320 traps from the 4 grids were set and baited for 2 consecutive nights approximately every 10 days. Traps were shut and left in place between trap periods. Prior to manipulations one grid was designated a control (Grid 1), two grids were designated to have P. maniculatus removed (Grids 2 and 3) and one was designated to have P. parvus removed (Grid 4). The experimental design was arbitrarily chosen so that preremoval densities of rodents on the experimentals and control were as similar as possible (Figs. 1-4). During the experimental period, 1 July until 19 October, 1980, the appropriate species was removed from each removal grid while rodents on the control grid were trapped and released on the grid. To enhance the likelihood of

detecting any removal effects an intensive trapping schedule was followed from 1 July until 1 September, 1980. During this period all traps were set for 4 or 8 consecutive nights with 3 non-trap days in between. A total of 40 trap days were recorded during this period. Trapping and removal continued during September and October. However, traps were only set for two consecutive nights every two weeks during these months.

Traps were always set during a 2-hour period prior to sunset and checked during a 3-hour period after sunrise. Traps were shut during the day. Captured rodents were toe clipped for identification, weighed, sexed, assessed for reproductive condition, aged and released at the point of capture or removed. The grid coordinates were recorded for each capture. Males were recorded as reproductively active if their testes were scrotal. Females with copulatory plugs, perforated vaginas, or that were lactating or pregnant were recorded as reproductive. P. maniculatus and P. parvus were recorded as adult if they weighed more than 13 grams (Redfield et al 1977, O'Farrell et al 1975).

Since conspecific and interspecific olfactory cues have been shown to bias trap preferences of some rodents (Daly et al 1980, Boonstra and Krebs 1976, Mazdzer et al 1976) an effort was made to uniformly disperse odors throughout all traps. Unused, soiled and presumably odoriferous bait from traps which caught rodents was mixed with fresh bait. The mixture of soiled seed and chaff, collected each morning, and fresh bait was used to bait the traps in the evening. Since washing all traps each night was not possible I thought that the uniform dispersion of odors

would alleviate problems associated with preferences for previously used traps.

Analysis of the Removal Effect on Demographic Parameters

Density Response - The minimum number alive (Hilborn et al 1976) of P. parvus on grids 1, 2 and 3 and the minimum number alive (MNA) of P. maniculatus on grids 1 and 4 were used to test the competition hypothesis by looking for shifts in density. Pre-removal MNA means for each species revealed initial differences in rodent numbers between the control grid and experimental grids (Figs 1-4). To compare changes in numbers of individuals associated with the removal affect, each day's MNA from the removal period was standardized by having the pre-removal mean MNA subtracted. Thus the removal data used in the statistic represented the increase in individuals above the pre-removal mean MNA (Figs 2, 4). The null hypothesis was that the increases in individuals above the pre-removal mean MNA on the control grid and experimental grid were equal. Since assumptions of ANOVA were violated (normality and nonindependence of error terms) the Wilcoxon matched-pairs signed-rank test was used (Neter and Wasserman 1973, Conover 1979). Twenty-one removal days were randomly selected from the total pool of 45 removal trap days. To determine if the removal differentially affected sexes, age classes or reproductive categories the total MNA for each species was broken down into reproductive adults, nonreproductive adults and juveniles for each sex (Fig. 2, 4). These demographic categories were then subjected to the same analysis as the totals.

Reproductive Response - To test interspecific effects on reproduction within and between grid differences in the proportions of MNA reproductive adults during the preremoval and removal periods were tested using chi square analysis. If there was an inhibitory effect on reproduction by one species over the other then two conditions should be met. The first is that the proportion of MNA reproductive adults from the unmanipulated species on the experimental grids should be larger during the removal period than during the pre-removal period. Chi square tests using 2 x 2 contingency tables were done comparing pre-removal and removal proportions of reproductive individuals for both sexes and species on control and experimental grids (Fig. 5). The null hypothesis was that the proportions of reproductive individuals on a grid during the pre-removal and removal periods was equal.

The second condition is that if within grid increases occurred on the experimental grids but not on the control grid, do these increases result in the experimental grids having significantly greater proportions of reproductive individuals than the control grid. Chi square analysis was used to determine if between grid differences in the proportion of reproductives existed for each species and sex during both the pre-removal and removal periods (Fig. 5). Numbers in the P. manipalatus analysis were tabulated from 21 randomly selected removal trap days and 6 randomly selected pre-removal trap days. The sample sizes represented approximately 50% of the total number of trap days during each period. Numbers used in the P. parvus analysis were tabulated from all trap days to satisfy the condition that the expected values in each cell of the contingency table exceeded 5 (Conover p. 152 1979).

Trappability - Redfield et al (1977) estimated trappability by dividing the number of individuals caught on a grid during a trap day by the MNA for that day. To assess if trappability was affected by interspecific competition the proportion of individuals caught on a grid during the pre-removal phase was compared with the proportion caught during the removal period. If interspecific competition were occurring and affected activity as measured by trappability then the proportion of individuals caught during the removal phase would be larger than the pre-removal proportion. Further tests were done to determine if predicted between grid differences occurred (Fig. 6). The analysis and null hypotheses were similar to those discussed in the preceding section on reproductive responses. Numbers tabulated for both animals were from the 21 randomly selected removal days and the 6 randomly selected pre-removal days.

Analysis of Microhabitat Use and Arboreality

Thirty percent of the traps were randomly set on platforms in bushes, leaving 56 ground level traps per grid. The ground level traps were assigned to one of three microhabitat categories. The classification reflected the observed local pattern of blocks of vegetation, generally less than 1 m in height and less than 1.5 m in diameter, separated from each other by trail like openings of sparsely vegetated ground. The categories were defined as 1) Block - any vegetated area taller than 25 cm and having a diameter > 50 cm, 2) Avenue - any nonblock area more than 25 cm away from a block area and 3)

Sidewalk - a nonblock area less than 25 cm from a block. The traps were set next to the stakes marking the grid coordinates. The total numbers of individuals caught in each category were used in the chi square analysis. The removal data were divided into 3 time periods, July, August and Sept/Oct, to test for temporal shifts in microhabitat use. Pre-removal data were left as a single time, May/June. The null hypotheses were 1) the proportionate use of microhabitat by each species, during each time period, is equal to the available proportions of each microhabitat category, 2) the proportionate use of microhabitat by each species does not change through time as a consequence of seasonality or the removal and 3) the proportionate use of microhabitat, during each time period, does not differ between the species (Table 1).

Use of the vertical dimension was assessed by comparing total captures in platform traps with the total ground level captures. Data were grouped by month as with the ground level data. Chi square analysis was used to test 3 hypotheses which were analogous to the ground level microhabitat hypotheses. To obtain the hypotheses substitute arboreality for microhabitat in the preceding paragraph (Table 2).

Field Behavior Experiments

Two behavioral studies were done to test if interspecific aggression was a potential mode of competition. In the first study, I matched a single P. parvus with a single P. maniculatus in an outdoor enclosure.

The enclosure consisted of 4 pieces of plywood, taped together around a single bush, several forbs and grasses (150 x 150 cm). An incandescent red light was taped on one corner of the box. The box was dismantled at the end of each observation night leaving the area readily accessible to other animals, seed dispersal and wind.

All rodents were caught in the morning of the day that they were observed. None were held for more than 14 hours. Animals tested were from the removal grids or trap areas within two miles of the study grids. Rodents were caught using Sherman live traps and were kept with food in traps until dark. It was thought that the trap more closely mimicked a burrow than standard mouse cages. Trials were conducted between 1900 and 0100.

For each encounter I matched naive adults by weight, using all sexual combinations. I simultaneously released the paired animals in the center of the enclosure. Each species was scored for every occurrence of 5 overt behaviors during a 15 min period immediately following release. The five behaviors were Approach - movement of one rodent toward the other, Retreat - movement of one rodent away from the other, Attack - initiating a fight with the other rodent by physical contact, Chase - pursuit of a retreating rodent, and Defend - retaliating an attack. The Mann-Whitney U test was used to determine if there were differences in behavior between the two species. The 5 null hypotheses were that each species used the 5 behavioral categories with equal frequency. Attacks, Chases and Defense were considered overt aggressive behaviors. Thus the dominant individual in encounters was the species which utilized the aggressive behaviors most often.

An alternate indicator of behavioral dominance would be differential use of microhabitats within the enclosure when with an individual of another species and when alone. As a second test for interspecific aggression, I compared the amount of time each P. maniculatus spent in the bush during the paired encounters with the amount of time P. maniculatus spent in the bush when placed in the observation box alone. It was hypothesized that P. maniculatus might be arboreal so as to forage, behaviorally thermoregulate, avoid predators or avoid competitors. If P. maniculatus uses the bush for the first 3 reasons there should be no difference in bush use when it is with P. parvus or alone. The null hypothesis of the Mann-Whitney U test was that P. maniculatus spends an equal amount of time in the bush whether with P. parvus or alone. The outcome of these results should corroborate the results on aggressive behavior encounters, if dominance is independent of measurement criteria. P. parvus rarely climbs (personal observation), so the reciprocal study was not done.

RESULTS

Removal Effect on Demographic Parameters

Density Response - The removal mean increases in the total MNA of P. parvus on experimental grids 2 and 3 were 9.1 and 10.1 respectively. These increases were significantly greater ($p \ll .01$) than the mean increase of 3.2 on the control grid (Fig. 2) indicating that P. maniculatus has a negative effect on P. parvus thus supporting the hypothesis that these rodents compete. Analysis of the demographic categories indicated that juvenile, reproductive adult and nonreproductive adult male P. parvus had significantly larger mean increases on both removal grids (Fig. 2). Female reproductive adults increased to a larger extent on both removal grids relative to the control (Fig. 2). Female juvenile increases were similar on all three grids. Female nonreproductive adults were significantly less numerous on Grid 2 but not on Grid 3 (Fig. 2). The results indicate that there was a definite competitive response and that the response varies with sex, age and reproductive condition. Adult reproductive females and all categories of males were affected by competition from P. maniculatus, whereas the inconsistent results in the other female categories suggest they were not affected by competition.

The reciprocal removal suggested biotic interactions are important, but competition was not implicated. The P. maniculatus mean increase in MNA on the removal grid ($\bar{X} = 7.4$) was significantly smaller than the control grid ($\bar{X} = 11.7$, $p < .01$, see Fig. 4). The data showed that

P. parvus has a positive effect on P. maniculatus. Demographic analysis revealed males and nonreproductive females show no removal effect (Fig. 4). The two other female categories show highly significant differences with increases being smaller on the removal grid. As with the P. maniculatus removals the response to the manipulation was dependent on an organism's demographic status. Reproductive and juvenile categories of female P. maniculatus showed a significant dependence on the presence of P. parvus (Fig. 4).

Reproductive Response - The proportion of reproductive female P. parvus in the grid populations ranged from .15 to .89. The proportion of reproductive females significantly increased during the removal period on the experimental grids from .15 to .88 and .80 to .89. On the control grid there was a nonsignificant decrease, from .81 to .71 (Fig. 5). Significant between grid differences existed in the proportion of reproductive females. The pre-removal between grid difference was attributed to experimental grid 2 having only .15 reproductive females whereas the control grid and experimental grid 3 had initial proportions of .81 and .80 (Fig 5). The removal between grid difference was due to both experimental grids having greater proportions of reproductive females relative to the control (.88 and .89 vs. .71 $p < .005$). The data do not support the null hypotheses predicting no within or between grid changes. There were significant within grid increases in the proportion of reproductive females on the experimentals, but not on the control. In addition there were significantly greater proportions of reproductive females on the experimental grids than on the control grid, during the removal period. The data support the hypothesis that these

rodents compete. Reproduction by female P. parvus was apparently inhibited by the presence of P. maniculatus. The percent of reproductive male P. parvus ranged from 65 to 100 (Fig. 5). The proportion of reproductive males were similar on the control grid and experimental grid 2, but significantly decreased on grid 3 (Fig. 5). Shifts in the numbers of scrotal males are not consistent with the competition hypothesis.

When comparing the reciprocal removal data from Grid 4 with the control, the proportion of male reproductive P. maniculatus decreased during the removal period on both grids (.60 to .45 on the control and .64 to .39 on the removal, Fig. 5). The pattern did not suggest competition was important. Reproductive female P. maniculatus significantly increased by 33% on the control and did not significantly increase on the removal grid. These data weakly suggested that female P. maniculatus reproduction was enhanced by the presence of P. parvus. However no between grid differences resulted as a consequence of the differential within grid increases (Fig. 5).

Trappability - Female P. parvus trappability ranged from 33% to 53% and did not significantly change on either the control or experimental grids (Fig. 6). However, female trappability decreased 13% on the control grid and increased on the experimental grids by 14% and 8%. Enhanced trappability during the removal phase on the experimental grids and a decrease on the control suggested that P. maniculatus may suppress female P. parvus trappability. Between grid differences further supported the competition hypothesis. Both experimental grids had nonsignificant but larger proportions of trapped females than the

control (.47 and .52 vs .40 on the control, Fig. 6). The observed trends indicated that the negative effect P. maniculatus has on P. parvus may be mediated, by suppressing female P. parvus trappability. Since the number of traps capturing nocturnal rodents was always less than 25%, trappability may reflect changes in activity. No readily interpretable trend is reflected in the male P. parvus data (Fig. 6).

Female P. maniculatus trappability significantly decreased during the removal period on the control grid (.89 to .17, Fig. 6) and showed a nonsignificant increase on the removal grid (.67 to .80, Fig. 6). These within grid shifts resulted in female P. maniculatus being significantly more active on the experimental grid than on the control, during the removal period. Thus, P. parvus may have a negative effect on female P. maniculatus activity. Contrary to the numerical response data, these data are supportive of the competition hypothesis. As with male P. parvus, male P. maniculatus activity showed no removal effect (Fig. 6).

Microhabitat Use and Arboreality

Ground level traps located in different microhabitats were not used preferentially by either species in any month (Table 1). Of 20 tests for preferential microhabitat use only one was significant (Table 1). During the month of July, on grid 3, P. parvus showed a preference for sidewalk areas (Table 1). P. maniculatus never evinced a temporal shift on any grid (4 time periods x 3 microhabitat contingency table). P. parvus showed a temporal shift in microhabitat use on Grid 3. This

shift was attributed to the preference for sidewalks during July. Since no other preferences or shifts occurred it is unlikely that this shift was biologically relevant. All chi squares testing for differences in microhabitat use between the two species on the control grid were not significant. It appears that microhabitat, as defined, was not partitioned.

Arboreal activity in both species was nonrandom. Arboreality was much greater in P. maniculatus than in P. parvus. The percent of captures in platform traps for the deer mouse ranged from 0 to 39. Of the 8 chi squares testing for platform preference, ground traps were preferred 4 times, platforms once and there was no preference 3 times (Table 2). The only statistically apparent temporal shift in platform use occurred on Grid 4 where P. maniculatus switched from no preference to a ground preference in August. However, during each time period, Peromyscus arboreality was always less on the experimental grids than the control. During July the difference was such that the controls preferred climbing bushes and the experimentals showed no preference. The difference between the grids during July was almost significant ($\chi^2 = 3.46$, df 1, $p = .063$). One possible explanation, supportive of the competition hypothesis, is that P. maniculatus responds to the presence of P. parvus by being more arboreal.

P. parvus always preferred the ground and percent arboreality never exceeded 3 (Table 2). No seasonal shifts or removal effects in P. parvus arboreality were apparent (Table 3). P. parvus restricted its spatial utilization to two dimensions and consequently vertical use of space is not affected by the presence of P. maniculatus.

Behavioral Experiments

Peromyscus - Perognathus interactions were generally non-aggressive. Of the 87 total approaches by individuals of either species, Peromyscus approached more often (64%) than Perognathus (36%). The mean number of approaches per trial by Peromyscus (3.3) and Perognathus (1.8) were significantly different (Table 3). Approaches by either species generally resulted in a retreat by the other species. Retreats often occurred when the two species were in close proximity to each other although no approach behavior had been initiated. Perognathus retreated (58%) more often than Peromyscus (42%) when considering all retreats by both species. The mean number of retreats per trial by Peromyscus (3.1) and Perognathus (4.4) were not significantly different (Table 3).

Perognathus attacked Peromyscus only twice and never chased or defended an area. Peromyscus attacked 7 times, chased Perognathus 3 times and never defended. There were no significant differences between the species within these categories (Table 3). Summing the 5 categories by both species gave a total 227 behavioral interactions. Only 5% of the behaviors can be characterized as overtly aggressive. These data do not support the hypothesis that overt aggressive behavior by a dominant is a mechanism mediating competition between Perognathus and Peromyscus. Although Peromyscus approached more often than Perognathus neither species can clearly be labeled as a behavioral dominant. Alternate mechanisms of competition such as subtle aggressive behavioral

cues, vocalization, chemical cues or exploitation competition may be more important.

The mean amount of time spent in the bush by Peromyscus was 164 seconds when alone and 317 seconds when with Perognathus (Table 3). Although the means were not significantly different, the data suggest that Peromyscus arboreality within the enclosure increases in the presence of Perognathus. As with the data on arboreality from the removal experiments there is a trend towards increased arboreality in the presence of Perognathus suggesting competition. These results do not corroborate the aggression study and suggest that dominance may vary with the criteria used to define superiority.

DISCUSSION

Demographic Parameters

Density Response - The data presented indicate that biotic interactions are important in determining the abundance of P. parvus and P. maniculatus in the northern Great Basin. The shifts in density by both species due to the manipulations suggest that the type of interaction was not amensalism or mutually detrimental competition, but was more like parasitism or predation. The density response had three alternate explanations. The first possibility is that the single P. parvus removal did not have an effect. The enhanced P. maniculatus population growth may be an unreplicated statistical artifact due to some biotic or abiotic event occurring on one grid but not the others. If there are some parameters acting in a stochastic manner and resulting in qualitative differences between grids one would not expect the three P. parvus or the two P. maniculatus populations to show the same shaped population curves (Fig. 1, 3). Random events acting on each grid should result in grid populations exhibiting different patterns of population growth and demographic structure. My data do not support this contention. The second possibility also assumes that the removal did not have an effect. However, instead of qualitative differences, the enhanced P. maniculatus growth is an artifact due to the same variables acting with different magnitudes. Under these conditions population curves could have the same overall shape but have different rates of increases or decreases. However, all grids were within 6 km of each

other and located in an area of homogeneous terrain and vegetation. No significant differences between grids existed in the availability of microhabitat ($\chi^2 = 6.756$ df = 6 $p > .05$). Since the grids were so close to each other, it is likely that they received similar schedules of solar radiation, precipitation, temperature fluctuation and other abiotic parameters. That plant physiogomy does not differ between grids and the grids are probably affected to the same degree by abiotic factors suggests that cover from predators and the production of seeds is similar between grids. The degree of grid similarity does not warrant support for the second possibility and further negates the first possibility.

The third possibility is that the removal effect is a real biological phenomenon. One hypothesis is that it is and due to species differences in foraging skills and seed cache thievery. P. parvus is the more specialized granivore and may be more adept at locating scattered seed in the arid shrub steppe than the more generalized P. maniculatus. It is feasible that P. maniculatus parasitized the foraging skills of P. parvus by stealing some seed from P. parvus seed caches. Many rodents store seeds (Eisenberg 1963, Hawbecker 1940, Shaw 1934, Tappe 1941, Blair 1937) and desert rodents are known to burglarize seed caches of other species (Clark and Comanor 1973, Vorhies and Taylor 1922). P. maniculatus numbers could be enhanced by the presence of P. parvus if the deermouse stole seeds either directly from the burrow or from scatter hoard caches of P. parvus. Although my data on behavior does not suggest that P. maniculatus is aggressive, Kritzman (1974) presented evidence that P. maniculatus is aggressively dominant to P.

parvus in confined situations such as burrows. In addition, during this study there were two occasions in which a semi-torpid P. parvus was introduced into the behavior enclosure with P. maniculatus, subsequently P. maniculatus attacked, bit and would have killed the P. parvus had it not been removed. It is feasible that P. maniculatus is a kleptocompetitor. The deer mouse gains added food by stealing from P. parvus, perhaps via aggressive encounters in burrows. The depleted seed reserve would then have a negative effect on P. parvus. This type of behavioral parasitism has its analogues with avian nest parasites (Barash 1977) and slave making ants (Wilson 1971). Although there is no strong evidence to support this hypothesis the occurrence of cache thievery by desert rodent systems (Clark and Comanor 1973, Vorhies and Taylor 1922) suggests that cleptocompetition may be an important force in structuring rodent communities.

Reproductive Response and Trappability - Data suggested that the negative effect P. maniculatus had on P. parvus may be mediated by reducing female Perognathus reproduction. Previous studies have indicated that a competitor, Microtus californicus (California vole), depressed the proportion of reproductive females in Reithrodontomys megalotis (western harvest mouse) and Mus musculus (house mouse) populations in California (Blaustein 1980, Lidicker 1966). Competitive effects such as reduced availability of food, suitable nesting sites and increased exposure to agonistic encounters may have a negative effect by usurping resources that would be channeled into reproduction even when the competitive effect is not strong enough to reduce availability of resources associated with self maintenance. The reciprocal removal

suggested that enhanced reproduction in female P. maniculatus was associated with the presence of P. parvus. Enhanced reproduction may be facilitated when resources are more available due to the activities of another species (i.e. seed caching).

Both P. parvus and P. maniculatus females reduced their activity in the presence of the other species. The decrease in activity may be associated with an increase in retreat or avoidance behaviors. Congdon's (1974) observations in the field and my enclosure experiments indicate that avoidance is probably common in desert rodents. Reduction in female P. parvus activity complements the results showing reduced female P. parvus reproduction. It suggests that the strong negative effect P. maniculatus had on Perognathus density was mediated primarily through females and that physiological condition, such as reproductive status, may also influence competitive effects. The reduced activity by female P. maniculatus suggest a competitive effect and is contrary to the density and reproduction results. This is discussed in the following section.

Microhabitat

Studies have shown that heteromyid rodents prefer certain types of microhabitats (Rosenzweig and Winakur 1969, Brown and Lieberman 1973, Rosenzweig 1973, Price 1978). Generally, the larger bipedal Dipodomys prefer the open ground and restrict the use of open space by smaller Perognathus and Peromyscus species. The findings reported here do not fit this pattern. P. parvus and P. maniculatus showed no microhabitat preferences. Whatever resource may be limiting, it was either not correlated with microhabitat or it was impossible to usurp from interspecific competitors. Perhaps only Dipodomys, due to their large size and keen foraging ability (Reichman and Oberstein 1977) can restrict use of open space by smaller interspecific competitors through either aggressive behavior or efficient removal of seeds. If this is true one would expect other rodent communities where species are small and similar in size, not to exhibit microhabitat preferences.

My study presents evidence that P. maniculatus tends to be more arboreal in the presence of P. parvus. The proportion of arboreal P. maniculatus was always smaller on the P. parvus removal grid and the trend in the behavior box was less time in the bush when P. maniculatus was alone. The data suggest that P. parvus restricts use of ground space by P. maniculatus. An alternate explanation is that P. maniculatus perceives movement as a potential predator and responds not to the rodent but to its movement by seeking refuge in a bush. There was no evidence to support either interpretation of the shift in arboreality by P. maniculatus, when P. parvus is removed.

The evidence that P. maniculatus arboreality and activity, as measured by trappability, are influenced by P. parvus suggests that interspecific competition was occurring. However, the data on density and reproduction indicates that P. parvus enhanced P. maniculatus populations. Apparently the negative effects are smaller than the gains accrued through association as measured by density. Perhaps if resource availability were such that Peromyscus gained no benefit from its association with Parvus then competitive effects acting on arboreality and activity might negatively affect density. In a variable environment, shifts in the importance of the various biotic interactions, may be important determinants of structure. In addition, the data underscores the need to study several aspects of a community so as to more accurately assess which biotic interactions are important.

Behavior

The field behavior experiments suggest that overt aggression between these rodent species was not common. Avoidance was the most common type of behavior observed in the behavior box (see also Congdon 1974). Similar encounter studies in the laboratory on desert rodents (Blaustein and Risser 1974a, 1974b, 1976) and microtines (Colvin 1973, Murie 1972, Randall 1978) have noted avoidance by subordinate rodent species. However, both Kritzman (1974) and Ambrose and Meehan (1977) suggest that aggression is important in interspecific encounters. The importance of aggression may be much greater than suggested by the frequency of observation. Agonism could modify the types of behavior that occur in

future encounters. Avoidance may be a learned behavior stemming from a previous agonistic encounter. Reinforcement for avoidance may be mediated through olfactory, acoustical or more subtle behavioral cues. Thus in enclosure studies where aggression was not observed in high frequency, aggressive interference cannot be eliminated as a potential competitive mechanism.

The two measures of dominance, aggressive behavior and shifts in bush climbing did not yield parallel results. In a variable environment one would expect behavioral encounters to vary in concordance with costs and benefits. Costs of aggression may vary with the location of encounters. Thus it is possible that in confined situations, such as burrows, P. maniculatus may be dominant and in open terrain P. parvus may have an advantage. The outcome will be dependent on how well the animal is adapted to the particular situation. The dominant species may vary with the site of the local encounter. There is no a priori reason to believe a species will be dominant in all types of encounters.

Conclusions

In efforts to elucidate the mechanisms involved in structuring rodent communities, investigators have consistently studied the role of competition (Grant 1972, 1978, Brown et al 1979, others cited herein). These reviews suggest that competition affects rodent community organization. However, few investigators have simultaneously studied the effect of competition on rodent (and terrestrial vertebrates in general) demography, density and microhabitat use. This approach allows

one to determine, not only if competition is occurring, but also how competition affects variables such as microhabitat use, reproduction and population structure. Thus one can assess how competition determines community structure. In this study simultaneous reciprocal removals in a two species rodent system suggested that a type of interaction termed kleptocompetition may be occurring. Kleptocompetition occurs when one species enhances its population growth by parasitizing on the cached food of another species. The parasite simultaneously depresses the population growth of the victim. These results are in marked contrast to most previous removal experiments between presumed competitors where either mutually detrimental competition or amensalism (Lawton and Hassell 1981) has been suggested to be the principle interaction.

The hypothesized kleptocompetition appears to affect the two species community by depressing the reproduction and activity of P. parvus females while enhancing the reproduction of P. maniculatus females. Although the data indicate that P. maniculatus numbers are enhanced by the presence of P. parvus, P. parvus seems to cause P. maniculatus to be more arboreal and for females to restrict their activity. These results suggest that the benefits accrued by P. maniculatus from associating with P. parvus was greater than any costs incurred from restricted activity and use of space. A shift due to a removal experiment along any one dimension of an organisms hyperspace may not completely reflect the biotic interaction suggested by the density shift. Deductions, regarding biotic interactions, based on a meticulous study of a single dimension of community structure may lead to erroneous conclusions. However, studies which simultaneously investigate several life history

traits in conjunction with monitoring density may reveal how competition and other biotic interactions determine structure.

LITERATURE CITED

- Abramsky, Z., M.I. Dyer and P.D. Harrison. 1979. Competition among small mammals in experimentally perturbed areas of the shortgrass prairie. *Ecology* 60:530-536.
- Ambrose, R.F. and T.E. Meehan. 1977. Aggressive behavior of Perognathus parvus and Peromyscus maniculatus. *Journal of Mammalogy* 58:665-668.
- Barash, D.P. 1977. *Sociobiology and Behavior*. Elsevier, New York.
- Blair, W.F. 1937. The burrows and food of the prairie pocket mouse. *Journal of Mammalogy* 18:188-191.
- Blaustein, A.R. 1980. Behavioral aspects of competition in a three-species rodent guild of coastal southern California. *Behavioral Ecology and Sociobiology* 6:247-255.
- Blaustein, A.R. and A.C. Risser. 1974a. Interspecific interactions between the great basin pocket mouse (Perognathous parvus) and the little pocket mouse (P. longimentris) in captivity. *Murrelet* 55:23-25.
- Blaustein, A.R. and A.C. Risser. 1974b. Dominance relationships of the dark kangaroo mouse (Microdipodops megacephalus) and the little pocket mouse (Perognathous longimembris) in captivity. *The Great Basin Naturalist*. 34:312-316.
- Blaustein, A.R. and A.C. Risser. 1976. Interspecific interactions between three sympatric species of kangaroo rats (Dipodomys). *Animal Behaviour* 24:381-385.
- Boonstra, R. and C.J. Krebs. 1976. The effect of odour on trap response in Microtus townsendii. *Journal of Zoology (London)* 180:467-476.
- Brown, J.H. and G.A. Lieberman. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. *Ecology* 54:788-797.
- Brown, J.H., O.J. Reichman and D.W. Davidson. 1979. Granivory in desert ecosystems. *Annual Review of Ecology and Systematics* 10:201-227.
- Chappell, M. 1978. Behavioral factors in the altitudinal zonation of chipmunks (Eutamias). *Ecology* 59:565-579.

- Clark, W.H. and P.L. Comanor. 1973. The use of western harvester ant, Pogonomyrmex occidentalis (Cresson), seed stores by heteromyid rodents. Occasional Papers of the Biological Society of Nevada. 34:1-6.
- Colvin, D.V. Agonistic Behavior in males of five species of voles Microtus. Animal Behaviour 21:471-480.
- Congdon, J. 1974. Effect of habitat quality on the distribution of three sympatric species of desert rodents. Journal of Mammalogy. 55:659-662.
- Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle, Chthamalus stellatus. Ecology 42:710-723.
- Connell, J.H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. pp. 460-490. In: M.L. Cody and J.M. Diamond (eds.). Ecology and evolution of communities. Harvard University Press, Cambridge.
- Conover, J.W. 1971. Practical Nonparametric statistics. John Wiley and Sons New York.
- Daly, M., M.I. Wilson and P. Behrends. 1980. Factors affecting rodent's responses to odours of strangers encountered in the field: experiments with odour-baited traps. Behavioral Ecology and Sociobiology 6:323-329.
- Davis, J. 1973. Habitat, preference and competition of wintering juncos and golden-crowned sparrows. Ecology 54:174-180.
- Delong, K.T. 1966. Population ecology of feral house mice: interference by Microtus Ecology 47:481-484.
- Dhondt, A.A. and R. Eyckerman. 1980. Competition between the Great Tit and the Blue Tit outside the breeding season in field experiments. Ecology 61:1291-1296.
- Eisenberg, J.F. 1963. The behavior of heteromyid rodents. University of California Publications in Zoology. 69:1-114.
- Flake, L.D. 1973. Food habits of four species of rodents on a short grass prairie in Colorado. Journal of Mammalogy. 54:636-647.
- Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. Forest Service General Technical Report PNW-8.
- Gause, G.F., 1934. The struggle for existence. Williams and Wilkins, Baltimore.

- Glass, G.E. and N.A. Slade. 1980. The effect of Sigmodon hispidus on spatial and temporal activity of Microtus ochrogaster: evidence for competition. *Ecology* 61:358-370.
- Grant, P.R. 1972. Interspecific competition among rodents. *Annual Review of Ecology and Systematics*. 3:79-106.
- Grant, P.R. 1978. Competition between species of small mammals. pp. 38-51 In: D.P. Synder (ed.). *Populations of small mammals under natural conditions*. Vol. 5. Special Publication Series Pymatuning Lab. of Ecology. U. of Pittsburg Press, Pittsburg.
- Hairston, N.G. 1980. The experimental test of an analysis of field distributions: competition in terrestrial salamanders. *Ecology* 61:817-826.
- Hall, E.R. and K.R. Kelson. 1959. *The Mammals of North America*. The Ronald Press Company, New York.
- Hawbecker, A.C. 1940. The burrowing and feeding habits of Dipodomys venustus. *Journal of Mammalogy* 21:388-396.
- Hilborn, R., J.A. Redfield and C.J. Krebs. 1976. On the reliability of enumeration for mark and recapture census of voles. *Canadian Journal of Zoology*. 54:1019-1024.
- Holbrook, S. 1979. Habitat utilization, competitive interactions, and coexistence of three species of cricetine rodents in east-central Arizona. *Ecology*. 60:758-769.
- Koplin, J.R. and R.S. Hoffman. 1968. Habitat overlap and competitive exclusion in voles (Microtus). *American Midland Naturalist* 80:494-507.
- Krebs, C.J., B.L. Keller and R.H. Tamarin. 1969. Microtus population biology: demographic changes in fluctuating populations of M. ochrogaster and M. pennsylvanicus in southern Indiana. *Ecology* 50:587-607.
- Krebs, C.J. and J.H. Myers. 1974. Population cycles in small mammals. *Advances in Ecological Research* 8:267-399.
- Kritzman, E.B. 1974. Ecological relationships of Peromyscus maniculatus and Perognathus parvus in eastern Washington. *Journal of Mammalogy*. 55:172-188.
- Lawton, J.H. and M.P. Hassel. 1981. Asymmetrical competition in insects. *Nature* 289:793-795.
- Levine, S. 1976. Competitive interactions in ecosystems. *American Naturalist* 110:903-910.

- Levins, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton.
- Lidicker, W.Z. 1966. Ecological observations on a feral house mouse population declining to extinction. *Ecological Monographs* 36:27-50.
- Lotka, A.J. 1925. Elements of physical biology. Williams and Wilkins, Baltimore (reprinted as Elements of mathematical biology, Dover Press, 1956).
- May, R.A. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton.
- Mazdzer, E., M.R. Capone and L.C. Drickamer. 1976. Conspecific odors and trappability of deer mice (Peromyscus leucopus noveboracensis). *Journal of Mammalogy* 57:607-609.
- McCabe, T.T. and B.D. Blanchard. 1950. Three species of *Peromyscus*. Rood Associates, Publishers, Santa Barbara, California.
- Meserve, P.L. 1976. Food relationships of a rodent fauna in a California coastal range scrub community. *Journal of Mammalogy* 57:300-319.
- Munger, J.C. and J.H. Brown. 1981. Competition in desert rodents: An experiment with semipermeable exclosures. *Science* 211:510-512.
- Murie, J.O. 1971. Dominance relationships between Peromyscus and Microtus in captivity. *American Midland Naturalist* 86:229-231.
- Neter, J. and W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc. Homewood, Illinois.
- O'Farrell, T.P., R.J. Olson, R.O. Gilbert, and J.D. Hedlund. 1975. A population of great basin pocket mice, Perognathus parvus, in the shrub-steppe of south-central Washington. *Ecological Monographs* 45:1-28.
- Peterson, M.K. 1973. Interactions between the cotton rats, Sigmodon fulviventer and S. hispidus. *American Midland Naturalist* 90:319-333.
- Pianka, E.R. 1976. Competition and niche Theory. pp. 114-141. In: R.M. May (ed.) *Theoretical Ecology Principles and Applications*. W.B. Saunders Co., Philadelphia.
- Platt, J.R. 1964. Strong inference. *Science* 146:347-353.
- Price, M.V. 1978. The role of microhabitat in structuring desert rodent communities. *Ecology* 59:910-921.

- Randall, J.A. 1978. Behavioral mechanisms of habitat segregation between sympatric species of Microtus: habitat preference and interspecific dominance. Behavioral Ecology and Sociobiology 3:187-202.
- Redfield, J.A., C.J. Krebs, and M.J. Taitt. 1977. Competition between Peromyscus maniculatus and Microtus townsendii in grasslands of coastal British Columbia. Journal of Animal Ecology 46:607-616.
- Reichman, O.J. and D. Oberstein. 1977. Selection of Seed Distribution Types by Dipodomys merriami and Perognathus amplus. Ecology 58:636-643.
- Rosenzweig, M.L. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. Ecology 54:111-117.
- Rosenzweig, M.L., B.W. Smigel, and A. Kraft. 1975. Patterns of food, space and diversity. pp. 241-268. In I. Prakash and P.K. Ghosh (eds.) Rodents in desert environments. Dr. W. Junk, The Hague
- Rosenzweig, M.L. and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology 50:558-572.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185:27-39.
- Shaw, W.T. 1934. The ability of the giant kangaroo rat as a harvester and storer of seeds. Journal of Mammalogy 15:275-286.
- Tappe, D.T. 1941. Natural history of the tulare kangaroo rat. Journal of Mammalogy 22:117-148.
- Thomson, J.D. 1980. Implications of different sorts of evidence for competition. American Naturalist 116:719-726.
- Tilman, D. 1980. Resources: a graphical-mechanistic approach to competition and predation. American Naturalist 116:362-393.
- Vorhies, C.T. and W.P. Taylor. 1922. Life history of the kangaroo rat, Dipodomys spectabilis spectabilis Merriam. U.S. Department of Agriculture Bulletin 1091, 40 pp., illus.
- Wiens, J.A. 1977. On competition and variable environments. American Scientist 65:590-597.
- Wilson, E.O. 1971. The Insect Societies. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.

APPENDIX I

Table I - Percent use of ground level microhabitat and total captures for P. maniculatus (Pm) and P. parvus (Pp) during each time period on the control and experimental grids. Trap availability for each microhabitat is given for all grids. See text for description of microhabitat categories (SW=Sidewalk, AVE=Avenue). The asterisks indicates the only time a species demonstrated a microhabitat preference $p < .005$.

GRID	TIME	SPECIES/ TRAPS	MICROHABITAT (%)			TOTAL NO. CAPTURES OR TRAPS	
			BLOCK	SW	AVE		
1 Control	Pre-removal	Pm	15	62	23	60	
		Pp	14	61	25	49	
	July	Pm	14	51	35	144	
		Pp	13	59	28	46	
	August	Pm	14	52	33	237	
		Pp	14	65	21	71	
	September	Pm	14	57	29	58	
		Pp	15	55	22	72	
			Traps	16	53	31	56
	2 Pm removal	Pre-removal	Pp	15	23	62	26
July		Pp	10	35	54	79	
August		Pp	16	35	48	147	
September		Pp	12	41	47	66	
			Traps	18	38	44	56
3 Pm removal		Pre-removal	Pp	7	58	35	59
	July	Pp	4	67	29	122	
	August	Pp	4	49	46	198	
	September	Pp	6	44	50	86	
			Traps	8	51	41	56
	4 Pp removal	Pre-removal	Pm	7	54	41	44
July		Pm	9	60	47	123	
August		Pm	19	49	20	232	
September		Pm	19	58	46	48	
			Traps	15	51	34	56

Table II - Percent use of arboreal traps and (total number of captures) in arboreal traps for each species on the control and experimental grids. The percent of arboreal traps and (total number of arboreal traps) per grid is given below. The letter following (total numbers) refers to the preference of the species during that time period. N=no preference, G=significant ground preference and A=significant arboreal preference. REM=removal period, Pm=P. maniculatus, and Pp=P. parvus.

SPECIES	TIME	GRID 1 Control	GRID 2 Pm removal	GRID 3 Pm removal	GRID 4 Pp removal
<u>P. maniculatus</u>	Pre-removal	25 (20) N	---	---	21 (12) N
	July	39 (92) A	---	---	30 (50) N
	August	18 (52) G	---	---	15 (42) G
	September	17 (12) G	---	---	6 (3) G
<u>P. parvus</u>	Pre-removal	2 (1) G	0 (0) G	2 (1) G	---
	July	2 (1) G	2 (2) G	0 (0) G	---
	August	0 (0) G	1 (2) G	0 (0) G	---
	September	1 (1) G	3 (2) G	1 (1) G	---
Trap Availability		30 (24)	30 (24)	30 (24)	30 (24)

Table III - Field Tests for Dominance: 1) Behavioral Interactions - The average weight and average occurrence of each behavioral category per trial and per species. The H_0 for each Mann-Whitney U Test was that the two species did not differ. 2) Bush Climbing Data - The average (S.E.) amount of time P. manipulatus spent in a bush with P. parvus vs alone.

BEHAVIORAL INTERACTIONS

	<u>P. parvus</u>	<u>P. maniculatus</u>	Sig. level
∑ Approaches	1.8	3.3	<.02
∑ Retreats	4.4	3.1	NS
∑ Attacks	.1	.4	NS
∑ Chases	0.0	.2	NS
∑ Defends	0.0	0.0	NS
∑ Weight	15.5	16.0	NS
N	17.0	17.0	

BUSH CLIMBING DATA

	<u>P. maniculatus</u> with <u>P. parvus</u>	<u>P. maniculatus</u> alone
∑ Seconds in Bush	317 (250)	164 (114)
Number of trials	6	14
Sig. level		NS

Figure 1. The minimum number alive (MNA) of P. parvus on the two P. maniculatus removal grids and the control grid during May - Sept., 1980. The tic marks on the X axis represent trap days and the arrow represents the initiation of the removal period.

RESULTS OF P. maniculatus REMOVAL

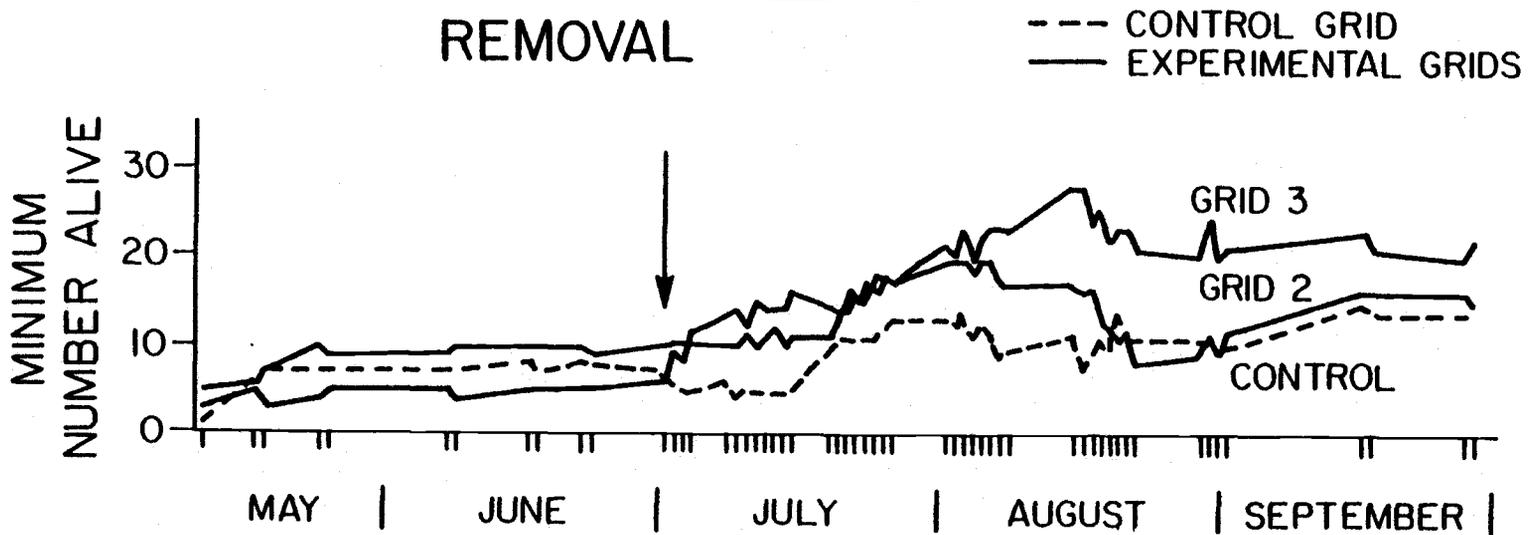


Figure 2. Control and experimental mean changes in P. parvus MNA relative to the preremoval mean MNA for the combined totals and the six demographic categories. * = $p < .05$ and ** = $p < .01$ using the Wilcoxon matched-pairs signed-rank statistic to test if the mean change is larger on the experimental grids than on the control.

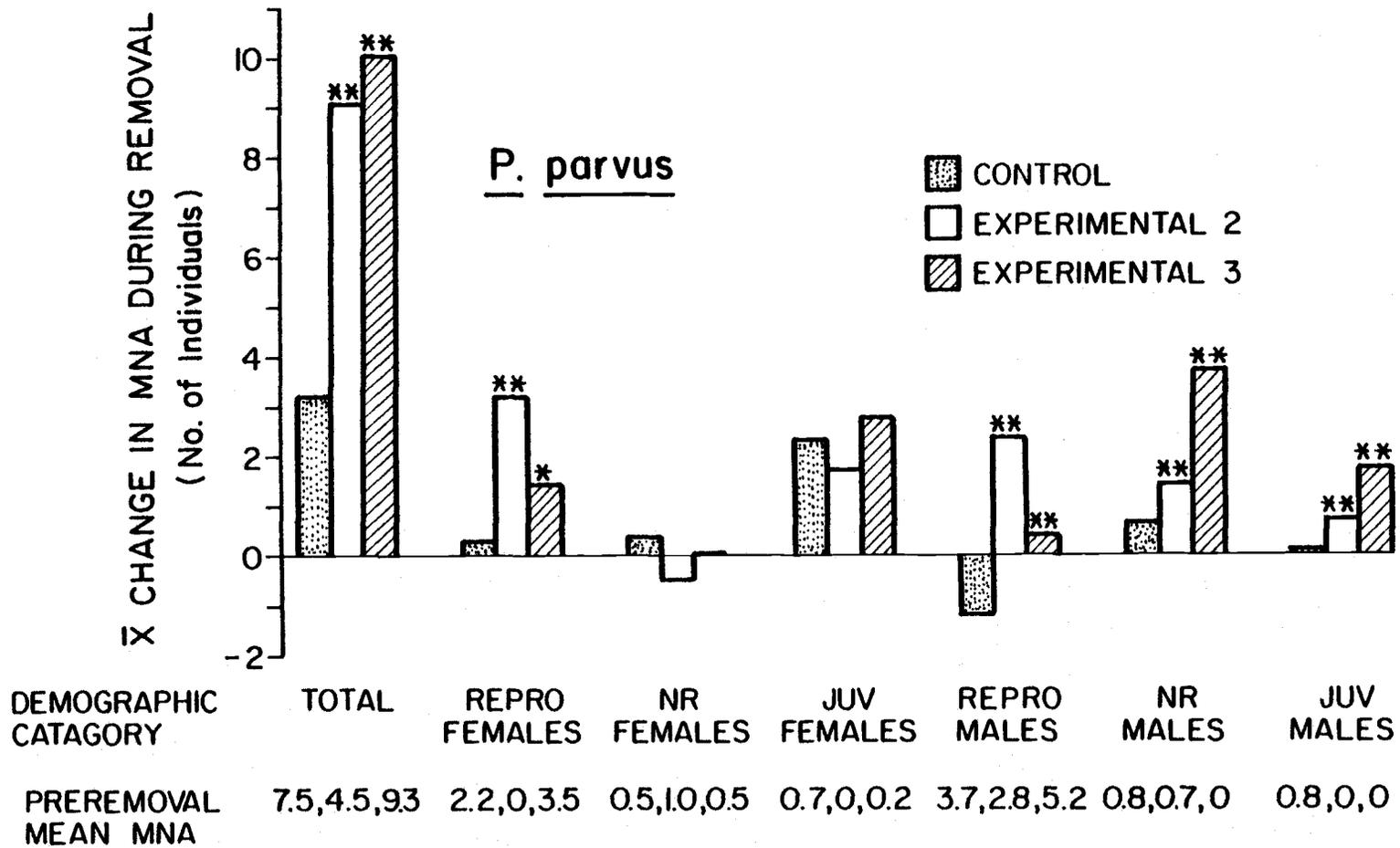


Figure 3. The minimum number alive (MNA) of P. maniculatus on the P. parvus removal grid and the control grid during May - Sept, 1980. The tic marks on the X axis represent trap days and the arrow represents the initiation of the removal period.

RESULTS OF P. parvus

REMOVAL

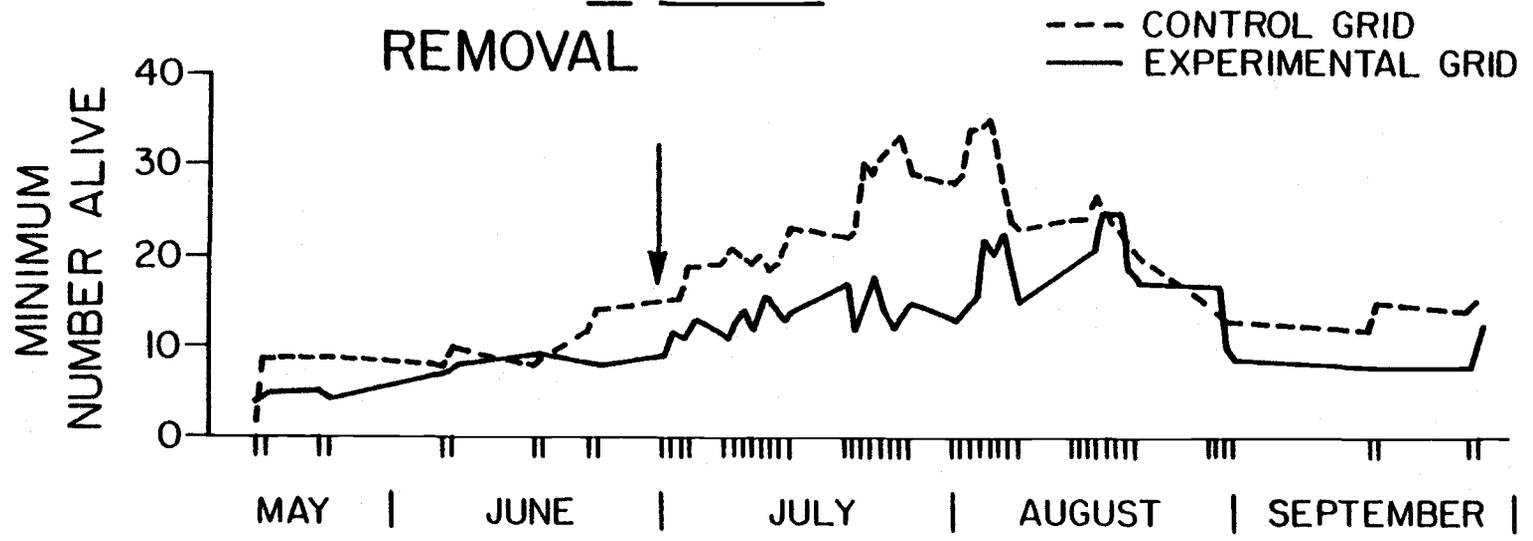
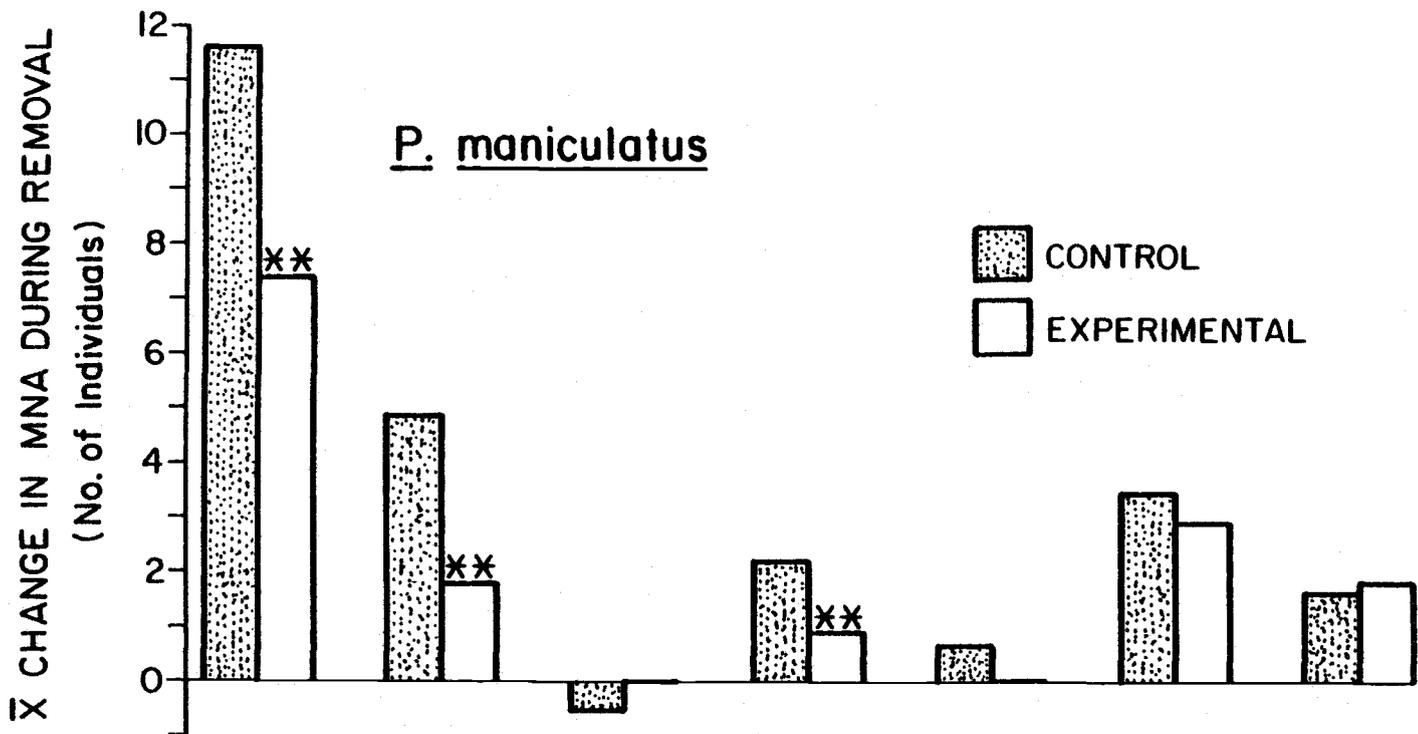


Figure 4. Control and experimental mean changes in P. maniculatus MNA relative to the preremoval mean MNA for the combined totals and the six demographic categories. ** = $p < .01$ using the Wilcoxon matched-pairs signed-rank statistic to test if the mean change is larger on the experimental grid than on the control.

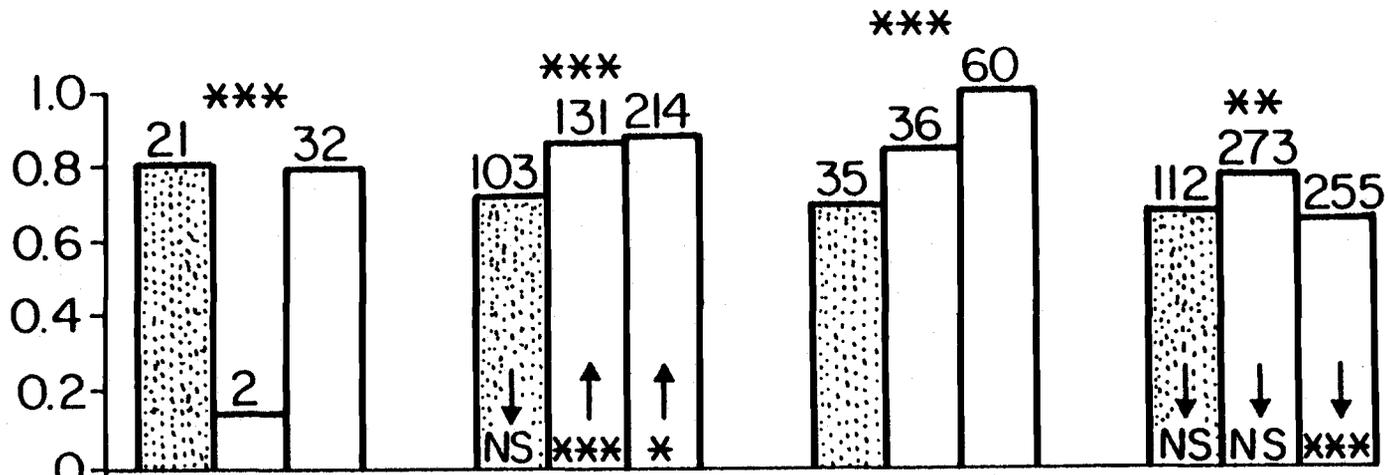


DEMOGRAPHIC CATAGORY	TOTALS	REPRO FEMALES	NR FEMALES	JUV FEMALES	REPRO MALES	NR MALES	JUV MALES
PREREMOVAL MEAN MNA	10.4, 7.8	1.5, 1.5	1.5, 0.8	0.2, 0.7	4.3, 3.0	2.8, 1.7	0, 0

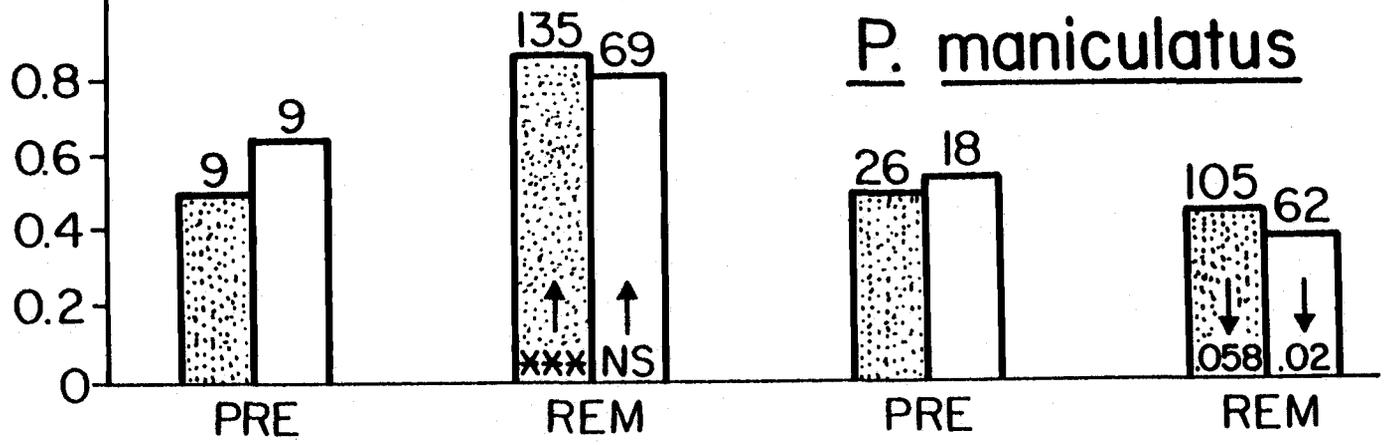
Figure 5. Frequency of reproductive males and females, for both P. parvus (upper histograms) and P. maniculatus (lower histograms) on the control grid (stippled) and experimental grids during the preremoval (PRE) and removal (REM) periods. The middle histograms for the P. parvus data refer to grid 2. Numbers above each histogram give the number of MNA reproductives. Arrows in each REM histogram indicate the direction of change in proportion relative to the PRE period for that grid. Asterisks inside a histogram indicate significant within grid changes in proportions from the PRE to REM period. Asterisks above each group of histograms indicate significant between grid differences for that time period. NS = nonsignificant, * = $p < .05$, ** = $p < .01$, and *** = $p < .005$.

FREQUENCY OF REPRODUCTIVE ADULTS

P. parvus



P. maniculatus



FEMALES

MALES

Figure 6. Male and female trappability, for both P. parvus (upper histograms) and P. maniculatus (lower histograms) on the control grid (stippled) and experimental grids during the preremoval (PRE) and removal (REM) periods. See Fig. 5 legend for further explanation.

