ABSTRACT

INTERACTIONS BETWEEN SYMPATRIC *MICROTUS* AND *SIGMODON* (RODENTIA: CRICETIDAE)

By

Max Robert Terman

Two species of grass eating, runway making myomorph rodents, *Microtus ochrogaster* and *Sigmodon hispidus*, were occupying a common habitat (vegetationally dominated by bluestem grasses--*Andropogon spp.*) in central Kansas. Since these two rodents were living in the same area, and since a decline in *M. ochrogaster* coincided with a northward spread of *S. hispidus*, it was hypothesized that these two species were interacting negatively with each other.

To test this hypothesis, a field and laboratory investigation was carried out. It was hypothesized that the presence of *Sigmodon* in the field would decrease mean body weights, change sex ratios, shorten survival rates, reduce mean residence times, increase range overlaps, produce negative measures of interspecific association, decrease individual and population movements, reduce home ranges, and reduce trappability in *Microtus*. In the laboratory, it was hypothesized that *Sigmodon* would aggressively dominate and spatially exclude *Microtus*.

Six study plots were live trapped from April 16 through December 6, 1971 and then again on March 17 and April 14, 1972. In two plots all *Microtus* were removed, in another all *Sigmodon* were removed, in the fourth both species were removed and in two more plots neither species was removed. *Sigmodon* did not appear in the traps until late summer which shortened the time of interspecific contact. The late appearance

of Sigmodon reduced the between-the-plot comparisons but facilitated the observation of single plots over time (before and after Sigmodon).

In the presence of Sigmodon, Microtus had a lower survival rate and changed sex ratio in one of the two-species plots. Also, the two species when left together were negatively associated. The population movements of Microtus in the absence of Sigmodon were more widespread than when Sigmodon was present. The number of captures per individual Microtus dropped significantly after the appearance of Sigmodon in one of the dual species plots. Microtus also became less trappable in the presence of Sigmodon. These results and the presence of wounds on Microtus after the appearance of Sigmodon suggested a negative interaction between the two species in the field. The severity of the Kansas winter may limit Sigmodon populations sufficiently for Microtus to coexist.

Both genera were paired in a terrarium divided into two sections. Sigmodon was clearly the dominant animal. The spatial distribution of the two species was observed in a three-compartment laboratory arena. Sigmodon excluded Microtus except under conditions of dense cover. In a specially designed tunnel, the movements of Microtus were reduced by a free ranging Sigmodon but not by a confined one.

The frequency of interspecific contact appeared to determine the presence or absence of a negative interaction. A model utilizing the contribution of various factors to the frequency of interspecific contact was constructed. This offers a possible explanation of the relationship between Microtus ochrogaster and Sigmodon hispidus. Also, a model was proposed to explain the mechanism of competitive exclusion as it might occur in myomorph rodents as a group.

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INTRODUCTION

The prairie vole, *Microtus ochrogaster* (Wagner) and the hispid cotton rat, *Sigmodon hispidus* Say and Ord, are near the edges of their respective ranges in central Kansas where they overlap. A field and laboratory study of their relationship in a sympatric area was carried out from April, 1971, through April, 1972. The purpose of this investigation was to examine their relationship for a suspected negative interaction.

The distribution of *Microtus ochrogaster* and *Sigmodon hispidus* is shown in Figure 1. *Microtus ochrogaster* has been a long time resident of the Southern Great Plains, whereas *Sigmodon hispidus* is an invader from the south, appearing in the central Kansas area about 40 years ago (Cockrum, 1948). The northward spread of *S. hispidus* has coincided with a decline in *M. ochrogaster*. For example, in Kansas Martin (1956, 1960) and Frydendall (1969) found decreased *Microtus* population levels with increasing *Sigmodon* populations. *Microtus ochrogaster* formerly was trapped in north central Oklahoma but has not been taken there since 1957 and then only with a crash in the *Sigmodon* population (Bryan Glass, personal communication). In South Carolina, Wiegert (1972) reported that *Microtus pennsylvanicus* lived and reproduced in field enclosures when not in contact with *Sigmodon hispidus*. Odum (1955) noted a rare occurrence of *Microtus pennsylvanicus* in Georgia following a low population year for *Sigmodon*. Although the observed decline of *M.*

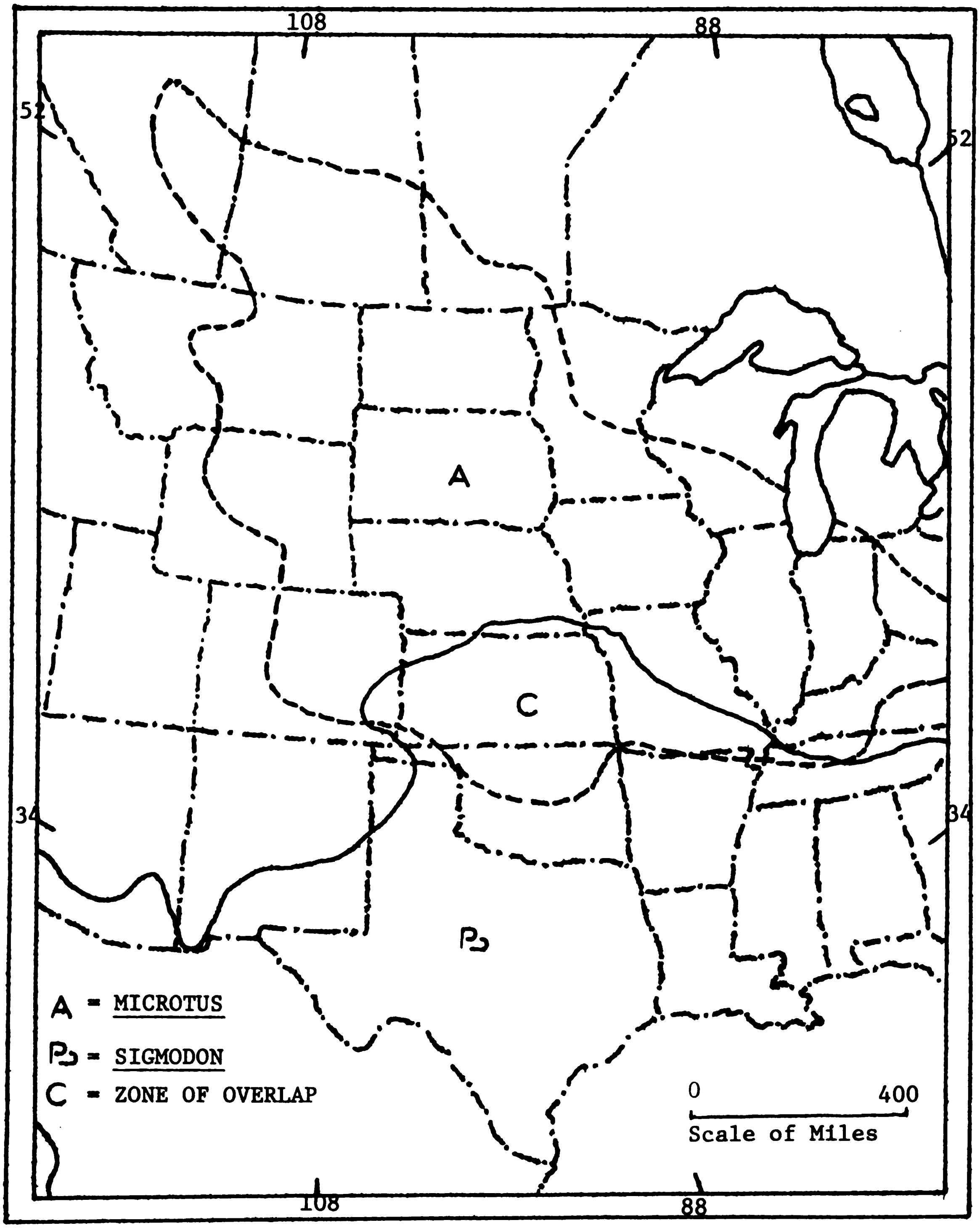


Figure 1. Distribution of *Microtus ochrogaster* and *Sigmodon hispidus* in central United States (from Hall and Kelson, 1959; with modifications from Easterla, 1968; Genoways and Schlitter, 1966; and Jones, 1960).

ochrogaster might be the result of environmental factors having nothing to do with the "newly arrived" Sigmodon in Kansas, these studies and other observations (Baker, 1969, 1971; Dimmick, 1969; Fleharty and Olson, 1969; Goertz, 1971; Hays, 1958; Whittaker and Zimmerman, 1968) point to some kind of negative interaction between these two rodents. These reports stimulated the questions which formed the basis for this study.

Objectives

The objectives of the present study were (1) to investigate and present data on the ecological relationship between *Microtus ochrogaster* and *Sigmodon hispidus* in their common habitat; (2) to test hypotheses on the presence or absence of a negative interaction between these two species in (a) the field situation; and (b) in a controlled laboratory situation.

Hypotheses

Baker (1969, 1971) has contended that when two species of grass eating, runway making rodents of the genera *Microtus* and *Sigmodon* live in the same area, *Microtus* is generally replaced by the cotton rat or there is spatial separation of the two species. Since *M. ochrogaster* and *S. hispidus* were resident in the mixed grass habitat of Marion County, Kansas, this area offered an excellent opportunity to study the alleged incompatibility of the two species.

Because of their apparent niche similarity (Calhoun, 1945; Svihla, 1929), it was postulated that the two rodent populations would negatively affect each other. To test this concept the following two hypotheses were developed:

(1) It was hypothesized that *Sigmodon* would decrease mean body weights, change sex ratios, shorten survival rates, reduce mean residence times, increase range overlaps, produce negative measures of interspecific association, decrease individual and population movements, reduce home ranges, and reduce trappability in *Microtus*.

(2) It was hypothesized that *Sigmodon* would aggressively dominate and spatially exclude *Microtus* in laboratory experiments.

FIELD INVESTIGATION

Description of the Study Area

Trapping was conducted on a grassy pasture owned by Robert Navrat located two miles north of the city of Marion in Marion County, Kansas. Marion County is near the border between two biotic districts, the Mixed Grass Plains and the Osage Savanna (Cockrum, 1952). The study area itself is dominated by big bluestem (*Andropogon gerardi*), little bluestem (*Andropogon scoparius*), switchgrass (*Panicum virgatum*), and Indian grass (*Sorghastrum nutans*). The pasture in which the study area was located was placed in the Soil Bank for ten years prior to the study, according to owner Robert Navrat, and had not been disturbed by grazing, plowing or burning during this time.

Cockrum (1952) lists Marion County as containing mammals of the Great Plains Mammalian Distributional Area and mammals of the Central Lowland Mammalian Distributional Area. Small mammal species observed or captured on the study area were *Sylvilagus floridanus*, *Lepus californicus*, *Peromyscus maniculatus*, *Reithrodontomys megalotis*, *Mus musculus*, *Microtus ochrogaster*, *Sigmodon hispidus*, and *Cryptotis parva*. *Peromyscus maniculatus*, *R. megalotis*, *M. ochrogaster*, *S. hispidus*, and *C. parva* were the most common species observed.

Notable features of the Kansas climate are frequent and abrupt changes. Summers are usually warm often with periods of high temperatures and low humidity. Winters are drier than the summers. The average annual precipitation for the county of Marion is 782 mm. and the average annual temperature is 13.5° C (56.6° F). Table 1 gives the weather data for the study period.

Plot Vegetation and Topography

Moderately grazed pastures bordered the study area on all sides. To the west and south there were fence rows with sparse to dense woody vegetation. On the northern border there was a small creek with associated woody vegetation. Grassland similar to that which composed the study area was on the east border.

Six study plots, each 60 meters square, were chosen for this experiment (see Figure 2). Each was placed at least 30 meters away from any other plot or adjacent boundary. The percent coverage of the common plant species (see Table 2) was determined for each plot during September by the line intercept technique described in Cox (1967). A Gossen Luna-Pro light meter was used to measure relative cover by comparing the amount of light penetration reaching the ground level beneath the vegetation in each plot (Mossman, 1955). The relative cover corresponded directly with the percent coverage of bare ground in Table 2 (*i.e.* plot 1 was most dense, then plot 3, and so on).

Plots 1 and 3 were located in a drainage area which was relatively moist. This accounted for the relatively dense cover in these plots. Plots 2, 4, and 5 were located on gentle slopes (Figure 2). Plot 6 was on higher ground which gently sloped down into the drainage area containing plots 1 and 3. The plots were not exact duplicates of each other in terms of plant cover and species density. However, all plots were part of a homogenous prairie area which occupied 80 acres, and the

Table 1. Weather data (1969 - 1972) taken from Marion Dam (8 km. west of study area).*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean temperature (°C)												
1969	---	---	---	13	18	21	28	26	20	12	7	0
1970	-5	2	4	12	20	22	26	28	20	12	5	3
1971	-5	-6	4	14	16	25	24	24	21	16	6	1
1972	-5	-1	9	13	18							
Mean precipitation (mm.)												
1969	---	---	---	125	190	128	158	12	80	104	4	34
1970	1	5	22	89	76	127	62	20	139	80	4	5
1971	27	31	6	44	118	204	260	13	52	121	86	13
1972	2	2	32	64	91							
Mean soil temperature at 10.2 cm. (°C) (taken at Hutchinson, Kansas)												
1969	---	---	---	17	23	24	29	28	23	16	9	5
1970	1	5	7	14	24	24	29	32	23	16	7	6
1971	1	3	7	15	24	25	30	27	24	19	10	6
1972	3	5	12	17	21							
Total snowfall (cm.) and number of days on ground												
1969	---	---	---							0(0)	0(0)	152(7)
1970	51(2)	0(0)	102(3)	203(3)						25(1)	0(0)	0(0)
1971	76(17)	558(16)	101(9)							0(0)	51(2)	51(1)
1972	0(0)	0(0)	0(0)									

* From Environmental Data Service, U. S. Department of Commerce, Manhattan, Kansas

Table 2. Percent coverage of common plant species found in each plot.

Species	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
Andropogon gerardi	40.0	42.5	54.0	40.1	59.6	35.0
Panicum virgatum	35.0	4.3	25.5	0.5	15.3	10.5
Andropogon scoparius	9.6	35.0	10.3	44.6	19.8	43.5
Sorghastrum nutans	9.3	1.3	2.0	4.5	2.0	1.2
Agrostis alba	1.5	1.5	0.8	0.1	0.3	0.2
Agropyron smithii	1.9	1.7	1.5	0.2	0.7	0.4
Sporobolus asper	0.9	1.5	0.8	1.5	0.6	0.3
Aristida spp.	0.7	1.7	3.3	0.5	0.1	0.5
woody plants	0.2	0.2	0.3	0.3	0.2	0.2
Bouteloua curtipendula	0.3	2.1	0.2	0.9	0.1	0.5
herbs	0.3	0.7	0.5	0.7	0.5	0.5
Paspalum circulare	0.2	0.2	0.5	---	0.2	---
bare ground	0.1	7.3	0.4	6.0	.6	7.0
	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%
cover rank*	1	6	2	4	3	5

* Determined by a light meter, ranked from most dense to least dense.
Rank also related to amount of bare ground.

differences in cover, ground litter, soil type, and species composition were not extensive.

Field Methods

On each 60-meter-square plot a live trap was placed at every 15 meter interval. Every plot thus contained 25 live traps of the type described by Fitch (1950). Every three weeks traps were baited in late afternoon, checked early the following morning, closed during the day and opened again in late afternoon for four continuous days. Oats were used for bait and the traps were partially wrapped in aluminum foil to provide some overhead protection for the captured animals.

All plots were live-trapped from April 16 through December 6, 1971 and then again on March 17 and April 14, 1972. The catch of *Microtus* and *Sigmodon* at each plot was manipulated according to the procedure given in Figure 2. Other species of small mammals captured were identified and released.

The following information was recorded from each prairie vole and cotton rat in each plot throughout the entire period of trapping (6300 trap nights): Species, sex, individual number (by toe-clipping), weight, trap station, breeding condition, and presence or absence of wounds.

Weights were taken to the nearest gram using a spring balance with an alligator clip from which animals were suspended by their tails while being weighed (see Krebs, 1969). Breeding condition was determined by the position of the testes in males and by the condition of the vaginal opening, lactation, and pregnancy in females. Juveniles, subadults, and adults were categorized by weights. In *Microtus* juveniles were animals

$\leq$ 22 grams, young adults were between 23 and 32 grams, and adults were $\geq$ 33 grams (Krebs, 1969). In cotton rats juveniles were $\leq$ 46 grams, young adults were between 47 and 111 grams, and adults were $\geq$ 112 grams (Sealander and Walker, 1955). After information was gathered on each rodent, the animal was marked (unless a recapture or one to be removed) and released at its point of capture.

Field Hypotheses

The six field plots containing the two species were trapped utilizing selective release or removal procedures (see Figure 2). In two plots all *Microtus* were removed, in another all *Sigmodon* were removed, in the fourth both species were removed and in two more plots neither species was removed. Once the field data were collected, comparisons were made between the plots and within single plots. Between-the-plot comparisons were made difficult by a late appearance of the cotton rats. *Sigmodon* did not appear in the traps until late August which prevented a year-around comparison as was originally intended. The late occurrence of the cotton rats did, however, facilitate the single plot comparisons since each *Microtus* population could be observed both before and after the *Sigmodon* invasion. It must be stated that the latter comparisons can introduce such variables as seasonal influences which can not be controlled. For this reason, much field data can only be considered as suggestive and not confirmative.

Where possible, the field data were subjected to statistical tests in an effort to confirm or reject specific hypotheses. Much of the data, for example population levels, were not testable by presently known procedures. These types of data were not used to confirm or

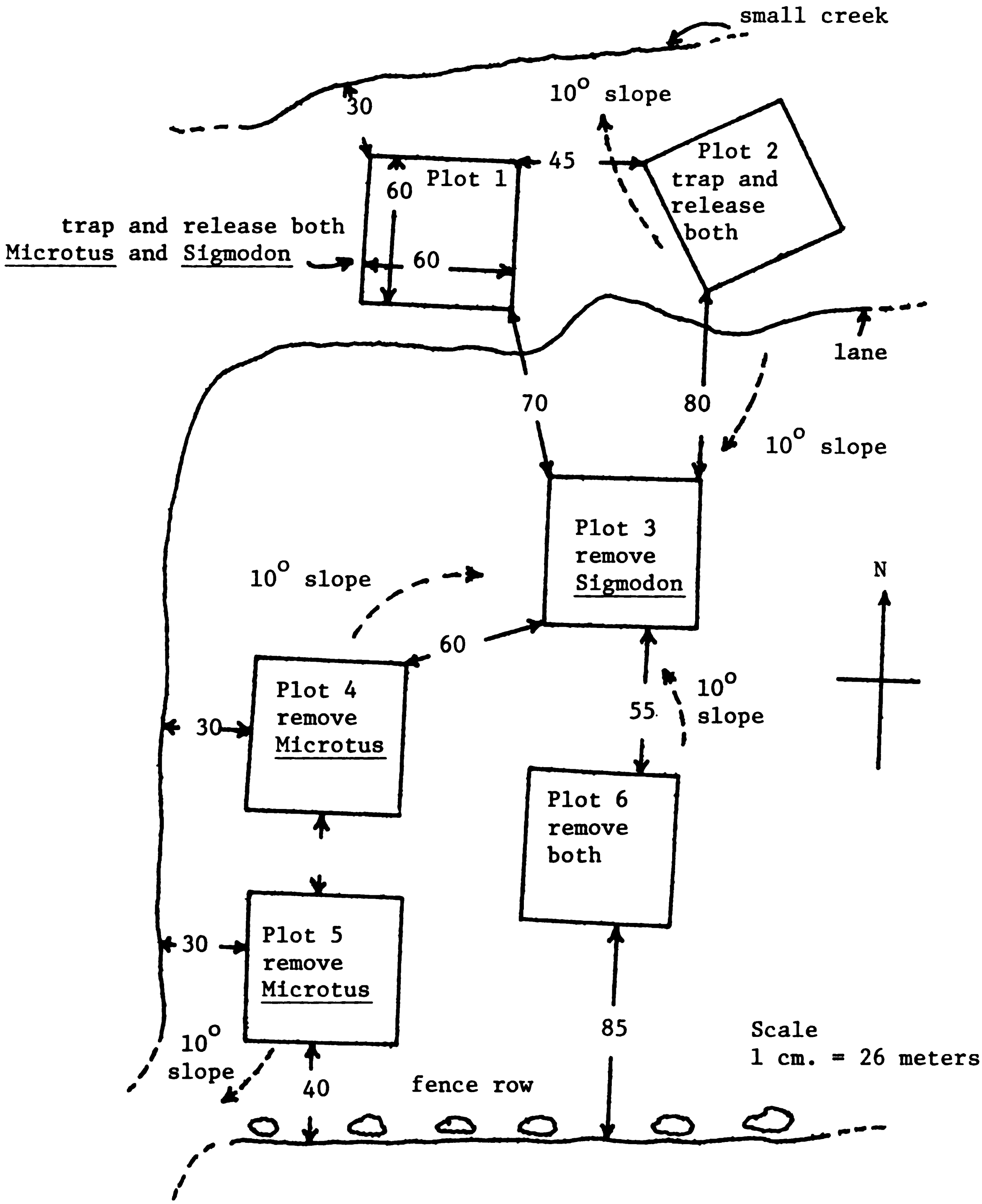


Figure 2. Map of the study plots on the trapping area (distances in meters).

reject hypotheses but were discussed because of their descriptive values and the information they provided about the interspecific situation.

In the two field plots where both species were trapped, marked and released (see Figure 2) it was expected that the Sigmodon populations would cause certain changes to occur in the Microtus populations. When compared with the plot from which Sigmodon was removed (plot 3) it was hypothesized that the former two plots would have significantly lower Microtus survival rates, lower mean residence times, more range overlap, negative measures of interspecific association, decreased individual and population movements and home ranges, and would be less trappable. I hypothesized these things because of the suspected niche similarity and dominance of Sigmodon (Martin, 1956). It should be noted now that the late appearance of the cotton rat handicapped this design by reducing the time of interspecific contact.

Because of the sudden appearance of Sigmodon, it was anticipated that each plot would experience temporal changes in the respective vole populations. In the plots containing both species, it was hypothesized that the Microtus populations would change significantly in mean body weights, sex ratios, mean residence times, range overlaps, trap capture rates, individual movements, and individual and population home ranges. The Sigmodon removal plot should experience changes of lesser magnitude.

The plots from which only Microtus were removed were expected to provide data on Sigmodon survivorship in the absence of Microtus and on interspecific association. It was hypothesized that the voles would not affect cotton rat survival and that these plots would have neutral indices of interspecific association. It was expected that plot 6 (both species removed) would provide data on the total cotton rat and vole populations available to the plots. If the animals of either species were common and mobile on the grassland area as a whole, then there should be a constant removal of that species from plot 6. Also, this plot was hypothesized to have neutral indices of interspecific association because of the removal program.

This trapping regime was also expected to produce useful data on population levels, recruitment, immigration and emigration, and spatial distribution in single and dual species conditions.

Analysis of Data

All field data were placed on paper and magnetic tape and were analyzed on a PDP8 (Digital Equipment) computor through the time-sharing facilities of the Associated Colleges of Central Kansas and Tabor College.

Population estimates were made using the direct enumeration technique (Krebs, 1966), which reveals the minimum number of animals on each area at time *t*. The resulting figure is a summation of two counts: (1) the actual number of individuals caught at time *t*; and (2) the number of individuals marked previous to time *t* but caught after time *t*, and not at time *t* (Peterson, 1970).

Survival rates were calculated by computing the percentage of animals surviving between successive trapping periods (per three weeks). The mean residence times were computed by averaging the length of time from first to last capture for all individual rodents in a given time interval. Mortality here is assumed to include emigration or death.

Dispersion was determined by computing the center of activity for each multi-captured individual (more than 2 captures) and for each population in a given time interval. The center of activity is an average x-y coordinate of all points of capture for an individual or population. Centers of activity were then placed on grids representing particular plots so that individual and population movements could be observed in varying situations.

Another index of population dispersion was gained by counting the number of trap sites which captured none, one, two, etc., individual rodents. These data were then put on graphs to reveal population distributions in different situations.

Cole's (1949) coefficient of interspecific association was used to ascertain the degree to which Microtus and Sigmodon associated with each other in each plot. This involved the calculation of a coefficient of association for data arranged in a 2 x 2 contingency table. This coefficient was then tested for statistical significance by using Cole's specially designed Chi-square test formula. In addition, correlation coefficients were calculated between the two species by using the number of individuals of both species caught at every trapsite.

To get a further insight into species association, traps were first categorized according to the number of different cotton rat individuals caught. Then the mean number of Microtus individuals was determined for each trap of a particular category.

The last measure which gave an indication of species association was the percentage capture rate for each trap station where both species were taken. The vole capture rate at a trap should decrease when that trap began to capture Sigmodon.

An index to population movements was gained by noting the monthly movement of population centers of activity for Microtus and Sigmodon.

Other indices of movements included the mean number of different traps and the mean number of captures per individual *Microtus*. Individual and population home ranges were also indices to movements and were calculated by the computer using a method developed by Jennrich and Turner (1969). This method is based on the determinant of the covariance matrix of the capture points and can measure noncircular as well as circular home ranges. The resulting figure is an A4 statistic which is an index to the size of the home range.

Field Results

Populations

Preliminary trapping during October-December 1970, indicated that both *Microtus* and *Sigmodon* were present on the study area and that there seemed to be some degree of spatial separation between areas of similar habitat.

When experimental trapping commenced on April 16, 1971, *Microtus* was present in all plots except plot 2. In the next trapping period, however, *Microtus* was trapped in plot 2 in numbers comparable to the other plots. *Sigmodon*, on the other hand, was not captured until the August trapping period in plots 1, 4, and 5 and not until the September trapping period in plots 2, 3, and 6. This late arrival of *Sigmodon* allowed the analysis of *Microtus* populations over time, *i.e.* before *Sigmodon* and after *Sigmodon*. Figures 3 through 8 show the population levels for each species on each plot for the entire study (1971-1972).

The *Microtus* populations and removals showed a September-October decline in all of the plots. This coincided with the first sign of cotton rats. The voles appeared to recover in all plots by December

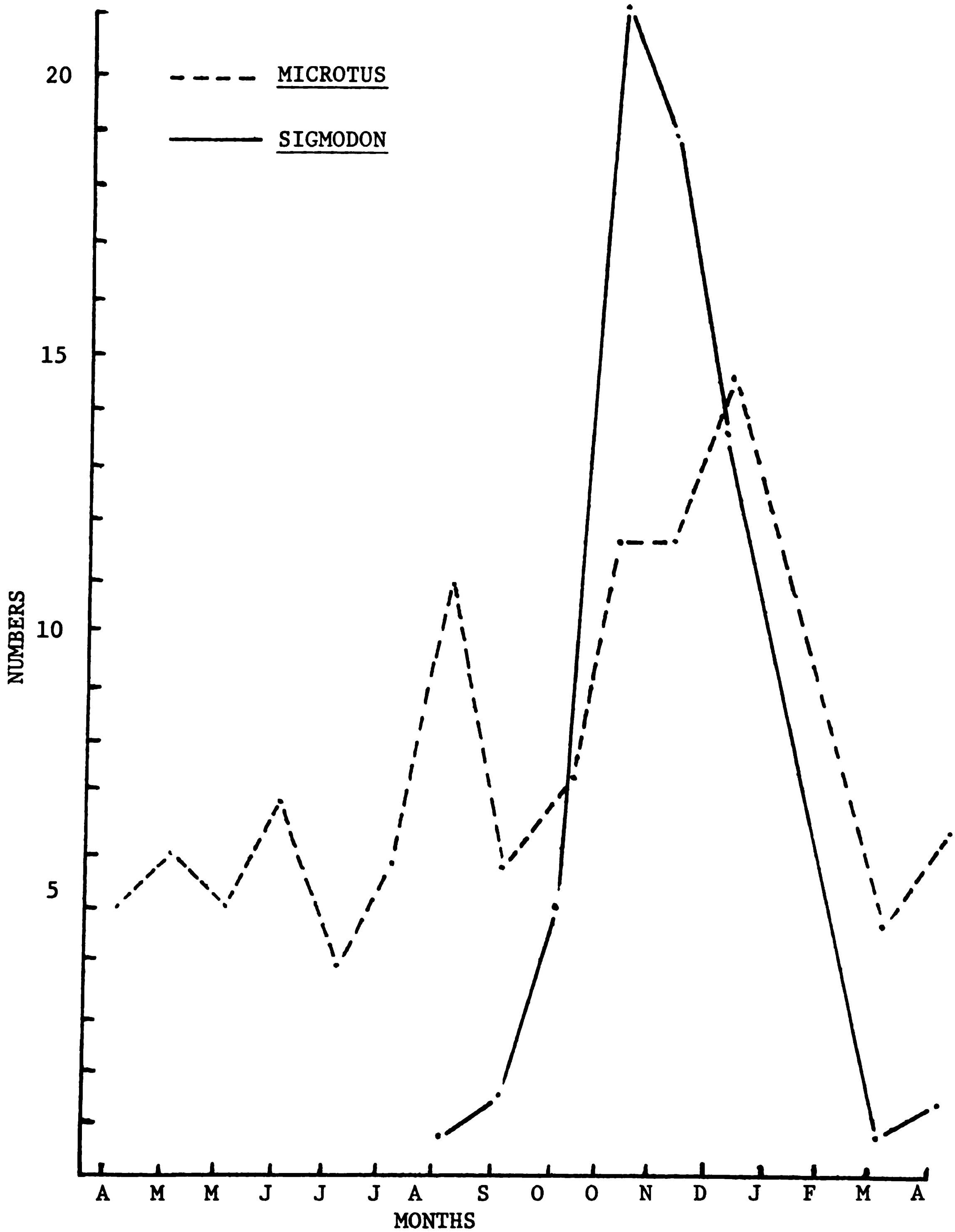


Figure 3. Minimum numbers of <u>Microtus</u> and <u>Sigmodon</u> on plot 1 (1971-1972).

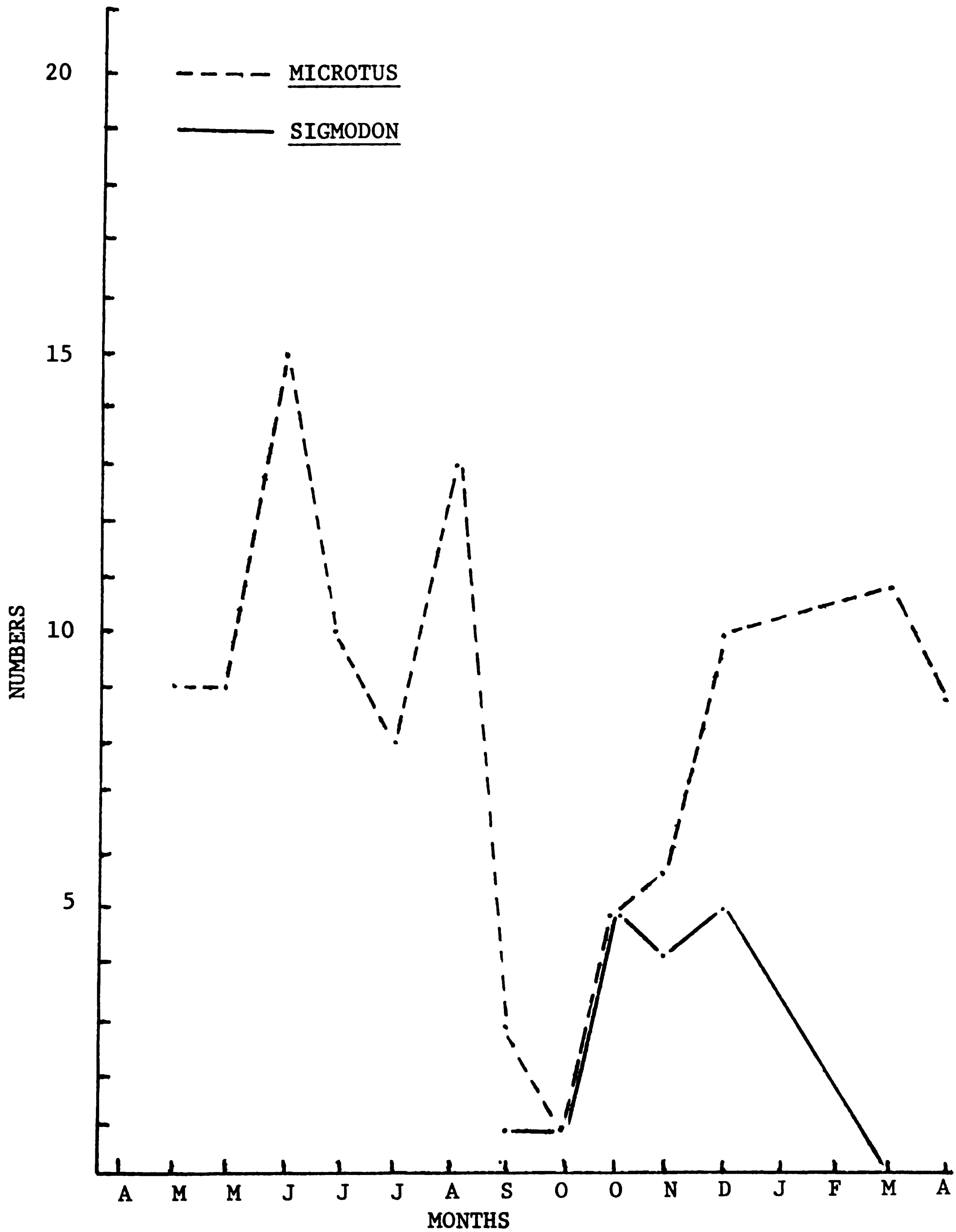


Figure 4. Minimum numbers of Microtus and Sigmodon on plot 2 (1971-1972).

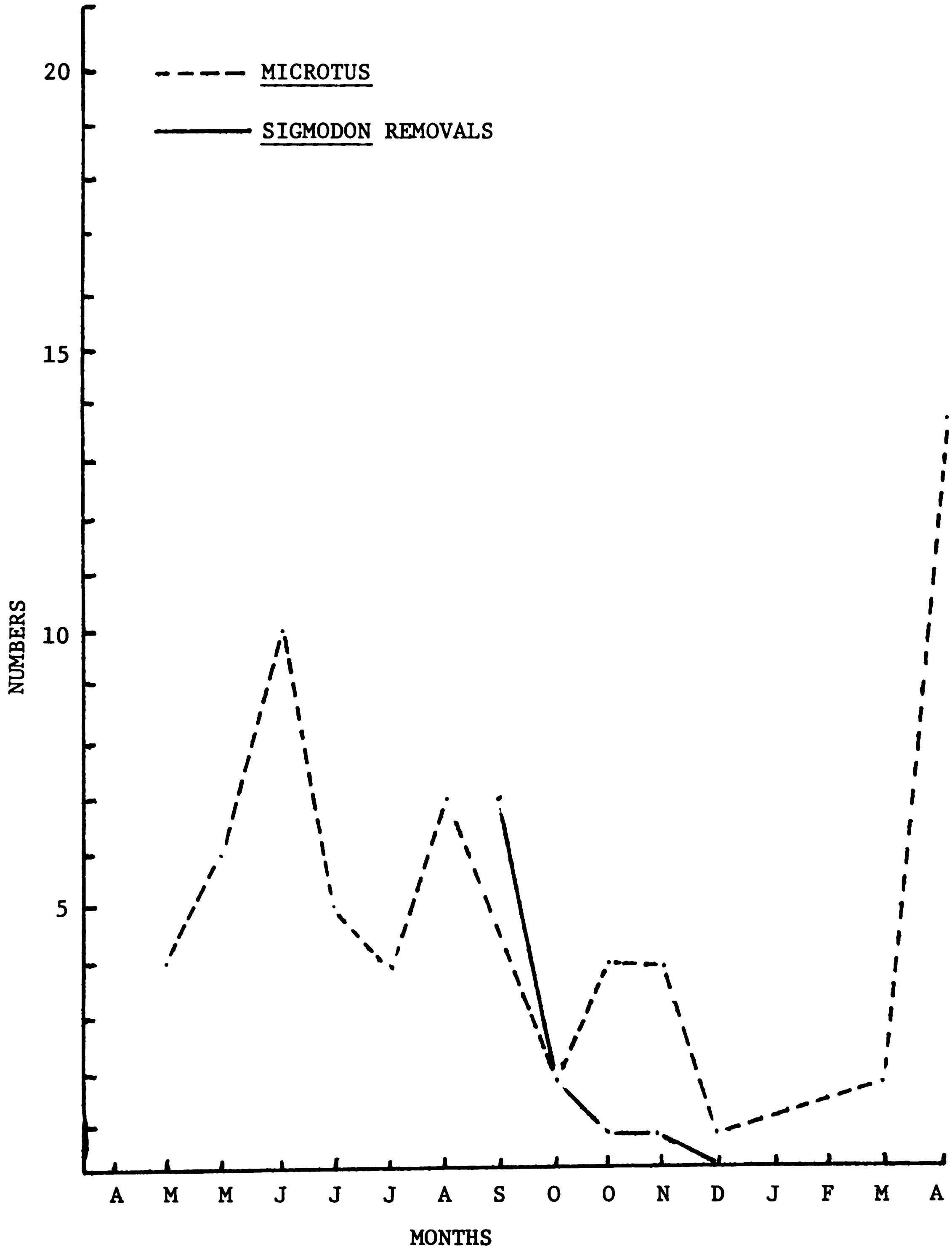


Figure 5. Minimum numbers of Microtus and the numbers of Sigmodon removals on plot 3 (1971-1972).

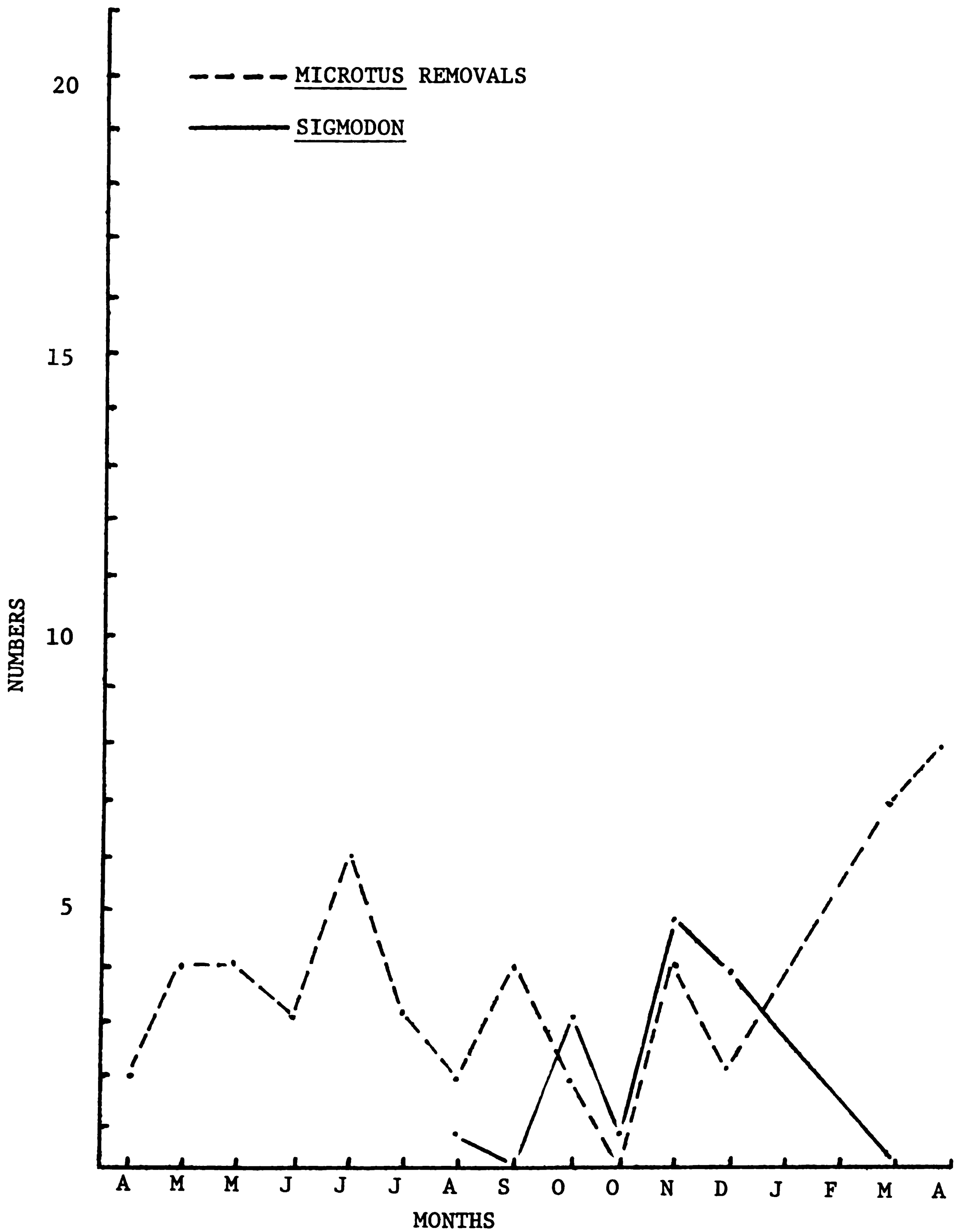


Figure 6. Minimum numbers of Sigmodon and the numbers of Microtus removals on plot 4 (1971-1972).

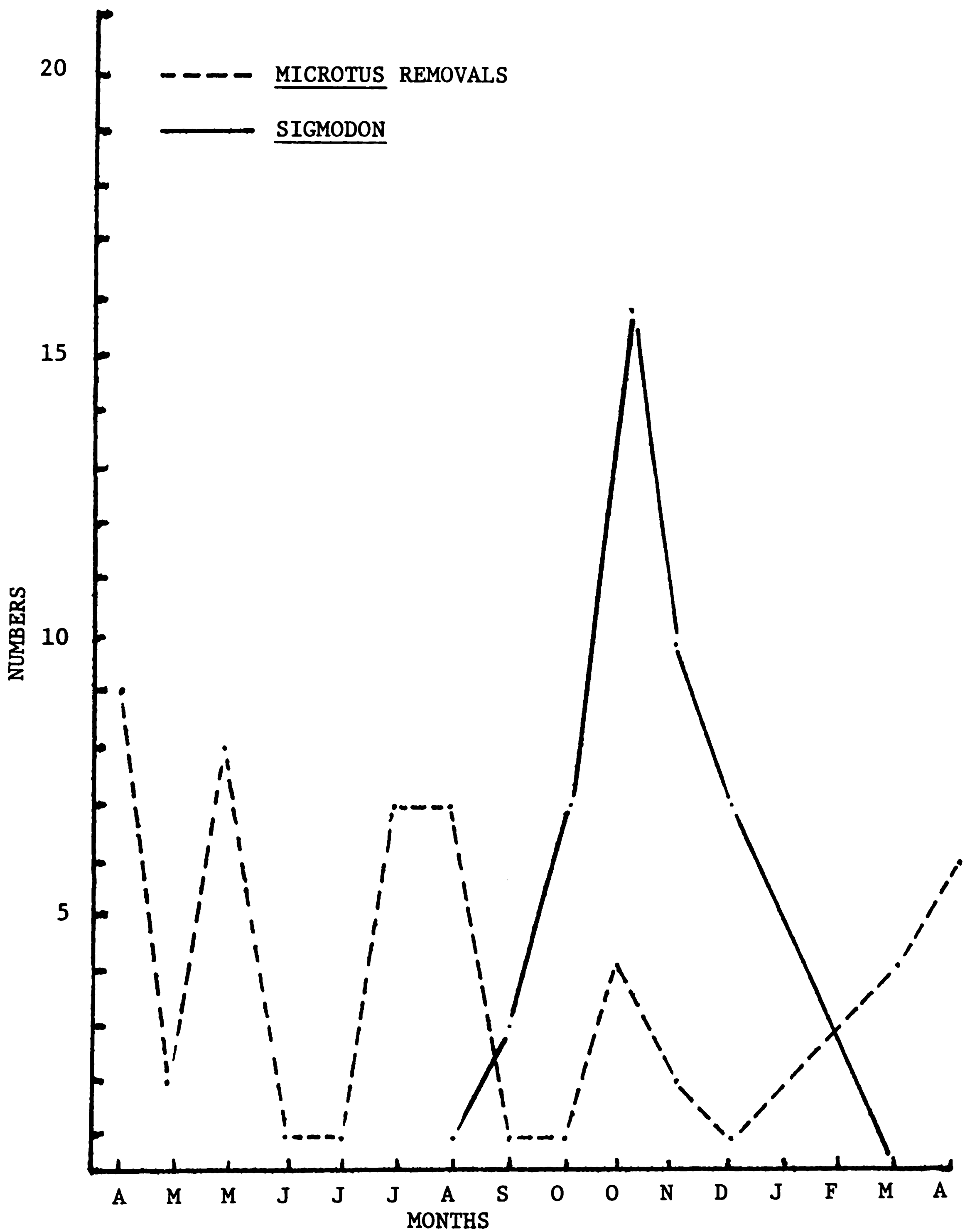


Figure 7. Minimum numbers of Sigmodon and the numbers of Microtus removals on plot 5 (1971-1972).

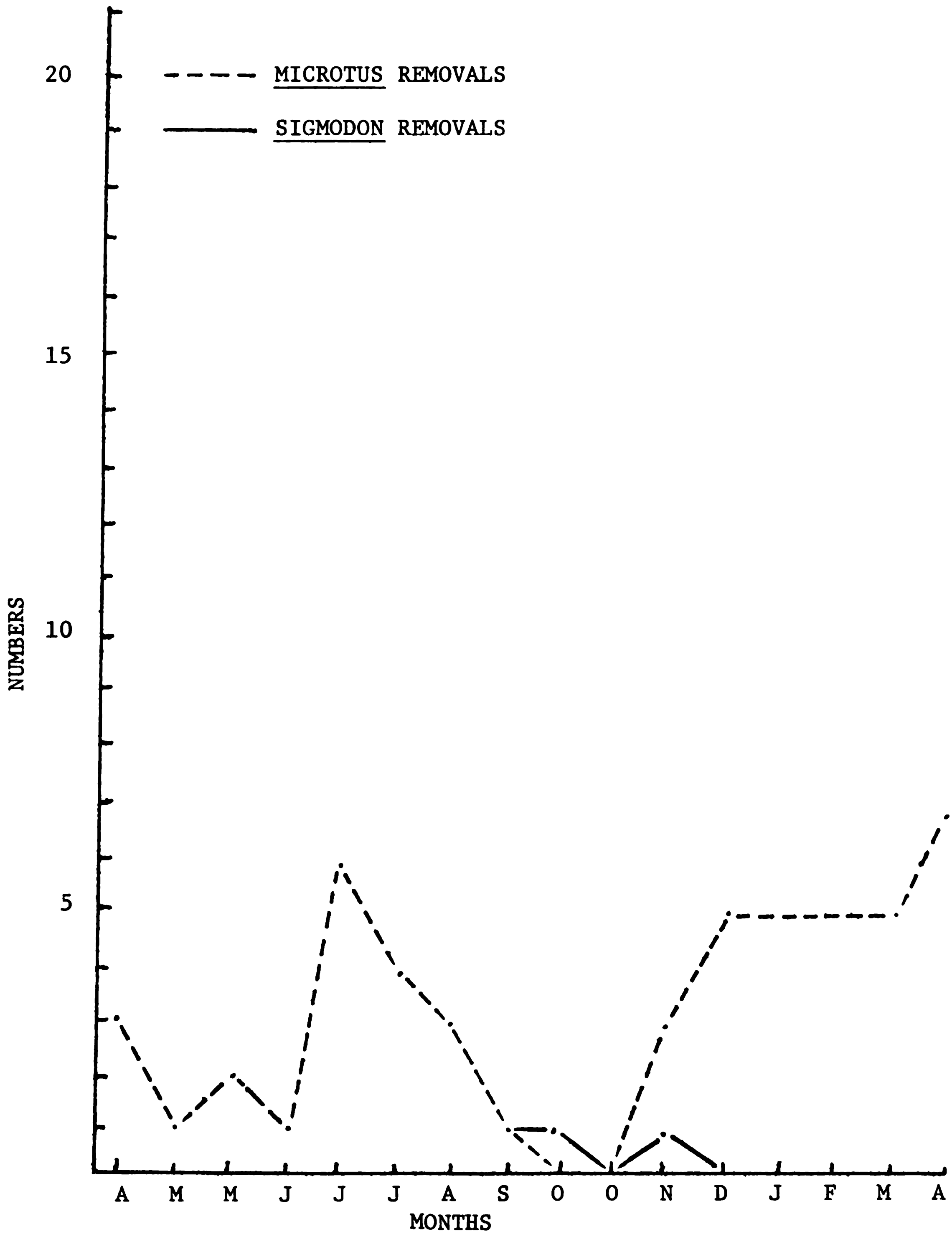


Figure 8. The numbers of *Microtus* and *Sigmodon* removals on plot 6 (1971-1972).

and increased thereafter, except in plot 1. Resident *Sigmodon* populations increased during September and October and then decreased in December. *Sigmodon* removals from plot 3 decreased steadily, while those from plot 6 were minimal, never more than one per period. Plots 2, 4, and 6 showed a complete cessation of vole captures in October.

There were only two *Sigmodon* captured in the spring of 1972, both in plot 1. *Microtus* populations were higher in the spring of 1972 than in the spring of 1971 in all plots except plots 1 (where neither *Microtus* nor *Sigmodon* was removed) and 5 (where *Microtus*, but not *Sigmodon* was removed). Nine *Microtus* were known to overwinter, four in plot 1, four in plot 2, and one in plot 3. One *Sigmodon* overwintered (plot 1). Plots 3 and 6 were the only ones that had captures of *Microtus* juveniles in 1972.

Figures 9 through 11 reveal the numbers of new and recaptured *Microtus* and *Sigmodon* on plots 1-5. From these records, an indication of recruitment and immigration can be gained. In plot 1, the recruitment of voles and cotton rats increased steadily from September through October. In November both rates decreased substantially. *Microtus* recruitment increased again in December.

In plot 2, *Microtus* recruitment dropped to zero in early October. In October, *Sigmodon* had no new captures and one recapture. From late October, *Microtus* exhibited renewed recruitment and steady population growth. From late October through December, *Sigmodon* had a constant recruitment but little population growth.

In plot 3, *Microtus* recaptures dropped to zero in early October. The population, however, remained constant until it declined in December. In December no *Sigmodon* were captured in plot 3.

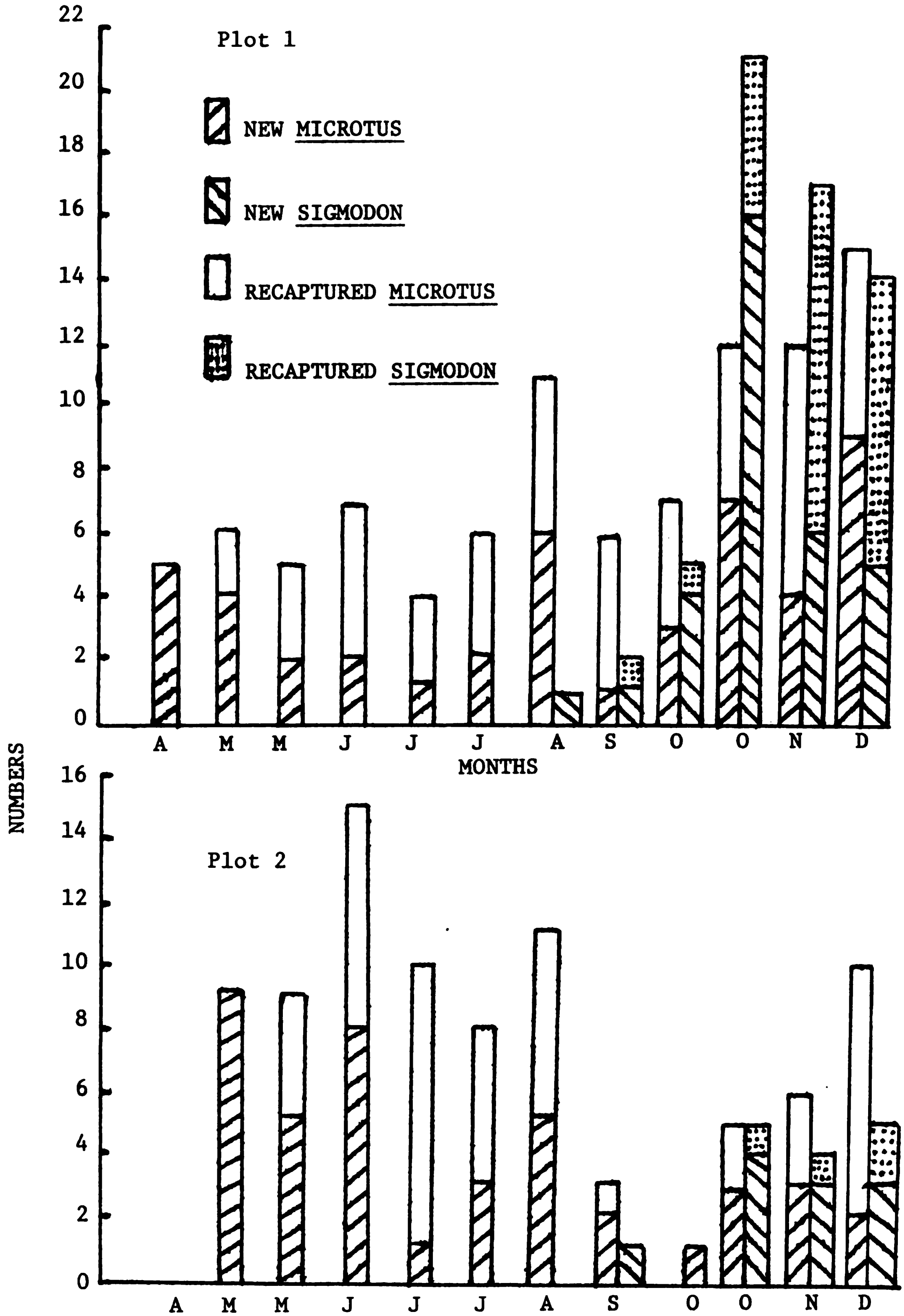


Figure 9. Relative numbers of new and recaptured *Microtus* and *Sigmodon* on plots 1 and 2 (1971).

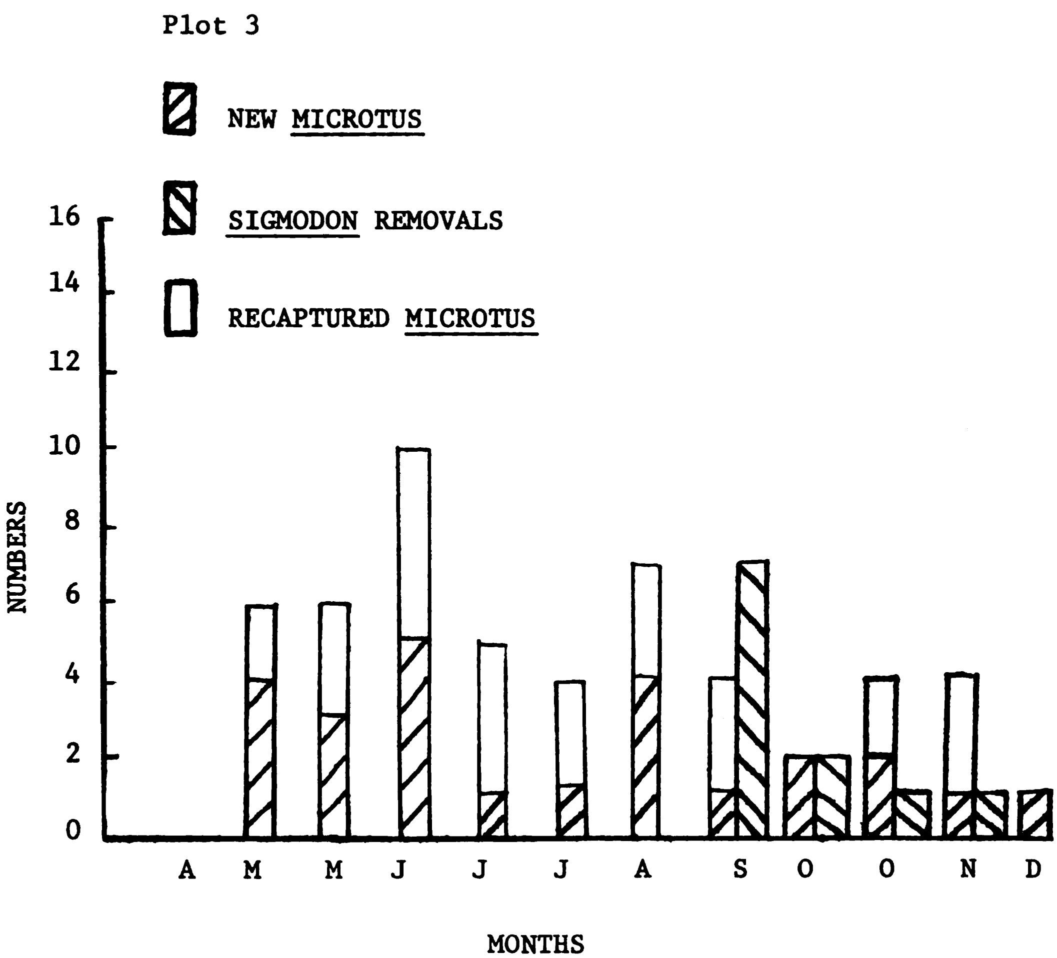


Figure 10. Relative numbers of new and recaptured Microtus and the numbers of Sigmodon removals on plot 3 (1971).

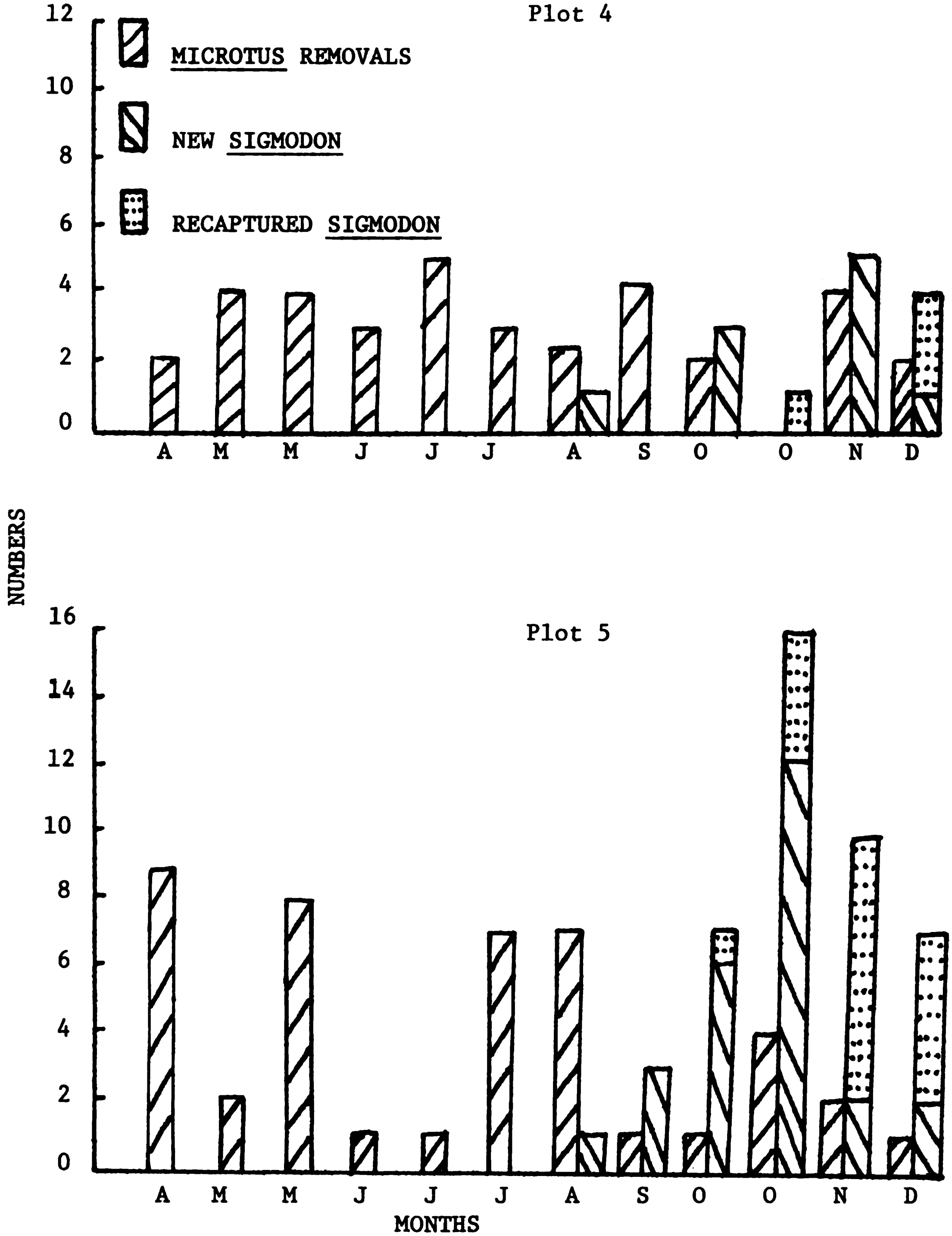


Figure 11. Relative numbers of new and recaptured *Sigmodon* and the numbers of *Microtus* removals on plots 4 and 5 (1971).

The *Sigmodon* population in plot 4 showed sporadic recruitment. *Microtus* removals declined in late October and recovered in November. The *Sigmodon* population in plot 5, like that in plot 1, showed constant recruitment from September through October when it also fell off to a lower, more constant rate. Removals of *Microtus* declined steadily from late October in this plot.

Mean Body Weights and Sex Ratios

The mean body weights and sex ratios (Joule and Jameson, 1972) of *Microtus* were calculated for plots 1, 2, and 3 for the trapping periods before and after the appearance of *Sigmodon*. For plot 1 (neither species removed) the *Microtus* mean body weights before and after *Sigmodon* were respectively 35.2 grams and 35.8 grams. For plot 2 (neither species removed) these values were 36.7 grams and 32.4 grams. The values for plot 3 (*Sigmodon* removed) were 34.0 grams and 38.3 grams. Even though plot 3 differed from the two-species plots, none of the differences were significant.

The sex ratio for *Microtus* in plot 2 (neither species removed) changed significantly after the appearance of *Sigmodon* ($p < .05$, $x^2 = 5.6$). The proportion of females increased in the presence of *Sigmodon*. *Microtus* sex ratios in plots 1 and 3 did not change.

Since *Sigmodon* did not appear until late August, it was not possible to get the response of the *Microtus* populations to the cotton rats over what can be considered a reasonable amount of time. Also, the cotton rats which did appear were mainly juveniles and subadults which further reduced the likelihood that the voles came under the necessary interspecific pressure to reveal substantial declines. Other than providing an indication of a negative interaction, the above data on Microtus were experimentally inconclusive.

The late occurrence of the cotton rats indicated a low overwinter survival for Sigmodon in Kansas. Preliminary trapping in 1969 and 1970 also revealed small or non-existent Sigmodon populations in the early spring and summer. As will be discussed later, this is an important point to consider since this might allow Microtus the time it needs to complete its reproductive cycle.

Survivorship

Table 3 illustrates survivorship in Microtus and Sigmodon. The Microtus survival rate was lower in the presence of Sigmodon (plot 2) than in the plot without Sigmodon (plot 3) ($p < .05$, Mann-Whitney U test). It was difficult to conclude, however, that the cotton rats were the cause of this difference because of the low numbers of Sigmodon which were caught in plot 2 (see Figure 4). Also the vole survival was lowest on plot 2 for the year and for the interval before the appearance of Sigmodon. This suggested that some other factors probably limited Microtus survival rates before Sigmodon appeared and that the influence of Sigmodon on Microtus was no more than slight. Microtus did not affect the survival rates of the Sigmodon in any apparent way. The plots from which Microtus were removed had the lowest Sigmodon survival rates.

Mean Residence Times

Table 4 gives the mean residence times for all Microtus in plots 1, 2, and 3. There were no significant differences when the dual species plots were compared to the Sigmodon removal plot. The appearance of the

Table 3. Survival rates in *Microtus* and *Sigmodon* (per three weeks) (1971).

Plot	Species	Time	Survival rate for all animals
1	*Microtus*	year	.59
2	*Microtus*	year	.36
3	*Microtus*	year	.57
1	*Microtus*	before *Sigmodon*	.60
2	*Microtus*	before *Sigmodon*	.49
3	*Microtus*	before *Sigmodon*	.62
1	*Microtus*	after *Sigmodon*	.57
2	*Microtus*	after *Sigmodon*	.18
3	*Microtus*	after *Sigmodon*	.67
1	*Sigmodon*	year	.72
2	*Sigmodon*	year	.67
4	*Sigmodon*	year	.46
5	*Sigmodon*	year	.48

Table 4. Mean residence times (weeks) for *Microtus* (± 1 SE).

	Plot 1	Plot 2	Plot 3
Before *Sigmodon*	6.6 ± 2.7	6.9 ± 2.6	6.9 ± 2.9
After *Sigmodon*	6.3 ± 1.7	3.6 ± 1.7	5.4 ± 3.0

cotton rats did not significantly alter the residence times of the voles when their use of the plots was compared over time. The values for plot 2 were the only indication that the Sigmodon occupation had any effect on the voles. Perhaps a longer exposure to a larger cotton rat population would produce significant results.

Spatial Distribution

Figures 12 through 16 reveal the spatial distribution of centers of activity of individual Microtus and Sigmodon in plots 1, 2, and 3. It appeared that there was a change in the spatial distribution of the centers of activity of the voles when the plots were compared over time. It is debatable whether this change was a result of the Sigmodon invasion or other factors related to the response of the Microtus populations to seasonal influences. This change in dispersion in plot 3 (Sigmodon removed) also could have been the result of undetermined factors. Again, a longer period of exposure to cotton rats might have produced more useful data to look at this alleged interaction.

Microtus Range Overlap

An index to the range overlap of a population can be gained by counting the number of trapsites which have captured two or more individuals (Metzgar and Hill, 1971). Figure 17 illustrates these data for plots 1, 2, and 3. When the dual species plots were compared to the Sigmodon removal plot, there were no significant differences in the vole range overlaps ($X^2 = 2.77$, $p < .30$). When the findings from the plots were compared over time, the Microtus in plot 2 were the only ones to change significantly in range overlap after the appearance of Sigmodon (18 trapsites to 7 trapsites, $X^2 = 4.8$, $p < .05$). In plot 3, the

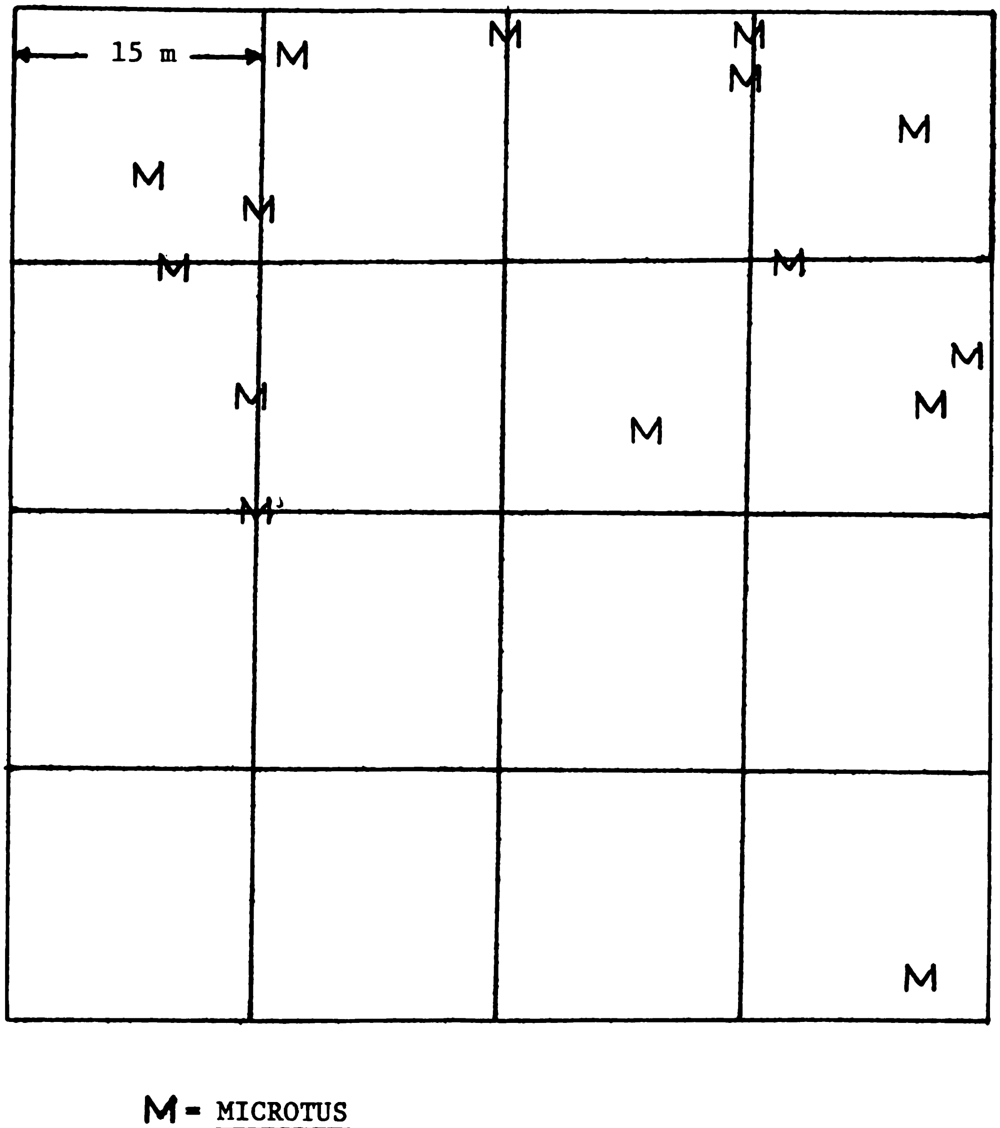
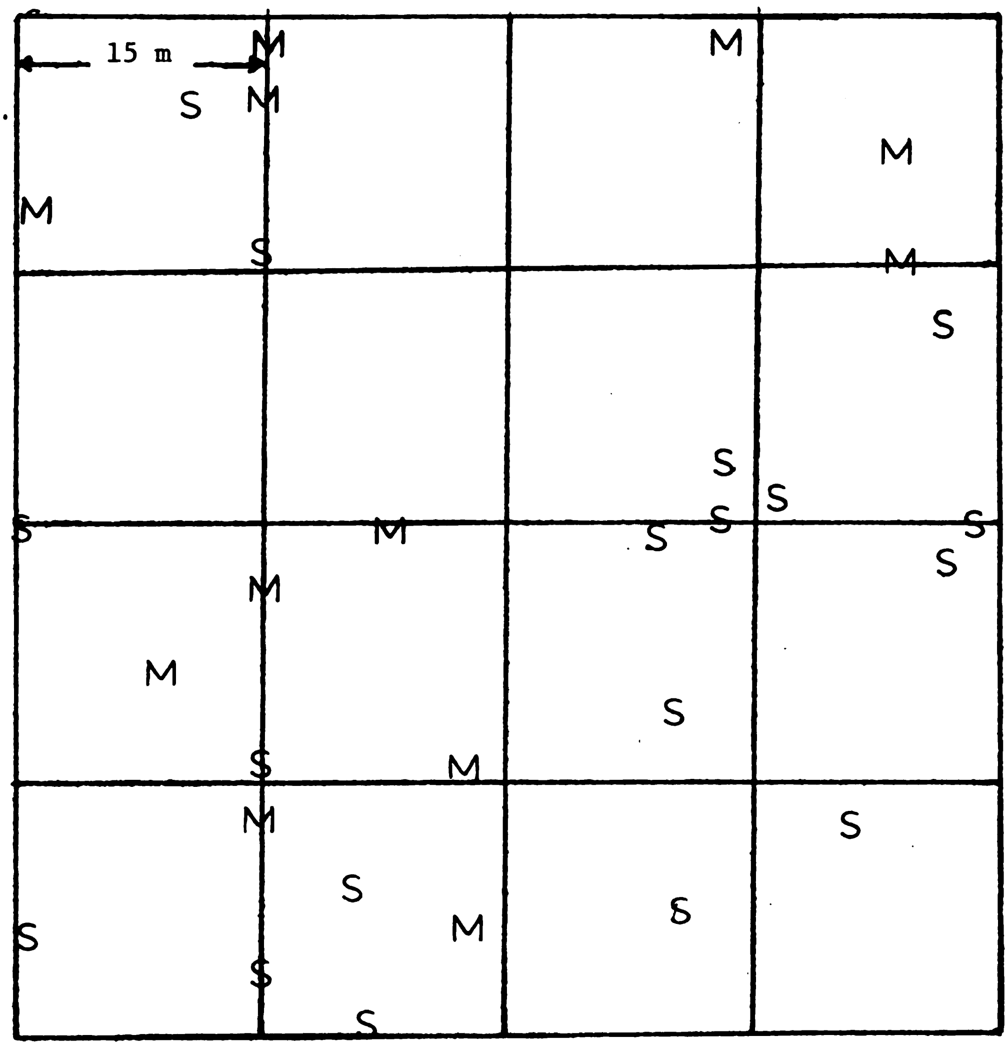


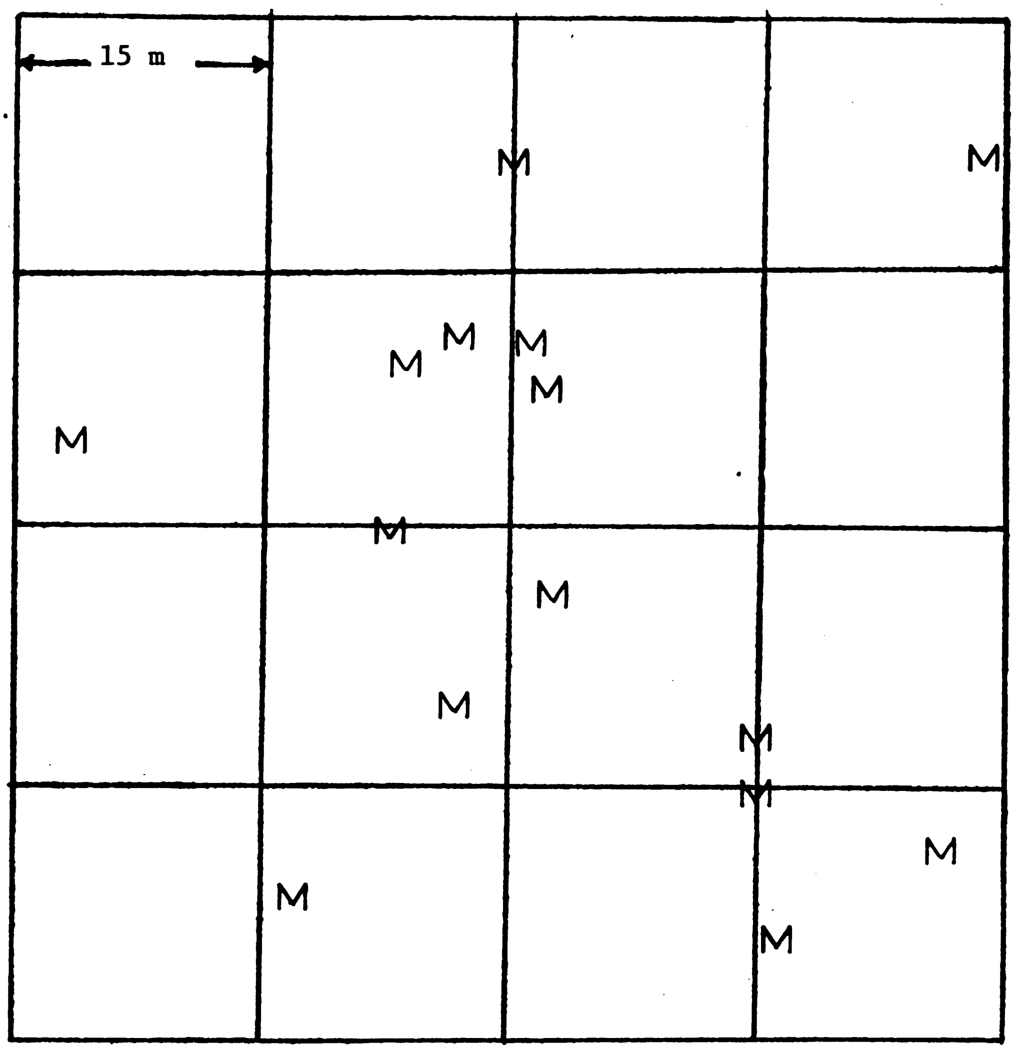
Figure 12. Spatial distribution of centers of activity of individual Microtus (Plot 1 - before appearance of Sigmodon).



M = MICROTUS

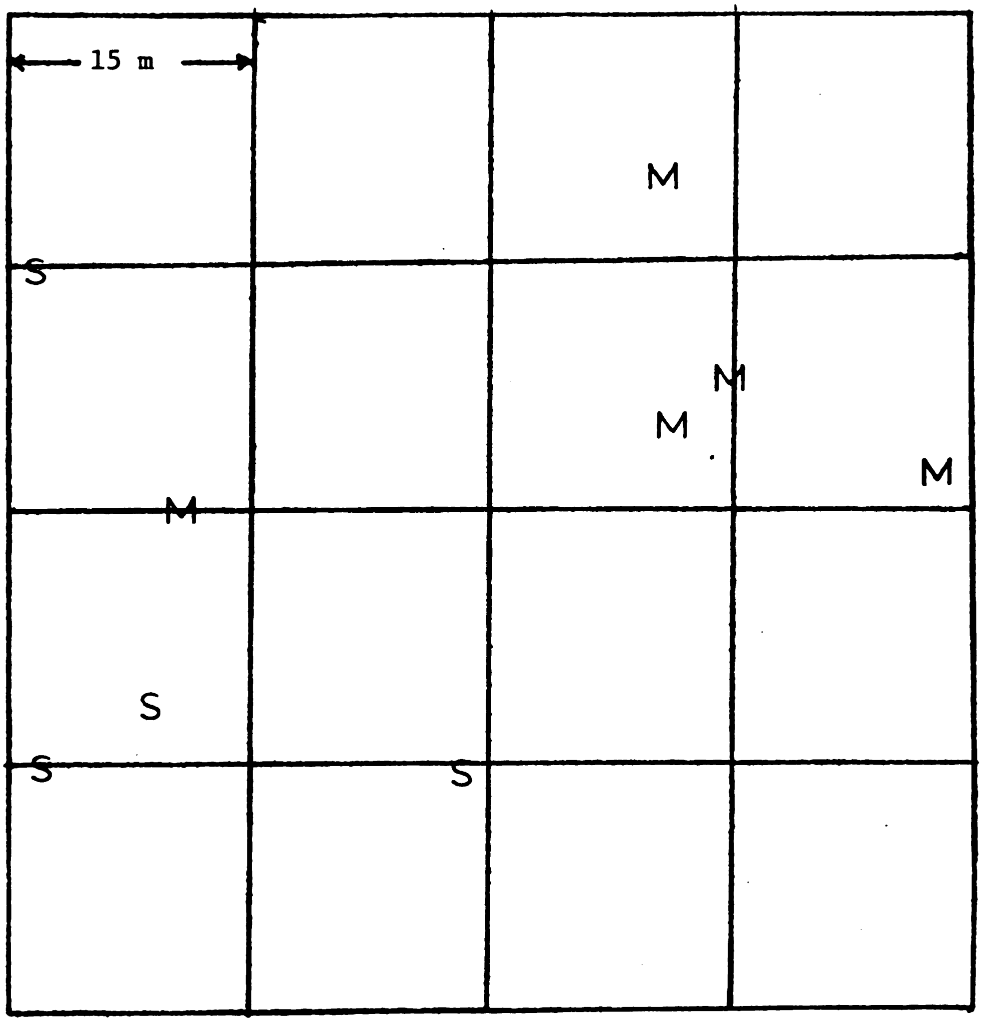
S = SIGMODON

Figure 13. Spatial distribution of centers of activity of individual Microtus and Sigmodon (Plot 1 - after appearance of Sigmodon).



M = MICROTUS

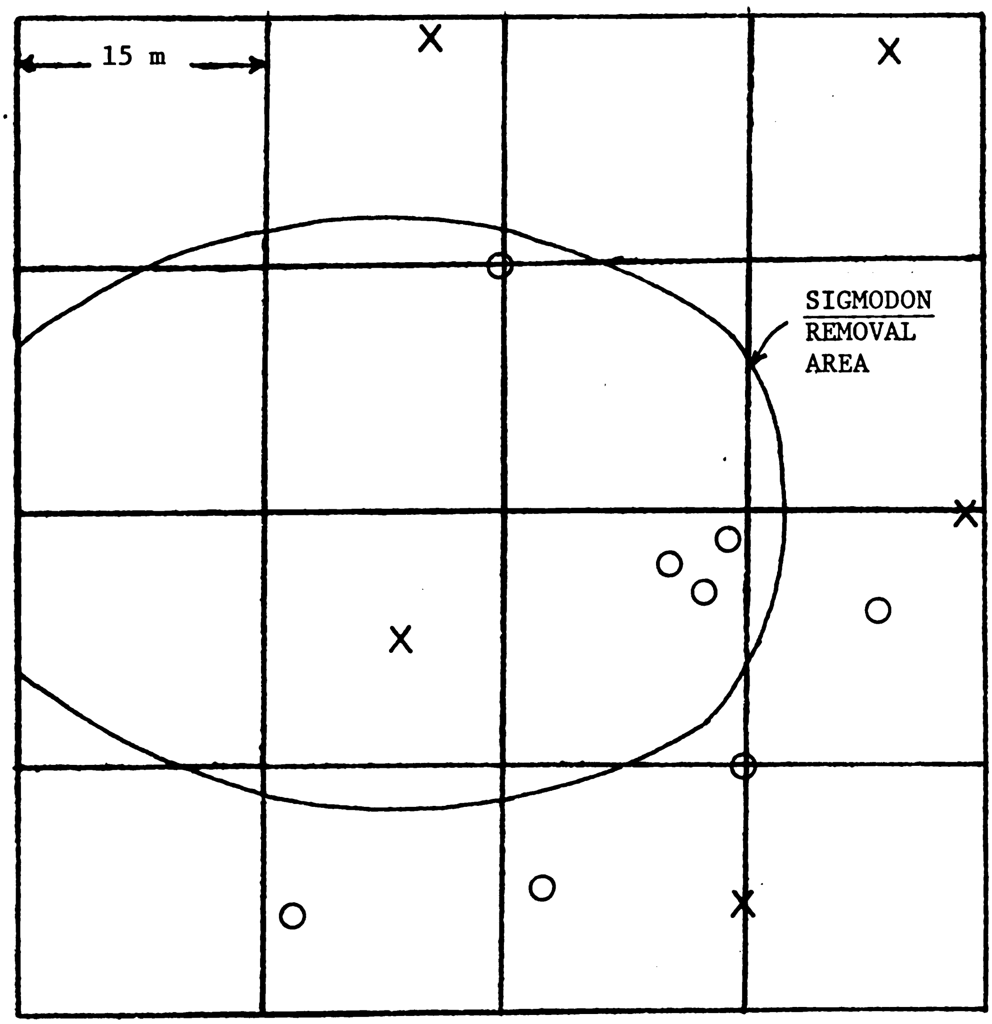
Figure 14. Spatial distribution of centers of activity of individual *Microtus* (Plot 2 - before appearance of *Sigmodon*).



M = MICROTUS

S = SIGMODON

Figure 15. Spatial distribution of centers of activity of individual *Microtus* and *Sigmodon* (Plot 2 - after appearance of *Sigmodon*).



O = Microtus before Sigmodon

X = Microtus after Sigmodon

Figure 16. Spatial distribution of centers of activity of individual Microtus (Plot 3 - before appearance of and after removal of Sigmodon).

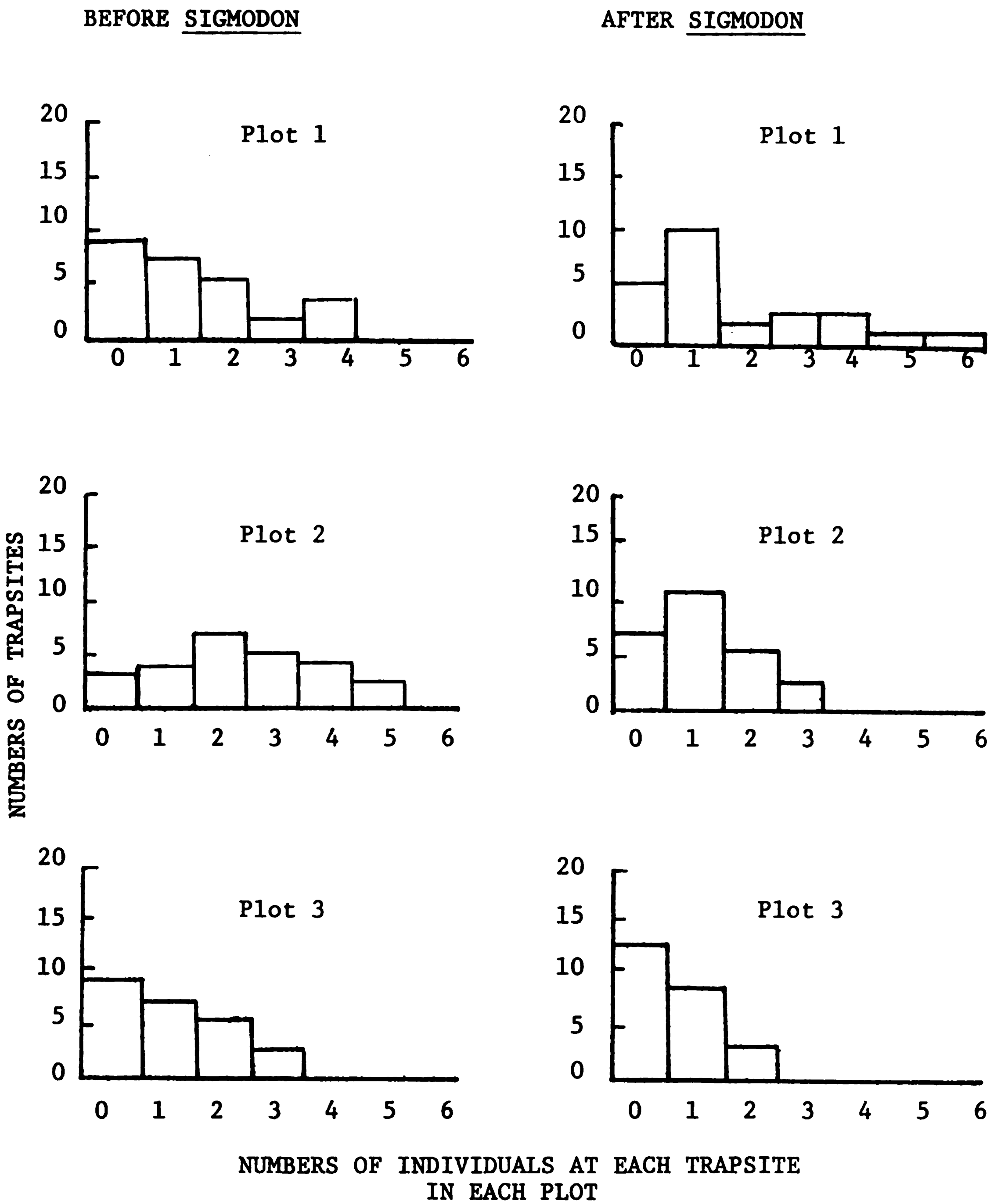


Figure 17. The numbers of trapsites with captures of none, one, two, etc. individual <u>Microtus</u> (before and after appearance of <u>Sigmodon</u> - 1971).

difference was fairly large ($X^2 = 1.60$, $p < .2$) but the range overlaps did not differ enough to be significant. This index is probably affected by radical changes in population density (Metzgar and Hill, 1971) and since plot 2 experienced a population decline in *Microtus* in October, the value was suspect.

Indices of Association

Coefficients - Table 5 gives the coefficients of association (C) for *Microtus* and *Sigmodon*. Plot 1 had the only significant negative association as revealed by the number of traps which captured none, one, or both species (see Cole, 1949). The *Sigmodon* were most dense in this plot which probably resulted in more frequent interspecific contact. Plot 2 did not have many *Sigmodon* at any time which probably resulted in the neutral index revealed in this plot. Plots 3, 4, 5, and 6 were expected to have neutral coefficients due to the removal of one or both species. This reduced the opportunity for interspecific contact on a prolonged basis. In contrast to the sign negative association index (Cole, 1949), no plot had a significantly negative correlation coefficient. The lack of conformity between the two tests may be due to a difference in their ability to reveal differences in trap utilization by the two species.

Trap and Capture Indices of Association - When the mean number of *Microtus* individuals per trap was compared to the number of *Sigmodon* individuals per trap, it was noticed that there were no significant differences in the numbers of voles at a trap due to the presence of two or more cotton rats. The reduced numbers at highly frequented *Sigmodon* traps and the near significant values for these comparisons

Table 5. Coefficients of interspecific association (C) for *Microtus* and *Sigmodon* (all plots) (August-December 1971).

Plot	C
1	-1.0 *
2	0.10
3	0.08
4	0.09
5	0.03
6	-0.07

C is computed from the number of traps catching none, one, or both species. Values run from -1.0 to +1.0 (negative association to positive association).

* Significant negative association.

($p < .1$, Mann-Whitney U test) did, however, suggest that a negative interaction could be suspected. Table 6 gives the values for the selected plots.

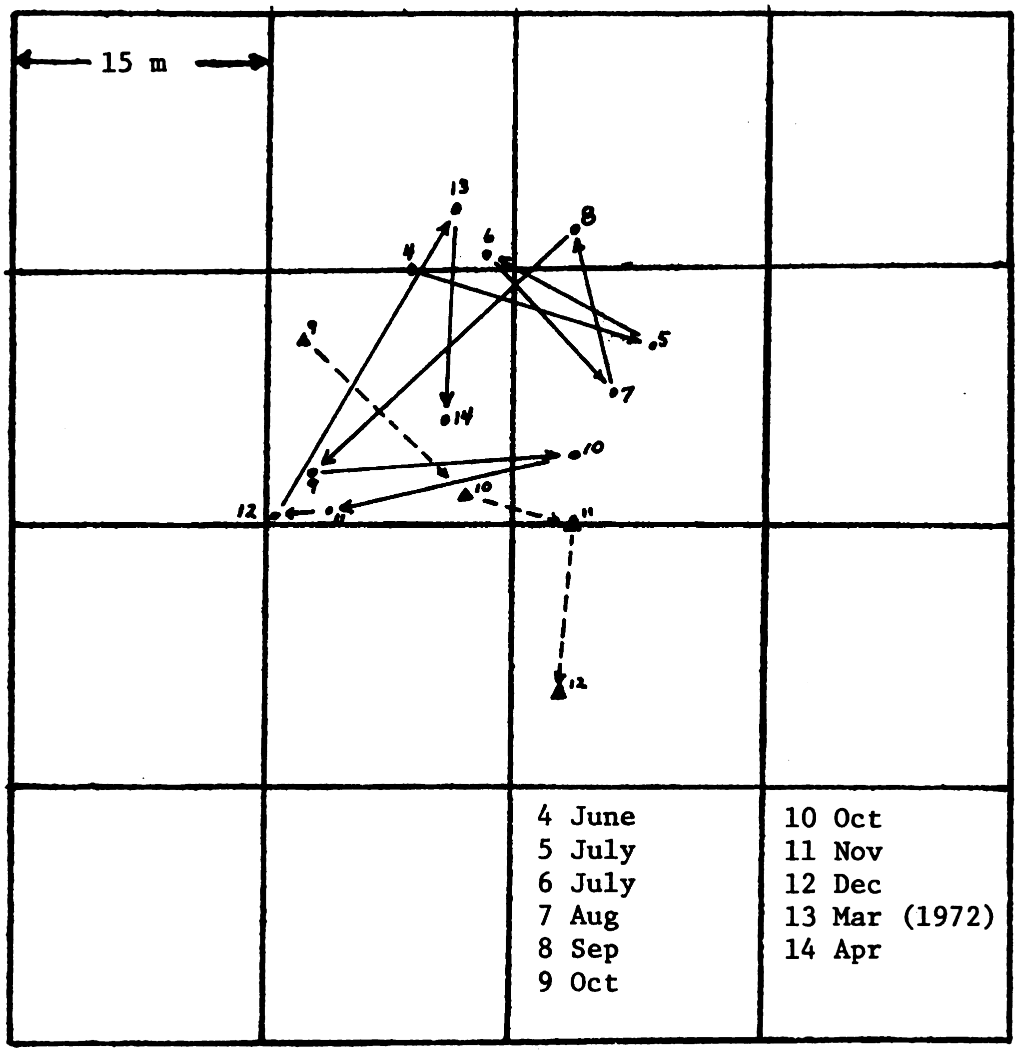
When the capture rates of the stations taking both *Microtus* and *Sigmodon* were compared over time, plots 1 and 2 had significantly different percentage capture rates of *Microtus* after the cotton rats appeared ($p < .05$, Mann-Whitney U test). The traps in plot 3 (where *Sigmodon* was removed) were not different in their vole capture rates. It is reasonable to at least partly attribute this change to the cotton rats since any seasonal factors would have caused the capture rates in plot 3 to change also. Ecological differences in the plots may have produced these effects but such seems unlikely.

Movements

Figures 18 through 20 show the monthly movements of the *Microtus* and *Sigmodon* populations. These data were analyzed by measuring the distances moved by each vole population in each plot. Before the appearance of *Sigmodon*, there were not significant differences between the dual species plots and the *Sigmodon* removal plot (the monthly movements were between 2 - 16 meters). After the appearance of *Sigmodon*, the population of *Microtus* in plot 3 (*Sigmodon* removed) moved significantly greater distances (6 - 52 meters) than the voles in plots 1 and 2 ($p < .05$, Mann-Whitney U test). This indicated that the *Microtus* population in plot 3 was more wide-ranging. This difference might have been due to the absence of *Sigmodon* or to intraspecific factors operating in the individual *Microtus* populations.

Table 6. The mean number of individual Microtus per trap according to the number of Sigmodon per trap (1971).

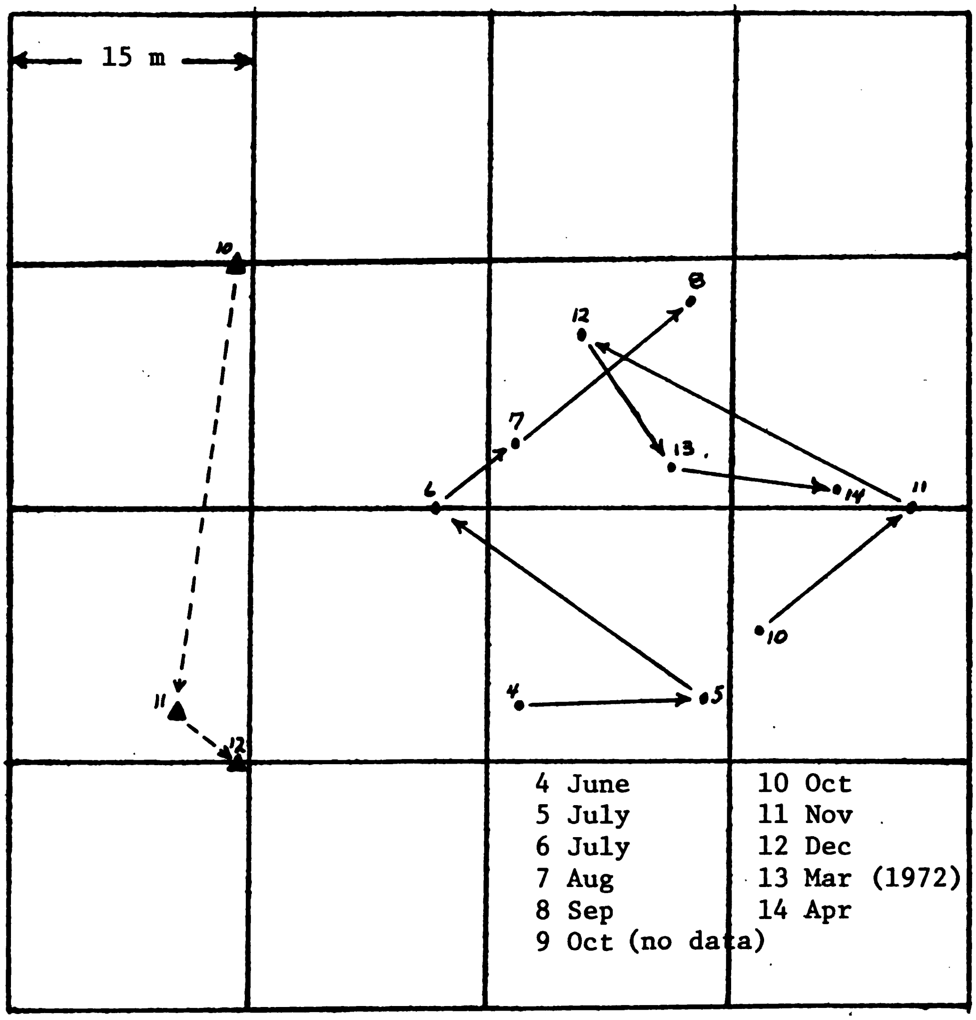
	Mean number of individual Microtus per trap	
Plot	$\leq$ 1 Sigmodon	$\geq$ 2 Sigmodon
1	3.50	1.73
2	1.11	0.60
4	0.72	0.75
5	1.0	0.75



——— *Microtus* population movements

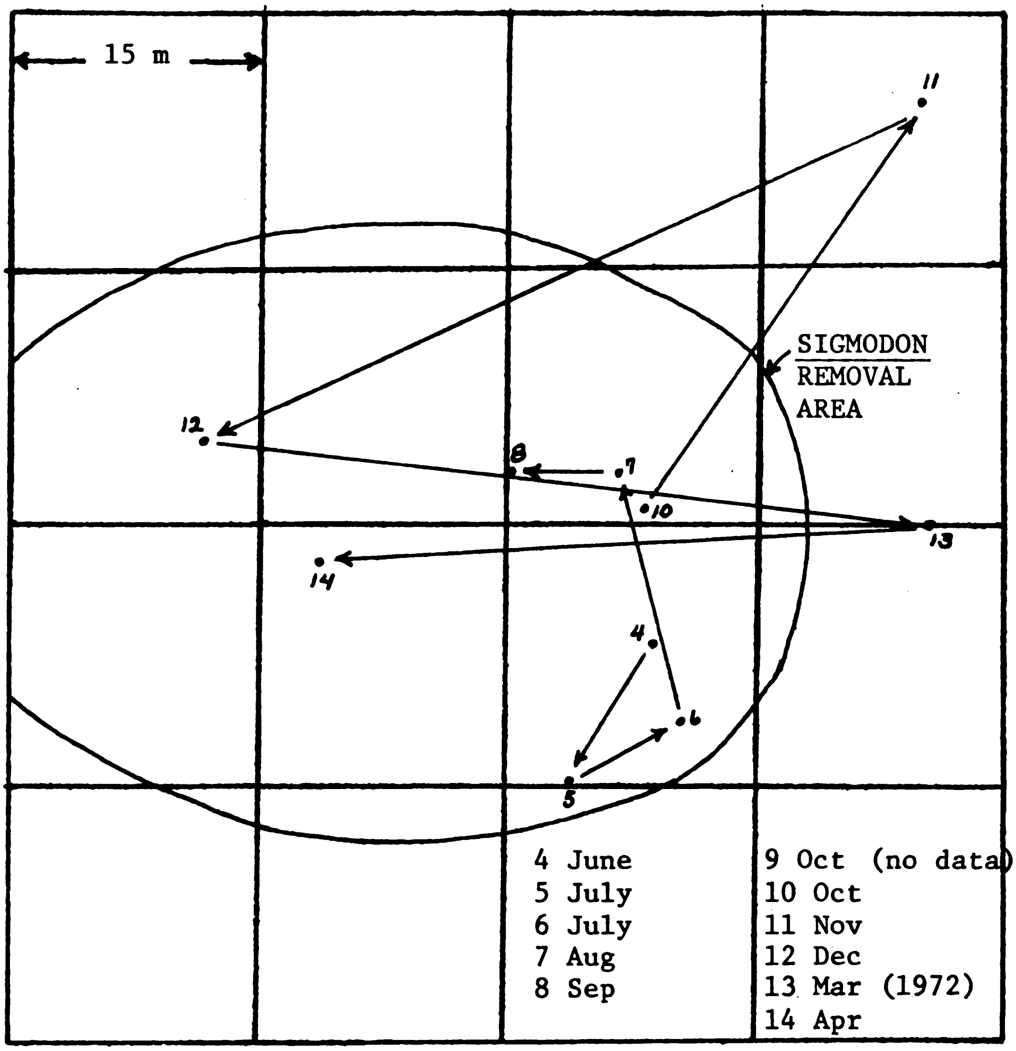
- - - - *Sigmodon* population movements

Figure 18. Population movements of *Microtus* and *Sigmodon* on plot 1 (1971-1972). (Locations numbered according to legend.)



——— Microtus population movements
- - - - Sigmodon population movements

Figure 19. Population movements of *Microtus* and *Sigmodon* on plot 2 (1971-1972). (Locations numbered according to legend.)



———— Microtus population movements

Figure 20. Population movements of Microtus on plot 3 (1971-1972). (Locations numbered according to legend.)

An index to individual movements is given in Table 7. The median number of different traps and the median number of captures per individual Microtus were not significantly different between the plots when Sigmodon was present. The only significant change occurred when the plots were compared over time (each plot before and after Sigmodon). The number of captures per individual Microtus dropped significantly after the occurrence of Sigmodon in plot 1 ($p < .05$, Mann-Whitney U test). The number of traps per individual Microtus dropped also but the difference was not significant ($p < .07$). If the Sigmodon had been more dense in plot 2 perhaps this plot would have shown a difference comparable to plot 1.

Migration Between Plots

The plots were invaded or vacated by Microtus and Sigmodon as shown in Table 8. Migration between plots characterized 13 percent of the recaptured voles and 16 percent of the Sigmodon individuals. Twenty-six percent of the Microtus migrants were active in the April-July period; 74 percent were active in the August-December period. These migrants were released or removed according to the experimental treatment of the plot that they invaded. The increased migration of the voles during the autumn periods may have been due to seasonal influences rather than the occurrence of the cotton rats.

Individual and Population Home Ranges

Tables 9 and 10 give the individual and population home range statistics (A4) for Microtus. When compared over time the major changes in the individual home ranges occurred in plots 1 and 2. These changes were not significant however, and the home ranges for the individuals

Table 7. The median number of different traps and the median number of captures per individual *Microtus* (1971). (Numbers of individuals are in parentheses.)

Plot	Median number of different traps per individual		Median number of captures per individual	
	Before *Sigmodon*	After *Sigmodon*	Before *Sigmodon*	After *Sigmodon*
1	2 (19)	1 (27)	2 (19)	1 (27)
2	1 (26)	1 (15)	1 (26)	1 (15)
3	1 (17)	1 (11)	1 (17)	1 (11)

The only significant difference was in captures per individual in plot 1 when compared before and after *Sigmodon*.

Table 8. The numbers of *Microtus* and *Sigmodon* invading or leaving the plots (1971).

Plot	Invaders		Departures	
	Microtus	*Sigmodon*	*Microtus*	*Sigmodon*
1	6	6	6	3
2	7	4	2	5
3	0	1	9	--
4	3	3	--	1
5	0	0	--	4
6	1	1	--	--

Table 9. Mean home range statistics (A4) for *Microtus* individuals in plots 1, 2, and 3 (1971).

Plot	N	Before *Sigmodon*	N	After *Sigmodon*
1	4	17.7	4	11.5
2	6	16.3	1	0.0
3	2	8.3	2	6.7
All	12	15.4	7	7.5 *

N equals the number of individuals captured 4 times.
* Significantly different after *Sigmodon* when compared to before *Sigmodon* (Mann-Whitney U test, see Siegel, 1956).

Table 10. Mean home range statistics (A4) for populations of *Microtus* in plots 1, 2, and 3 (1971).

Plot	Before *Sigmodon*	After *Sigmodon*
1	34.12	35.22
2	35.80	40.30
3	33.80	44.10

had to be pooled for all three plots before the ranges were significantly reduced over time ($p < .05$, Mann-Whitney U test). The numbers of individuals were too few to allow valid comparisons between the plots. Table 10 reveals that there likewise were no significant differences between the plots and over time using the population home ranges. This failure to find significant changes makes it difficult to derive conclusions regarding the effect of *Sigmodon* on the home ranges of *Microtus*. The pooled comparison using individual home ranges was complicated by many uncontrolled variables. The population home range increase in plot 3 was nearly twice that in the other plots but the difference was not significant.

Trappability

Trappability (Krebs, 1969) was computed for the *Microtus* and *Sigmodon* populations. For the year *Microtus* had a trappability of .80; *Sigmodon* had a trappability of .85. In plots 1 and 2, the vole trappability was, respectively, .82 and .86 before *Sigmodon* and .76 and .62 after *Sigmodon*. In plot 3, the trappability was .81 before *Sigmodon* and .90 after *Sigmodon*. The *Microtus* in plot 2 were the only ones which differed significantly from those in plot 3 in trappability during the cotton rat occupation ($p < .05$, Mann-Whitney U test). If *Microtus* is less trappable in the presence of *Sigmodon* then they should have become less trappable in plot 1 also since it had the highest cotton rat densities. Unless the plot vegetation (dense in plot 1, sparce in plot 2, see Table 2) affected the *Microtus*-*Sigmodon* frequency of contact, it is difficult to explain this discrepancy in the results.

All captured Microtus were examined for the presence of wounds, especially the large slashes indicative of a Sigmodon encounter (Terman and Johnson, 1971). During autumn, plots 1, 2, and 4 had voles which showed large slashes on the back and hindquarters. Such individuals, however, were rare in the samples. No wounds were noticed before the cotton rats were on the plots.

Field results of experimental studies on interspecific interaction are rarely conclusive because of the many environmental factors which remain uncontrolled. These field results were complicated by seasonal factors, plot differences, and changes in population densities. If a negative interaction occurred, it probably was not well detected because techniques for monitoring the individual interactions were not available. Such individual interactions appear to be the mechanism of competition (Grant, 1970). In order to investigate these interactions a laboratory study was undertaken.

LABORATORY INVESTIGATIONS

Many of the variables which complicate the field experiment can be controlled in the laboratory. For this reason, the alleged *Microtus-Sigmodon* interaction was examined in the laboratory. The hypotheses tested were suggested by the field results of the present study and by the observations and comments of other investigators.

(1) If interspecific aggression between *Microtus* and *Sigmodon* is the mechanism favoring cotton rats over voles (Baker, 1971; Martin, 1956), then *Sigmodon* should be aggressive toward *Microtus* and dominant in the interspecific encounters. I hypothesized that *Sigmodon* would actively attack *Microtus* and would be aggressively dominant in interspecific pairings.

(2) If *Sigmodon* limits the spatial distribution of *Microtus* (Baker, 1969; Fleharty and Olson, 1969; Terman and Johnson, 1971), this phenomenon should be observable in a laboratory arena. I hypothesized that voles would reduce their use of areas occupied by *Sigmodon*. Further, if the amount of habitat cover (complexity) affects this relationship (Crombie, 1946; Krebs *et al.*, 1971; MacArthur, 1972), then I hypothesized that dense cover would enable *Microtus* and *Sigmodon* to occupy the same area.

(3) If the *Microtus-Sigmodon* interaction lacks interspecific recognition and avoidance (Baker, 1971; Brown, 1966; Calhoun,

1963; Jameson, 1947), cotton rats should affect the movement of voles only when *Sigmodon* comes into actual physical contact with *Microtus*. I hypothesized that vole movements would not be affected by a confined cotton rat but would be affected by a free ranging cotton rat.

Should most of these questions be answered, a model of the *Microtus*-*Sigmodon* interaction could then be constructed which might help explain the numerical and spatial observations on these two species throughout their geographical ranges.

Rodents used for the laboratory experiments were removed from the field during 1970-1972. These animals were maintained in the live animal facility of the Department of Biology, Tabor College, Hillsboro, Kansas, and were caged under conditions described by Colvin and Colvin (1970). The facility at Tabor College is located in a heated basement which remains relatively cool in the summer and warm in the winter. Relative humidity was always rather high and light was supplied through overhead windows and by a 100 watt incandescent bulb. Light intensity in the room during the day was always near 10 fc. The animals were kept on a light cycle of 12 hours daylight and 12 hours darkness. Water and food (oats and grass) were given *ad lib*.

Aggressive Behavior

Interspecific aggression has been proposed as a mechanism by which *Sigmodon* may exclude *Microtus* (Baker, 1971; Martin, 1956). Terman and Johnson (1971) noted aggressive behavior between *Sigmodon hispidus* and *Microtus pennsylvanicus* when the two were together in a confined laboratory arena. *Sigmodon* appeared to be dominant and actually killed and ate some juvenile *Microtus*. Martin (1956) reported that *S. hispidus* killed and ate *Microtus* when the two were captured in the same live trap. Eugene Fleharty (personal communication) observed *S. hispidus* to be dominant over *Microtus ochrogaster* when the two were placed together in a terrarium.

On the basis of this information, I hypothesized that *Sigmodon hispidus* would be aggressive towards and dominant over *Microtus ochrogaster* in interspecific encounters.

Subjects

All animals tested were wild males recently taken from the field. Before being used, each rodent was caged for one month to allow it to acclimate to the laboratory environment. Only adult animals (as defined under Field Methods) were used and each animal was tested only once.

Treatments

The purpose of this experiment was to determine if *Sigmodon* was aggressive towards and dominant over *Microtus*. Individuals of each species were tested in (1) a neutral arena; and (2) in an arena formerly inhabited by the other species. If one species was aggressive towards and dominant over the other species in both of these treatments, it was concluded that this species would be victorious in most of the encounters that might take place in the field.

Apparatus and Procedures

Each test arena consisted of a terrarium (91 x 30 x 30 cm.) with a solid, central, removable partition and a floor covering of soil and grass. For each test a cotton rat was placed in one section and a vole in the other. The test animals were allowed to acclimate, and then the partition which separated them was removed. The behavior patterns exhibited were observed and recorded for 30 minutes (under red light, following Finley, 1959), and the dominant animal was determined by the aggressiveness (attack) or avoidance that was exhibited. Thirty interspecific pairings were observed, 15 in each of the treatments (neutral and resident arenas).

Analysis and Results

A noticeable interaction occurred in all but 8 of the 30 pairings. *Sigmodon* dominated *Microtus* in each encounter. *Sigmodon* was aggressive towards *Microtus* even in those trials where *Microtus* had been the resident species in the arena. Ten *Microtus* eventually died as a result of injuries which were received in the pairings. Three of eight trials without interactions were in the neutral arena, one occurred when *Sigmodon* was the resident species, and four occurred when *Microtus* was resident.

Sigmodon exhibited either attack (Krebs, 1970) or did not react to *Microtus*. *Microtus* exhibited agonistic behavior only after it came into physical contact with the cotton rat. Teeth chattering (Getz, 1962) was a common reaction as was submission, avoidance, and threat (Krebs, 1970).

During 10 preliminary interspecific pairings, it was noticed that *Sigmodon* subadults ($\leq$ 60 grams) were non-aggressive toward *Microtus*. This point deserves further study for it could be important to the interaction in the field.

Spatial Distribution

When *Sigmodon* becomes abundant in an area, it is often noted that *Microtus* becomes scarce or nonexistent (Baker, 1969; Fleharty and Olson, 1969; Frydendall, 1969; Martin, 1956, 1960). Terman and Johnson (1971) reported that *S. hispidus* limited the movements of *M. pennsylvanicus* when the two were in a confined area. The purpose of the present experiment was to determine if *Microtus* would use areas occupied by *Sigmodon* under (1) sparse cover conditions, and (2) under dense cover conditions. I hypothesized that *Microtus* would reduce their use of those areas occupied by *Sigmodon* when cover was sparse but would not reduce their use of those areas when cover was dense. The data from Terman and Johnson (1971) indicated that co-utilization would not occur under sparse cover conditions. The results of Crombie (1946), Morris (1969), and the theories of MacArthur (1972) suggested that dense cover would allow co-utilization of an area.

Subjects

All *Microtus* and *Sigmodon* used in these tests were adults recently captured from the field. For the tests using sparse cover conditions, 15 groups of three male adult *Microtus* and 15 bisexual pairs of adult *Sigmodon* were used. For the tests using dense cover conditions, 13 different groups of *Microtus* and *Sigmodon* were tested. Each group was used only once so all animals were naive to the experimental conditions.

Apparatus

A test chamber (2.4 x 1.2 x 1.2 m.) similar to that described by Terman and Johnson (1971) was constructed (see Figure 21). Observations could be made over the top of the 1.2 m. sides of the chamber without disturbing the animals. Also, a red light was used to make the observations. Water and food (oats) were supplied in excess in each compartment. The compartments were connected by holes measuring 2.5 cm. and 1.3 cm. in the partitions at floor level. These openings could be closed at will. *Sigmodon* was able to go through the large holes but not through the small holes. Between observations the arena was covered with a canvas which caused the floor area to be similar to natural habitat in light intensity.

Two environmental conditions were used: sparse and dense cover. Sparse cover consisted of a mixture of grass and soil placed on the floor of the arena allowing the animals to be easily seen from overhead. Dense cover consisted of the grass-soil substratum with shredded paper added in excess so that the animals could not be seen from overhead without moving the cover material. A stiff wire probe was used to separate the cover at places where there was activity in order for the observer to see the animals.

Treatments and Procedures

To test the hypothesis that voles would reduce their use of those parts of a confined area occupied by cotton rats (restriction of spatial distribution), fifteen groups of three male adult voles and fifteen bisexual pairs of adult cotton rats were subjected to the following three trials under sparse cover conditions. After the voles had acclimated to the entire arena for three days, the first experimental trial consisted of introducing the pair of *Sigmodon* into compartment A. Subsequently, locations of the individuals by compartment were recorded at 18

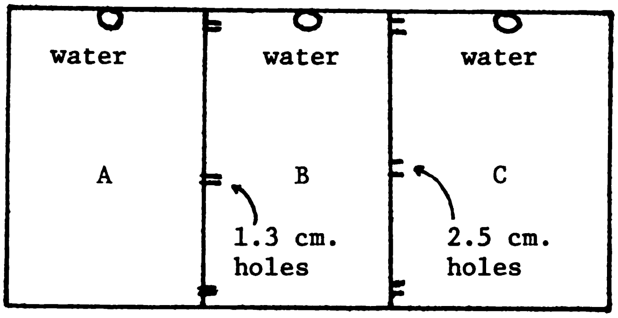


Figure 21. The experimental arena used to test for spatial restriction.

irregular intervals over a three-day period. The voles could freely move throughout all sections but the cotton rats were confined to section A.

The second experimental trial consisted of placing the pair of cotton rats in compartments B and C. The voles were left in the compartments in which they were found at the end of trial one. They could freely move throughout all the sections, but the cotton rats were now confined to sections B and C. Observations were recorded as in trial one.

To exclude the possibility of position effect, a control test (trial 3) in which only voles were used was run. During these observations the voles were able to move freely from one compartment to another. During the trials, if an animal died it was replaced by another.

To determine the effect of dense cover on this interaction, thirteen different groups of _Microtus_ and _Sigmodon_ were tested with compartments B and C containing dense cover. After the voles had acclimated for three days, trial one in this experiment consisted of placing the _Sigmodon_ in B and C. Observations were carefully taken at 18 intervals over a three-day period as in the first experiment.

For the second trial, the cover material was carefully removed, leaving the animals in sparse cover as in the first experiment. After one day, observations were recorded for the three-day period. This trial was used to verify the effect of the cover in trial one.

Trial three was a control test in which only voles were used. Before these observations, the cover was replaced in the compartments B and C.

Two different groups of three male adult _Microtus_ were examined in a third experiment. Two pairs of _Sigmodon_ were placed in dense cover along with the voles. At this high _Sigmodon_ density, it was expected that the voles would not coexist with the cotton rats.

Analysis and Results

The results are presented in Table 11. The number of _Microtus_ in each compartment was compared between treatments using the Friedman two-way analysis of variance for the data from the sparse cover conditions. The number of _Microtus_ in each compartment varied significantly between the treatments ($p < .001$) under sparse cover. This indicated that the _Sigmodon_ significantly excluded _Microtus_ from compartments it occupied under sparse cover conditions.

Under dense cover conditions, the number of _Microtus_ in each compartment was examined when _Sigmodon_ was present in compartments B and C and when _Sigmodon_ was absent from these compartments. The Wilcoxon matched-pairs signed-ranks test was used to make this comparison. The number of _Microtus_ in each compartment did not vary significantly between these two treatments. This indicated that dense cover allowed the _Microtus_ to use those areas occupied by _Sigmodon_. When the cover material was removed (but not the _Sigmodon_) the distribution per compartment differed significantly from when the cover was present with the _Sigmodon_ ($p < .001$). This again indicated that cover was essential for the co-utilization of compartments.

Although not enough groups were tested to be statistically evaluated, the experiment using four _Sigmodon_ instead of two suggested that a high density of _Sigmodon_ might override the effect of the cover. Both

Table 11. The median number of *Microtus* in each compartment per observation under sparse cover (15 replications) and under dense cover (13 replications).

Treatment	Compartment A	SPARSE COVER Compartment B	Compartment C
Sigmodon in A	0 (0)	1 (12)	2 (17)
Sigmodon in B, C	3 (17)	0 (1)	0 (1)
Sigmodon not present	1 (15)	1 (11)	1 (12)
		DENSE COVER (in B, C)	
Sigmodon in B, C	0 (6)	1 (12)	1 (11)
Sigmodon in B, C - cover removed	3 (17)	0 (3)	0 (3)
Sigmodon not present - cover in B, C	0 (6)	1 (15)	1 (14)

Numbers in parentheses are the mean numbers of observations (rounded off) per three-day observation period that *Microtus* was observed in each compartment.

of the observed groups of <u>Microtus</u> declined to enter the compartments containing the four <u>Sigmodon</u>. They were noticed to remain in compartment A much more than did the <u>Microtus</u> in the other dense cover experiments.

I also observed that <u>Microtus</u> would spend more time in compartment A (not accessible to <u>Sigmodon</u>) when <u>Sigmodon</u> was especially active, even in situations of dense cover. A rustling of the cover material usually signaled increased movement by <u>Sigmodon</u> and this observation was often coupled with the presence of <u>Microtus</u> in compartment A.

Other observations were taken on the location of nests, water usage, and tracks on smoked cards. Table 12 gives these data. A nest was recorded as being in a compartment if a nest was noticed in 70 percent of the groups. Water usage was termed "considerable" for a compartment when an average of $\geq$ 30 percent was used during the trials and "slight" when an average of $\leq$ 30 percent was used. In each compartment smoked cards were placed in a small cage accessible only to <u>Microtus</u>. At the end of every trial, these cards were checked for vole tracks. The percentage of groups making tracks in a particular compartment was then computed. These observations supported the distribution revealed by the animal counts.

Upon removal from the arena, all animals were checked for the presence of wounds. Only <u>Microtus</u> exhibited visible lacerations. In experiment one (sparse cover), 12 percent of the animals were wounded and 12 percent were found dead. In experiment two (dense cover), 35 percent of the animals were wounded and 7 percent died. In the two trials using four cotton rats, four of the voles had wounds and three of the voles died. One cotton rat died in the high density trials,

Table 12. Summary of nest location, water usage, and tracks in the test chamber (all experiments combined).

Test	Nest Location			Water Usage *			Percent of groups making tracks		
Sparse Cover	A	B	C	A	B	C	A	B	C
Sigmodon in A	0	X	X	0	+	+	0	100	100
Sigmodon in B, C	X	0	0	+	0	0	100	0	0
Sigmodon not present	X	X	X	+	+	+	100	100	100
Dense Cover									
Sigmodon in B, C	X	X	0	+	+	+	31	69	61
Sigmodon in B, C (cover removed)	X	0	0	+	0	0	38	0	0
Sigmodon not present (cover replaced)	0	X	X	+	+	+	15	54	46
Four *Sigmodon* in B, C (dense cover)	X	0	0	+	+	0	50	50	0

* + Considerable water usage ($\geq$30 percent of water used)
0 Slight water usage ($\leq$30 percent of water used)

presumably from intraspecific strife.

The Effect of *Sigmodon* on *Microtus* Movements

Baker (1971) has contended that since *Microtus* and *Sigmodon* are both runway prone grass eaters, they may have many head-on meetings in the narrow trails that are used by both species. Jameson (1947) reported capturing both species in the same runways. It has also been suggested that neither *Microtus* nor *Sigmodon* seem to have the complex social organization required to avoid frequent inter-individual contacts (Brown, 1966; Calhoun, 1963; Getz, 1972). The question arises as to what mechanism may then allow *Sigmodon* to restrict the movements of *Microtus*. I hypothesized that *Sigmodon* would only affect the movements of individual *Microtus* when there were frequent contacts (tactile) between the two.

Subjects

A total of 16 male adult *Microtus* and 16 adult *Sigmodon* were used for this experiment. All animals tested were recently removed from the field and thus new to the experimental situation. The animals were kept in the laboratory for at least a week before they were used for experimental purposes.

Apparatus

To test the hypothesis that *Microtus* movements would only be affected by frequent contact with a cotton rat, a tunnel was constructed (1.8 x 0.5 x 0.5 m.) with an adjoining cage (see Figure 22). For non-contact encounters a wild-caught, healthy, active cotton rat was placed in the cage. The cage was then closed and placed midway across the

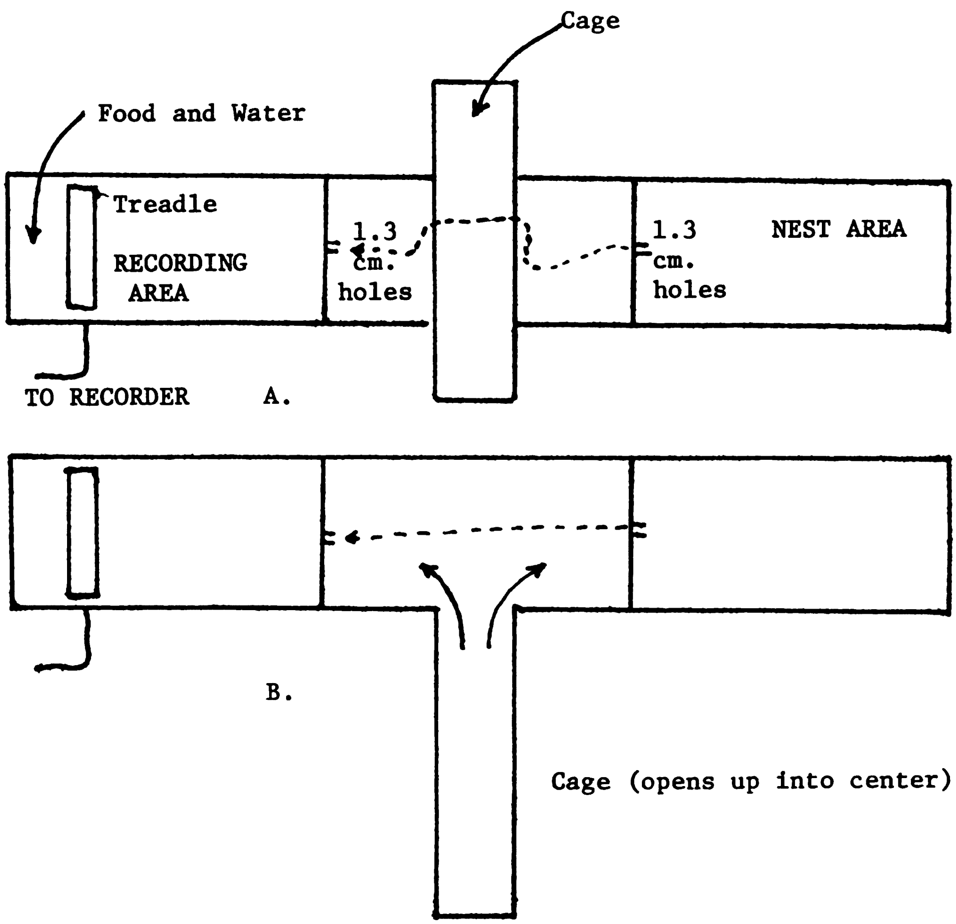


Figure 22. The movement tunnel apparatus (A - no contact; B - contact).

tunnel (Figure 22-A). The approaching *Microtus* could see, hear, and smell the cotton rat but could not enter into combat. The vole was free to pass over the cage and enter the recording area which had a treadle connected to a recorder (Heath-Kit) on a 24 hour cycle. When the vole stepped on the treadle, an electrical circuit was closed which caused the recorder to make a mark at the corresponding time of the cycle. The lights in the laboratory were set to turn on and off at sunrise and sunset.

To allow contact, the cage was simply moved to one side so that it opened up into the central part of the tunnel (Figure 22-B). The tunnel had sliding panels with 1.3 cm. sized holes which prevented the *Sigmodon* from entering the recording area and the nest area of *Microtus*. The nest area was darkened and contained cotton batting. The recording area was painted white and contained approximately 75 percent of the food and water required by an individual rodent in 24 hours. The nest area contained the rest of the food and water which prevented starvation but did not remove the motivation to go into the recording area.

To determine the activity of *Sigmodon*, the partitions were removed. The cotton rat could be tested alone or with a *Microtus* confined in the cage.

Treatments and Procedures

Eight adult *Microtus* were subjected to noncontact encounters with *Sigmodon* and eight other adult voles were subjected to contact encounters. All animals tested were unfamiliar with the tunnel and in most cases were recently captured from the field. Ten adult *Sigmodon* were also tested with a *Microtus* confined in the cage.

Each animal was acclimated to the tunnel for one day. It was then tested alone, with the other species, and then alone again. The tests were run in sequence. The last test should reveal any lasting effects of the interspecific encounter.

Activity periods were defined as 30-minute intervals with at least two marks. The number of activity periods was tallied for each animal and then recorded for each test. Table 13 gives the results of this experiment.

The proportion of total marks falling into three-hour intervals was computed. Figure 23 illustrates these data. The peaks of activity for both species occurred during 1800 - 0300 hours. This agrees favorably with Calhoun's data (1945) for these same animals.

Analysis and Results

That *Microtus* lived in the nest area and had to pass the *Sigmodon* to get to the recording area was indicated by the presence of nests and the abundant feces in the nest end of the tunnel. Also, when the animals were checked periodically during the experiment, *Microtus* was invariably in or near the nest area. Evidently the presence of cotton batting, the small amount of food and water (one-fourth of daily requirement), and the closed, darkened area were more desirable to the *Microtus* than the open recording area with its more abundant food and water but whitened background and no nest material. *Microtus* evidently moved to the recording area for the desired food and water but quickly returned to the seclusion of the nest area.

In both tests (contact and no contact) the number of *Microtus* activity periods was less when *Sigmodon* was in the tunnel. However, the

Table 13. The number of activity periods for individual *Microtus* under no contact and contact conditions.

No Contact (*Sigmodon* confined)

Animal	Alone	*Sigmodon* in cage	Difference
1	13	6	+ 7
2	10	6	+ 4
3	13	1	+12
4	5	7	- 2
5	17	13	+ 4
6	24	20	+ 4
7	9	3	+ 6
8	19	11	+ 8

Contact (*Sigmodon* free)

Animal	Alone	*Sigmodon* free	Difference
1	19	2	+17
2	18	0	+18
3	14	0	+14
4	8	0	+ 8
5	20	3	+17
6	16	1	+15
7	20	0	+20
8	17	9	+ 8

Differences were ranked and compared using the Mann-Whitney U test.

free ranging *Sigmodon* caused these differences to be much greater than the confined *Sigmodon* ($p < .01$, Mann-Whitney U test). This indicated that *Microtus* movements were more affected by *Sigmodon* when the two animals could physically contact each other. Inspection of the raw data indicated that this contact was sufficient to keep some *Microtus* from ever crossing the center area of the tunnel. Four of the voles remained in the nest area despite a shortage of food and water. After each test with the *Sigmodon*, the *Microtus* were again tested when alone. There was also a reduction in the number of activity periods in this last test. The differences between the treatments were not significant. This activity reduction may have been due to an increased familiarity with the tunnel.

Cotton rats did not significantly reduce their activity in the presence of voles although the number of activity periods was less. Cotton rats did not show the reduced activity in the last test as did *Microtus*.

The *Microtus* activity pattern during *Sigmodon* contact did not appear to be different from the other activity patterns (see Figure 23). It appeared that the amount of activity changed but not the scheduling of the activity. The peaks of activity for both species were in the same time interval (1800 - 0300 hours). This supported Calhoun's (1945) contention that these two species may be active at the same time in the field.

These laboratory results suggested that *Sigmodon* would be dominant in an interspecific encounter should it occur in the field. *Sigmodon* also seemed to have the ability to exclude *Microtus* spatially. Dense cover affects this relationship by allowing *Microtus* to enter areas occupied by *Sigmodon*. At higher *Sigmodon* densities, however, this

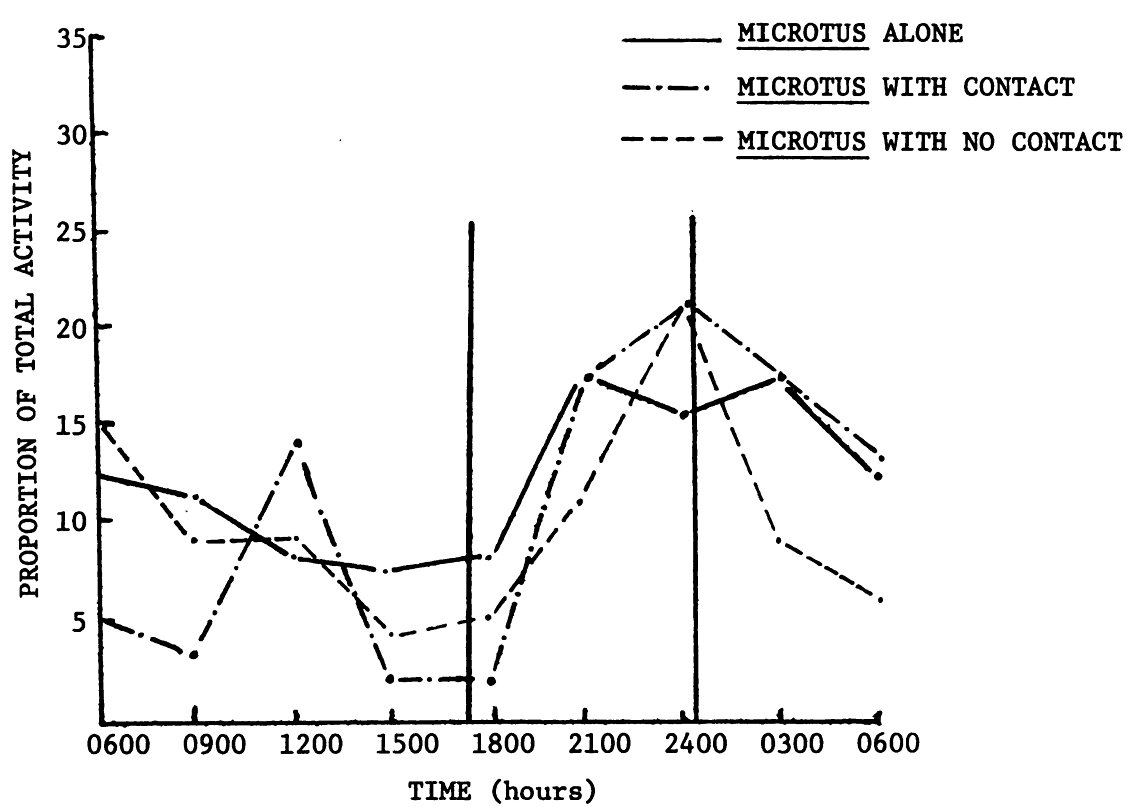


Figure 23. Activity pattern of *Microtus* alone, with *Sigmodon* contact, and without *Sigmodon* contact. (Vertical lines delineate a range of time in which *Sigmodon* activity was high.)

effect seemed to be lessened. The freedom of *Sigmodon* to contact *Microtus* seemed to be necessary before it could significantly affect the movements of *Microtus*.

DISCUSSION

Field Populations

Ayala (1972), Hutchinson (1953), Klopfer (1969), Fretwell (1972), and MacArthur (1972) point out the significance of environmental factors to the outcome of interspecific competition. Since Sigmodon is near the northern edge of its range (Cockrum, 1948), it was expected that over-winter survival in this species would be low in Kansas thus releasing Microtus from any major competitive pressures in early spring.

The late occurrence of Sigmodon in 1971 and the low population levels in the spring of 1969, 1970, and 1972 did strongly suggest that overwinter survival for this southern species may be low in Kansas. This phenomenon would appear to allow Microtus to be free from heavy Sigmodon contact for a relatively long time (for my data, late December until August). The severity of the Kansas winter is probably the principal factor. The climatic data in Table 1 reveal that the winters of 1970 and 1971 were severe in terms of snowfall. The spring trapping periods of these years yielded not a single cotton rat. The winter of 1972 was mild in comparison (little snowfall) and the April trapping period of that year was the only one that yielded any Sigmodon at all. The trapping records reported by Gier (1967) indicated a similar situation throughout the state of Kansas. There were only isolated instances of cotton rats being abundant in the spring of the year and it was a common observation to see them disappear after a severe winter. The states south of Kansas experience a milder winter which presumably allows more Sigmodon to overwinter. This permanent Sigmodon residence may contribute to the absence of the prairie vole from states such as Oklahoma.

The late summer emergence of Sigmodon and the shortened time of interspecific contact affected the experimental design of the field investigation. It was originally intended to observe the year-around response of one species population to the presence or absence of the other. As it happened, this situation was only partially realized. Between-the-plot comparisons were made over a relatively short period of time and with only a small population of Sigmodon being present. It is doubtful whether such conditions allowed the time and frequency of contact necessary to produce reliable results. The single plot comparisons (one plot observed over time) was affected by the presence of seasonal factors which may obscure any effects of interspecific interaction. The field results, consequently, merely suggested a negative interaction between the two species. The laboratory experiments examined this relationship between the two species in order to learn if their interactions were negative.

The October appearance of Sigmodon coincided with a sharp drop off in Microtus captures and recruitment. Data from Carley et al. (1970), Cooksey (1971), Fitch (1957), Keller and Krebs (1970), Krebs et al. (1969), Martin (1956), Meserve (1970), and Yang et al. (1970) did not indicate that a normal Microtus population cycle should crash this abruptly in October. At the same time, it was not possible to attribute the vole decline solely to the presence of the cotton rats because of the decline in plot 3, a plot which continually had its Sigmodon population removed. Since the plots were all part of a contiguous grassland area, it can be argued that all the plots, regardless of treatment, were equally affected by the Sigmodon invasion. Such things as immigration might be affected when field plots are contiguous. Such statements speak to the designs of future experiments. It may not be possible to look for population changes in plots which are in the same area and contiguous.

The plots containing both species did indicate that some coexistence was possible for the observed time interval. It may also be stated that the presence of good cover and food supply facilitated the coexistence. Plot 1 (abundant vegetation and cover) had a more constant Microtus population growth than plot 2 (lesser vegetation and cover). If these two plots had been observed over a longer period, this relationship might have become more evident.

The plots with low Sigmodon densities (plots 2, 3, 4, and 6) in 1971 had the highest Microtus densities in 1972. Although it can not be verified that the cotton rats caused this, such data do suggest a possible negative interaction. The presence of wounds on Microtus, the absence of Microtus juveniles from all plots except the Sigmodon removal plots, the winter increases in Microtus population levels, and plot differences in immigration also suggest that the interaction between the two species is negative.

Mean Body Weights and Sex Ratios

It was hypothesized that the mean body weights of Microtus would decrease over time in those plots where neither species was removed.

Joule and Jameson (1972) noticed a weight increase in *Sigmodon hispidus* females when *Reithrodontomys* and *Oryzomys* were removed from the habitat being used in common. Although the mean body weights decreased in the dual species plots and not in the *Sigmodon* removal plot, the differences were not significant. A longer period of interspecific contact may have produced significant results.

It was also hypothesized that the sex ratios of *Microtus* would change in the presence of *Sigmodon*. Joule and Jameson (1972) found this to occur in *Sigmodon* when its competitors were removed. This hypothesis was confirmed for plot 2 ($p < .05$) but not for plot 1 ($p < .1$). Again, the period of interspecific contact may not have been long enough for both plots to have significant values. These results, although not conclusive, suggest that *Sigmodon* might affect *Microtus* negatively in situations providing sufficient interspecific contact.

Survivorship and Mean Residence Times

If *Sigmodon* affects *Microtus* adversely, this should show up in reduced survival rates for *Microtus* in the dual species plots. It was hypothesized that *Microtus* survivorship would be lower in the presence than in the absence of *Sigmodon*. This hypothesis for lower vole survivorship was confirmed for plot 2 but not for plot 1. The reason for this was not clear. It seemed more probable that *Microtus* survival rates in plot 1 would drop since it had more *Sigmodon*. Unless the differences in cover between the two plots caused this discrepancy, it seems more likely that *Microtus* survival in plot 2 was more affected by environmental factors than by the few cotton rats which were captured on the plot.

It was also hypothesized that the mean residence times of Microtus would be lower in the presence of Sigmodon than in their absence. This hypothesis was not confirmed for either plot. All that can be said is that there might have been an inhibitory influence. The time of interspecific contact was probably too brief to cause significant differences. Also, the numbers of Sigmodon on the study area as a whole were probably low as was shown by the removal rates from plot 6 (both species removed). While Microtus were taken with regularity from this plot, Sigmodon were taken only sporadically with never more than one individual being taken in a trapping period.

Spatial Distribution

In the absence of procedures for analyzing the data on spatial distribution, examination of the raw data did not suggest any plot differences between the dual species plots and the Sigmodon removal plot during the Sigmodon occupation. There did seem to be major differences which appeared when the plots were compared individually over time. When Sigmodon appeared in plot 1, Microtus seemed to leave former areas of concentration. Also, there were few Microtus around areas of concentrated Sigmodon activity. This was also the case in plot 2. Since the Sigmodon in plot 3 were removed, it was expected that this plot would not show obvious changes in Microtus spatial distribution over time. However, Microtus in this plot also appeared to change which leads to the conclusion that factors other than the presence of Sigmodon were operative. It was not possible to ascertain the role of interspecific strife in these distributional changes which again means that the data were only suggestive.

Microtus Range Overlap

At the onset of the field experiment, it was expected that the *Sigmodon* would cause the individual ranges of *Microtus* to overlap due to the movement limitations that the cotton rats might impose on the voles. This hypothesis was rejected when the plots were compared with each other. When the individual plots were compared over time, plot 2 was the only plot which changed significantly in range overlaps. However, this change was not in the expected direction. The ranges became more exclusive which indicated that something other than the *Sigmodon* (which were few in number) caused this change. Since both plots 2 and 3 showed large changes, it was concluded that changes in population density were the cause of these changes. Both plots experienced sudden declines which probably reduced the chances for any given trap to capture more than two voles. This measure is probably not very useful in long term studies where population densities may change radically.

Indices of Association

Coefficients - Cole's (1949) coefficient of association indicated a negative interaction between the two species in plot 1 (see Table 5). Plot 2 presumably did not show this because of lower densities of *Sigmodon* which resulted in reduced opporunities for interspecific contact. Plots 3, 4, 5, and 6 showed neutral values primarily because of the reduced contact due to the removal program. Since plot 2 did not have an adequate density of cotton rats, plot 1 was the only one that could be used to verify the hypothesis that the two species were negatively associated. Even though the correlation coefficient for this plot was not significantly negative, the very significant value for Cole's index remains as convincing evidence for a negative interaction. In summary, this index revealed a negative interaction where the opportunity for interspecific contact was high. Seasonal influences, plot differences, and fluctuating rodent populations all acted to reduce the statistical validity of the index. Even considering these factors, there does appear to be evidence that the *Sigmodon* and *Microtus* reacted negatively to each other.

Trap and Capture Indices of Association - It was expected that traps which captured two or more *Sigmodon* would capture lower numbers of *Microtus* than traps which had fewer *Sigmodon* (Table 6). Although the number of *Microtus* at these traps was lower, the difference was not significant. It was also expected that the trap capture rates of *Microtus* in the dual species plots would change more than the trap capture rates in the removal plots. The rates in the dual species plot did change significantly while those in the removal plots did not change. This indicated that *Sigmodon* caused *Microtus* to use different traps or to become less trappable (see discussion of trappability). This suggested a negative association between the two species. The spatial distribution of *Microtus* and *Sigmodon* in plot 1 (see Figures 12 and 13) also suggested that the trap capture rates of *Microtus* might change with the appearance of *Sigmodon*.

Movements, Migration, Home Ranges, and Trappability

The hypothesis for significantly different population movements between the dual species plots and the *Sigmodon* removal was confirmed.

These results suggested that *Sigmodon* may limit the normal population movements of *Microtus*.

It was hypothesized that there would be significant differences between the plots in the median numbers of different traps and captures per individual *Microtus*. This hypothesis was not confirmed. It was also hypothesized that the plots containing both species would change significantly in the number of traps and captures per *Microtus* when compared over time. This hypothesis was confirmed for plot 1 but not for plot 2. The interplot differences were not significant but the over time comparison (before and after *Sigmodon*) for plot 1 was significant. This makes it difficult to conclude that *Sigmodon* negatively influenced *Microtus*. Were seasonal factors the cause of the change over time in plot 1? Also, why were there no interplot differences between the removal plots and the plots containing both species?

The increased amount of inter-plot movement by *Microtus* in autumn probably illustrated a response to seasonal factors rather than to the presence of cotton rats. That this increased movement takes place casts further doubt on the validity of making certain comparisons on the voles over time. Future experiments should take this into consideration.

It was hypothesized that individual and population home ranges of *Microtus* in the dual species plots would be smaller than those in the *Sigmodon* removal plot. However, there were too few individuals to make any comparisons between the plots using the individual home ranges. The individual home ranges were then pooled for all three plots and the difference was significant when the three plots were compared over time. Although seasonal factors complicated the comparison, it is noteworthy that the individual ranges decreased in size when it was expected that they would increase (as the autumn inter-plot movements would indicate). The hypothesis for decreased Microtus population home ranges was also rejected although the voles on the dual species plots had smaller home ranges than on the Sigmodon removal plot. When the population home ranges on each plot were compared over time they showed an increase. Plot 3 (Sigmodon removed) showed the largest increase but this was not significant.

It was hypothesized that Microtus trappability would be lower in those plots containing Sigmodon than in the Sigmodon removal plot. The Microtus in plot 2 were the only ones that were significantly less trappable than the ones in the Sigmodon removal plot. This result also should have been observed in plot 1 since it had the highest cotton rat densities. This is difficult to explain unless the differences in cover between the plots allowed for differing degrees of interspecific contact.

In summary, the field results of this study were at most suggestive of a negative interaction between Microtus and Sigmodon. The results were inconclusive mainly because of the late appearance and low numbers of Sigmodon. Also, the weaknesses of live-trapping as a technique for monitoring small mammal interactions were apparent. Results of the present study suggest that in Kansas, this negative interaction may only occasionally become severe enough to result in the exclusion of Microtus. If Sigmodon can adapt to the severe winters so that it can maintain a more stable population level, or if winters become less severe Sigmodon may eventually exclude Microtus.

Aggressive Behavior

It was hypothesized that *Sigmodon* would be aggressive towards and dominant over *Microtus* in interspecific encounters. This hypothesis was confirmed. If interspecific encounters between individuals occur in the field and if the laboratory behaviors are real, *Sigmodon* should have a negative survival influence on *Microtus*. How many encounters are necessary to affect noticeably a population of *Microtus* is debatable. Also, how long might it take? With what frequency must these interactions occur? These questions must be answered if the mechanism of interference is to be understood.

Spatial Distribution

It was hypothesized that *Microtus* would not use those areas of a laboratory arena occupied by *Sigmodon*. This hypothesis was confirmed under sparse cover conditions. It was also hypothesized that dense cover would allow co-utilization of the compartments. This was also confirmed for the experimental conditions. At higher *Sigmodon* densities the degree of co-utilization of a compartment by the two species seemed to be lessened. It appeared that the cover conditions affected the frequency at which the two species came into contact. If this frequency was high (as under sparse cover conditions which allowed the animals to see and smell each other) the *Sigmodon* would exclude *Microtus*. If the frequency of contact was low (as under dense cover conditions which permit concealment) coexistence resulted. High densities (and greater activity) increase the frequency of contact which leads to spatial exclusion. It appeared that the densities used in the laboratory were sufficient to reveal interference in space utilization. What densities are required in the field? Does there have to be a certain number of adults? The tentative observation that subadult Sigmodon were non-aggressive toward Microtus suggests that there might be a certain number required. Are such sensory modalities as sight and smell operative in the exclusion? Microtus did not stay out of areas which had been previously occupied by Sigmodon, whose remaining odors did not seem to affect Microtus. The frequency of interspecific contact seems to be a crucial point.

The Effect of Sigmodon on Microtus Movements

It was hypothesized that Sigmodon would only affect the movements of individual Microtus when the two species made frequent contact. This hypothesis was confirmed when it was observed that a free ranging Sigmodon affected Microtus movements more than a confined Sigmodon. Here again a situation, which provided contact, resulted in spatial exclusion. Why did the contact and not the mere presence of the cotton rat result in restriction of movements? Is the learning ability of Microtus involved? An aggressive encounter is a stimulus which may not be forgotten. If enough of these encounters occur, would the learning of avoidance by all members of a population then result in complete exclusion? The animals are active at the same times (see Figure 23), they are both runway oriented, and they seem to strive for the same food resources (Fleharty and Olson, 1969). The possibilities for contact appear to be present. The question arises as to what factors may control the number of interspecific contacts.

The results from the laboratory investigations suggested that the *Microtus*-*Sigmodon* interaction might be one based on the frequency of interspecific contact. If this is the case, it might be possible to explain many of the observations on these two species in terms of this concept. Since this concept will be referred to later, it is abbreviated to FIC.

INTERACTION BETWEEN *SIGMODON* AND *MICROTUS*

From the results of the present study, it was difficult to conclude with confidence that *Microtus ochrogaster* and *Sigmodon hispidus* were in competition. The most that can be said is that they interact negatively and frequent interactions are necessary before the effect of *Sigmodon* on *Microtus* can be measured in the field.

Other workers have suggested that these two genera may be in competition as it is described by Birch (1957) and Miller (1967). Fleharty and Olson (1967) noted that *Microtus ochrogaster* and *Sigmodon hispidus* in Kansas consumed the same species of plants, lived in the same area, and appeared to be in competition for space. Since both species seem to under-utilize food resources (Golley, 1960; Fleharty and Olson, 1969), competition for space is a tenable hypothesis. Wiegert (1972) implicated competition in South Carolina when he observed that *Microtus pennsylvanicus*, which is rare or nonexistent in the state, lived and reproduced in enclosures when not in contact with *Sigmodon*. Odum (1955) indicated that there might be an interspecific interaction between these same two species in Georgia. Bryan Glass (personal communication) pointed to interspecific competition as a probable reason for the prairie vole's general absence from Oklahoma. Data from other Oklahoma studies (Calhoun, 1950; Goertz, 1964, 1971; Hays, 1958; Phillips, 1936) support this contention. Howell (1954) did not report any *M. ochrogaster* with the *Sigmodon* that he caught in Tennessee. Baker (1969) suspected competition between *Microtus* and *Sigmodon* in Mexico.

Occasionally small populations of *Microtus* have appeared sporadically in areas where *Sigmodon* was the dominant grass eating rodent. This occurred in Oklahoma in 1957 following a *Sigmodon* "crash" in population (Bryan Glass, personal communication). The same phenomenon appeared to happen in Georgia (Odum, 1955; Ramsey and Briese, 1971). Whittaker and Zimmerman (1968) noted an unusual appearance of *M. ochrogaster* in Alabama. In Tennessee, there was also an unexpected appearance of this species (Dimmick, 1969; Whittaker and Zimmerman, 1968). Baker (1969) observed presumed differential exclusion of *Microtus mexicanus* by *Sigmodon* in Mexico.

These observations indicated that if there was any competitive exclusion (Hardin, 1960) of the voles by the cotton rats, it was only partially realized. The question arises as to what mechanisms and factors could result in the above mentioned observations. It is proposed that a model of the interaction based upon the frequency of interspecific contact (FIC) could explain these observations. Such a model is given in Table 14.

The frequency of *Microtus*-*Sigmodon* contact (FIC) facilitated by each of the factors is the important point. In Kansas, *Microtus* experiences low FIC much of the time because severe winters seem to decimate *Sigmodon* populations (Gier, 1967). It follows that *Microtus* only occasionally comes into frequent contact with *Sigmodon*; this infrequency seems to permit voles to coexist with the sporadic cotton rats. This factor is probably important throughout the zone of overlap

Table 14. A tabular model of the *Microtus*-*Sigmodon* interaction: trends to be expected.

Factor	Factor value	*Microtus* FIC value *
A. *Sigmodon* overwinter survival	poor	1
	moderate	2
	good	3
B. Present *Sigmodon* population density	low	1
	moderate	2
	high	3
C. Adult proportion of *Sigmodon* population	always low	1
	periodically high	2
	constantly high	3
D. Habitat cover	dense	1
	moderate	2
	sparse	3
E. Extent of habitat area	$\geq$ 10 hectares	1
	2 hectares	2
	$\leq$ 1 hectare	3
F. Habitat diversity	high	1
	moderate	2
	low	3

Prediction formula	If:	equals	expect
	A + B + C + D + E + F =	13 - 18	exclusion
		8 - 12	noticeable inhibition
		6 - 7	coexistence

* Frequency of Interspecific Contact (a value of 1 indicates low FIC).

between the two genera (Dunaway and Kaye, 1961; Mohlenrich, 1961). Periodic Sigmodon crashes (Goertz, 1964; Haines, 1971; McCulloch, 1962) reduce FIC in southern states. The Sigmodon population, however, is stable enough in the southern states (Chipman, 1966) that this alone would not allow Microtus to exist there. The necessity for high FIC allows Microtus to inhabit refuges which, due to a variety of micro-climatic factors, maintain only small or occasional populations of Sigmodon. The low FIC in these areas provides for the presence of vole "reservoirs" which expand when the cotton rats experience a wide-spread population decline. Other factors which reduce the Microtus FIC are a low proportion of Sigmodon adults, dense habitat cover, extensive habitat area, and high habitat diversity (for discussions of these concepts see Caldwell and Gentry, 1965; Klopfer, 1962; and MacArthur, 1972). Martin (1956) reported that during periods of high Sigmodon densities, the voles in his Kansas study retreated to refuge areas which were rarely used by Sigmodon. Barbehenn and Strecker (1962) and Ecke (1954) reported this phenomenon as being important in the interaction between Old World rats (Muridae).

In the field experiment of the present study there are many factors which could result in low FIC. First, the winter before the period of trapping was severe and Sigmodon was absent during spring and early summer. Second, when the cotton rats did appear, most of the individuals were juveniles and subadults. Third, the densities of Sigmodon were relatively low. Fourth, the plots were dense in habitat cover, structurally complex (refuges), and part of an extensive grassland area. These factors might have been reasons for the general lack of conclusive results from the field experiment. The high FIC facilitated by the laboratory experiments likewise may have exaggerated a negative interaction. Further studies using FIC as a hypothesis are needed to verify the meanings of these results.

FIC may characterize other competitive situations involving myomorph rodents (Findley, 1954; Delong, 1966; Getz, 1962; Koplin and Hoffman, 1968; Murie, 1971; Wendlend, 1970). Many other such cases are in the literature. Getz (1972) found no evidence of a formalized social structure in Microtus pennsylvanicus. This observation provides added support for the hypothesis that these animals need contact for their spatial organization. Batzli (1968), Goertz (1971), Grant (1971), and Van Vleck (1968) all listed high densities as being central to the competitive interactions documented. Raun and Wilks (1964) reported that dense cover was necessary for coexistence between Baiomys taylori and S. hispidus in Texas. Morris (1969) reported that snow cover facilitated coexistence between Microtus and Clethrionomys in Canada.

Explanations of the mechanism of competitive exclusion need to be generated. In addition to Table 14, I propose the following explanation concerning competitive exclusion as it may take place in myomorph rodents. When two ecologically similar species meet, the individuals of each species enter into aggressive encounters. When the frequency of these interspecific encounters (contacts) becomes high enough, individuals of the subordinate species develop an avoidance behavior. The acquisition of this behavior causes an individual rodent to leave an area should it continue to receive enough negative stimuli (contact, sight, smell) from the members of the dominant species. When enough subordinate individuals acquire the avoidance behavior and if the dominant species continues to provide negative reinforcements, exclusion results. The time required for exclusion to occur depends upon the frequency and the duration of interspecific contacts (FIC) and on the ability of the subordinate species to learn and exercise avoidance behavior.

If situations of species coexistence and exclusion are to be explained, testable hypotheses need to be generated. Models such as the one described provide a source for these hypotheses. Whether this one, or others like it, stand or fall depends on further experimentation.

SUMMARY AND CONCLUSIONS

1. The hispid cotton rat, *Sigmodon hispidus*, and the prairie vole, *Microtus ochrogaster*, are sympatric in central Kansas.
2. *Sigmodon* did not reach a substantial population density until late summer and early autumn. This allowed *Microtus* to be free from heavy *Sigmodon* contact during winter, spring, and summer. The severity of the Kansas winter was probably responsible for this relationship.
3. The results of the field experiment were only suggestive and not confirmative of a negative interaction between *Microtus* and *Sigmodon*. A late appearance of the cotton rats affected the experimental design of the field experiment.
4. *Sigmodon* (adults but not subadults) was aggressive towards *Microtus* and was dominant in interspecific encounters.
5. Prairie voles did not use the areas of a confined space occupied by cotton rats unless the cover was dense. However, high *Sigmodon* densities excluded the voles even in dense cover.
6. *Microtus* movements were not affected by a confined cotton rat but were affected by a free-ranging one.
7. A high frequency of interspecific contact between the two species was proposed as the necessary condition for a negative interaction.

8. A model utilizing the contribution of various factors to the frequency of interspecific contact was constructed to explain observations on these two species.
9. A model attempting to explain the mechanism of competitive exclusion in myomorph rodents was proposed.

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