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SPATIAL RELATIONSHIPS OF RODENTS IN A SAGEBRUSH COMMUNITY

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ABSTRACT.—Twelve species of nocturnal rodents were studied on a 2.7-ha plot of sagebrush desert in westcentral Nevada. Species richness appeared to be augmented by food resource allocation, microhabitat selection, temporal partitioning, and the establishment of an interspecific dominance hierarchy. Three species (*Dipodomys microps, Perognathus formosus,* and *Neotoma lepida*) were restricted to the shadscale habitat. One species, *D. ordii* was restricted to sand dunes, and one species, *D. panamintinus,* was restricted to big sage habitat. Three species, *D. merriami, P. longimembris,* and *Peromyscus maniculatus,* appear to be habitat generalists. Intraspecific overlap values indicate that *D. merriami* and *P. longimembris* are the most social of the heteromyids studied, although *Peromyscus maniculatus* was the only species exhibiting intraspecific overlap throughout the year. Between-sex overlap was greatest during reproduction. Male-male overlap was most prevalent for all species except *P. longimembris,* which exhibited greater female-female overlap. The magnitude of total overlap tolerated by a species showed a positive density relationship although on an individual basis, overlap values tended to remain fairly constant. Interspecific overlap was low except for the habitat generalists, which tended to use more habitat patches. By using principal component analysis to study changes in home range shape, size, and orientation, one can assess changes in overlap and space utilization. This technique should enhance our knowledge of small mammal social structure.

The distribution of an individual in time and space is influenced by the presence or absence of other individuals (Brown and Orians, 1970), the distribution of food resources (Covich, 1976), and the presence of suitable habitat. Spatial relationships of vertebrates have been examined largely on the basis of generalized home range size, food resource allocation, or microhabitat selection. These approaches have been used to examine spacing patterns (Maza et al., 1973; O'Farrell, 1978) and mechanisms for coexistence (Brown and Lieberman, 1973; Rosenzweig, 1973; Schroder and Rosenzweig, 1975; Hoover et al., 1977; Mares and Williams, 1977; Reichman and Oberstein, 1977) for desert rodents. Changes in species diversity should influence spatial organization within the small mammal community. Whitford (1976) has shown that species diversity in desert rodents is variable and dependent on temporal fluctuations of productivity.

The social use of space has been examined in several species of rodents (e.g., Calhoun, 1963; Myton, 1974), but desert species have largely been ignored. Heteromyid rodents are important components of North American deserts and have been shown to be highly aggressive in the laboratory, exhibiting a closed-dispersed social system (Eisenberg, 1963; Schroder and Geluso, 1975). Recently, interspecific agonistic behavior has been proposed as a mechanism for heteromyid coexistence and as a factor affecting spatial distribution (Blaustein and Risser, 1974, 1976).

The present study is a portion of a larger effort to examine the structure of a small mammal community in the Great Basin Desert (O'Farrell, 1974, 1978). The purpose of this report is to describe interspecific interactions based on indices of overlap. Laboratory data indicate that a complex social structure may exist intraspecifically for heteromyids (Eisenberg, 1963), described for coastal sage scrub in California (MacMillen, 1964), and that an interspecific social hierarchy is present within the species-rich rodent community in westcentral Nevada (Blaustein and Risser, 1974, 1976). A secondary aim is to provide field documentation of predictions based on the above laboratory studies: 1) heteromyid aggression suggests that individual intraspecific spatial overlap should be low regardless of population numbers; 2) intraspecific overlap between sexes should be greatest during the reproductive season, whereas within a sex, overlap should be lowest during the same period; 3) social hierarchy should be reflected by spatial separation of the dominant species with subordinate species exhibiting increasing levels of spatial overlap; 4) subordinate species are habitat generalists and dominant species are habitat specialists (Miller, 1967), therefore spatial overlap on dominant species areas should be greater due to the size of specialized habitat patches relative to the overall generalized habitat. In addition, the graphic use of home range, determined by principal component analysis, is described and evaluated.

STUDY AREA

The study area was located at the northern end of Warm Springs Valley, about 40 km N Sparks, Highway 33, Washoe Co., Nevada (1,363 m elev.). The selected site was approximately 200 m east of the highway. A 12- by 12-station grid, 2.7 ha, was staked out at 15-m intervals. Sand dunes occurred at the western side of the grid. Slope increased to the east with the last line situated below a rocky outcrop, which constituted a hilltop.

Soil was variable over the grid. The dunes and immediate vicinity were composed of fine, wind-blown sand. Soil on most of the study plot consisted of fine sand with a fragile crust of pebbles and small stones. The soil on the eastern portion of the plot was composed of coarse sand with a harder surface layer of stones or rocks.

Vegetation on the grid was variable and exhibited a notable change from the low dune area to the hilltop. Shrubs on the area were basin sagebrush (*Artemisia tridentata* and *A. spinescens*), saltbush (*Atriplex canescens* and *A. confertifolia*), hopsage (*Grayia spinosa*), cotton thorn (*Tetradymia glabrata*), rabbit-brush (*Chrysothamnus viscidiflorus* and *C. nauseosus*), and winter fat (*Eurotia lanata*). Common and scientific names follow the usage of Munz and Keck (1965). Vegetation analysis of shrubs on the grid was determined by the line intercept method (Canfield, 1941). Except for *A. tridentata*, the only shrubs found on the eastern portion of the grid were halophytes; this area may be categorized as a shadscale scrub association (Munz and Keck, 1965). Shrub cover was sparse, with the central portion of the grid exhibiting the densest cover of 43%. Many shrubs were clumped with several individuals of the same species and up to four different species within a clump.

Except for the vegetation associated with the western portion of the grid, which was influenced by the presence of sand dunes, the dominant species was *A. tridentata* and the dominant shrub association was *A. tridentata-G. spinosa*. Based on vegetation transects and edaphic features, I have subdivided the grid into several habitat patches: 1) sand dune habitat—characterized by the presence of dunes, *Tetradymia-Grayia-Atriplex-Chrysothamnus* with a concomitant lack of *Artemisia*, <30% shrub cover, and a substrate of fine wind-blown sand; 2) big sage canopy habitat—representative of the central portion of the grid, characterized by relatively dense stands of *Artemisia* and *Grayia* forming a protective canopy, moderate slopes, and sandy substrate; 3) shadscale scrub habitat—represented mainly on the eastern portion of the area, characterized by the presence of halophytic vegetation (e.g., *Atriplex confertifolia*), <30% shrub cover, coarse compact soil, and steep slopes.

The common forbs on the study area were fiddleneck (*Amsinckia* spp.), tansy-mustard (*Descurainia pinnata*), wild buckwheat (*Eriogonum baileyi*), and prince's plume (*Stanleya pinnata*).

Forbs were usually located next to or under the clusters of shrubs. Lichens and mosses were also common beneath the cover of the shrubs. The common grasses were rice grass (*Oryzopsis hymenoides*), cheat grass (*Bromus tectorum*), squirreltail (*Sitanion hystrix*), and salt grass (*Distichlis stricta*) which was the most abundant and widely distributed grass over the entire grid.

MATERIALS AND METHODS

Trapping was conducted from 18 January 1972 to 7 January 1973. One Sherman live-trap was placed at each station. Trapping was carried out for 6 nights each month (on 3 consecutive nights during the first part and again in the latter part of the month). The trapping regimen included checking traps at 2-h intervals throughout the night and is detailed elsewhere (O'Farrell, 1974). For each animal captured, trap number, time, species, sex, relative age, reproductive condition, and weight were recorded. All animals were toe-clipped for identification.

Rodents captured on the grid belonged to two families (Heteromyidae and Muridae). Heteromyid species were: Perognathinae—*Perognathus longimembris, P. formosus,* and *Microdipodops megacephalus*; Dipodomyinae—*Dipodomys merriami, D. ordii, D. panamintinus,* and *D. microps.* Murid species were: Cricetinae—*Peromyscus maniculatus, Reithrodontomys megalotis, Onychomys torridus, O. leucogaster,* and *Neotoma lepida.*

Spatial relationships were examined using several approaches: 1) distribution of each species on the grid area was studied on the basis of season and habitat type; 2) intraspecific overlap was assessed on a point-in-time basis where each point-in-time refers to a 3-day trapping set; 3) interspecific overlap was calculated on a monthly and annual basis to examine short and long term relationships; 4) intraspecific space utilization was examined using home range data such as size, shape, and orientation of movements.

Using set theory notation, I calculated overlap with the following equation:

$$\mathrm{IO}_i = \frac{\mathrm{L}_i \cap \mathrm{L}_j}{\mathrm{L}_{iTot}}, \tag{1}$$

where $\mathrm{L}_i \cap \mathrm{L}_j$ = the number of capture loci that individual or species i shared with individual or species j; and L_{Tot} = the total number of capture loci for a given individual or species. Likewise the converse was calculated:

$$\mathrm{IO}_j = \frac{\mathrm{L}_i \cap \mathrm{L}_j}{\mathrm{L}_{jTot}}. \tag{2}$$

Equation 1 calculates the overlap of j on i and Equation 2 calculates the overlap of i on j.

To examine the mean total overlap experienced by individual i from all other individuals within the species:

$$\mathrm{IO}_{\mathrm{T}} = \frac{1}{K}\sum_{i=1}^{K}\sum_{j=1}^{n}\frac{\mathrm{L}_i \cap \mathrm{L}_j}{\mathrm{L}_{iTot}}, \tag{3}$$

where n = the total number of individuals overlapping individual i, and K = the number of individuals within the species used for the overlap measure. Similarly, the mean individual overlap (pairwise overlap) was calculated by:

$$\mathrm{IO}_{\mathrm{I}} = \frac{1}{m}\sum_{i=1}^{m}\sum_{j=1}^{n}\left(\frac{\mathrm{L}_i \cap \mathrm{L}_j}{n \cdot \mathrm{L}_{iTot}}\right), \tag{4}$$

where n = the number of individuals overlapping i; and m = the number of individuals within the species used for overlap calculations. An index of overlap multiplied by 100 yields a percentage value.

Home range data were obtained by live-trapping and use of principal component analysis, which yields information on the size, generalized shape, and orientation for each home range (Jennrich and Turner, 1969; Mazurkiewicz, 1971; O'Farrell, 1978). Inasmuch as the shape, size, and orientation of each animal's home range changes dramatically through time, home ranges for each species were plotted graphically by computer to allow visual examination of space utilization at discrete points in time.

TABLE 1.—*Variation in population numbers (number of different individuals) for each species of rodent on the study area. Tabulations are separated by first and second halves of each month.*

Species	J 2	F 1	F 2	M 1	M 2	A 1	A 2	M 1	M 2	J 1	J 2	J 1	J 2	A 1	A 2	S 1	S 2	O 1	O 2	N 1	N 2	D 1	D 2	J 1
Microdipodops megacephalus				2	6	5	5	2	1		2	2		3	5	7	9	4						
Perognathus longimembris							6	26	11	21	38	37	42	15	10	4			1	1	1			
Perognathus formosus								2	1	2	2	1		1										
Dipodomys merriami	8	8	8	14	8	10	7	10	11	8	7	5	5	5	5	7	5	4	5	6	2		3	2
Dipodomys ordii	3	3	3	2	5	3	3	2	4	3	1	2	2	2	2	2	2	2	2	2	1		2	1
Dipodomys panamintinus	4	4	4	4	2	2	2	2	2	2	1	1	2					1	1					
Dipodomys microps	3	3	3	4	3	3	3	4	4	5	3	4	2	1	1	4	4	6	5	5	2		5	2
Onychomys torridus	3	4	3	2	1	1	2		2			1	1					1			1			
Onychomys leucogaster	1							1										1						
Reithrodontomys megalotis				2	3	4	1	1	4	1	1													
Peromyscus maniculatus	6	9	8	7	7	6	8	3	7	2		3	1	2	3	4	6	6	7	13	9	4	9	6
Neotoma lepida												1		1	1	1	1	2	1	1	1			
Total	28	31	29	37	35	34	37	53	47	44	55	57	55	30	27	29	27	27	22	28	17	4	19	11

In addition, centers of activity were calculated as a two dimensional mean of capture coordinates using the method of Hayne (1949). Seasonal centers of activity for each individual of each species were calculated and plotted on grid maps. The outer points of each cluster of centers were enclosed in a convex polygon, which allows the examination of spatial use and separation of areas most heavily used.

RESULTS

Intraspecific overlap.—Although 12 species of rodents were captured on the study area, not all were permanent residents (i.e., sporadic occurrence indicating transient individuals). The grid was not large enough to include enough of the specialized habitat patches to yield sufficient data for certain species. A comparison of changes in population numbers for all species is given in Table 1. Variations can be seen in both number of individuals of a species present on the grid as well as changes in the number of species present for a given point-in-time. Such changes in composition of populations are expected to influence social behavior.

The tolerance of *D. merriami* to individual overlap exhibits several trends (Fig. 1). Mean total overlap (Equation 3) indicates the extent of intraspecific spatial pressures experienced by individuals. For example, *D. merriàmi* #17 experienced overlap by three conspecifics (#8, #10, #13) during the latter half of April. Indices of overlap on #17 were 0.25, 0.50, and 0.50, respectively, for a total of 1.25. Furthermore, six individuals experienced overlap at this time (total overlap: #1 = 0.40; #5 = 0.25; #8 = 1.00; #10 = 1.67; #13 = 2.01; #17 = 1.25) for a mean total overlap of 1.10 (see Fig. 1 for April 2). Variability in total overlap was usually great throughout the year; however, there was a low, but significant, correlation with population numbers ($r = 0.28$; d.f. = 77; $t = 2.36$; $P < 0.05$).

In contrast to total overlap, which illustrates encroachment of all individuals on single individuals, mean individual overlap (Equation 4) refers to separate measures of overlap (one-on-one situations). Utilizing the example above, mean overlap for each individual was as follows: #1 = 0.40; #5 = 0.25; #8 = 0.33; #10 = 0.56; #13 = 0.67; #17 = 0.42; and a mean individual overlap for the species of 0.44 (see Fig. 1 for April 2). It is apparent that during most of the winter and throughout the spring, *D. merriami* experienced greater infringements on home ranges; however, each individual was tolerated at a fairly consistent level of less than 45% overlap (Fig. 1).

Sexual differences in tolerated overlap were striking as shown in Fig. 2. Male-male combinations of overlap were the most prevalent. Female-female combinations were the least common and only occurred sporadically through late winter and spring. Between-sex combinations were intermediate in frequency of occurrence with a higher percentage of male overlap on female ranges than the reverse. Reproductive activity appears to account for much of the sexual differences in magnitude of overlap experienced (Fig. 1). During the reproductive season, males are less tolerant of male encroachment, whereas males overlap female areas to a great extent. In May and June, between-sex overlap decreased, corresponding to the period of pregnancy.

The remaining species of kangaroo rats were less abundant than *D. merriami* and tended to occur in more restricted habitat patches (see Fig. 5). Overlap patterns for *D. ordii* and *D. panamintinus* were similar to those presented in Fig. 1. Indices of overlap for *D. ordii* ranged from 0.6 to 1.0 from the last half of January through the first half of June. Observable overlap occurred twice at levels below 0.4 during the summer and none was observed the remainder of the year. Indices for *D. panamintinus* ranged from 0.4 to 0.9 from the last half of January through the first half of March, with no overlap observed beyond May. As in *D. merriami*, there was a positive relationship evident between magnitude of overlap experienced and numbers of individuals present on the grid. No such pattern existed for *D. microps*, which exhibited only slight overlap irrespective of population numbers.

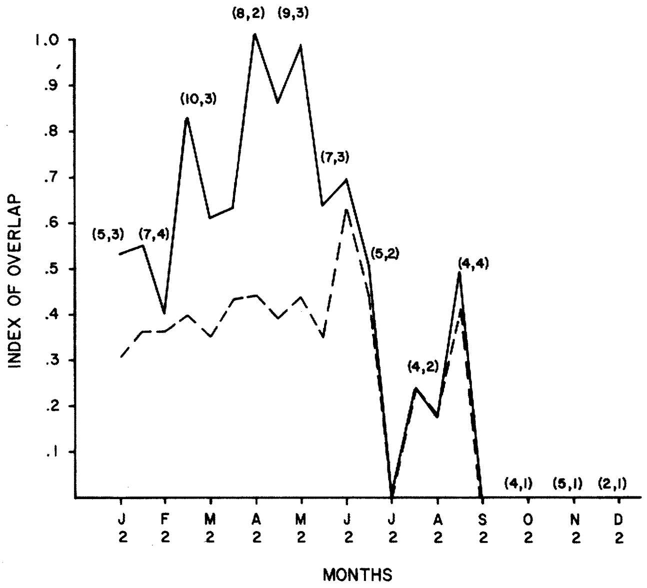

FIG. 1.—Indices of overlap for *Dipodomys merriami* determined at biweekly intervals at the first and second half of each month. Solid line gives mean total overlap, dashed line presents mean average overlap. Numbers of individuals captured for each month are in parentheses (♂♂, ♀♀).

Sexual combinations of overlap for *D. ordii* and *D. panamintinus* differed somewhat from the trends shown in Fig. 2 for *D. merriami*. Male-male interactions were the most numerous but occurred only in the spring for *D. ordii* and only in January for *D. panamintinus*. Inter-sex combinations occurred through a greater portion of the year for both species, with males overlapping females to a greater extent. Peak inter-sex encroachment occurred in late winter for both species as well as a second peak in May and June for *D. ordii*. No patterns were evident for *D. microps*. The relationship between overlap and reproductive activity was less apparent than that observed for *D. merriami* (Fig. 2).

Patterns of intraspecific overlap for *Peromyscus maniculatus* differed markedly from those exhibited by *Dipodomys* spp. (Fig. 3). The mean total overlap of this species varied erratically, but tended to decline through the spring, whereas the greatest overlap occurred in the fall. Mean individual overlap remained low throughout the year and did not remain as consistent as that exhibited by *D. merriami* (Figs. 1 and 3). The degree of encroachment tolerated by *P. maniculatus* tended to be less than that for *Dipodomys*, although individuals continually demonstrated overlap, with few exceptions, throughout the year. There is a positive relationship between population numbers and magnitude of overlap ($r = 0.24$; d.f. = 91; $t = 2.36$; $P < 0.05$). It should be noted that there was a complete population turnover in *P. maniculatus* in June, and the fall population consisted primarily of immigrating subadults.

Sexual differences in overlap were apparent in *P. maniculatus* (Fig. 4). Male-male combinations were most frequent, but the magnitude remained low. The greatest overlap exhibited was males for females, which coincided with early reproductive activity. In general, inter-sex overlaps were of similar magnitude.

The perognathine patterns of intraspecific overlap differed from those of *Dipodomys* and *Peromyscus* described above. Peak overlap in *Perognathus longimembris* oc-

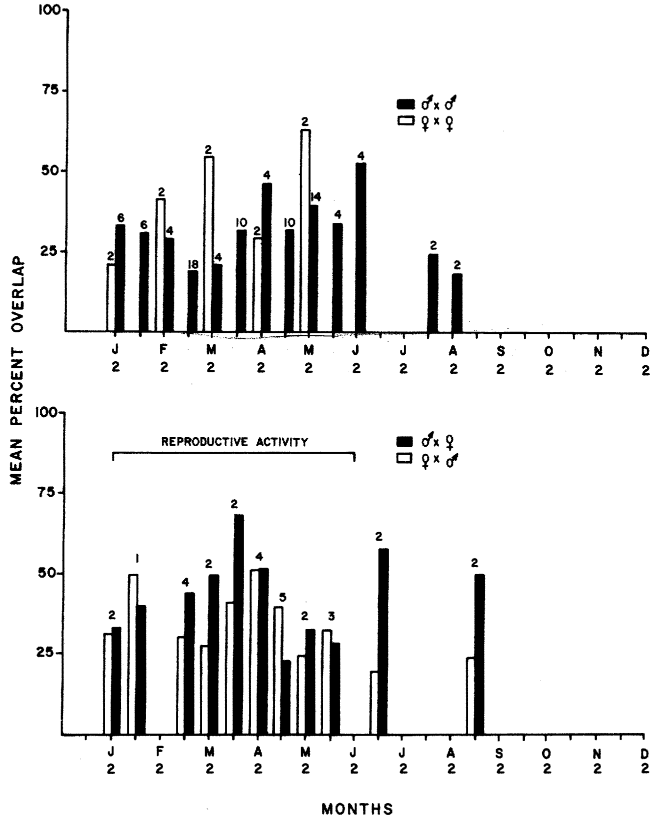

FIG. 2.—Percent overlap for *Dipodomys merriami* at biweekly intervals for different sexual combinations. Numbers above the bars indicate the number of combinations occurring in each category.

curred from May through July, with a later peak during the second half of August. No overlap occurred while the population numbers were low in April and September, October, and November. Perognathine overlap was observed during the time *D. merriami* and *P. maniculatus* exhibited low overlap in spring and summer (Figs. 1 and 3). Mean total overlap tolerated ranged between 60 and 150%. Mean individual overlap showed an almost linear decline from May through August with values ranging from 100 to 40%. A positive relationship was apparent between population size and mean total overlap, whereas mean individual overlap did not show this relationship.

Sexual differences in overlap were pronounced in *P. longimembris* but the trends were different from the other species. Female-female combinations of overlap occurred most frequently, whereas male-male combinations were the least frequent. The magnitude of overlap for the majority of interactions of all sexual combinations tended to range from 50 to 100%. Because successful reproduction did not occur during the tenure of the study for this species, the examination of effects of reproductive activity on intraspecific behavior was not possible.

Microdipodops megacephalus was present on the grid from March through the first half of October (Table 1). Through this entire time, observable overlap occurred only during the first half of April and the second half of September. This observed overlap

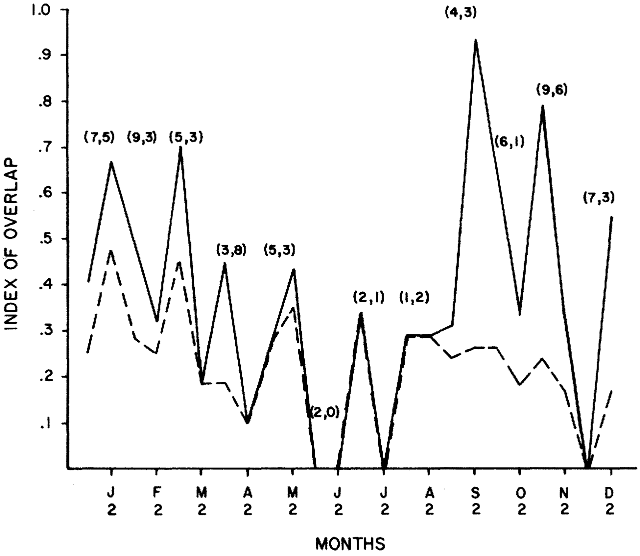

FIG. 3.—Indices of overlap for *Peromyscus maniculatus* determined at biweekly intervals at the first and second half of each month. Solid line gives mean total overlap; dashed line presents mean average overlap. Numbers of individuals captured for each month are in parentheses (♂♂, ♀♀).

corresponded to times of high population numbers. However, indices of overlap were variable and data are too few to yield trends. Perhaps the major pattern prevalent during the study was low population size spread over sufficient habitat area to allow little or no overlap.

Interspecific overlap and habitat utilization.—Centers of activity, as defined by Hayne (1949), were calculated for each individual of every species. Based on recaptures, the center of activity corresponds to a core area where an animal is most active. Presumably, a center of activity is close to the home burrow and therefore would be the most actively defended area within the animal's home range. This area would be most protected from overlap. Plotting the calculated centers of activity for each individual yields a mosaic of intensively used areas for each species within the habitat sampled.

Seasonal variations in spatial patterns for the four species of *Dipodomys* are shown in Fig. 5. The upper portion of the grid was exclusively utilized by *D. microps,* which indicates the preference for shadscale habitat, steep ground slope, and compact rocky soil. Two other habitat specialists were *D. ordii* and *D. panamintinus. D. ordii* was captured primarily in the sand dune habitat. During the summer and autumn, this species did considerable traveling between the dunes on and off the grid, thereby exhibiting centers of activity between dune sites. *D. panamintinus* was captured most frequently in the sagebrush habitat containing the greatest cover (up to 43% aerial cover). The habitat generalist of the group appears to be *D. merriami,* which occurred throughout the sagebrush habitat. Fig. 5 indicates two separate clusters and only marginal overlap occurred between them.

Indices of overlap between species agree with the spatial isolation observed from centers of activity (Table 2; Fig. 5). Hierarchical status may be inferred tentatively from the indices. Overlap is low between the species except for *D. merriami* on the other species (Table 2). This suggests that *D. merriami* is the generalist within the

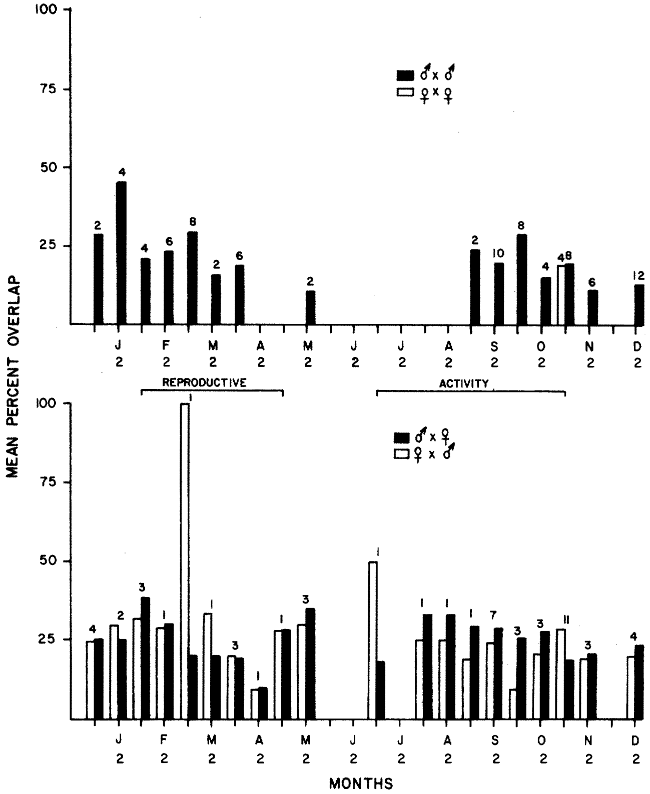

FIG. 4.—Percent overlap for *Peromyscus maniculatus* at biweekly intervals for different sexual combinations. Numbers above the bars indicate the number of combinations occurring in each category.

group, using all available habitats, and should be the subordinate species (Miller, 1967; Meserve, 1976). The other species are classified as habitat specialists. It should be noted that *D. merriami* was not captured in the shadscale habitat utilized by *D. microps*. There is low habitat similarity between *D. ordii* and *D. panamintinus* (Table 2). An examination of the summary annual interspecific overlap clarifies differences in habitat specificity. It should be stressed that although population numbers are low for certain species, calculated values are still a valid reflection of the results of species interactions under conditions of high species packing. Low density with habitat patchiness is a reality, therefore it is necessary to include all species to examine social relationships.

The perognathine group demonstrates an interesting set of seasonal patterns in spatial and habitat separation, as well as temporal differences in activity (Fig. 6; Table 1). *Microdipodops* emerged from hibernation a month and a half earlier than *P. longimembris* and demonstrated an increase in numbers, as well as intensity of activity, until the latter half of April. As numbers of *P. longimembris* increased, the trappability of *M. megacephalus* decreased. The integrity of spatial separation between the three species of perognathines is evident in Fig. 6. Distribution of *Perognathus formosus* on the study area was marginal and restricted to the upper edge of the grid exclusively in shadscale habitat. The summer is not represented on Fig. 6 because *P. longimembris* was distributed over the entire area. The autumn expansion of spatial use for *M.*

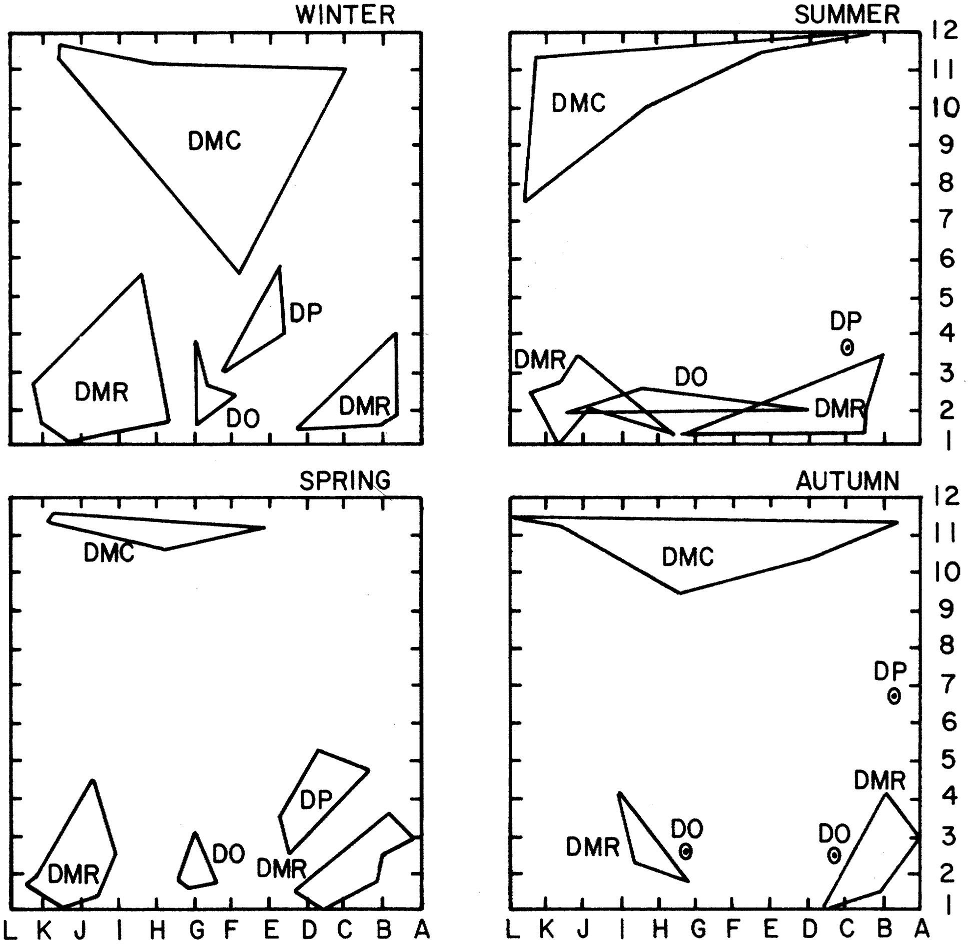

FIG. 5.—Seasonal variations of centers of activity for the four species of *Dipodomys*. DMR = *D. merriami*; DO = *D. ordii*; DP = *D. panamintinus*; DMC = *D. microps*.

megacephalus concomitant with the early entrance into hibernation by *P. longimembris* indicates a subordinate status for *Microdipodops*. The observed patterns in spatial distribution by season also correspond to apparent changes I observed in dietary habits of *M. megacephalus*, which reflects back to the decrease in trappability. While *P. longimembris* was either not present on the grid or only present in low numbers, primary food items found in cheek pouches of *Microdipodops* consisted of seeds. However, during periods with high numbers of *Perognathus*, cheek pouches of *Microdipodops* contained mainly insects. On the basis of cheek pouch contents, *P. longimembris* remained granivorous throughout the study.

Seasonal changes in overlap indices support the results of the centers of activity analysis (Table 3). Considerable spatial separation between perognathines was evident in the spring and fall. During the summer *P. longimembris* demonstrated a high degree of overlap, with *M. megacephalus* solely occupying approximately 17% of the habitat. An annual examination revealed great similarity of preferred habitat with *Microdipodops* exhibiting a more restricted distribution.

TABLE 2.—*Mean percent overlap for the species of* Dipodomys *on a seasonal and annual basis. The first value is species 1 on species 2 and the second value is the reverse. Dmr* = D. merriami; *Do* = D. ordii; *Dp* = D. panamintinus; *Dmc* = D. microps.

Species	Winter		Spring		Summer		Autumn		Annual	
Do × Dmr	2	10	10	28	16	44	13	35	36	94
Dp × Dmr	9	34	12	29	10	35	7	40	34	83
Dmc × Dmr	2	2	2	5	0	0	1	2	18	24
Dp × Do	23	15	21	17	5	7	0	0	48	46
Dp × Dmc	6	9	0	0	0	0	0	0	13	23
Do × Dmc	0	0	0	0	2	4	0	0	5	9

The cricetine group presented difficulties in analysis due to the infrequent or unpredictable occurrence of many of the species (Table 1). During the two seasons *Neotoma lepida* was trapped on the grid, it was restricted to the upper shadscale habitat exclusively. *Onychomys leucogaster* occurred only during the winter and fall and apparently represented individual migrators. *Reithrodontomys megalotis* occurred only in the spring with the species distribution confined to the lower central portion of the grid on and around the main sand dune. Distribution of *Onychomys torridus* during the entire year was centered primarily in the lower northwest quadrant. The greatest quantity of data on distribution concerns *Peromyscus maniculatus* and will be discussed in reference to Figs. 5 and 6.

First, the general distribution of centers of activity for *P. maniculatus* during all seasons was primarily in the central portion of the grid. Spatial separation between all species of cricetines based on centers of activity was the rule except for *O. torridus-P. maniculatus* in the winter and *O. torridus-R. megalotis* in the spring. Spatial separation between cricetines and heteromyids likewise was maintained each season with few exceptions. The magnitude of overlap and similarity of habitats utilized are given in Table 4. Overlap tended to be moderate each season, and there also tended to be great similarity of habitat used by *P. maniculatus* with all the heteromyid species.

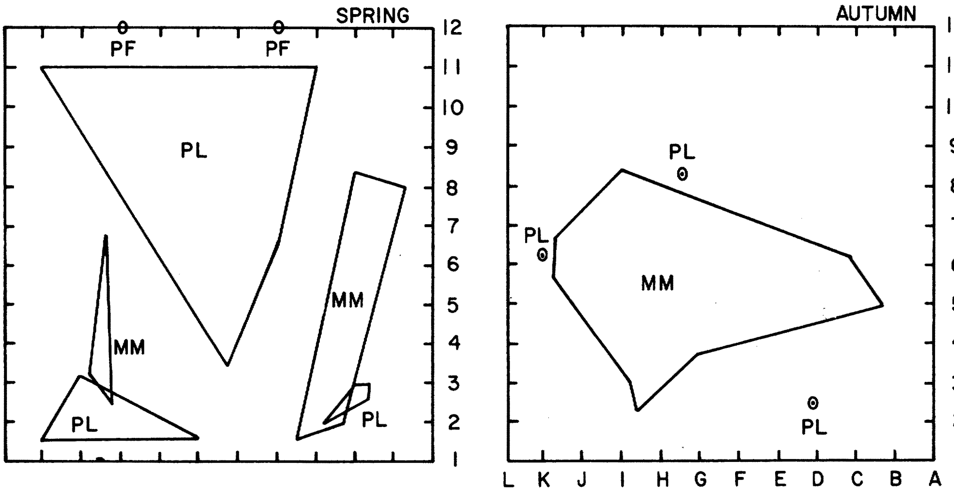

FIG. 6.—Seasonal variations of centers of activity for the Perognathinae. MM = *Microdipodops megacephalus*; PL = *Perognathus longimembris*; PF = *P. formosus*.

TABLE 3.—*Seasonal and annual percentage overlap between* Perognathus longimembris *(Pl) and* Microdipodops megacephalus *(Mm).*

Species	Spring	Summer	Autumn	Annual
Pl × Mm	32	83	23	81
Mm × Pl	21	15	26	42

Home range considerations.—The home ranges of the rodents in the present study fluctuated greatly in size, shape and orientation throughout the year (O'Farrell, 1978). Analyses of home range dynamics allow a new perspective of space utilization as well as social interactions. This type of analysis was an unexpected spin-off subsequent to data collection; therefore the full potential was not realized. When home ranges of all animals are graphically depicted on a grid map for a given time period, the result is a complex of circles, ellipses, and lines which are difficult to separate. Separating the graphics by species at discrete points in time reveals an interesting pattern.

As an example of the potential use of home range analysis, Fig. 7 presents movement and distribution patterns of *D. merriami* through four sequential biweekly trapping sets. The most striking feature is the rapidity with which individual spatial use patterns change. The presence or absence of individuals seems to influence the orientation and size of home range. Social structure appears to be an important factor in spatial relations. Physiological condition, as well as social position, should also influence spacing patterns. Fig. 2 indicates sexual and reproductive effects on spatial overlap, and Fig. 7 may be examined in this manner. During Jan-2 and Feb-1, individuals #1 and #5 were reproductively inactive and demonstrated a high percentage of overlap (40–65%). With the onset of reproductive activity in March, overlap values dropped to 10–15%. As reproductive activity waned in late spring and early summer, overlap indices returned to winter values.

The pulsating pattern of home range size through time strikingly accents the orientation of the major axis. As axis orientation changes, so does the impact of foraging by a given individual. Availability of resources may be the primary factor influencing the rotation of axes, although encroachment of dominant individuals or increased density may be equally accountable. The patterns observed in Fig. 7 are representative of the types of changes that occur throughout the year for all the species studied. Superimposing additional species onto a grid map illustrates that interspecific hierarchy and space use is operating similarly to that at the intraspecific level.

DISCUSSION

Many studies have been conducted to examine niche relations in coexisting desert rodents, almost exclusively dealing with heteromyids (for summary see Rosenzweig

TABLE 4.—*Mean percent overlap between* Peromyscus maniculatus *and the heteromyid rodents on a seasonal and annual basis. The first value is species 1 on species 2 and the second value is the reverse. Pm* = P. maniculatus; *Dmr* = D. merriami; *Do* = D. ordii; *Dp* = D. panamintinus; *Dmc* = D. microps; *Mm* = M. megacephalus; *Pl* = P. longimembris.

Species	Winter		Spring		Summer		Autumn		Annual	
Pm × Dmr	39	27	30	21	1	2	39	19	94	59
Pm × Do	16	2	10	3	0	0	28	4	85	21
Pm × Dp	54	10	17	5	0	0	80	5	89	24
Pm × Dmc	18	5	38	11	23	12	47	12	92	43
Pm × Mm			73	19	6	3	68	24	82	41
Pm × Pl			48	22	20	69	78	19	84	77

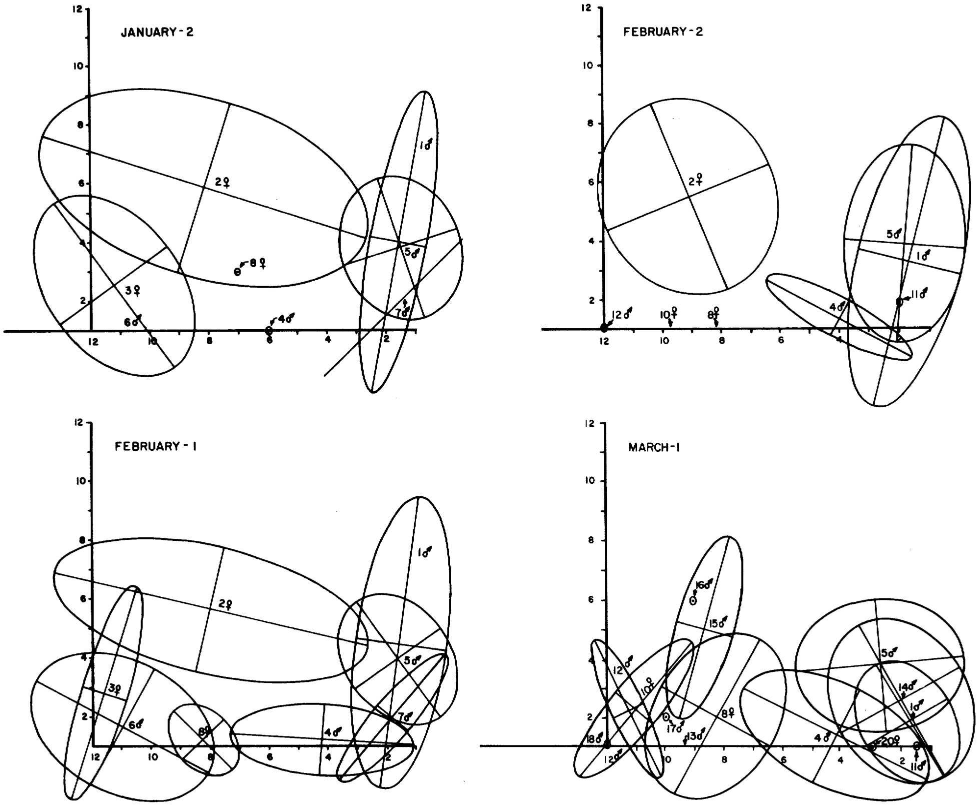

FIG. 7.—Biweekly variations in home range size, shape and orientation for *Dipodomys merriami*. Totally linear and single locations for individuals are also included.

et al., 1975; Mares and Williams, 1977; M'Closkey, 1978). An examination of dietary separation based on size of food particles has yielded conflicting results, although several studies have shown a tendency towards a positive relationship with body size (Brown and Lieberman, 1973; Mares and Williams, 1977). Microhabitat selection in relation to complexity of vegetative structure appears to be the most important factor in niche separation for desert rodents (Rosenzweig, 1973; Rosenzweig et al., 1975; M'Closkey, 1976, 1978; Price, 1978). Price (1978) suggested that interspecific competition maintains differences in microhabitats used for foraging. M'Closkey (1976) further indicated that seasonal variation in habitat use facilitates greater species packing and coexistence.

In the present study, a heterogeneous habitat in the Great Basin Desert was examined. Of the 12 species of nocturnal rodents studied (Table 1), one species (*Onychomys leucogaster*) was transient and two species (*Perognathus formosus* and *Neotoma lepida*) were marginal in occurrence, presumably due to insufficient microhabitat on the study area. The remaining nine species may be considered primary residents and separate readily into seasonal and year-round use patterns. The seasonal species represent the lower range of body size, hibernate, and during the summer constitute the greatest number of individuals (Table 1).

An examination of species distribution based on capture-recapture sites in relation to the habitat mosaic (see Description of Study Area) reveals that microhabitat selection is apparent. Three species were restricted to the shadscale habitat, although *P. formosus* and *N. lepida* were probably influenced more by the presence of rocky outcrops, which characterize preferred habitats elsewhere (Hall, 1946). Kenagy (1972, 1973) described the reliance of *Dipodomys microps* upon *Atriplex* leaves, which probably account for this species' distribution in the present study. Of the other two large kangaroo rats that may be considered potential competitors, *D. ordii* was restricted to sand dunes and *D. panamintinus* was trapped exclusively in the big sage canopy habitat. The edaphic relationship of *D. ordii* with loose sand has been documented by Schroder and Rosenzweig (1975). The vegetative differences between these two habitats suggest differences in feeding strategies, as well as vegetative cover provided, for the large *D. panamintinus*. Distributions of *Microdipodops megacephalus* and *Peromyscus maniculatus* were also concentrated primarily in the big sage canopy habitat. The remaining species were relegated to the base of the dunes as well as the sparser interface between this habitat and that of the big sage canopy. Only *Perognathus longimembris* was found distributed throughout all habitats.

The discrete separation of the species along a body weight continuum was documented previously (O'Farrell, 1978). Such an array in coexisting sand dune rodent species was discussed by Brown and Liberman (1973) in relation to resource utilization. These workers, as well as Mares and Williams (1977), gave evidence for a positive correlation between body size and seed size selected. The hypothesis presented was that differential seed size selection accounts for decreased interspecific competition, although there was substantial overlap in seed size selection among species. A more acceptable hypothesis suggests that because seeds are differentially distributed, resources may be allocated by selective foraging behavior (Reichman and Oberstein, 1977; Hutto, 1978). Kangaroo rats would forage primarily on seeds with a clumped distribution whereas pocket mice would utilize randomly dispersed seeds. Feeding habits were not analyzed in the present study, but inferences based on the literature, the body size continuum, and gross examination of cheek pouch contents yield the following conclusion. Seed size selection, spatial distribution differences of seeds in foraging areas, seasonal changes in occurrence, and changes in dietary habits (i.e., seeds to insects) serve to reduce interspecific competition.

Temporal partitioning as a means of promoting coexistence in desert rodents has been discussed by Kenagy (1973) and O'Farrell (1974). Such partitioning as demonstrated in these two studies would further serve to reduce competition, particularly when there is overlap in space and diet. This does not imply competition for food, rather the separation of social space of two highly aggressive species with similar foraging strategies (e.g., *D. merriami* and *D. ordii*; rapid, bipedal searching for seed clumps). Thus temporal partitioning would reduce interference behavior and enhance coexistence.

Social structure and consequent spatial utilization has largely been ignored for desert rodents, although the aggressive nature of desert heteromyids has been summarized and documented in the laboratory by Eisenberg (1963). A behavioral continuum seems to exist where increasing intra- and interspecific aggression follows increasing body size. Eisenberg (1963) categorized desert heteromyids as having a closed-dispersed social system with the tendency towards adult isolation. Because heteromyids are relatively long-lived species (French et al., 1974) and tend to remain loyal to a given home range area (Maza et al., 1973; O'Farrell, 1978), it may be inferred as suggested by Eisenberg (1963) that a permanent complex social organization is present. Social structure of the small mammal community would tend to stabilize the community and provides another important niche dimension.

In the present study intra- and interspecific overlap in spatial distribution are used as an index of social interactions. Overlap within a species may be considered indicative of individual crowding (density) and may also express social tolerance. Resource distribution may also influence overlap but was not dealt with in the present study. A population experiencing an increase in density can be expected to exhibit a concomitant increase in total overlap or a decrease in size of home range. Likewise, a species that exhibits a great deal of spatial overlap can be considered socially tolerant. On an individual basis, overlap may express social hierarchy, with the dominant individuals tolerating the least amount of overlap.

Interspecific overlap may be used as an index of spatial partitioning and may shed light on differential habitat specificity. This analysis also allows prediction of social hierarchy within the community and may serve as an index of the social dimension of the niche. Such a behavioral analysis is judged to reflect competitive pressures of microhabitat selection and resource allocation.

Species of *Dipodomys* were characterized by only seasonal occurrences of spatial overlap. Summer and fall overlap was either minimal or nonexistent. *D. merriami* exhibited the longest period of intraspecific overlap and also the highest level, whereas *D. microps* the least and most sporadic. This tendency of *D. merriami* indicates a less aggressive nature, which agrees with the findings of Eisenberg (1963). As population numbers increased, the total amount of overlap per individual tended to increase, but the amount of encroachment tolerated on an individual basis remained relatively constant (Fig. 1). It should be expected that as populations increase overlap should increase correspondingly or home range size should decrease. A comparison of overlap (Fig. 1) with home range size for the same individuals (O'Farrell, 1978) indicated decreasing home range coupled with increasing total overlap. It appears that at least for *D. merriami* individual tolerance to overlap is maintained by both decreasing home range size and allowing more individuals to overlap slightly.

Perognathine intraspecific patterns demonstrated opposite trends. Low population numbers, moderate home range size, and little to no spatial overlap were demonstrated by *M. megacephalus*. On the other hand, *P. longimembris* has the least aggressive intraspecific social structure of the heteromyids examined. *Peromyscus maniculatus* differed from the heteromyids in that mean home range remained relatively constant although intraspecific overlap fluctuated dramatically through the year (Fig. 3).

The role of sexual overlap as it relates to the overall intraspecific overlap observed above, exhibits several patterns indicative of species social structure. Where data were sufficient, all *Dipodomys* species showed primarily male-male spatial overlap. Between-sex overlap occurred mainly during the reproductive period. This common trend reflects the disproportionately greater abundance of males. Reproductively inactive males seemed more tolerant to spatial overlap than did females (Fig. 7). *Perognathus longimembris* demonstrated the reverse, with female-female combinations occurring most frequently, indicating a greater level of male aggressiveness. Sex ratios for *P. longimembris* show little difference between male and female abundance (O'Farrell, 1974). In most cases, *Peromyscus maniculatus* showed less overlap than *Dipodomys* spp. with no female-female combinations observed. This is contrary to the generalization that *Peromyscus* is more social than heteromyids (Eisenberg, 1968). I suggest that in desert habitats, *Peromyscus* adopts a more isolated dispersion to decrease intraspecific competitive pressure.

The dispersion of mathematical centers of activity provides a clear visual analysis of habitat utilization in relation to the environmental mosaic (Figs. 5 and 6). General contiguous allopatry suggests strong interference behavior and/or ecological specialization. However, individual movements are large (O'Farrell, 1978) and habitat patches are small, which is evident when annual interspecific overlap is examined (Tables 2 and 3). Without formal testing, I am assuming that interspecific overlap is an index of habitat similarity. Seasonal overlap is low, suggesting that although preferred habitats are similar in most cases, temporal differences in use of available space effectively isolate potential competitors.

Spatial separation at discrete points in time must be accomplished, at least in part, by behavioral means. Four species of *Dipodomys,* for example, present on a limited study area suggest a hierarchical social structure. Blaustein and Risser (1976) studied agonistic behavior of three of these species in the laboratory concurrently with the present study. They determined that behavioral dominance followed the body size gradient, with *D. merriami* being the most subordinate and *D. panamintinus* the most dominant. On the other hand, *P. longimembris,* the smallest perognathine, was always dominant to *M. megacephalus* (Blaustein and Risser, 1974). Conclusions of these laboratory studies are supported in the present study (Tables 2 and 3; Results).

The predictions stated in the Introduction are borne out based on overlap analysis as follows. (1) Intraspecific overlap for heteromyids increased as population size increased, although individual encroachment remained at a relatively low, constant level. Overlap was absent during portions of the year and occurred less frequently in the larger, presumably more aggressive species. (2) Intraspecific overlap between sexes was greatest during the reproductive season; within sex combinations were lowest during this same period. Male overlap on female home range was the rule except for *P. longimembris.* (3) Species judged dominant in laboratory encounters exhibited low overlap, indicating high spatial separation. Subordinate species exhibited great overlap with most of the dominant species, indicating generalized habitat use. However, for specific points-in-time, overlap was low indicating avoidance. (4) Habitat generalists (i.e., those species using a wide variety of habitat patches) were those that were behaviorally subordinate in laboratory encounters. Likewise, dominant species demonstrated restricted distribution to discrete habitat patches.

A final point of consideration is the use of short, but intensive, point-in-time examinations of home range movements with principal component analysis. Mazurkiewicz (1971) demonstrated the value of this analysis in studying differences in shape and orientation of small mammal movements. More recently, Hawes (1977) carried this procedure farther and for *Sorex* demonstrated changes in orientation, size, and shape of home ranges between breeding and nonbreeding seasons. I propose that more detailed studies are required. I have shown that home range fluctuates in size, shape, and orientation, not only in relation to breeding, but throughout the year (O'Farrell, 1978; Fig. 7). It is apparent that social factors, as well as physiological condition and resource availability, are accounting for the fluctuations in spatial distribution. Properly designed studies using the techniques discussed in the present study should result in the description of the social structure of small mammal communities and its role as a stabilizing influence in these communities.

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