Patterns of Coexistence in *Synaptomys Cooperi* and *Microtus Pennsylvanicus*

Author(s): Alicia V. Linzey

Source: *Ecology*, Vol. 65, No. 2 (Apr., 1984), pp. 382-393

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/1941401>

Accessed: 13/03/2014 09:45

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

PATTERNS OF COEXISTENCE IN *SYNAPTOMYS COOPERI* AND *MICROTUS PENNSYLVANICUS*¹

ALICIA V. LINZEY²

Department of Biology, Virginia Polytechnic Institute and State University,
Blacksburg, Virginia 24061 USA

Abstract. The microtine rodents *Synaptomys cooperi* and *Microtus pennsylvanicus* are sympatric, have similar life styles, and occur in the same general habitats. The object of this study was to determine the importance of competition in a *Microtus-Synaptomys* system in southwestern Virginia as a test of the general hypothesis that herbivorous rodents compete directly for space and indirectly for food.

The following patterns were observed: (1) Undisturbed populations of *Microtus* and *Synaptomys* exhibited microhabitat partitioning when coexisting in heterogeneous habitats that were marginal for *Microtus*. (2) In the presence of *Microtus*, *Synaptomys* microhabitats were characterized by significantly higher densities of deciduous trees and shrubs. (3) Disappearance of *Microtus* from some habitats during a population decline was accompanied by a shift of *Synaptomys* into areas formerly occupied by *Microtus*. Recolonization by *Microtus* resulted in a return to the previous pattern of microhabitat segregation. (4) Removal of *Microtus* from an experimental grid was followed by immediate colonization by *Synaptomys*. (5) One year following removal of *Synaptomys* from an experimental grid, most of the former *Synaptomys* habitat remained empty even though *Microtus* numbers were increasing. (6) Fecal analysis indicated that *Synaptomys* diet consisted largely of vegetation that is low in digestible nutrients (*Andropogon* in summer, moss in winter). Although *Microtus* ate *Andropogon*, this species included more dicotyledons and other monocotyledons in its diet. (7) When *Synaptomys* was living on a grid from which *Microtus* had been removed, similarity to food habits of *Microtus* previously living on the removal grid was much greater than on a grid where the two species coexisted in separate microhabitats (72 vs. 37%).

These results suggest that in the southern Appalachians, *Synaptomys* is excluded from preferred habitats by *Microtus* and, as a result, lives where cover is sparse and food is low in nutritional value. Although these species do compete, this competition is relaxed when *Microtus* populations decline. When given access to preferred habitats the food habits of *Synaptomys* change and resemble those of *Microtus*, suggesting that the ultimate limiting resource is food. The combination of wider habitat tolerances by *Synaptomys* and temporal variation in intensity of competition allows coexistence of these species on a regional basis.

Key words: competition; food habits; microhabitat; *Microtus*; *Synaptomys*.

INTRODUCTION

Many authors have considered competition a primary factor determining the structural organization of animal communities (Hutchinson 1957, Hairston 1964, Mac Arthur 1972, Schoener 1974). Either the historical role of competition or its contemporary action can account for present-day patterns of resource partitioning and community composition (Rosenzweig 1966, Rosenzweig and Sterner 1970, Grant 1972, Brown and Lieberman 1973, M'Closkey 1976, Brown 1978, Grant 1978). However, acceptance of resource partitioning as evidence for competition is weakened by the circular logic that partitioning must occur in order for similar species to coexist (Peters 1976, Connor and Simberloff 1979, Dunham 1980). Furthermore, competition may be intermittent or absent if unpredictable climatic variability prevents species' numbers from closely tracking resources (Menge and Sutherland 1976, Wiens 1977, Grant 1978, Rotenberry 1980), or if the population of one competitor undergoes wide fluctuations in density

(Blaustein 1980). When these variations occur asynchronously over a large geographic area, the result is a dynamic system within which competing species can coexist on a regional basis (Horn and Mac Arthur 1972, Slatkin 1974). If contemporary competition is important, then species' densities or resource use should differ over time, depending on whether a competitor is present or absent. This deduction forms the basis for the increasing emphasis on experimental approaches to competition (Inger and Greenberg 1966, Jaeger 1970, 1971, 1972, Grant 1972, Schroder and Rosenzweig 1975, Brown and Davidson 1977, Dunham 1980).

The microtine rodents *Synaptomys cooperi* and *Microtus pennsylvanicus* are sympatric species that are similar in size, appearance, and diet (herbaceous vegetation). While low population densities are typical of *Synaptomys* (Stegeman 1930, Blair 1948, Connor 1959), *Microtus* is often abundant and undergoes cyclic population fluctuations in suitable habitat (Krebs and Myers 1974). Interspecific competition, predicted because of similarities in life styles, should vary in intensity with temporal variation in *Microtus* density. In areas of geographic sympatry with *Microtus pennsylvanicus*, *Synaptomys cooperi* has been reported from sphagnum bogs, dense forests, sedge/grass marshes, recent clearcuts, sparsely grassed openings in both deciduous and

¹ Manuscript received 27 October 1981; revised 15 March 1983; accepted 22 March 1983.

² Present address: Department of Biology, Indiana University of Pennsylvania, Indiana, Pennsylvania 15705 USA.

coniferous forests, and upland fields (Howell 1927, Coventry 1937, Hamilton 1941, Hooper and Cady 1941, Poole 1943, Stewart 1943, Smyth 1946, Odum 1948, Richmond and Rosland 1949, Barbour 1951, Connor 1959, Getz 1961, West and Hutchison 1964, Linzey and Linzey 1968, Doult et al. 1973, Kirkland 1977). *Microtus* occurs in habitats with dense herbaceous ground cover, but avoids woodlands except at times of high population density (Eadie 1953, Mossman 1955, Getz 1967, 1970a, Grant 1972, Birney et al. 1976).

Demographic and behavioral studies in eastern Kansas suggest that *Synaptomys* is forced to disperse when *Microtus* undergoes rapid population increase (Rose and Spevak 1978, Gaines et al. 1979). These observations support suggestions that the occurrence of *Synaptomys* in diverse habitat types may be the result of competitive exclusion by *Microtus*, with *Synaptomys* being relegated to marginal *Microtus* habitat (Richmond and Rosland 1949, Doult et al. 1973).

This study investigated habitat use by *Microtus* and *Synaptomys* and tested the general hypothesis that herbivorous rodents compete directly for space and indirectly for food. I expected that: (1) *Microtus* and *Synaptomys* would exhibit microhabitat partitioning according to vegetational characteristics; (2) population fluctuations in *Microtus* would be accompanied by temporal variation in habitat use by *Synaptomys*; (3) experimental removal of *Synaptomys* would not significantly affect *Microtus* distribution; and (4) the diets of *Microtus* and *Synaptomys* would be more similar when they use similar microhabitat.

STUDY AREA

The study area was located east of Blacksburg (Montgomery County), Virginia, USA, on slopes above the North Fork of the Roanoke River at elevations between 518 and 533 m. Unless the land was cultivated or heavily grazed, the dominant plant species were eastern red cedar (*Juniperus virginiana*) and little bluestem (*Andropogon scoparius*). Infrequent pockets of deeper soils with relatively high water-holding capacity supported deciduous trees (primarily *Quercus*). A detailed description of the vegetation can be found in Linzey (1981). Although the underlying rock was limestone, outcrops were not a dominant feature, and these habitats were more similar to cedar glades of Wisconsin and Missouri than to the geographically nearer Tennessee glades (Quarterman 1950, Kucera and Martin 1957, Curtis 1959).

Specific sites (0.2-ha grids) were chosen after preliminary live-trapping and represented a range of habitat suitability. Four sites were located near or within the narrow ecotone between *Juniperus-Andropogon* and deciduous woodland; three of these were undisturbed throughout the study (Cedar Grids I, II, III); one was used for experimental removal of *Synaptomys* (*Synaptomys* Removal Grid). Small-mammal density was

comparatively low on these grids, the most frequently recorded species being *Synaptomys cooperi*, *Microtus pennsylvanicus*, *Peromyscus leucopus*, and *Blarina brevicauda*.

Two additional grids were located in an area with very few deciduous trees. These grids were 50 m apart and had similar aspect and slope, but were separated by a road and steep embankment. *Microtus* was ultimately removed from one grid (*Microtus* Removal), while the other served as a control (*Microtus* Control). Small-mammal density was higher than on the ecotonal grids, and before perturbation, species recorded included *Microtus pennsylvanicus*, *Peromyscus leucopus*, and *Blarina brevicauda*.

The seventh grid (Layne Field Grid) was in an abandoned pasture that supported a dense cover of introduced grasses, an abundance of forbs, and a scattering of large, widely spaced eastern red cedars. This habitat was bounded on three sides by a *Juniperus-Andropogon* association. *Microtus pennsylvanicus* occurred in moderate densities and was the only small mammal recorded on the grid.

MATERIALS AND METHODS

Mammal sampling

Mark and recapture studies extended from July 1978 to June 1979 on Cedar Grid I and from October 1978 to June 1979 on Cedar Grid II. Grids were staked at 5-m intervals and live-trapped each month for four consecutive nights; one small Sherman live trap was placed at each station. Live-trapping was inefficient because of low population density and poor recapture of *Synaptomys*. Unbaited dropping boards were used throughout the remainder of the study (Eadie 1948, Emlen et al. 1957, Linzey 1981). One board (1 × 6.5 × 15 cm) was placed near each grid station and one in the middle of each square formed by four stations (sampling interval ≈ 3 m). During a sampling period, 870 to 905 boards per grid were set for 10 d and checked at 2-d intervals (five times). At each check, droppings were identified and boards were cleared. Successful use of dropping board technique depends on accurate identification of droppings. Droppings of *Synaptomys* are distinctly green, blunt at both ends, and deposited singly; those of *Microtus* are brown or black, pointed at one end, and often deposited in adhering clusters (Burt 1928, Cockrum 1952, Connor 1959, Linzey 1981).

The relationship between frequency of board use and population size for *Microtus* was tested by conducting 10-d board surveys followed by 4-d live-trapping sessions ($n = 5$). Population size was estimated by minimum number known to be alive (Krebs 1966). Regression of number of board visits on population size (one board visit = one board with droppings during a 2-d interval) indicated that the two measures were highly correlated ($r = 0.90$, $y = 10.25x + 11.28$, $P < .05$). For *Synaptomys*, six animals (determined by removal trapping) visited 55 boards on one grid during a 10-d pe-

FIG. 1. Distribution of *Microtus* (○) and *Synaptomys* (●) on Cedar Grid I. A. July 1978–June 1979 (live-trap records); B. Summer 1979 (dropping boards); C. Summer 1980 (dropping boards). Size of symbol indicates number of records per station.

riod, and five animals (determined by mark-and-recapture trapping) visited 59 boards on a second grid. These points fell reasonably close to the *Microtus* regression line (71 and 61 boards predicted). The number of visits to dropping boards during a sample period was therefore used as an index of relative population densities both within and between species.

Spatial distribution of *Synaptomys* relative to *Microtus* was tested for nonrandomness by chi-square tests of heterogeneity based upon cumulative frequencies of occurrence at stations in six equal parts of each grid (Sokal and Rohlf 1969).

Vegetation analysis

Vegetation analyses were conducted on Cedar Grids I and II in an attempt to determine how the grids differed, because *Synaptomys* was a permanent resident on Cedar Grid I but only occurred on Cedar Grid II in the absence of *Microtus*. Variables reflecting density of ground cover, trees, and shrubs were selected on the basis of earlier research suggesting that these are important factors in habitat selection by *Microtus* and *Synaptomys* (Eadie 1953, Getz 1961, 1967, 1970b). All cover estimates were made during August at peak grass/forb development and again during winter when cover was minimal (between December and February). Tree/shrub counts were made during two summers (1979, 1980) and were completed before leaf fall. Sampling units were squares formed by grid stations (25 m²). Sampling intensity was 100% ($n = 78$) on Cedar Grid I and 33% ($n = 26$, randomly chosen) on Cedar Grid II.

Cover estimates were obtained by using a 0.5 × 1 m cover board divided into three vertical levels on both sides (0–25, 25–50, 50–10 cm), with each level marked off in equal units (M'Closkey and Fieldwick

1975, Schreiber et al. 1976). The board was placed vertically in the center of a grid square in a randomly chosen position. Percentage of area covered by vegetation at each level of the cover board was estimated for both sides of the board, and final values for each category were obtained by averaging the two sides. Distance from observer to board was standardized at 75 cm because on the grid with densest ground cover, this resulted in values consistently below 100%. This technique was designed primarily to quantify grass/forb cover and was less efficient as an estimator of tree/shrub density. Hence, direct counts of trees and shrubs in several height classes were also made on each sampled square. Shrub counts were based on numbers of vertical stems. When density of blackberries (including dewberries) and roses exceeded 100 stems/square, the square was assigned a value of 100 stems/square.

Statistical tests for normality indicated that nearly all variables showed significant skewness and/or kurtosis, although distributions of all variables were unimodal. Data were not transformed because of a preponderance of zero values for some variables. Discriminant-function analysis (DFA) was used as a statistical tool to distinguish groups of samples relative to habitat use by *Microtus* and *Synaptomys*. A stepwise routine (SPSS STEPWISE) selected variables that, in linear combination, contributed most to group separation (Nie et al. 1975). The criterion for entering variables was Wilk's lambda, with minimum $F = 1.0$ to enter for stepwise selection. The percentage of samples that would be assigned to the correct group based on the selected variables was subsequently determined.

DFA has been widely used by ecologists in recent years and is discussed in several publications (Cooley and Lohnes 1971, Green 1974, 1979, Dueser and Shugart 1978, 1979). Caution must be used in interpreting results of DFA if there are violations of assumptions of normality and homogeneity of within-group variance-covariance matrices. Since some data sets in the present analysis violate these assumptions, a formal test of the hypothesis of no difference in species' microhabitat is not statistically valid. Because of such problems, Green (1974) suggested that the validity of the discriminant function be judged by whether it has an ecologically meaningful and consistent interpretation. In this paper, DFA is used to detect those vegetation variables most likely to contribute to the discrimination of *Synaptomys* and *Microtus* habitat. These results are compared to differences in variable means to see if they allow consistent interpretations.

Analysis of food habits

For determination of food habits, droppings were collected during summer (July–September) and winter (November–January) and were examined microscopically using modifications of techniques developed by Baumgartner and Martin (1939), Dusi (1949), Williams (1962), and Hansson (1970). All fecal material

TABLE 1. Number of visits to dropping boards during a single 10-d sample period (boards cleared every 2 d). Sampling intensity is given in parentheses as number of board units (one board unit = one board set for 2 d). Dashes indicate when sampling was not conducted.

Grid	Species	Summer 1979	Fall 1979	Winter 1979-1980	Spring 1980	Summer 1980
Cedar I (880)	<i>Microtus</i>	0	18	2	12	27
	<i>Synaptomys</i>	59	11	6	27	24
Cedar II (870)	<i>Microtus</i>	4	...	9	1	7
	<i>Synaptomys</i>	40	...	8	2	10
Cedar III (905)	<i>Microtus</i>	5	26	17	2	21
	<i>Synaptomys</i>	52	36	26	6	14
Layne Field (905)	<i>Microtus</i>	444	...	127	473	360
	<i>Synaptomys</i>	0	...	0	0	0
<i>Microtus</i> removal (905)	<i>Microtus</i>	55	...	97	<i>Microtus</i> removed	19
	<i>Synaptomys</i>	0	...	3		27
<i>Microtus</i> control (905)	<i>Microtus</i>	...	...	...	...	47
	<i>Synaptomys</i>	...	...	...	...	3
<i>Synaptomys</i> removal (880)	<i>Microtus</i>	14	<i>Synaptomys</i> removed	...	...	43
	<i>Synaptomys</i>	55		...	...	7

was obtained from dropping boards except for winter samples of *Microtus* from Cedar Grid I, which were collected from trapped animals. In this case, only droppings from the first capture of a given individual were used. Freshly collected droppings were oven-dried for 24 h at 70°C and stored until processing.

To prepare samples for analysis, 10 droppings per sample were rehydrated and ground to form a water suspension. Several drops of the suspension were spread evenly over a slide and ten randomly chosen fields were examined microscopically. Ten slides were prepared for each locality and season. Plant remains were assigned to the following categories: *Andropogon*, other monocot, dicot, or moss. Because of differential digestibility, fecal samples probably overestimate moss and monocotyledon content of the diet and underestimate forbs (Batzli and Pitelka 1971). However, the bias should be consistent for both species of microtines so that comparisons of diets can still be made.

The frequency of fields in which a given food item occurred was converted to density per field, using a table developed by Fracker and Brischle (1944), and then to relative density. For this conversion to be fully valid, plant fragments must be randomly distributed over the slide and the density of fragments must be such that the most common species does not occur in >86% of fields (Sparks and Malechek 1968). The second requirement could not be met for all samples because *Andropogon* occurred so frequently in *Synaptomys* droppings that procedural adjustments to lower its density resulted in virtual elimination of other plant remains. Degree of dietary similarity was calculated using proportional similarity (simplification of Pielou 1975):

$$PS = \sum p_{\min}$$

where $p_{\min}$ was the smaller percentage of a food category in the two diets.

RESULTS

Microdistribution on undisturbed grids

Microdistribution of *Microtus* and *Synaptomys* on Cedar Grid I during mark-and-recapture studies is shown in Fig. 1A. Eight *Microtus* individuals were trapped in 39 captures and six *Synaptomys* were trapped in 16 captures over a 1-yr period (5894 trap nights). Distributions did not vary seasonally. *Microtus* ranged diagonally across the center of the grid, *Synaptomys* occurred in the lower portion and along the left edge, and the upper portion was avoided by both species. *Synaptomys* visited 13% of the 98 trap stations, *Microtus* visited 19%, and 2% were visited by both species (not in the same month). In a given month, a maximum of four *Microtus* (17 individuals/ha) and two *Synaptomys* (8 individuals/ha) were captured. Neither species was taken from February-June, although fresh *Synaptomys* sign was noted throughout the spring months.

Dropping boards were initiated in July 1979 and, although *Microtus* was not recorded on Cedar Grid I during spring and summer 1979, this species was present during fall sampling and throughout the remainder of the study (Table 1). The 7-mo disappearance of *Microtus* from Cedar Grid I coincided with the low-density phase of a 4-yr population cycle in the Blacksburg area. On a permanent live-trap grid, *Microtus* numbers peaked in October 1978 at 398 individuals/ha and declined to 27 individuals/ha in March 1979 (J. A. Cranford, *personal communication*). In the absence of *Microtus*, *Synaptomys* visited 25% of the 176 board stations, and its range shifted to include virtually all of the former *Microtus* range (Fig. 1B). By October, *Microtus* recolonized its former range and *Synaptomys* was again located primarily in the lower portion and along the left edge of the grid. This microdistributional pattern persisted through the end of the study (Fig. 1C). In summer 1980, 8 and 11% of board stations

FIG. 2. Distribution of *Microtus* (O) and *Synaptomys* (●) on Cedar Grid II. A. October 1978–June 1979 (live-trap records); B. Summer 1979 (dropping boards); C. Summer 1980 (dropping boards). Size of symbol indicates number of records per station.

were visited by *Synaptomys* and *Microtus*, respectively, and no sampling stations recorded both species. *Synaptomys* records (data of Fig. 1A and C) tended to occur at stations without *Microtus* records ($\chi^2 = 56.5$, 5 df, $P < .001$).

Live-trapping on Cedar Grid II resulted in 49 *Microtus* captures, including 13 individuals, and 2 *Synaptomys* captures, representing 2 individuals (4000 trap nights) (Fig. 2A). There were up to 6 *Microtus* (30 individuals/ha) present in a given month, with most *Microtus* captures occurring between October and March. *Synaptomys* was first recorded in late spring at a peripheral grid station. *Microtus* visited 22% of the 98 trap stations, *Synaptomys* visited 2%, and 1% were visited by both species (not in the same month). During summer 1979, when *Microtus* numbers had declined in the general area, dropping board records indicated that *Synaptomys* was evenly distributed over the grid except for areas of poor cover associated with a rock outcrop and dense tree canopy (Fig. 2B). *Synaptomys* visited 18% of the stations, while *Microtus* visited 2%.

Two percent were visited by both species, although not during a single 2-d period. Sparse records for the remainder of the study (Table 1) apparently reflected slow recovery of populations from low winter density. By summer 1980, *Microtus* had only recolonized one edge of the grid and *Synaptomys* was scattered throughout the remainder (Fig. 2C). *Synaptomys* and *Microtus* visited 8 and 4% of board stations, respectively. One percent of stations were visited by both species, although not during a single 2-d period. Statistical tests indicated that *Synaptomys* visited grid stations different from those frequented by *Microtus* ($\chi^2 = 14.8$, 5 df, $P < .05$).

Initial board sampling on Cedar Grid III during summer 1979 indicated that *Synaptomys* occurred over much of the grid, but avoided local areas where ground cover was poor (Fig. 3A). *Synaptomys* visited 20% of the 181 board stations, while *Microtus* visited 2%. One station (0.5%) was visited by both species, although not in the same 10-d period. As *Microtus* records increased through fall and winter (Table 1), there was an intermingling of stations visited by the two species. A distributional shift of *Synaptomys* did not occur until summer 1980 (Fig. 3B). By this time, *Microtus* occurred over a large portion of the grid, while (except for one station) *Synaptomys* had withdrawn to the right half. *Synaptomys* and *Microtus* visited 7 and 9% of board stations, respectively. Three stations (2%) were visited by both species, although not within a 2-d period. *Synaptomys* distribution was significantly different from that of *Microtus* during summer 1980 ($\chi^2 = 11.4$, 5 df, $P < .05$).

The Layne Field Grid had moderate densities of *Microtus*, even during the low phase of the population cycle (Table 1). Live-trapping during two summers (1979–1980, 450 trap nights each) revealed densities varying from 120–190 *Microtus*/ha. Fewer winter board visits may have partially reflected technical problems, because large numbers of slugs frequented the boards and may have consumed all droppings on some boards. During the summer of 1979 (population low), *Microtus*

FIG. 3. Distribution of *Microtus* (O) and *Synaptomys* (●) on Cedar Grid III (dropping boards). A. Summer 1979; B. Summer 1980. Size of symbol indicates number of records per station.

showed no obvious microhabitat preference in this homogeneous habitat, and 90% of 181 board stations were visited during a 10-d sample period. *Synaptomys* was never recorded.

Vegetation analysis

Comparisons of means for vegetation variables (summer) on Cedar Grids I and II indicated that Cedar Grid II had significantly greater numbers of deciduous trees (height-classes <1 m, 1–4 m) and shrubs (*Rubus/Rosa* <0.5 m; other shrubs <0.5 m, >0.5 m) (Table 2). This suggested that the deciduous tree/shrub component on Cedar Grid I served as a refugium for *Synaptomys* and enabled *Microtus* and *Synaptomys* to co-exist on the grid. Coexistence was not possible on Cedar Grid II where this component was lacking.

Vegetation data from Cedar Grid I were used to characterize microhabitat use at times when *Microtus* and *Synaptomys* coexisted on the grid and when *Synaptomys* occurred alone (Table 3). Analyses were based on summer distributions of microtines and vegetation, as animal records in winter were insufficient to define ranges.

When both species were present on the grid, squares visited by the two microtines differed only in that *Synaptomys*' range included higher densities of deciduous trees and shrubs (other than *Rubus/Rosa*). Squares not occupied by either species (nonrange) had significantly less grass cover, but were generally similar to *Synaptomys* squares in regard to shrub and tree cover.

DFA was used to determine which variables were most important in distinguishing squares within *Microtus* microhabitat from squares within *Synaptomys* microhabitat (Table 4). Eight parameters contributed to the discriminant function; one of these had means that were significantly different (deciduous trees 1–4 m, Table 3). All discriminating variables except one (grass 26–50 cm) were measures of tree/shrub abundance and were higher on *Synaptomys* squares. The power of discriminating functions can be tested by determining their accuracy in predicting whether squares should be assigned to *Microtus* or *Synaptomys* microhabitat. A high percentage of squares were correctly classified (81.4%), with a slightly higher accuracy for *Microtus* (84%) than for *Synaptomys* (78%) (Table 4).

During the absence of *Microtus* from Cedar Grid I, *Synaptomys* microdistribution shifted to include most of former *Microtus* range (Fig. 1). Comparison of means for *Synaptomys* microhabitat with and without *Microtus* present indicates that *Synaptomys* chose areas with denser grass/forb cover and fewer trees and shrubs when living alone on this grid (Table 3). Furthermore, means for *Synaptomys* microhabitat without *Microtus* were not significantly different from *Microtus* microhabitat (t test, $P > .05$). Results of DFA comparing *Synaptomys* microhabitat with *Microtus* present to *Synaptomys* microhabitat without *Microtus* indicated that six variables contributed to the discrimination be-

TABLE 2. Comparison of habitat variables on Cedar Grids I and II in summer. Significant differences between sample estimates of the mean (standard error in parentheses) are indicated by an asterisk (t test, $P < .05$). n = number of squares sampled.

Vegetation variables	Cedar I ($n = 78$)	Cedar II ($n = 26$)
% cover		
0–25 cm high		
Grass	53.7 (3.34)	56.4 (4.61)
Forbs	3.4 (0.47)	5.4 (1.24)
Shrubs	3.1 (0.56)	1.2 (0.40)
Trees*	2.2 (0.53)	5.5 (1.71)
26–50 cm high		
Grass	5.1 (0.66)	4.6 (1.20)
Forbs	1.4 (0.28)	2.2 (0.48)
Shrubs	3.2 (0.70)	1.4 (0.36)
Trees*	3.6 (0.73)	11.8 (2.49)
51–100 cm high		
Grass	0.2 (0.04)	0.1 (0.03)
Forbs	0.4 (0.18)	0.3 (0.12)
Shrubs	1.0 (0.46)	0.1 (0.06)
Trees*	6.8 (1.06)	14.7 (2.40)
Numbers per 25 m ²		
Trees		
<1 m high		
Deciduous*	13.0 (1.93)	1.5 (0.34)
Evergreen*	10.2 (1.09)	29.6 (3.16)
1–4 m high		
Deciduous*	8.0 (2.00)	0.0 (0.04)
Evergreen*	6.4 (0.57)	19.9 (2.27)
>4 m high		
Deciduous	0.2 (0.09)	0.0 (0.00)
Evergreen	1.2 (0.12)	1.8 (0.40)
Shrubs		
<0.5 m high		
<i>Rubus/Rosa</i> *	94.6 (1.55)	62.8 (9.12)
Other*	15.1 (3.27)	0.6 (0.24)
>0.5 m high		
<i>Rubus/Rosa</i>	0.6 (0.34)	0.5 (0.24)
Other*	6.1 (1.72)	1.0 (0.33)

tween groups (Table 5). With one exception (grass 26–50 cm), all these variables measured densities of trees and shrubs, which were present in lesser quantities in squares preferred by *Synaptomys* in the absence of *Microtus* (Table 3). Accuracy of classification was higher for *Synaptomys* microhabitat without *Microtus* (85%) than for *Synaptomys* microhabitat with *Microtus* (72%) (Table 5), indicating that squares preferred by *Synaptomys* in the absence of *Microtus* exhibit less variability.

Microtus removal experiment

Microtus Removal and *Microtus* Control grids were trapped prior to board sampling (860 trap nights) and the only microtine captured was *Microtus* (winter density on Removal Grid 50 *Microtus*/ha; population density not determined on Control Grid). Before removal,

TABLE 3. Sample estimates of the means and standard errors (in parentheses) for vegetation variables in the microhabitats of *Microtus* and *Synaptomys* on Cedar Grid I. *n* = number of grid squares. Means in each row not differing significantly are designated by the same letter (Duncan's Multiple Range Test, *P* > .05). Asterisks indicate significant differences between *Synaptomys* habitat choices with and without *Microtus* (*t* test, *P* < .05).

Vegetation variables	With <i>Microtus</i>			Without <i>Microtus</i>
	<i>Synaptomys</i> (<i>n</i> = 18)	<i>Microtus</i> (<i>n</i> = 25)	Nonrange (<i>n</i> = 39)	<i>Synaptomys</i> (<i>n</i> = 34)
% cover				
0–25 cm high				
Grass	^a 63.7 (6.91)	^a 69.9 (4.51)	^b 41.7 (4.41)	66.3 (4.21)
Forbs	^a 2.2 (0.69)	^a 2.8 (0.60)	^a 4.0 (0.80)	4.0 (0.83)
Shrubs	^a 1.9 (0.66)	^a 1.8 (0.47)	^a 4.1 (1.02)	1.7 (0.36)
Trees	^a 3.6 (1.28)	^a 1.2 (0.62)	^a 2.5 (0.83)	1.8 (0.79)
26–50 cm high				
Grass	^a 8.4 (1.57)	^a 8.3 (1.27)	^b 2.1 (0.46)	7.7 (1.12)
Forbs	^a 1.3 (0.32)	^a 1.2 (0.28)	^a 1.5 (0.50)	1.8 (0.56)
Shrubs	^a 1.9 (0.54)	^a 3.9 (1.51)	^a 3.1 (1.00)	2.6 (0.96)
Trees	^a 5.1 (1.85)	^a 2.5 (1.22)	^a 4.0 (1.03)	3.2 (1.11)
51–100 cm high				
Grass	^{ab} 0.3 (0.10)	^a 0.4 (0.09)	^b 0.1 (0.02)	0.3 (0.07)
Forbs	^a 0.4 (0.21)	^a 0.1 (0.08)	^a 0.5 (0.35)	0.5 (0.40)
Shrubs	^a 0.1 (0.14)	^a 1.4 (1.01)	^a 1.1 (0.63)	1.4 (0.97)
Trees	^a 8.7 (2.80)	^a 6.6 (1.65)	^a 7.1 (1.49)	6.9 (1.64)
Numbers per 25 m ²				
Trees				
<1 m high				
Deciduous	^a 11.9 (5.19)	^a 6.4 (0.70)	^a 17.1 (2.84)	10.3 (1.65)
Evergreen	^a 10.7 (1.90)	^a 9.6 (1.18)	^a 10.7 (1.89)	9.5 (1.26)
1–4 m high				
Deciduous	^a 19.1 (7.38)	^b 1.9 (0.59)	^b 6.0 (1.60)	*2.8 (0.80)
Evergreen	^a 8.2 (1.55)	^a 7.1 (1.10)	^a 6.1 (0.81)	7.0 (0.73)
>4 m high				
Deciduous	^a 0.3 (0.16)	^a 0.0 (0.00)	^a 0.3 (0.16)	0.1 (0.04)
Evergreen	^a 1.7 (0.25)	^b 0.9 (0.23)	^{ab} 1.1 (0.15)	1.1 (0.19)
Shrubs				
<0.5 m high				
<i>Rubus/Rosa</i>	^a 89.4 (4.02)	^a 93.8 (2.74)	^a 94.9 (2.34)	94.7 (2.54)
Other	^{ab} 17.6 (7.43)	^b 3.1 (0.55)	^a 19.9 (5.36)	*3.2 (0.62)
>0.5 m high				
<i>Rubus/Rosa</i>	^a 0.2 (0.10)	^a 1.0 (1.04)	^a 0.3 (0.13)	0.8 (0.71)
Other	^a 5.7 (3.66)	^a 2.4 (0.55)	^a 8.0 (2.94)	1.6 (0.34)

frequency of *Microtus* visits to dropping boards on the Removal Grid was moderately high (Table 1). A composite of two 10-d board samples in summer and winter 1979 indicated that *Microtus* distribution was fairly uniform, although there were fewer visits to boards in areas on the right edge of the grid where forb cover dominated (Fig. 4A). Forty-seven percent of the 181 board stations were visited by *Microtus* (23% summer, 39% winter). In December, three stations (2%) on the edge of the grid were visited by *Synaptomys*. During March, 15 *Microtus* were removed from the grid and 23 from a buffer zone around the grid (900 trap nights). Four *Synaptomys* were captured, marked, and released during removal trapping in the buffer zone. Periodic board monitoring and additional trapping every few weeks throughout the spring months indicated that few

Microtus had recolonized the grid and that *Synaptomys* was visiting boards at stations well within grid boundaries.

A simultaneous 10-d board survey of the *Microtus* Removal and Control grids was conducted during late June. On the Removal Grid, *Synaptomys* records were concentrated toward the center and nonexistent in the areas of heavy forb cover (Fig. 4B). *Microtus* was not recorded on the Removal Grid during the 1st 6 d of the sampling period. Extremely heavy rain on the 6th d resulted in a rapid rise of water level in a low wet area below the grid and caused local movement of *Microtus*. By the 8th d, *Microtus* visited boards in the lower sector of the grid, and by the 10th d scattered records extended across the grid. During the 10-d sample, 13 and 10% of the 181 board stations were visited

by *Synaptomys* and *Microtus*, respectively. On the *Microtus* Control Grid, the number of board visits by *Microtus* (47) was similar to the number recorded on the Removal Grid the previous summer (55) (Table 1). While 13% of board stations on the Removal Grid were visited by *Synaptomys* after *Microtus* removal, only 1% were visited by this species on the Control Grid (Fig. 4C). These results indicate that *Synaptomys* will colonize *Microtus* habitat if *Microtus* has been removed.

Synaptomys removal experiment

Cedar Grids I and III were most similar in vegetation structure to the *Synaptomys* Removal Grid and served as controls for this experiment. Sampling on the Removal Grid during summer 1979 (before removal) indicated that *Synaptomys* numbers were approximately the same on Removal and Control grids, but that *Microtus* were more abundant on the Removal Grid than on the Control Grids (Table 1). *Synaptomys* ranged over most of the grid, but avoided a corner where *Microtus* records were concentrated (Fig. 5A). *Synaptomys* and *Microtus* visited 21 and 7% of the 176 board stations, respectively.

Synaptomys was removed during fall 1979, and by summer 1980, two individuals had recolonized a moss bed at one corner of the grid (Fig. 5B). The density and distribution of *Microtus* increased somewhat by summer 1980, with 14% of board stations visited during a 10-d sample period. However, most of *Synaptomys* former range remained unoccupied. An additional 10-d sample in January–February 1981 (880 board units) indicated that this distributional pattern was stable.

TABLE 4. Summary of stepwise discriminant-function analysis comparing squares in *Synaptomys* and *Microtus* microhabitat on Cedar Grid I during co-occurrence. Absolute values of standardized coefficients are proportional to the contribution of each variable to the separation of the groups.

Eigenvalue	1.02568		
Chi-square statistic	26.1		
Significance	0.001		
Degrees of freedom	8		
Variable	Standardized DF coefficient		
Shrub 0–25 cm	0.51593		
Grass 26–50 cm	0.74632		
Tree 26–50 cm	0.40132		
Deciduous trees 1–4 m	0.61268		
Evergreen trees 1–4 m	0.53558		
Deciduous trees >4 m	0.66879		
Evergreen trees >4 m	0.89898		
Shrubs (other than <i>Rubus/Rosa</i>) >0.5 m	0.36251		
Classification matrix			
Predicted group membership			
Actual group	<i>n</i>	<i>Synaptomys</i>	<i>Microtus</i>
<i>Synaptomys</i>	18	14 (78%)	4 (22%)
<i>Microtus</i>	25	4 (16%)	21 (84%)

TABLE 5. Summary of stepwise discriminant analysis comparing *Synaptomys* microhabitat with *Microtus* present, to *Synaptomys* microhabitat without *Microtus* on Cedar Grid I. Absolute values of standardized coefficients are proportional to the contribution of each variable to the separation of the groups.

Eigenvalue	0.75110
Chi-square statistic	26.3
Significance	0.0002
Degrees of freedom	6

Variable	Standardized DF Coefficient
Grass 26–50 cm	0.608
Deciduous trees 1–4 m	0.944
Evergreen trees 1–4 m	0.555
Deciduous trees >4 m	0.455
Evergreen >4 m	0.618
Shrubs (other than <i>Rubus/Rosa</i>) >0.5 m	0.446

Classification matrix

		Predicted group membership	
		<i>Synaptomys</i> with <i>Microtus</i>	<i>Synaptomys</i> without <i>Microtus</i>
Actual group	<i>n</i>		
<i>Synaptomys</i> with <i>Microtus</i>	18	13 (72%)	5 (28%)
<i>Synaptomys</i> without <i>Microtus</i>	34	5 (15%)	29 (85%)

Food habits analysis

Diets of *Microtus* and *Synaptomys* were examined to test the hypothesis that exclusion of *Synaptomys* from habitats preferred by *Microtus* reduces competition for food. If this hypothesis is correct, dietary overlap of *Synaptomys* and *Microtus* would be greater when the species are not competing for space (*Microtus* absent) than when competing (*Microtus* present). Thus, overlap should be greater between *Microtus* from the summer before removal and *Synaptomys* from the summer after removal (living in the same microhabitat) than between the two species on Cedar Grid I where they coexist in separate microhabitats.

Fecal analysis indicated that *Synaptomys* fed primarily on *Andropogon* in summer, while *Microtus* ate considerable quantities of other monocots and dicots (Table 6). While moss was always part of the diet of *Synaptomys* (especially on Cedar Grid I), it was only eaten by *Microtus* during winter, and then to a lesser extent than by *Synaptomys*. During summer, *Synaptomys* inhabiting the *Microtus* Removal Grid (after *Microtus* removal) had a more diverse diet than individuals living on Cedar Grid I and consumed considerably more of other monocots, although *Andropogon* remained the dominant food. In winter, *Andropogon* became a minor *Synaptomys* food, and mosses became a major food item. Other monocots (rare on Cedar Grid I) also became a major food item on the *Microtus* Removal Grid. In contrast, *Microtus* consumed more *Andropogon*, fewer other monocots

FIG. 4. Distribution of *Microtus* (○) and *Synaptomys* (●). A. *Microtus* Removal Grid (dropping boards) in summer 1979 and winter 1980 (before *Microtus* removal); B. *Microtus* Removal Grid in June 1980 (after *Microtus* removal); C. *Microtus* Control Grid in June 1980. Size of symbol indicates number of records per station.

and forbs, and, on Cedar Grid I, much more moss during winter.

Microtus diets on the *Microtus* Removal Grid and Cedar Grid I were very similar during summer ($PS = 78\%$) despite quantitative differences in availability of food items. On Cedar Grid I, coexisting *Microtus* and *Synaptomys* had relatively low dietary overlap during summer ($PS = 37\%$). On the *Microtus* Removal Grid, the diet of *Microtus* during summer 1979 was very similar to *Synaptomys* during summer 1980 (*Microtus* absent) ($PS = 72\%$). Thus, summer food habits data support the hypothesis that exclusion of *Synaptomys* from preferred living space reduces competition for food.

In winter, dietary shifts by both species reduced the extent of dietary overlap slightly on Cedar Grid I ($PS = 29\%$) and dramatically on the *Microtus* Removal Grid ($PS = 30\%$). If competition for food is the ultimate cause of habitat partitioning, more overlap in habitat use might be expected during winter than summer. However, winter data are too few to evaluate this possibility.

DISCUSSION

Synaptomys and *Microtus* are sympatric over much of their geographic distributions and may occur in the same general habitats, but they seldom co-occur on a microhabitat scale in southwestern Virginia. My observations and experiments support the hypothesis that these herbivores compete for space. First, where these species coexisted in *Juniperus-Andropogon* habitats, *Synaptomys* occupied microhabitats with greater numbers of deciduous trees and shrubs, patchier grass cover, and more leaf litter and mosses. *Synaptomys* did not coexist with *Microtus* in *Juniperus-Andropogon* habitats that lack the deciduous tree/shrub component. These results suggest that on a larger geographic scale, sparsely grassed woodlands are the primary habitat for *Synaptomys* in the eastern United States. Colonization by *Synaptomys* of man-made clearings within exten-

sive forested areas (Barbour 1951, Kirkland 1977) is consistent with this view, as is the capture of *Synaptomys* in forested habitats (Coventry 1937, Hamilton 1941) and in shrubby areas within bogs and grasslands (Connor 1959, Getz 1961, Gaines et al. 1977, Rose and Spevak 1978). A common feature of these habitats is that *Microtus* is sparse or absent.

Second, expansion of the *Synaptomys* niche following natural population decline of *Microtus*, as well as after experimental removal of *Microtus*, indicates that microhabitat partitioning in ecotonal areas is due to active competition that varies temporally in intensity. Furthermore, retreat of *Synaptomys* to the tree/shrub habitat component when *Microtus* returned indicates that occupation of woodland habitats by *Synaptomys* is not due to preference, but to competitive exclusion by *Microtus* from adjacent grasslands.

My data do not indicate whether the colonization of former *Microtus* microhabitat by *Synaptomys* results from dispersal of young, a microdistributional shift of adults, or a combination of both factors. On Cedar Grid I, it appeared that the microhabitat of *Synaptomys* shifted rather than expanded because some formerly occupied locations were vacated (Fig. 1). Also, colonization of the *Microtus* Removal Grid by *Synaptomys* (Fig. 4) occurred very quickly and probably represented a shift by extant animals. Other studies have recorded similar immediate responses of small mammals to vacant territories (Schroder and Rosenzweig 1975, Blaustein 1980). Wiens (1977) suggested that density fluctuations on small plots often reflect local or regional redistribution of individuals rather than actual changes in numbers. However, Blaustein (1980) noted increased numbers of pregnant and lactating *Mus* and *Reithrodontomys* during a 7-mo period following a *Microtus* population crash, which suggests a long-term numerical response.

Habitats with dense populations of *Microtus* (Layne Field Grid) are probably not used by *Synaptomys*. Opportunistic use of *Juniperus-Andropogon* habitats by

Synaptomys is possible because these habitats support relatively low densities of *Microtus*, even where *Andropogon* forms dense mats. The poor quality of *Juniperus-Andropogon* habitats for *Microtus* probably results from the fact that *Andropogon* is a poor food. In laboratory feeding experiments with *Andropogon*, *Microtus ochrogaster* lost mass rapidly and died within a week (Cole and Batzli 1979). The ability of *Microtus* to occupy *Andropogon* habitats in southwestern Virginia may be dependent on the presence of forbs, which are higher in nutrient content than grasses (Keys and Van Soest 1970, Cole and Batzli 1979). On Cedar Grid I, for example, forbs constituted the largest portion of the diet (Table 6), even though they were a very sparse vegetational component (Table 2). Greater reliance on *Andropogon* during winter may reflect lower quality of other available forage and may be related to decreased breeding.

Comparison of food habits supported the hypothesis that the ultimate object of competition between *Microtus* and *Synaptomys* was food. *Synaptomys* diet became more diversified when living alone in preferred habitat (*Microtus* Removal Grid), which suggests that *Microtus* kept *Synaptomys* from some foods. However, *Synaptomys* did not abandon its apparent preference for *Andropogon*, which is puzzling because laboratory feeding trials indicated that both *Microtus* and *Synaptomys* lost mass when fed *Andropogon* (Linzey 1981). During these trials, *Synaptomys* did eat more *Andropogon* and lose less mass. Unlike *Microtus*, *Synaptomys* on the *Microtus* Removal Grid in winter fed heavily

TABLE 6. Relative densities of food items (see Methods: Analysis of Food Habits) in the diets of *Microtus* and *Synaptomys* during summer and winter ($n = 10$ slides for all samples).

	<i>Andropogon</i>	Other mono-cot	Dicot	Moss
Summer				
<i>Synaptomys</i>				
<i>Microtus</i> Removal Grid (after removal, 1980)	74.1	18.9	5.3	1.6
Cedar Grid I (1980)	88.5	0.9	0.0	10.5
<i>Microtus</i>				
<i>Microtus</i> Removal Grid (before removal, 1979)	48.3	34.8	16.8	0.0
Cedar Grid I (1980)	36.3	25.3	38.4	0.0
Winter				
<i>Synaptomys</i>				
<i>Microtus</i> Removal Grid (after removal, 1979–1980)	14.7	41.8	1.8	41.8
Cedar Grid I (1979–1980)	7.2	8.3	7.1	77.3
<i>Microtus</i>				
<i>Microtus</i> Removal Grid (before removal, 1979)	84.4	13.5	1.7	0.4
Cedar Grid I (1978)	41.4	15.0	19.1	24.4

ly on moss, which further indicates different nutritional adaptations.

Field and laboratory studies on *Microtus ochrogaster* and *Synaptomys* suggest that behavioral interactions may be important in maintaining microhabitat segregation. Rose and Spevak (1978) found that *Microtus ochrogaster* was dominant to *Synaptomys*. Field data from the same area of Kansas indicated that dispersal of *Synaptomys* increased as population density of *Microtus* increased (Gaines et al. 1979). Since *Microtus pennsylvanicus* is considerably larger and more abundant than *Synaptomys* in the southern Appalachians, defense of living space by *Synaptomys* against its more numerous antagonist would be costly in terms of time and energy. Under these circumstances *Synaptomys* would be expected to withdraw to microhabitats that are unacceptable to *Microtus*. The fact that *Synaptomys* microdistribution changed with population density of *Microtus* suggests that frequency of contact (Terman 1974) is the critical factor maintaining spatial distribution. As numbers of *Microtus* increase and contact frequency exceeds a critical level, *Synaptomys* is displaced.

The ability of *Synaptomys* to live in habitats and eat foods that are only marginally acceptable to *Microtus* and to expand its habitat and diet in the absence of *Microtus* indicates that *Synaptomys* is a generalist compared with *Microtus*. Apparently, the fundamental niche of *Synaptomys* includes that of *Microtus*, but the realized niche is considerably narrower due to inter-

FIG. 5. Distribution of *Microtus* (O) and *Synaptomys* (●) on *Synaptomys* Removal Grid (dropping boards). A. Summer 1979 (before *Synaptomys* removal); B. Summer 1980 (after *Synaptomys* removal). Size of symbol indicates number of records per station.

ference competition (Miller 1967, Grant 1972). This conclusion is consistent with the observation that when interference competition occurs between generalist and specialist species, the specialist usually prevents access by the generalist (Colwell and Fuentes 1975).

Criticisms regarding the relevance of competition in temporally variable environments (Wiens 1977, Rotenberry 1980) seem most justified when environments (or competing species) vary in an unpredictable fashion. When environments and populations of competitors vary in a predictable rhythm (seasonal or multi-year), closer tracking of animal densities to resources would be expected. Furthermore, behavioral interactions may be such that competing species are excluded before resources become directly limiting. Thus, the local distribution of animals may be determined by competitive interactions, even if populations do not reach equilibrium levels.

ACKNOWLEDGMENTS

This work was done in partial fulfillment of requirements for the degree of Doctor of Philosophy in the Department of Biology, Virginia Polytechnic Institute and State University. I am pleased to acknowledge the guidance of doctoral committee members Jack A. Cranford (Chairman), Robin M. Andrews, W. Carter Johnson, Alan R. Tipton, and Robert A. Paterson, and the support of my family and fellow graduate students. Robert K. Rose of Old Dominion University graciously reviewed an earlier version of the manuscript. Valuable assistance was provided by Statistical and Computer Consulting Services at Virginia Tech. This work was supported by Grants-in-Aid from Sigma Xi and the Theodore Roosevelt Fund, American Museum of Natural History, as well as by Grant Number 203-11-110-372-949-1 (United States Department of the Interior) to J. A. Cranford.

LITERATURE CITED

- Barbour, R. W. 1951. The mammals of Big Black Mountain, Harlan County, Kentucky. *Journal of Mammalogy* 32:100–110.
- Batzli, G. O., and F. A. Pitelka. 1971. Condition and diet of cycling populations of the California vole, *Microtus californicus*. *Journal of Mammalogy* 52:141–163.
- Baumgartner, L. L., and A. C. Martin. 1939. Plant histology as an aid in squirrel food-habits studies. *Journal of Wildlife Management* 3:266–268.
- Birney, E. C., W. E. Grant, and D. D. Baird. 1976. Importance of vegetative cover to cycles of *Microtus* populations. *Ecology* 57:1043–1051.
- Blair, F. 1948. Population density, life span, and mortality rates of small mammals in the bluegrass meadow and bluegrass field associations of southern Michigan. *American Midland Naturalist* 40:395–419.
- 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.
- Brown, J. H. 1978. Effects of mammalian competitors on the ecology and evolution of communities. Pages 52–57 in D. P. Snyder, editor. *Populations of small mammals under natural conditions*. Volume 5. Special Publication Series, Pymatuning Laboratory of Ecology, University of Pittsburgh, Pittsburgh, Pennsylvania, USA.
- Brown, J. H., and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. *Science* 196:880–882.
- 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.
- Burt, W. H. 1928. Additional notes on the life history of the Goss lemming mouse. *Journal of Mammalogy* 9:212–216.
- Cockrum, E. L. 1952. *Mammals of Kansas*. University of Kansas Publications of the Museum of Natural History 7: 1–303.
- Cole, F. R., and G. O. Batzli. 1979. Nutrition and population dynamics of the prairie vole, *Microtus ochrogaster*, in central Illinois. *Journal of Animal Ecology* 48:455–470.
- Colwell, R. K., and E. R. Fuentes. 1975. Experimental studies of the niche. *Annual Reviews of Ecology and Systematics* 6:281–310.
- Connor, E. F., and D. Simberloff. 1979. The assembly of species communities: chance or competition? *Ecology* 60: 1132–1140.
- Connor, P. F. 1959. The bog lemming *Synaptomys cooperi* in southern New Jersey. Publications of the Museum, Michigan State University, Biological Series 1:161–248.
- Cooley, W. W., and P. R. Lohnes. 1971. *Multivariate data analysis*. John Wiley and Sons, New York, New York, USA.
- Coventry, A. F. 1942. *Synaptomys cooperi* in forested regions. *Journal of Mammalogy* 23:450–451.
- Curtis, J. T. 1959. *The vegetation of Wisconsin, an ordination of plant communities*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Doutt, J. K., C. A. Heppenstall, and J. E. Guilday. 1973. Pages 163–165 in R. M. Latham, editor. *Mammals of Pennsylvania*. Pennsylvania Game Commission, Harrisburg, Pennsylvania, USA.
- Dueser, R. D., and H. H. Shugart, Jr. 1978. Microhabitats in a forest-floor small mammal fauna. *Ecology* 59:89–98.
- Dueser, R. D., and H. H. Shugart, Jr. 1979. Niche pattern in a forest-floor small-mammal fauna. *Ecology* 60:108–118.
- Dunham, A. E. 1980. An experimental study of interspecific competition between the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. *Ecological Monographs* 50: 309–330.
- Dusi, J. L. 1949. Methods for the determination of food habits by plant microtechniques and histology and their application to cottontail rabbit food habits. *Journal of Wildlife Management* 13:295–298.
- Eadie, W. R. 1948. Shrew-mouse predation during low mouse abundance. *Journal of Mammalogy* 29:35–37.
- . 1953. Response of *Microtus* to vegetative cover. *Journal of Mammalogy* 34:263–264.
- Emlen, J. T., Jr., R. L. Hine, W. A. Fuller, and P. Alfonso. 1957. Dropping boards for population studies of small mammals. *Journal of Wildlife Management* 21:300–314.
- Fracker, S. B., and H. A. Brischle. 1944. Measuring the local distribution of *Ribes*. *Ecology* 25:283–303.
- Gaines, M. S., C. L. Baker, and A. M. Vivas. 1979. Demographic attributes of dispersing southern bog lemmings (*Synaptomys cooperi*) in eastern Kansas. *Oecologia (Berlin)* 40:91–101.
- Gaines, M. S., R. K. Rose, and L. R. McClenaghan, Jr. 1977. The demography of *Synaptomys cooperi* populations in eastern Kansas. *Canadian Journal of Zoology* 55:1584–1594.
- Getz, L. L. 1961. Factors influencing the local distribution of *Microtus* and *Synaptomys* in southern Michigan. *Ecology* 42:110–119.
- . 1967. Responses of the meadow vole to woody vegetation. University of Connecticut Occasional Papers (Biological Science Series) 1:63–69.
- . 1970a. Habitat of the meadow vole during a 'population low.' *American Midland Naturalist* 83:455–461.
- . 1970b. Influence of vegetation on the local distribution of the meadow vole in southern Wisconsin. University of Connecticut Occasional Papers (Biological Science Series) 1:213–241.
- Grant, P. R. 1972. Interspecific competition among rodents. *Annual Reviews of Ecology and Systematics* 3:79–106.
- . 1978. Competition between species of small mam-

- mals. Pages 38–51 in D. P. Snyder, editor. Populations of small mammals under natural conditions. Volume 5. Special Publication Series, Pymatuning Laboratory of Ecology, University of Pittsburgh, Pittsburgh, Pennsylvania, USA.
- Green, R. H. 1974. Multivariate niche analysis with temporally varying environmental factors. *Ecology* **55**:73–83.
- . 1979. Sampling design and statistical methods for environmental biologists. John Wiley and Sons, New York, New York, USA.
- Hairston, N. G. 1964. Studies on the organization of animal communities. *Journal of Animal Ecology* **33**(Supplement): 227–239.
- Hamilton, W. J., Jr. 1941. On the occurrence of *Synaptomys cooperi* in forested regions. *Journal of Mammalogy* **22**:195.
- Hansson, L. 1970. Methods of morphological diet microanalysis in rodents. *Oikos* **21**:255–266.
- Hooper, E. T., and E. R. Cady. 1941. Notes on certain mammals of the mountains of southwestern Virginia. *Journal of Mammalogy* **22**:323–325.
- Horn, H. S., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. *Ecology* **53**:749–752.
- Howell, A. B. 1927. Revision of the American lemming mice (Genus *Synaptomys*). *North American Fauna* **50**:1–38.
- Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium in Quantitative Biology **22**:415–427.
- Inger, R. F., and B. Greenberg. 1966. Ecological and competitive relations among three species of frogs (genus *Rana*). *Ecology* **47**:746–759.
- Jaeger, R. G. 1970. Potential extinction through competition between two species of terrestrial salamanders. *Evolution* **24**:632–642.
- . 1971. Competitive exclusion as a factor influencing the distributions of two species of terrestrial salamanders. *Ecology* **52**:632–637.
- . 1972. Food as a limited resource in competition between two species of terrestrial salamanders. *Ecology* **53**: 535–546.
- Keys, J. E., Jr., and P. J. Van Soest. 1970. Digestibility of forages by the meadow vole (*Microtus pennsylvanicus*). *Journal of Dairy Science* **53**:1502–1508.
- Kirkland, G. L., Jr. 1977. Responses of small mammals to the clearcutting of northern Appalachian forests. *Journal of Mammalogy* **58**:600–609.
- Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs* **36**:239–273.
- Krebs, C. J., and J. H. Myers. 1974. Population cycles in small mammals. *Advances in Ecological Research* **8**:267–399.
- Kucera, C. L., and S. C. Martin. 1957. Vegetation and soil relationships in the glade region of the southwestern Missouri Ozarks. *Ecology* **38**:285–291.
- Linzey, A. V. 1981. Patterns of coexistence in *Microtus pennsylvanicus* and *Synaptomys cooperi*. Dissertation. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.
- Linzey, D. W., and A. V. Linzey. 1968. Mammals of the Great Smoky Mountains National Park. *Journal of Elisha Mitchell Scientific Society* **84**:384–414.
- MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York, New York, USA.
- M'Closkey, R. T. 1976. Community structure in sympatric rodents. *Ecology* **57**:728–739.
- M'Closkey, R. T., and B. Fieldwick. 1975. Ecological separation of sympatric rodents (*Peromyscus* and *Microtus*). *Journal of Mammalogy* **56**:119–129.
- Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* **110**:351–369.
- Miller, R. S. 1967. Pattern and process in competition. *Advances in Ecological Research* **4**:1–74.
- Mossman, A. S. 1955. Light penetration in relation to small mammal abundance. *Journal of Mammalogy* **36**:564–566.
- Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. SPSS statistical package for the social sciences. Second edition. McGraw-Hill, New York, New York, USA.
- Odum, E. P. 1948. *Synaptomys* on the Highlands, North Carolina, Plateau. *Journal of Mammalogy* **29**:74.
- Peters, R. H. 1976. Tautology in evolution and ecology. *American Naturalist* **110**:1–12.
- Pielou, E. C. 1975. Ecological diversity. John Wiley and Sons, New York, New York, USA.
- Poole, E. L. 1943. *Synaptomys cooperi stonei* from the eastern shore of Maryland. *Journal of Mammalogy* **24**:103.
- Quarterman, E. 1950. Major plant communities of Tennessee cedar glades. *Ecology* **31**:234–254.
- Richmond, N. D., and H. R. Rosland. 1949. Pages 49–50 in Mammal survey of northwestern Pennsylvania. Pennsylvania Game Commission, Harrisburg, Pennsylvania, USA.
- Rose, R. K., and A. M. Spevak. 1978. Aggressive behavior in two sympatric microtine rodents. *Journal of Mammalogy* **59**:213–216.
- Rosenzweig, M. L. 1966. Community structure in sympatric carnivora. *Journal of Mammalogy* **47**:602–612.
- Rosenzweig, M. L., and P. W. Sterner. 1970. Population ecology of desert rodent communities: body size and seed-husking as bases for heteromyid coexistence. *Ecology* **51**: 217–224.
- Rotenberry, J. T. 1980. Dietary relationships among shrub-steppe passerine birds: competition or opportunism in a variable environment? *Ecological Monographs* **50**:93–110.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* **185**:27–39.
- Schreiber, R. K., W. C. Johnson, J. D. Story, C. Wenzel, and J. T. Kitchings. 1976. Effects of powerline rights-of-way on small nongame mammal community structure. Pages 264–273 in R. Tillman, editor. Symposium on Environmental Concerns in Rights-of-way Management. Mississippi State University Press, Starkville, Mississippi, USA.
- Schroder, G. D., and M. L. Rosenzweig. 1975. Perturbation analysis of competition and overlap in habitat utilization between *Dipodomys ordii* and *Dipodomys merriami*. *Oecologia* (Berlin) **19**:9–28.
- Slatkin, M. 1974. Competition and regional coexistence. *Ecology* **55**:128–134.
- Smyth, T. 1946. *Synaptomys cooperi* in southwestern Virginia. *Journal of Mammalogy* **27**:277.
- Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California, USA.
- Sparks, D. R., and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscope technique. *Journal of Range Management* **21**:264–265.
- Stegeman, L. C. 1930. Notes on *Synaptomys cooperi cooperi* in Washtenaw County, Michigan. *Journal of Mammalogy* **11**:460–466.
- Stewart, R. E. 1943. The lemming mouse in Shenandoah Mountains, Virginia. *Journal of Mammalogy* **24**:104.
- Terman, M. R. 1974. Behavioral interactions between *Microtus* and *Sigmodon*: a model for competitive exclusion. *Journal of Mammalogy* **55**:705–719.
- West, G. C., and V. H. Hutchison. 1964. The southern bog lemming in Rhode Island. *Journal of Mammalogy* **45**:479–480.
- Wiens, J. A. 1977. On competition and variable environments. *American Scientist* **65**:590–597.
- Williams, O. 1962. A technique for studying microtine food habits. *Journal of Mammalogy* **43**:365–368.