SPATIAL PATTERNS IN TWO SYNTOPIC SPECIES OF MICROTONES: MICROTRUS OCHRORAGASTER AND SYNATOMYS COOPERI

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Abstract.—Two years of live-trapping data were analyzed for spatial patterns within and between the species Microtus ochrogaster and Synaptomys cooperi in eastern Kansas. Within species, each sex was frequently overdispersed and nearest neighbors were of the opposite sex. When sexes were combined, each species was frequently overdispersed. There was also frequent evidence of a negative association between species. However, there was no indication of seasonal or density dependent trends in any of the spacing indices. Although M. ochrogaster was often overdispersed within a season, on one of the study areas successive inhabitants tended to select the same locations. This result is suggestive of microhabitat selection, even though the study site had been selected to minimize spatial heterogeneity. S. cooperi did not exhibit any evidence of microhabitat selection.

There is a prodigious number of studies on dispersion patterns in rodent species. These studies fall primarily into two groups: those which examine spatial separation of two competing species, and those which examine dispersion patterns within species. Spatial separation between species is thought to be a mechanism allowing species to coexist (e.g., Conley, 1976; Grant, 1972; M’Closkey, 1976, 1978). Numerous studies have shown that two species will often separate themselves along an environmental gradient or ecotone, with each species having a preferred and a less preferred zone. Following the removal of one species, the other will use the empty space, indicating that interspecific competition rather than habitat selection is determining microhabitat utilization (e.g., Cameron, 1971; Grant, 1971, 1972; Koplin and Hoffmann, 1968; M’Closkey, 1978; Stoecker, 1972).

Dispersion patterns within a species have been studied in an attempt to understand the interactions of conspecifics (for reviews, see Brown and Orians, 1970; Waser and Wiley, 1979). The spacing of conspecifics can be the result of intraspecific competition (e.g., Brown and Orians, 1970; Smith, 1968; Waser and Wiley, 1979), mating systems (e.g., Hofmann et al., 1984; Madison, 1980; Metzgar, 1980; Metzgar and Hill, 1971), or a reflection of the distribution of microhabitats (e.g., Cockburn and Lidicker, 1983; Wondolleck, 1978).

This study examines spatial patterns within and between two microtine rodents, Microtus ochrogaster and Synaptomys cooperi, in an attempt to understand their patterns of habitat utilization and the nature of their interactions. Although these species are similar morphologically and ecologically, M. ochrogaster has been characterized as a more xeric and upland species than S. cooperi (Burt, 1948; Getz, 1961; Howell, 1927; Linduska, 1950; but see Shier, 1981). Wherever S. cooperi and Microtus sp. overlap together, it has been assumed they coexist by segregation along an environmental gradient such as moisture or vegetation type (Getz, 1961; Linduska, 1950; Linzey, 1984; Shier, 1981). However, Gaines et al. (1977) did not find substantial spatial separation between the two species nor was either species obviously associated with a microhabitat.

Gaines et al. (1977) made no attempt to quantify these anecdotal observations. The objective of this study is to examine the spatial patterns of these species in a more detailed fashion using the same data as Gaines et al. (1977).

Methods

Study Sites

Two live-trap grids, located 11 km north of Lawrence, Kansas, were separated by approximately 400 m of grassland and two fence rows overgrown with mixed deciduous shrub vegetation. These grids were

originally established in 1970 to study the demography of *M. ochrogaster* (Gaines and Rose, 1976; Rose, 1974); however, since no removals or introductions were made and *S. cooperi* and *M. ochrogaster* were consistently present over the course of the study, they are also suitable for an analysis of dispersion patterns.

Each grid consisted of 100 Longworth live traps arranged in 10 rows and 10 columns spaced 7.6 m apart. Traps were supplied with crimped oats and cotton bedding and covered with a board to protect them from direct sunlight. Within each block, trapping sessions were conducted on a biweekly schedule. During each session, traps were set for two consecutive nights and the intervening day. However, during the summer season, traps had to be closed during the day to prevent deaths due to heat stress. Animals were ear-tagged when first captured. For all captures, tag number, location, species, and sex were recorded, and the animal was immediately released.

Vegetation on both grids was predominantly grasses, in particular *Bromus* and *Agrostis* spp. (for a more detailed vegetational description, see Gaines and Rose, 1976, table 3; Rose, 1974). Grid B was evenly sloped to the north whereas grid D had little or no slope. However, this grid had several low terraces running north to south which were remnants of previous agricultural practices. With the exception of these terraces, neither grid was notably spatially heterogeneous.

**Demographic Data**

We analyzed mark-and-recapture data from December 1971 to November 1973 for seasonal as well as density effects. Each season consisted of a 10-week block. The winter season ran from mid-December to late February; spring, from early March to mid-May; summer, from mid-June to late August; and autumn, from mid-September to late November. The 2 to 4 weeks between each season were not used to avoid complications of seasonal transitions and to maximize the probability of detecting seasonal differences. This method also reduced the number of animals that occurred in more than one seasonal block. Nonetheless, 45% of the *M. ochrogaster* and 56% of the *S. cooperi* were caught in more than one season.

**Dispersion Analysis**

We excluded from the analysis all animals that resided on the grids for less than 1 month (i.e., transients without established home ranges and juveniles that died or dispersed early). This minimum tenure requirement ensured that all animals were caught at least twice. Although including individuals with as few as two captures may give a poor estimate of their use of space, a month’s residency is likely to have influenced the spatial distribution of the rest of the population. The mean number of captures per individual per season was 4.94 (±3.82 SD).

*Index of interspecific association.*—We tested trap stations for the presence or absence of each species with Cole’s index of association (Cole, 1949), as modified by Ratliff (1982). This index has been used by Blaustein (1980), Heske et al. (1984), and Petersen and Helland (1979) to determine if two rodent species avoid one another. If either species avoids areas used by the other, a nonrandom pattern of occurrence at trap stations would result. The method assigns presence or absence for each species to each grid coordinate. The number of stations with neither species, both species, *M. ochrogaster* only, or *S. cooperi* only was tested for nonrandomness with a 2 by 2 contingency table. The index of interspecific association was computed from the cell values using Ratliff’s (1982) corrected formulae. It varies from −1.0 for a negative association to 1.0 for a positive association.

*Center of activity.*—Centers of activity were computed for resident animals in each seasonal block. The center of activity is a bivariate point obtained from the capture locations by averaging the row values and column values for all captures of a given individual. Since both species exhibit a strong central tendency to their home range activities (Danielson and Swihart, 1987), the center of activity provides a reliable estimate of the location of the core area; the most heavily used portion of the home range. The spatial distribution of the centers of activities was then tested for nonrandomness. Under the null hypothesis of a random dispersion pattern, distances between each individual and its nearest neighbor can be expected to vary as a function of density. Clark and Evans (1954) formulated a method for determining the expected distance between nearest neighbors for a given density with a random dispersion pattern. The average observed distance can then be tested to determine if it differed significantly from the expected value. Additionally, the ratio of observed to expected averages can be used as an index of dispersion. Values greater than 1.0 indicate overdispersion; those less than 1.0 indicate underdispersion or aggregation. The index of dispersion is not symmetrical, having a range from 0.0 to 2.1491.

The analysis of dispersion was used on each sex of each species separately, on both sexes together, and on the two species combined. This series of analyses was used to examine intrasexual, interspecific, and intra-community spatial patterns. To test for intersexual spatial associations in each species, the frequency of
Fig. 1.—Population size of *M. ochrogaster* and *S. cooperi* from winter of 1971–72 to autumn 1973 on grid B (a) and grid D (b). WI = winter, SP = spring, SU = summer, AU = autumn.
Table 1.—Cole's index of interspecific association between M. ochrogaster and S. cooperi. Values greater than zero indicate a positive association. Values less than zero indicate a negative association.

<table>
<thead>
<tr>
<th>Grid</th>
<th>Year</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
<th>Autumn</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>1971–72</td>
<td>0.281*</td>
<td>-0.444</td>
<td>-0.487</td>
<td>0.040*</td>
</tr>
<tr>
<td></td>
<td>1972–73</td>
<td>-0.393</td>
<td>-0.003</td>
<td>-0.132</td>
<td>-0.146</td>
</tr>
<tr>
<td>D</td>
<td>1971–72</td>
<td>-0.256*</td>
<td>0.060</td>
<td>-0.335*</td>
<td>-0.111</td>
</tr>
<tr>
<td></td>
<td>1972–73</td>
<td>-0.019</td>
<td>-0.241</td>
<td>-0.188</td>
<td>-0.223</td>
</tr>
</tbody>
</table>

* P < 0.05.

conspecifics of the same sex and opposite sex being nearest neighbors was analyzed by a contingency test. Similarly, the frequencies of conspecific and heterospecific nearest neighbors for each individual in the community were tested for interspecific spatial associations.

Territoriality.—To further clarify intraspecific dispersion patterns, and in particular, to test for territoriality, we used the method described by Metzgar and Hill (1971). This procedure preserves the integrity of the home range shape and size for each individual. However, it assumes all portions of each home range are equally utilized. A computer simulation was used to compute the expected distribution of home range overlaps under the null hypothesis that the location of each home range is independent of all other home ranges on the grid. We used 300 iterations of the randomization procedure to derive our expected distributions. The observed and expected overlaps were then compared with a Chi-square test.

Results

Population Densities

The two grids differed substantially in densities of both M. ochrogaster and S. cooperi. Grid B averaged approximately 50% more animals than grid D. M. ochrogaster was always the more abundant species on grid B (Fig. 1), whereas grid D was predominantly populated by M. ochrogaster from the winter of 1971–72 through the summer of 1972; from autumn 1972 until the end of the study, S. cooperi was more abundant. The population of M. ochrogaster attained a peak in autumn 1972 on grid B followed by a precipitous drop in numbers through the spring before recovering slightly and then declining again. On grid D, a peak in the M. ochrogaster population occurred during the summer of 1972, followed by a decline and a smaller second

Table 2.—Ratios of observed to expected distances between centers of activity of nearest neighbors. Values greater than one indicate overdispersion. Values less than one indicate underdispersion or clumping.

<table>
<thead>
<tr>
<th>Species</th>
<th>Grid</th>
<th>Year</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
<th>Autumn</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. ochrogaster</td>
<td>Males</td>
<td>B</td>
<td>1971–72</td>
<td>1.218</td>
<td>1.212*</td>
<td>1.420*</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1972–73</td>
<td>0.836</td>
<td>1.296*</td>
<td>1.714*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>1971–72</td>
<td>0.943</td>
<td>1.240*</td>
<td>1.338*</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1972–73</td>
<td>1.370*</td>
<td>1.401*</td>
<td>1.626*</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>B</td>
<td>1971–72</td>
<td>1.117</td>
<td>1.201*</td>
<td>1.270*</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1972–73</td>
<td>1.127</td>
<td>1.140</td>
<td>1.231*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>1971–72</td>
<td>1.028</td>
<td>1.245*</td>
<td>0.868</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1972–73</td>
<td>1.067</td>
<td>0.974</td>
<td>1.250</td>
</tr>
<tr>
<td>S. cooperi</td>
<td>Males</td>
<td>B</td>
<td>1971–72</td>
<td>1.226</td>
<td>1.149</td>
<td>1.254</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1972–73</td>
<td>0.927</td>
<td>1.158</td>
<td>1.395*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>1971–72</td>
<td>0.485*</td>
<td>1.440*</td>
<td>1.479*</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1972–73</td>
<td>1.136</td>
<td>1.259*</td>
<td>0.980</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>B</td>
<td>1971–72</td>
<td>1.625*</td>
<td>1.237</td>
<td>1.269</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1972–73</td>
<td>1.051</td>
<td>1.020</td>
<td>1.409</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>1971–72</td>
<td>0.533</td>
<td>1.136</td>
<td>0.988</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1972–73</td>
<td>1.101</td>
<td>1.107</td>
<td>1.380*</td>
</tr>
</tbody>
</table>

* P < 0.05.
peak in the spring of 1973. *S. cooperti* reached its maximum numbers in the winter of 1972–73 on both grids.

**Index of Interspecific Association**

Cole’s index of interspecific association was significantly positive twice on grid B and significantly negative twice on grid D (Table 1). The index was less than zero in 13 of the 16 season-grid combinations, indicating a significant tendency for the species to avoid each other ($P = 0.011$, sign test). A regression of the index against the combined densities of both species showed no trend with changes in the numbers of individuals inhabiting the grids ($r^2 = 0.018$, $P > 0.5$), nor was there any consistent seasonal pattern ($P > 0.25$, Quade’s test; Conover, 1971). Taken together, these results imply that interspecific avoidance is relatively constant and independent of density and seasonal effects.

**Centers of Activity**

Considering distances between nearest neighbors for just male voles, the ratios of observed to expected distances were greater than 1.0 for 14 of the 16 data sets ($P = 0.002$, sign test). The ratios were significantly greater than 1.0 on nine of those 14 occasions ($P < 0.05$, Table 2). Females voles were also frequently overdispersed. The ratios were greater than 1.0 for 12 of the 16 data sets ($P = 0.038$, sign test); significantly so for six of those 12 ($P < 0.05$, Table 2). For five of the 16 data sets, the frequency with which nearest neighbors were of the opposite sex was significantly greater than that expected from random assortment ($P < 0.05$, contingency test). This positive association between males and females occurred once in each season and twice in autumn. A significantly negative association between the sexes occurred once on grid D during the autumn of 1972.

When both sexes of voles were combined, the ratios of observed to expected nearest neighbor distances were significantly greater than 1.0 during autumn 1973 on grid B, and during spring 1972, summer 1972, and spring 1973 on grid D (Table 3). They were significantly less than 1.0 during winter 1971–72 on grid D. Over both grids, there was a trend towards overdispersion for *M. ochrogaster*. The ratio of observed to expected distances was greater than 1.0 for 13 of the 16 season-grid combinations ($P = 0.011$, sign test). To test for density-dependent effects on distances between individuals, the ratio of observed to expected distance was treated as a dependent variable and a regression was performed with density as the independent variable. Density explained little of the variance ($r^2 = 0.033$, $P > 0.5$) and the slope of the regression did not differ significantly from zero. Similarly, there was no observable pattern correlated with seasons ($P > 0.25$, Quade’s test).

Dispersion patterns for *S. cooperti* were similar to *M. ochrogaster*. Within sexes, male lemmings
Table 4.—Species identity of nearest neighbor associations for M. ochrogaster and S. cooperi. C indicates that nearest neighbors were conspecifics more often than expected. H indicates nearest neighbors were biased towards heterospecifics.

<table>
<thead>
<tr>
<th>Grid</th>
<th>Year</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
<th>Autumn</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>1971–72</td>
<td>H</td>
<td>C</td>
<td>C</td>
<td>C*</td>
</tr>
<tr>
<td></td>
<td>1972–73</td>
<td></td>
<td></td>
<td></td>
<td>H</td>
</tr>
<tr>
<td>D</td>
<td>1971–72</td>
<td>C*</td>
<td>H*</td>
<td>C</td>
<td>H</td>
</tr>
<tr>
<td></td>
<td>1972–73</td>
<td>C*</td>
<td>C</td>
<td>C</td>
<td>H</td>
</tr>
</tbody>
</table>

* P < 0.05.

had observed to expected ratios that were greater than 1.0 on 13 of the 16 occasions (P = 0.011, sign test), five of which were significantly greater than 1.0 (P < 0.05, Table 2) and one which was significantly less (only seven lemmings resided on the grid at this time, Fig. 1). Females also had ratios greater than 1.0 on 14 of the 16 data sets (P = 0.002, sign test), but only four of the ratios were significantly larger than 1.0 (P < 0.05, Table 2). As with voles, significant positive associations of male and female centers of activity occurred for five of the data sets (P < 0.05, contingency test), once in each season and twice in autumn. There was a significant negative association during winter 1971–72 on grid D, when only seven lemmings were present.

When the sexes were combined, lemmings were significantly overdispersed on four occasions on grid B and once on grid D (Table 3). For the 16 season-grid combinations, the ratios of observed to expected distances were greater than 1.0 on 11 occasions (P = 0.105, sign test). Again, there was no detectable density dependence (r² = 0.083, P > 0.5) or seasonal pattern in the spacing of the centers of activity among S. cooperi individuals.

When the centers of activity for all individuals on the grid were combined for each season, overdispersion for the entire community was no more frequent than it was within a species. The combined species data sets were significantly overdispersed once on grid B and three times on grid D. Although this supports the results obtained with Cole’s index of interspecific association, because each occurrence of overdispersion in the two-species community coincided with overdispersion in one or both species alone (Table 3), these results may have been statistical artifacts of the within-species patterns.

Significantly more individuals than expected had conspecifics for nearest neighbors during winter 1972–73 on grid B and for both winters on grid D (Table 4). Only once were there significantly fewer individuals with conspecifics as nearest neighbors. This occurred during spring 1972 on grid D. In general, these results are compatible with those of Cole’s index and distances between centers of activity for the combined species data sets. However, there is one anomaly which occurred during autumn 1972 on grid B. This data set indicates a positive interspecific association with Cole’s index but shows nearest neighbors to be significantly biased towards conspecifics. The density of M. ochrogaster was exceedingly high at this time and the distance between individuals was less than half the distance between trap stations. At such high densities, there was little opportunity for S. cooperi to monopolize a trap station. This would bias the Cole’s index in a positive direction.

By combining the centers of activity for all seasons, each grid and species can be tested for less than expected distances between centers. This would indicate microhabitat selection if it can be safely assumed that microhabitat types were not temporally variable over the 2 years of the study. This assumption should be reasonable since most vegetation was perennial and should be relatively constant over this time span. The data for the 2 years were treated as a single block in which each individual had a single center of activity. The test is the same as the within-season tests already presented with the exception that the densities are much greater as they include all residents which existed over the entire 2-year period. The analysis shows evidence for microhabitat selection by M. ochrogaster on grid B only (Fig. 2). Voles on grid D, although underdispersed, did not differ significantly from random (P > 0.30). Underdispersion of centers indicates that several areas are consistently utilized more than expected by successive generations. S. cooperi did not exhibit evidence of microhabitat selection on either grid (Fig. 2).
Fig. 2.—Centers of activity of each *M. ochrogaster* and *S. cooperi* resident on grids B and D in at least one seasonal block. Each animal is represented by a single point, even if it occurred in more than one seasonal block. Over the entire 2 years, the ratio of the observed to expected distances between nearest centers for *M. ochrogaster* was 0.929 ($P < 0.03$) on grid B (A) and 0.979 ($P > 0.05$) on grid D (B). For *S. cooperi* the ratio was 1.04 ($P > 0.05$) on grid B (C) and 1.076 ($P > 0.05$) on grid D (D).

**Territoriality**

Metzgar and Hill's (1971) method of detecting territorial spacing behavior showed no evidence of strict territoriality in any season-grid combination for either species. However, this method will not detect the exclusive use of a defended central core area if the remainder of the home range is shared with neighboring animals.

**Discussion**

**Spacing within Species**

When centers of activity for *M. ochrogaster* on grid B were combined over the 2-year period, the species showed some indication of underdispersion (Fig. 2), yet within a season, the species tended to be overdispersed (Table 3). We have interpreted this to be a result of continual selection over time for relatively more desirable microhabitats. Though is was not apparent what factors may have dictated the selection of microhabitats, it seems likely that this selectivity reflects the distribution of resources on the grid. Intrasexual and intraspecific competition for such resources could result in the overdispersion we observed within seasons.
Linzey (1984) found *S. cooperi* to be more of a habitat generalist than the meadow vole *Microtus pennsylvanicus*. In her study, lemmings were frequently found in several types of habitats in addition to those preferred by meadow voles. Other studies have shown *S. cooperi* to be closely associated with mesic and shrubby habitats (Burt, 1948; Getz, 1961). Since bog lemmings were randomly dispersed when centers of activity were combined over the 2-year period, our results indicate that *S. cooperi* is more of a habitat generalist than *M. ochrogaster* on grid B.

Our results with the 10-week seasonal blocks indicate that individuals of both species are frequently overdispersed. There are three possible explanations for this overdispersion. First, if the species were selecting microhabitat patches and the preferred patches were uniformly distributed, overdispersion may occur (Brown and Orians, 1970; Waser and Wiley, 1979). Since overdispersion of nearest neighbors resulting from patch distribution implies there is one patch per individual per season, each cluster of centers of activity in Fig. 2 should be one patch which was occupied by sequential inhabitants. We cannot directly test for the number of clusters of centers of activity in Fig. 2, but by inspection, it seems unlikely that there are as many clusters as the minimum population size that occurred on the grid (Fig. 1). Hence, selection for overdispersed microhabitats is not a sufficient explanation of the observed pattern of overdispersion within a season.

Second, overdispersion may have been a function of the mating system of the species (Madison, 1980; Metzgar, 1980). Although nothing is known of *S. cooperi* mating systems, Thomas and Birney (1979) and Hofmann et al. (1984) have shown *M. ochrogaster* to be monogamous with both sexes exhibiting parental care. If the mating system of either species influenced dispersion patterns, we should have found a greater degree of underdispersion within each species as a result of male-female pairing in spring and autumn, when reproductive activity is higher, than in winter and summer (Gaines et al., 1977; Gaines and Rose, 1976). Within sexes, overdispersion may increase with breeding activity if males defend females or females defend nest sites. The observed results did not show these patterns although nearest neighbors were often of opposite sexes. Therefore, the mating system does not sufficiently account for the overdispersion observed in either species.

Third, overdispersion may have been a result of intraspecific competition (e.g., Brown and Orians, 1970; Smith, 1968; Waser and Wiley, 1979). Such a uniform dispersion pattern will minimize the risk of neighboring animals competing for available but limited resources, and will ensure that no pocket of resources will escape utilization. This explanation is compatible with the frequent overdispersion we observed in each species. However, we did not detect any evidence of territoriality with Metzgar and Hill’s (1971) method for detecting nonoverlapping territories as might be expected if resources could be defended in a manner which increases an individual’s fitness (Brown and Orians, 1970).

*Spacing between Species*

The effects of interspecific interactions are not easily dissected from intraspecific effects. However, the species did show a negative association as evidenced by Cole’s index and nearest neighbor preferences which are suggestive of interspecific competition. Interspecific competition for space has been shown in several species of microtines (e.g., Grant, 1969, 1970; Hansson, 1983; Koplin and Hoffmann, 1968; Linzey, 1984; Myllymaki, 1977). In these studies, the two competing species were usually segregated along some habitat gradient. In the absence of one species, the remaining species invaded the vacant habitat. However, *M. ochrogaster* and *S. cooperi* are not distributed along any observable gradient in eastern Kansas (Gaines et al., 1977; Rose and Spevack, 1978). Nevertheless, the negative association of the two species implies that each restricts the other’s use of otherwise useable habitat. This loss of access to resources could potentially have a negative effect on the fitnesses of those animals involved.

Two earlier studies of the populations on grids B and D found positive correlations between voles and lemmings for several demographic parameters (Gaines et al., 1977, 1979). However,
it can be misleading to interpret positive correlations between the demographic parameters of two ecologically similar species as evidence of no interspecific competition. Similarities between the two species which make them likely candidates for interspecific competition may also cause them to respond similarly to environmental factors such as vegetation quality, climatic events, and predation. Hence, a positive correlation between demographic parameters is not adequate to rule out competition as a factor in structuring the community. Furthermore, Gaines et al. (1979) did find a positive correlation between the population growth rate of *M. ochrogaster* and three measures of dispersal in *S. cooperi*. They suggested this may have been the result of the rapidly expanding vole population forcing lemmings out of habitat where the two species co-occurred.

Currently, there is considerable controversy surrounding the role of competition in structuring communities (e.g., Roughgarden, 1983; Strong, 1983). Competition is often difficult to detect (Schoener, 1983). Because there is so much variation in the mechanisms of competition and the communities in which competition may occur, there is no single protocol to test for competition (Roughgarden, 1983). Identifying and manipulating limiting resources are often impossible and the effects of the manipulation can be over-ridden by environmental variability (e.g., Brown and Batzli, 1985). Removal studies designed to detect competitive release are also subject to environmental variation between experimental and control populations, and the response to removals may be delayed for a long period of time (e.g., Brown and Munger, 1985). Although we did not experimentally manipulate our community, we suggest that the spatial patterns we observed in our analysis were most compatible with competition within as well as between species. Current experimentation on the effects of conspecific and heterospecific resident animals on colonization by dispersing voles and lemmings will provide a more detailed and mechanistic explanation of how this spatial structuring is created.

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LITERATURE CITED


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