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Effects of controlled burning on small mammal populations of a restored tallgrass prairie.

P. Lynne Vacanti

EFFECTS OF CONTROLLED BURNING ON SMALL MAMMAL POPULATIONS OF A RESTORED TALLGRASS PRAIRIE

A Thesis

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In Partial Fulfillment

of the Requirements for the Degree

Master of Arts

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by

P. Lynne Vacanti

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THESIS ACCEPTANCE

Accepted for the faculty of the Graduate College, University of Nebraska, in partial fulfillment of the requirements for the degree Master of Arts, University of Nebraska at Omaha.

Thesis Committee

Name	Department
Roger A. Sharpe	Biology
Thomas B. Bragg	Biology
Lawrence J. Stephens	Math/CS

Kenneth N. Geluso

Chairman

April 20, 1981

Date

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P.L.V.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

A field study was conducted on a reestablished grassland to investigate the effects of a controlled burn on resident mammals. Pre-burn populations were censused, and all small mammals eartagged so that comparisons with post-burn populations could be made; a control plot was similarly censused.

Following the fire, no animals were caught on the burn plot for one week, and no direct evidence of fire-induced mortality was observed. Evidence that mammals survived the fire was based on comparisons of recapture success on experimental and control plots before and after the burn.

Microtus pennsylvanicus (meadow voles) reinvaded the burned plot 93 days after the fire. The lack of dense vegetative cover appears to be the factor keeping voles from reinvading earlier, although the effect of increased predation may also be involved. The prolonged absence of voles apparently was not due to isolation of the burned plot from adjacent vole populations. Their absence cannot be attributed to the destruction of food, either, because grasses were growing on the burned area twelve weeks before voles reappeared. At the termination of this study, voles still had not become reestablished on the burned plot in numbers equal to those on the control plot or to those observed on the experimental plot before the fire. The lack of litter appears to be the primary factor keeping voles from reestablishing home ranges.

Peromyscus maniculatus (deer mice), which were not found on

either plot before the fire, invaded the burned area nine days after the fire when grasses had begun to emerge. Reithrodontomys megalotis (harvest mice), present in low numbers prior to the burn, reinvaded the experimental plot three months following the fire. Harvest mice increased in numbers and remained at relatively high densities until the termination of trapping. The positive response exhibited by both deer and harvest mice could have been caused by either changes in vegetation or the decrease in competition from voles.

Peromyscus leucopus (white-footed mice) were captured mainly in the woods and the fire had no noticable effect on this population. Too little data were collected for Blarina brevicauda (short-tailed shrews), Sorex cinereus (masked shrews), Spermophilus tridecemlineatus (thirteen-lined ground squirrels), S. franklinii (Franklin's ground squirrels), Mus musculus (house mice), Mustela nivalis (least weasels), Zapus hudsonius (meadow jumping mice), and Perognathus flavescens (plains pocket mice) to determine whether the fire had any effect on these species.

INTRODUCTION

Fire is a significant ecological factor in the lives of mammals, especially mammals inhabiting fire perpetuated environments like grasslands. The effect of fire has traditionally been considered only when discussing mortality; however, most mammals that live where fires occur regularly survive them (Handley, 1969). Some mammals even benefit due to the change in vegetation (Vogl, 1967).

Recently there has been increased interest in both short and long term effects of fire on small mammal populations. Many studies have consisted solely of observations and trapping after fires without knowledge of pre-burn populations. Results of these studies often have been inconclusive and varied due to differences in conditions under which the fires occurred. For example, Erwin and Stasiak (1979) reported high mortality of harvest mice pups and some deaths of voles, while Moreth and Schramm (1973) found no evidence of fire-induced mortality even though both studies were conducted on restored tallgrass prairies. Similarly varied findings have been described following fires in chaparral habitats containing similar species of mammals; Chew _et al_. (1959) observed very high mortality, especially of woodrats, while Lawrence (1966) found no evidence of death due to fire.

Experiments have been conducted to test the potential lethality of various physical characteristics of fire. Howard _et al_. (1959) conducted an experiment to test fire related mortality by burying caged rodents at two-inch and six-inch depths beneath a controlled brush fire. He discovered that most of the animals survived except in those areas where temperatures reached 63°C or above. In an experiment with *Peromyscus truei*, Lawrence (1966) demonstrated that in burrow systems which allowed underground air movement, increased temperatures caused by surface fire never reached lethal levels. According to Bendell (1974), when death does occur, suffocation from lack of O_2 and increased CO_2 is the more likely cause. Findings of Chew *et al.* (1959) tend to support this observation; 39 of 43 dead mammals found were untouched by flames.

A major effect of fire besides mortality is alteration of habitat, namely elimination of vegetative cover and litter. Researchers have reported varied responses of small mammals to these changes. Voles (*Microtus ochrogaster* and *M. pennsylvanicus*), which are primarily grazers, respond negatively to loss of vegetative cover (Tester and Marshall, 1961; Hayes, 1970; Schramm, 1970; Sims and Buckner, 1973). Cook (1959) suggested at least one year's accumulation of litter was necessary to afford *Microtus californicus* adequate cover for surface runs. Moreth and Schramm (1973) reported that immediately following a burn, *Microtus pennsylvanicus* was not present, then, as vegetation increased in density during the three months after the fire, voles increased slowly on the burned areas. Tester and Marshall (1961), who studied a native prairie, found that *M. pennsylvanicus* persisted after burning but at low density for a period of one year and then began to increase. Short-tailed shrews, *Blarina brevicauda*, also have been found to respond negatively to loss of litter cover caused by fire. Springer and Schramm (1972) observed that *B. brevicauda* populations were reduced for up to one and one-half years following a controlled burn.

Grassland fires appear to have the opposite effect on species that are primarily seedeaters. By reducing litter and vegetative cover, fire creates a more open habitat which is favorable to such species as Peromyscus maniculatus, provided seeds remain unharmed (Ahlgren, 1966; Daubenmire, 1968). Such positive effects on populations of both white-footed mice, Peromyscus leucopus, and deer mice, P. maniculatus, have been reported in numerous studies (Tevis, 1956; Cook, 1959; Gashwiler, 1959; Tester, 1965; Hayes, 1970; Beck and Vogl, 1972; Springer and Schramm, 1972; Moreth and Schramm, 1973; Sims and Buckner, 1973). Once litter starts to accumulate, however, these species tend to decline (Tester and Marshall, 1961). Cook (1959) also noted a similar invasion by harvest mice, Reithrodontomys megalotis.

I designed this study to elucidate further the effects of controlled burning on small mammal populations in a restored tallgrass prairie. This study was purposely set up on a small section of prairie where a burned plot would be surrounded by adjacent tallgrass areas containing potential populations that were present only a short distance from the plot. This way, the reason for absence of any animals would be resistance to some factor caused by the fire and not to isolation of the burned area. The intent of my experimental design was to determine: (1) whether the initial negative response to fire by small mammals is due to mortality or to emigration from the burned area; and (2) what factors are involved in reinvasion of the burned plot including when animals begin to reappear on the plot, the amount of vegetative cover and surface litter necessary for reinvasion, and the length of time it takes for populations to become reestablished at levels equal to those present before the burn.

METHODS AND MATERIALS

Study Area

The study was conducted at Allwine Prairie Preserve, a 65 ha reestablished grassland located in Douglas County, Nebraska approximately 19 km northwest of the University of Nebraska at Omaha. Previously a cultivated, terraced cropland, the area was seeded with native grasses in 1970 (Bragg, 1978).

The extensive grass cover on the study plots was dominated by big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), sideoats grama (*Bouteloua curtipendula*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). The northern two-thirds of the study area was a moist lowland dominated by big bluestem, Indiangrass, and switchgrass with a dense layer of litter. The southern one-third was a north-facing slope dominated by little bluestem and sideoats grama which was sparsely vegetated and littered compared to the north end. Waterways were dominated by smooth brome (*Bromus inermis*) and reed canarygrass (*Phalaris arundinacea*). The wooded area was dominated by boxelder (*Acer negundo*), white mulberry (*Morus alba*), cottonwood (*Populus deltoides*), black willow (*Salix nigra*), and American elm (*Ulmus americana*), with an understory consisting mainly of gooseberry (*Ribes missouriense*), wild plum (*Prunus americana*), dogwood (*Cornus amomum* and *C. drummondii*), white snakeroot (*Eupatorium rugosum*), violet (*Viola canadensis*), wild grape (*Vitis riparia*), and nettles (*Urtica dioica*). Soils are primarily silt and silty clay loams (Bragg, 1978).

Study Plots

The experimental plot and control plot were two contiguous areas selected for their similarity in vegetative composition, canopy cover, slope, elevation, water drainage, and signs of small mammal activity. They were located in the east-central portion of the Preserve (Appendix). Each plot was approximately 0.5 ha. The entire field was separated from the rest of the prairie by waterways on the west and north borders, a fence line and dirt road on the east, and a midgrass slope on the south. Beyond the waterway on the north boundary was a wooded area surrounding a pond (Fig. 1).

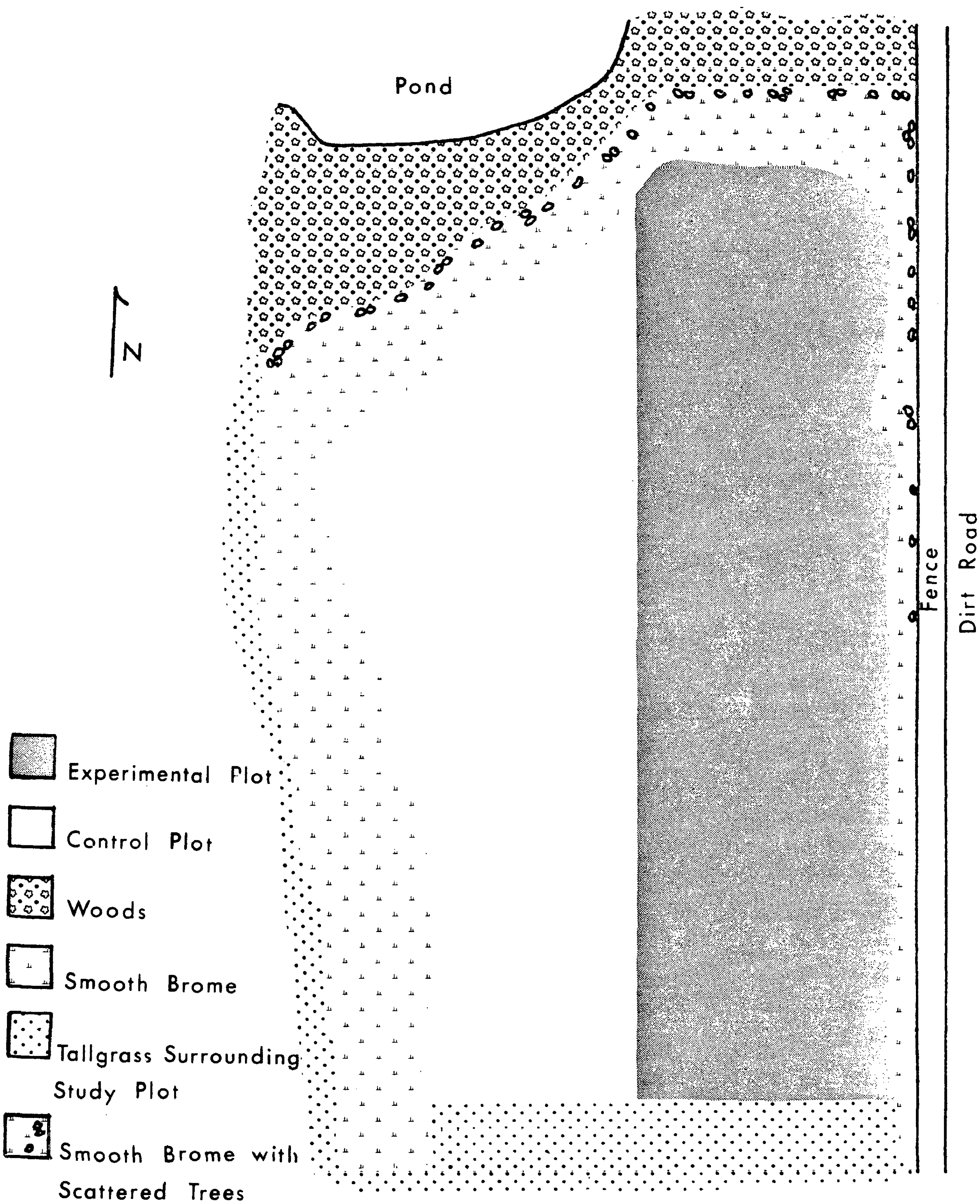
Previous management of the study plots consisted of mowing in 1971, 1972, 1976, and 1977, and burning in 1975. Previous management might have been responsible for the presence of a low number of voles compared to densities reported for *Microtus pennsylvanicus* in typical midwest tallgrass prairies which range from 73.6 per hectare (Blair, 1948) to 140.8 per hectare (Krebs, 1977).

Trapping Procedure

Trapping was conducted from 14 April 1979 to 20 October 1979, and from 28 April 1980 to 12 May 1980. Traps were placed on both the experimental and control plots in a grid pattern, at 10 m intervals. O'Farrell and Austin (1978) found that a grid pattern yielded more precise estimates of population density than a line transect. Grids also facilitate the study of daily movements, spatial relationships, and other aspects of small mammal community dynamics.

One hundred and nine large aluminum Sherman live-traps (nonfolding

Fig. 1. Study area on Allwine Prairie Preserve showing the arrangement of experimental and control plots and perimeter traplines. (Tallgrass area + experimental and control plots = *Andropogon gerardii*, *A. scoparius*, *Sorghastrum nutans*, *Panicum virgatum*, and *Bouteloua curtipendula*; Smooth brome = *Bromus inermis* and *Phalaris arundinacea*; Woods = *Acer negundo*, *Morus alba*, *Populus deltoides*, *Salix nigra*, and *Ulmus americana*.)


Pond
N
Fence
Dirt Road
Experimental Plot
Control Plot
Woods
Smooth Brome
Tallgrass Surrounding Study Plot
Smooth Brome with Scattered Trees

type = 7.6 cm X 7.6 cm X 25.4 cm; folding type = 7.6 cm X 8.9 cm X 22.8 cm) were placed on the two plots, sixty on the experimental plot and forty-nine on the control plot. Although eleven less traps were placed on the control plot because of its irregular shape (Fig. 1), the difference in actual size of these two plots was fairly small; the experimental plot was less than 17% larger than the control plot, an area approximately equal to the average size of the home range of one *Microtus pennsylvanicus* found in this study.

Fifty-two additional large Sherman live-traps were used to establish perimeter traplines around the entire boundary in order to study any movement across them. Each trap location was marked by a flag. Traps were provided with cotton for bedding and baited with rolled oats. Each trap was placed in a plastic bag for protection during rain (Maser and Maser, 1971). Traps were set daily at dusk and checked at dawn to correspond with the two periods of peak activity for *Microtus* (Hamilton, 1937). Trapping was not conducted on nights when temperatures dropped below freezing or when heavy frost was predicted; trapping was conducted, however, during rain (daily capture rates for this study were actually higher on nights with heavy rain). After each trapping, excrement and old bait were removed from traps because a preliminary study showed that *Microtus* would not enter dirty traps. Because of strong odors left in traps following capture of *Blarina*, *Sorex*, and *Mustela*, these traps were removed from the plots and thoroughly washed before being replaced. Following the end of trapping in October, all traps were removed from the study area, washed, repaired, and stored for the winter. Flags were left to mark trap sites on the grids. In the spring of 1980 all traps were replaced on the grids using the flags that marked each trap position.

Intensive trapping was conducted for 16 days during the one month period of 14 April to 14 May prior to the burn. It was divided into two trapping periods, Trapping Period A (April 14-28) and Trapping Period B (30 April-14 May), with eight trapping nights each. Following the burn on 14 May, traps were set that night, and trapping then continued for the next two weeks, resulting in another trapping period consisting of eight trapping nights over 15 days (Trapping Period C). Starting two weeks after the burn "spot" trapping was conducted until the end of trapping in the fall of 1979. I trapped every fifth night plus two nights consecutively in the middle of and at the end of each month until September. In September and October, monthly livetrapping censuses were made; traps were run for two consecutive nights, twice a month, until the end of October and the onset of adverse weather conditions. Trapping began again in the spring of 1980 on 28 April and was continued until 12 May with traps open eight out of the fifteen nights (Trapping Period D).

All animals captured were marked by eartagging with size #1 Monel Fingerling Fish Tags (National Band and Tag Company, 721 York Street, Newport, Kentucky 41072). Number, location, species, sex, body weight, reproductive condition, distinguishing characteristics, and age class were recorded for each animal trapped. Age classes consisted of adult and juvenile for all species except *Microtus* and *Peromyscus*, which were divided into juvenile, subadult, and adult classes. Microtus are commonly divided into these three age groups based on body weight (Krebs, 1966; Krebs et al., 1969). For my population, Microtus pennsylvanicus were classified on the basis of body weight as adults ($\geq$32 g), subadults (21 g - 31 g), and juveniles ($\leq$ 20 g). Peromyscus were divided into age classes based on pelage changes; juvenile pelage was entirely gray, adult pelage was all brown, and subadults were those animals in any stage of molting from juvenile into adult pelage. A rough measure of reproductive condition was obtained by recording external physical appearance of animals. The position of the testes was used as an index of reproductive condition in males. Females were considered pregnant if they showed an obviously bulging abdomen when examined; Krebs et al. (1969) suggest that only the last week of pregnancy can be detected using this observation alone. The size of the mammae (prominant nipples) was used as an index of lactation in females. At the end of the study voucher specimens were made for all species except Spermophilus franklinii, Zapus hudsonius, and Perognathus flavescens and were deposited in the mammal collection of the University of Nebraska at Omaha.

Burn Procedure

A controlled burn was carried out on the experimental plot at 11:45 am on 14 May 1979. Fire control lanes were mowed the morning of the burn to separate the experimental plot from the control plot and south perimeter trapline. To ensure a blaze of equal intensity in all areas and to provide extreme stress due to fire on small mammal populations, the entire plot was burned by backfire, resulting in a slow, hot fire. Seven people controlled the fire with water packs and fire swatters.

Traps on the control plot and on perimeter traplines were open during the fire in an attempt to monitor any animal movement in response to the burn. Those controlling the fire also watched for animal movements.

Flags were replaced and traps set for the night immediately after the fire; other disturbance of the burned area was avoided. A systematic search for dead animals was conducted over the experimental plot during the next week following the burn.

Vegetation Analysis

During this study, information was obtained concerning changes in maximum height and average percent vegetative cover on the experimental plot after the burn. Average, maximum vegetative height was determined by periodically measuring plants at 30 m intervals along a transect starting at the lowland north end and continuing up the slope. Average percent cover was ascertained within 1 m^2 quadrats at the same locations. The coverage categories used were: (1) 0-5%; (2) 5-25%; (3) 25-50%; (4) 50-75%; (5) 75-95%; (6) 95-100% (Daubenmire, 1959). Data were discussed using midpoint values for each category. Both types of measurement were averaged separately for the lowland and the slope portions of the plot.

Data Analysis

Because trapping methods were essentially the same for both plots, a comparable relative abundance of animals was obtained. One method used to estimate the size of populations is to determine the minimum number of animals known to be alive on each plot during each trapping period (Krebs, 1966). The Modified Lincoln Index also can be used for population estimates when the number of tagged animals recaptured is greater than seven (Pielou, 1974). In the ten instances where this requirement was met, Minimum Number estimates were compared with population estimates based on the Modified Lincoln Index; the estimates for the Modified Lincoln Index averaged two to three individuals fewer than the Minimum Number Alive estimates. Because recaptures usually were less than seven, I chose to use only the Minimum Number Alive estimates.

Another measure of relative abundance used was to compare the number of animals caught each trapping night (daily capture rates) during designated trapping periods; these data were statistically compared using the paired *t*-test. Population density was determined by calculating the number of animals trapped on an area per 100 trapnights; recaptures were not included in this determination. Any animal that was captured on both the experimental and control plots during the same trapping period was counted in the population estimate for each plot for that period.

Recapture rates of animals can be used to determine indirectly the loss of animals, due to death and predation, from a given population over a period of time. Survival rates are usually measured as minimum number of animals recaptured after a 28 day period (Krebs, 1966; Krebs *et al.*, 1969). In this study, survival rates were calculated by computing the percentage of animals surviving between successive trapping periods (15 days); since this is a shorter time period, survival of individuals should be even greater. Survival rates were measured as the percent of marked animals captured in one trapping period that were recaptured on the study area in the next trapping period. Any animal that was captured on both the experimental and control plots during the same trapping period was included in the calculations for both plots.

In all tests, probability values less than or equal to 0.05 were considered to be statistically significant.

RESULTS

During the course of this study, twelve species of small mammals were captured on the study area. The meadow vole (Microtus pennsylvanicus, white-footed mouse (Peromyscus leucopus), deer mouse (Peromyscus maniculatus), and western harvest mouse (Reithrodontomys megalotis) were the only species taken with sufficient frequency to permit population analyses, and thus determine the effects of the fire on population density (Table I). Enough data also were collected on meadow voles to examine the effects of fire on age and sex distribution and reproduction.

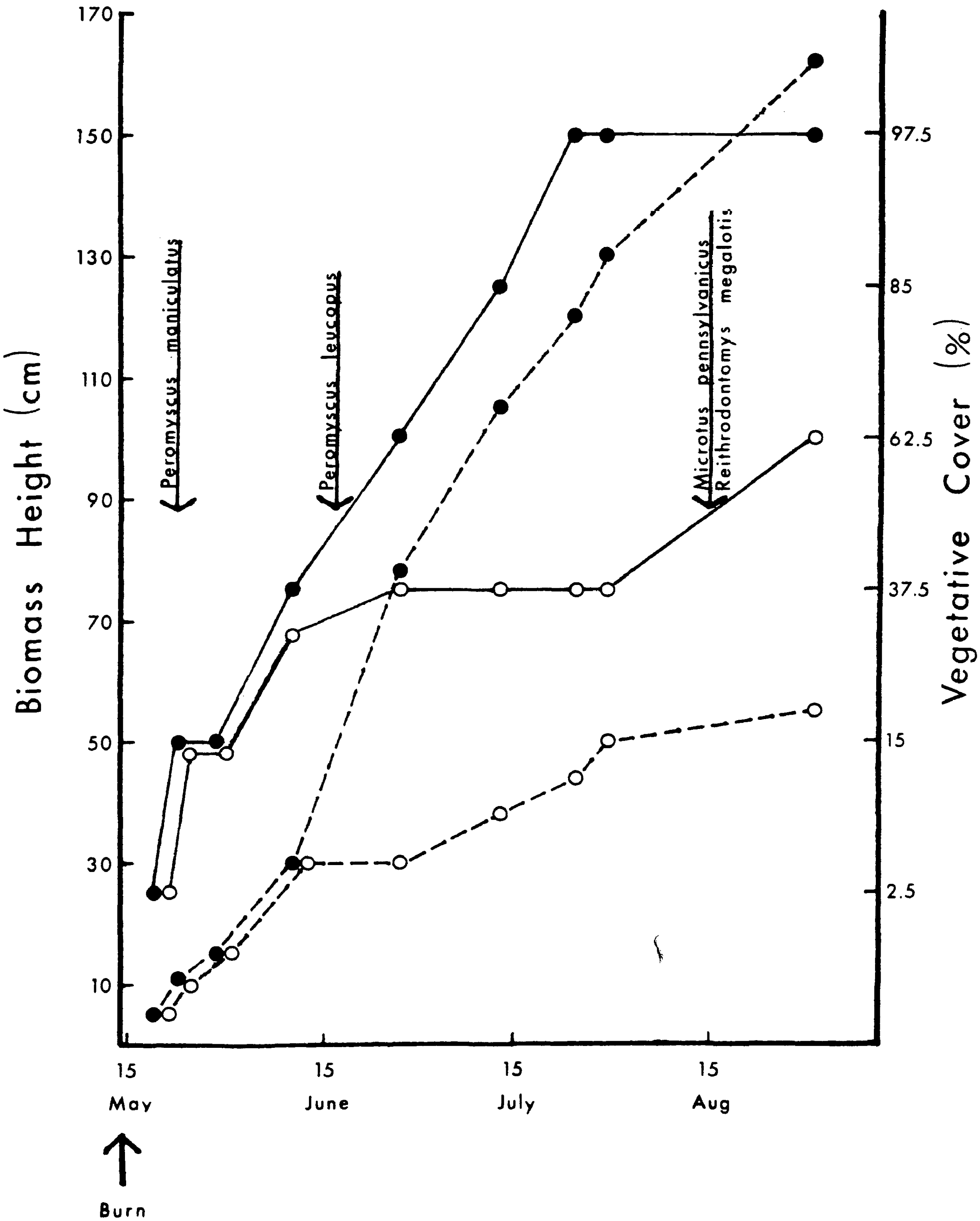
Vegetation

Percent vegetative cover, litter depth, and biomass height were observed to be similar on the experimental and control plots before burning. The fire completely destroyed all above ground vegetation and litter. Grasses began to emerge after three days and grew fairly rapidly and evenly over the entire plot for the first month. In mid-June, grasses began to grow at a much faster rate on the northern two-thirds of the plot than on the southern end. By the end of July, big bluestem on the lowland, north end had reached an average height of 130 cm, with flowering stalks up to 180 cm tall, and 100% vegetative cover. As one went up the slope, grasses gradually got shorter until, on the south end of the field dominated by little bluestem, grass height averaged 50 cm with flowering stalks up to 90 cm, and vegetative cover averaged 50%. Vegetation on the southern end of the plot never attained 100% cover (Fig. 2). Although growth of grasses on the

Table I. Small mammals captured on Allwine Prairie Preserve from 14 April 1979 to 12 May 1980.

Species	Individuals	Captures	Trap Deaths
Peromyscus leucopus (white-footed mouse)	107	564	1
Microtus pennsylvanicus (meadow vole)	81	583	5
Reithrodontomys megalotis (harvest mouse)	37	74	1
Blarina brevicauda (short-tailed shrew)	29	35	10
Peromyscus maniculatus (deer mouse)	23	99	3
Sorex cinereus (masked shrew)	13	13	8
Spermophilus tridecemlineatus (thirteen-lined ground squirrel)	11	38	1
Mus musculus (house mouse)	4	4	0
Mustela nivalis (least weasel)	4	4	0
Zapus hudsonius (meadow jumping mouse)	2	2	0
Perognathus flavescens (plains pocket mouse)	1	1	0
Spermophilus franklinii (Franklin's ground squirrel)	1	1	0
Totals	313	1418	29

Fig. 2. Change in vegetation on the experimental plot after the burn. The open circles (o) represent growth on the southern one-third of the plot; darkened circles (o) represent growth on the northern two-thirds of the plot; solid line indicates percent of vegetative cover; dashed line indicates biomass height; arrows with species names indicate the first time each species was captured on the experimental plot after the burn.


Biomass Height (cm)
Vegetative Cover (%)
170
150
130
110
90
70
50
30
10
97.5
85
62.5
37.5
15
2.5
Peromyscus maniculatus
Peromyscus leucopus
Microtus pennsylvanicus
Reithrodontomys megalotis
15
May
15
June
15
July
15
Aug
Burn

burned area, especially big bluestem, had surpassed that of grasses on the unburned area, there were still large bare areas of ground under the vegetation on the experimental plot in contrast to the dense litter layer which remained on the control plot.

In the spring of 1980, grasses were just emerging when trapping was conducted. The major difference between the experimental and control plots was the amount of litter present. While there was several years accumulation of litter on the control plot, there was only one year's accumulation on the experimental plot. Most of the litter present on the experimental plot was on the northern two-thirds; the southern one-third of the plot was relatively free of litter.

Microtus pennsylvanicus (meadow vole)

Effects on population density.--The number of voles on the experimental plot during the two trapping periods before the burn (Periods A and B) remained essentially the same (Tables II and III). During the burn, workers observed no animals running from the flames. Also, no voles were trapped in the perimeter traplines that were open during the fire. Directly following the burn, a careful search of the burned area did not reveal the remains of any vertebrates. Five hours after the burn, an adult male *Microtus*, which previously had been trapped mainly on the experimental plot, was captured in the woods. This was the only time a vole was trapped in the woods throughout my entire study (9982 trapnights), indicating a probable emigration in response to the fire; subsequent trappings of this animal were on the control plot. For the next 15 day trapping period only one *Microtus*

Table II. Number of *Microtus pennsylvanicus* known to be alive on experimental and control plots during Trapping Periods A, B, and C in 1979, and D in 1980. Burn occurred between Periods B and C.

Plot	Trapping Period			
	A April 14-28	B April 30-May 14	C May 15-29	D April 28-May 12
Experimental	18	16	1	2
Control	8	16	13	11

Table III. Number of animals captured per 100 trapnights for all species of small mammals trapped from 14 April 1979 to 12 May 1980 (recaptures not included); E = experimental plot; C = control plot; P = perimeter traplines; ST = spot trapping. Burn occurred between Periods B and C.

Species	Plot	Trapping Period				
		A April 14-28	B April 30-May 14	C May 15-29	ST June 4-Oct. 20	D April 28-May 12
Microtus pennsylvanicus	E	3.8	3.0	0.2	0.7	0.4
	C	2.0	3.6	3.0	2.1	2.5
	P	0.2	3.9	4.3	1.0	2.4
Peromyscus leucopus	E	0.8	0.2	0.0	1.5	0.4
	C	0.0	0.0	0.2	0.8	0.0
	P	0.0	3.4	5.1	5.3	2.4
Peromyscus maniculatus	E	0.0	0.0	0.7	0.7	1.1
	C	0.0	0.0	0.0	0.0	0.2
	P	0.0	0.2	0.9	0.3	1.3
Reithrodontomys megalotis	E	0.2	0.4	0.0	0.9	1.5
	C	0.5	0.0	0.0	0.3	0.5
	P	0.0	0.0	0.0	0.4	0.2
Blarina brevicauda	E	0.0	0.0	0.0	0.0	0.0
	C	0.0	0.5	0.2	0.7	0.2
	P	0.0	0.0	0.4	1.0	0.0

Sorex	E	0.0	0.0	0.0	0.1	0.0
cinereus	C	0.0	0.2	0.0	0.2	0.5
	P	0.2	0.4	0.0	0.1	0.4
Spermophilus	E	0.0	0.0	0.0	0.1	0.4
tridecemlineatus	C	0.0	0.5	0.2	0.0	0.0
	P	0.5	0.6	0.6	0.1	0.9
Mus	E	0.0	0.0	0.0	0.2	0.0
musculus	C	0.0	0.0	0.0	0.0	0.0
	P	0.0	0.0	0.0	0.0	0.0
Mustela	E	0.8	0.0	0.0	0.0	0.0
nivalis	C	0.0	0.0	0.0	0.0	0.0
	P	0.0	0.0	0.0	0.0	0.0
Zapus	E	0.0	0.0	0.0	0.1	0.0
hudsonius	C	0.0	0.0	0.0	0.0	0.0
	P	0.0	0.0	0.0	0.0	0.2
Spermophilus	E	0.0	0.0	0.0	0.1	0.0
franklinii	C	0.0	0.0	0.0	0.0	0.0
	P	0.0	0.0	0.0	0.0	0.0
Perognathus	E	0.0	0.0	0.0	0.1	0.0
flavescens	C	0.0	0.0	0.0	0.0	0.0
	P	0.0	0.0	0.0	0.0	0.0

was captured in the burned area. This individual, an adult female which previously had been trapped on the experimental plot, was caught on a small area of smooth brome that had not been destroyed in the fire. Thus, during the 15 day trapping period following the burn, there was actually an absence of voles on the area completely destroyed by fire (Figures 3 and 4).

Comparisons of vole populations between the control and experimental plots were made using daily capture rates. Although capture rates were initially higher on the experimental plot, they were almost identical during Trapping Period B just prior to the burn ($\underline{P} > 0.10$). Following the fire, capture rates decreased significantly on the experimental plot ($\underline{P} < 0.005$, Table IV).

Subsequent "spot" trapping during the months of June through October (trapping between Periods C and D) indicated that the size of the population of voles on the control plot continued to remain relatively stable and to be similar to the number just before and after the burn (Table III and Fig. 4). Spot trapping on the experimental plot revealed that *Microtus* continued to be absent from the burned area until 15 August, three months after the fire when vegetative cover had reached maximal cover (Fig. 2). From 15 August to the end of spot trapping in 1979, twelve voles were caught on the experimental plot. Although this number is only slightly lower than the number of voles present before the fire, if the number of animals captured during each of these time periods is examined, a decided difference can be seen. The number of animals caught on the burned

Fig. 3. Number of *Microtus pennsylvanicus* captured on the experimental and control plots during Trapping Periods A, B, and C in 1979, and D in 1980. The arrow indicates the burn which occurred between Periods B and C.

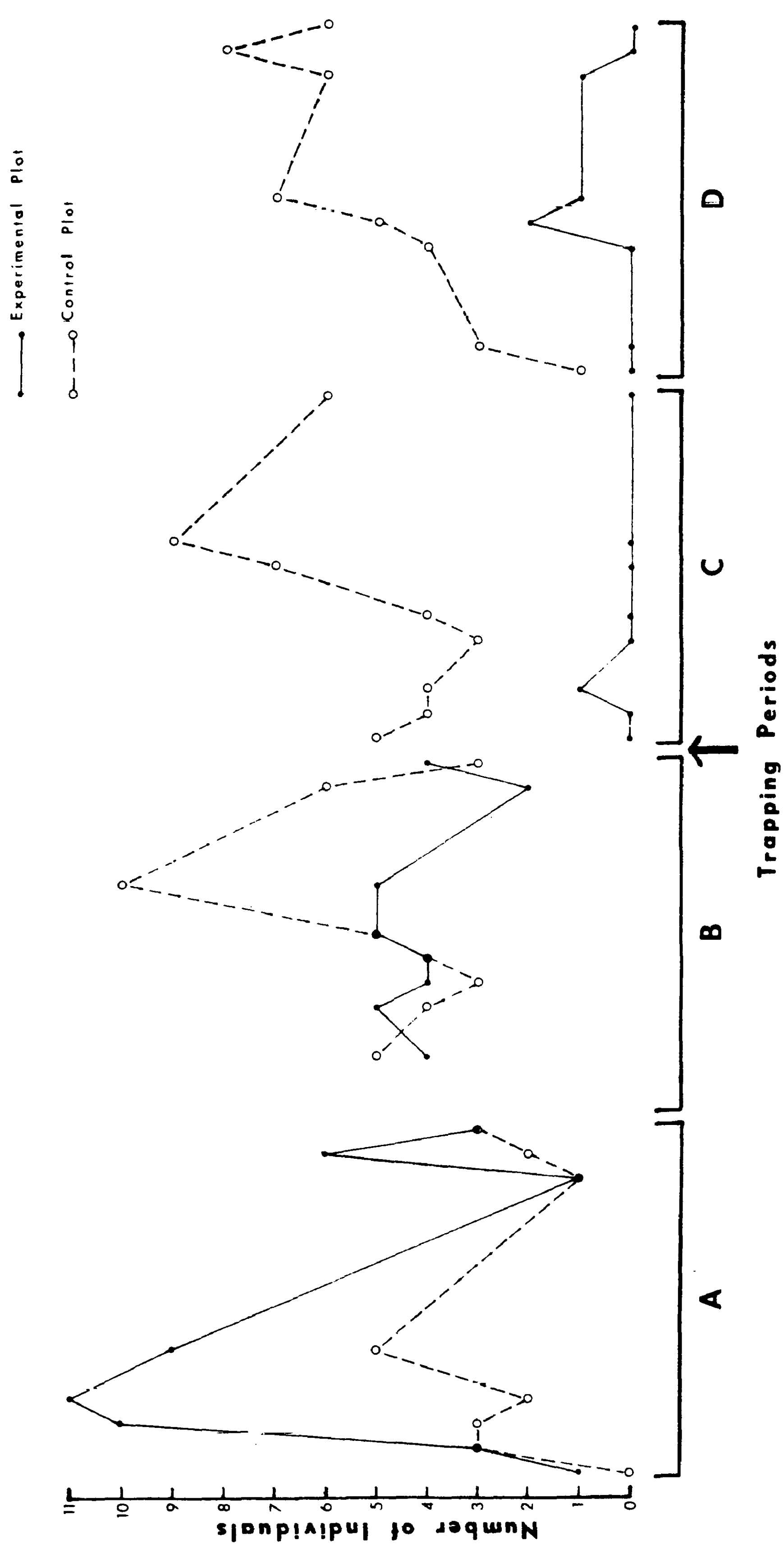
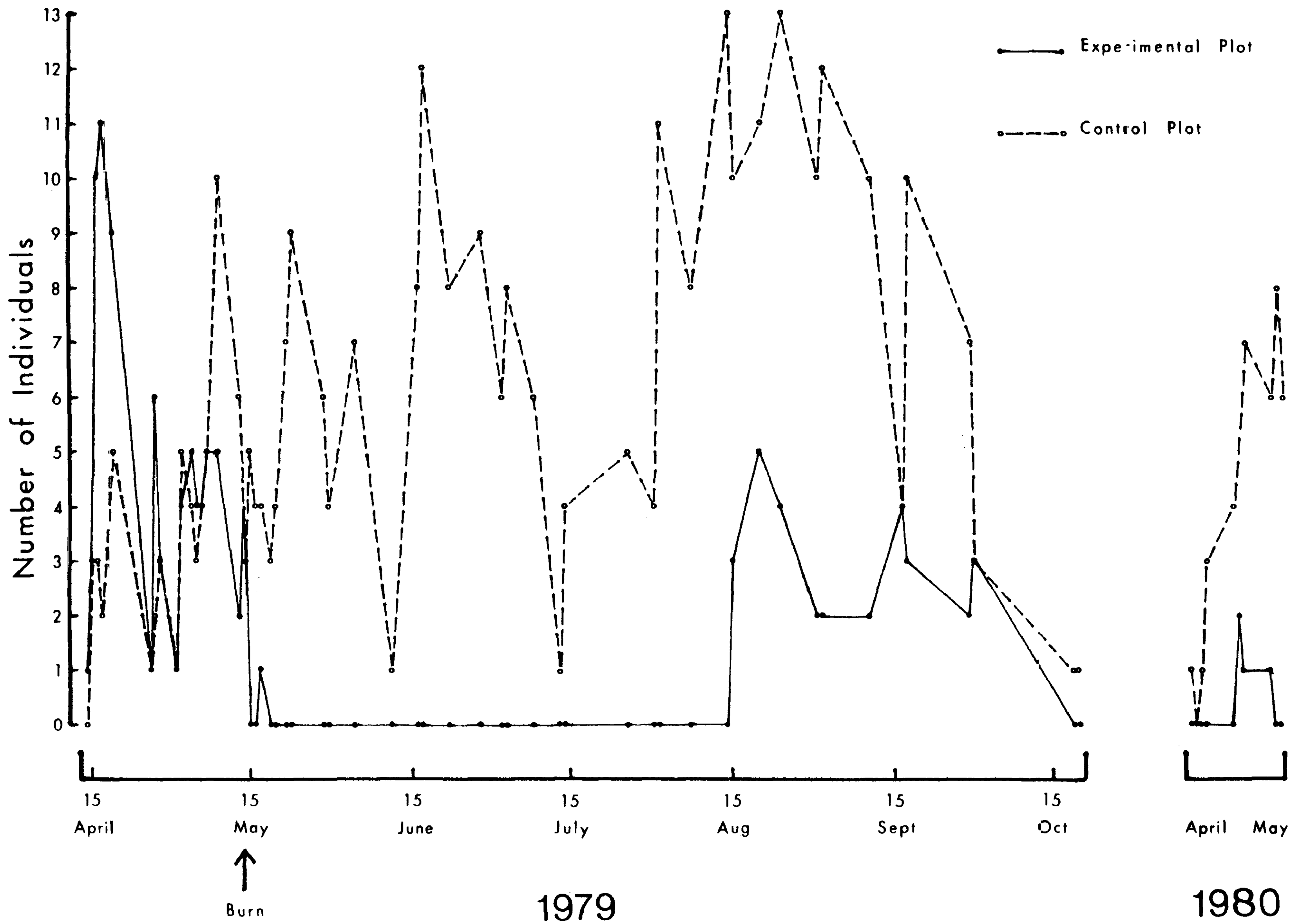

Experimental Plot
Control Plot
Number of Individuals
0
1
2
3
4
5
6
7
8
9
10
11
A
B
C
D
Trapping Periods

Fig. 4. Daily capture of *Microtus pennsylvanicus* on experimental and control plots from 14 April to 20 October, 1979, and from 25 April to 12 May, 1980.



Number of Individuals
13
12
11
10
9
8
7
6
5
4
3
2
1
0
Expe-imental Plot
Control Plot
15
April
15
May
Burn
15
June
15
July
15
Aug
15
Sept
15
Oct
April
May
1979
1980

Table IV. Daily capture rates of Microtus pennsylvanicus for experimental and control plots during Trapping Periods A through D.

Trapping Day	Trapping Period: A April 14-28 Exp.	A Con.	B April 30-May 14 Exp.	B Con.	C May 15-29 Exp.	C Con.	D April 28-May 12 Exp.	D Con.
1	1	0	4	5	0	5	0	1
2	3	3	5	4	0	4	0	3
3	10	3	4	3	1	4	0	4
4	11	2	4	4	0	3	2	5
5	9	5	5	5	0	4	1	7
6	1	1	5	10	0	7	1	6
7	6	2	2	6	0	9	0	8
8	3	3	4	3	0	6	0	6
Mean	5.5	2.4	4.1	5.0	0.1	5.3	0.5	5.0
t value*	2.54		1.05		6.90		5.78	
P value	<0.05		>0.10		<0.005		<0.005	

*Paired t-test

site per 100 trapnights during the two trapping periods before the fire, A and B, are 3.8 and 3.0 respectively, compared to 0.7 voles captured per 100 trapnights during the two month period between mid-August and mid-October (Table III). All captures occurred on the northern two-thirds of the plot where vegetative cover and height were the greatest. All twelve of these animals were taken on both the experimental and control plots during spot trapping, averaging two to three captures on the burned plot compared to seven on the control plot per individual. Three of these voles were ones that had emigrated from the burned plot to the control plot following the burn (see below). Unlike prior to the burn, no individuals were captured exclusively on the burned area during spot trapping. The number of *M. pennsylvanicus* trapped in October decreased dramatically with the onset of cold weather; only two animals were caught on the control plot and none on the experimental plot (Fig. 4).

In the spring of 1980, one year following the fire (Trapping Period D), two voles were trapped on the experimental plot. This number was significantly lower than the control population for this same period ($P < 0.005$, Table IV) and also substantially lower than the pre-burn experimental population in the spring of 1979 (Tables II and III). This low population size was similar, however, to the post-burn experimental population of 1979. One of these animals was an adult male trapped five times, twice on the burned area and three times on the unburned area. The other was a subadult male captured only twice, both times on the same part of the experimental plot.

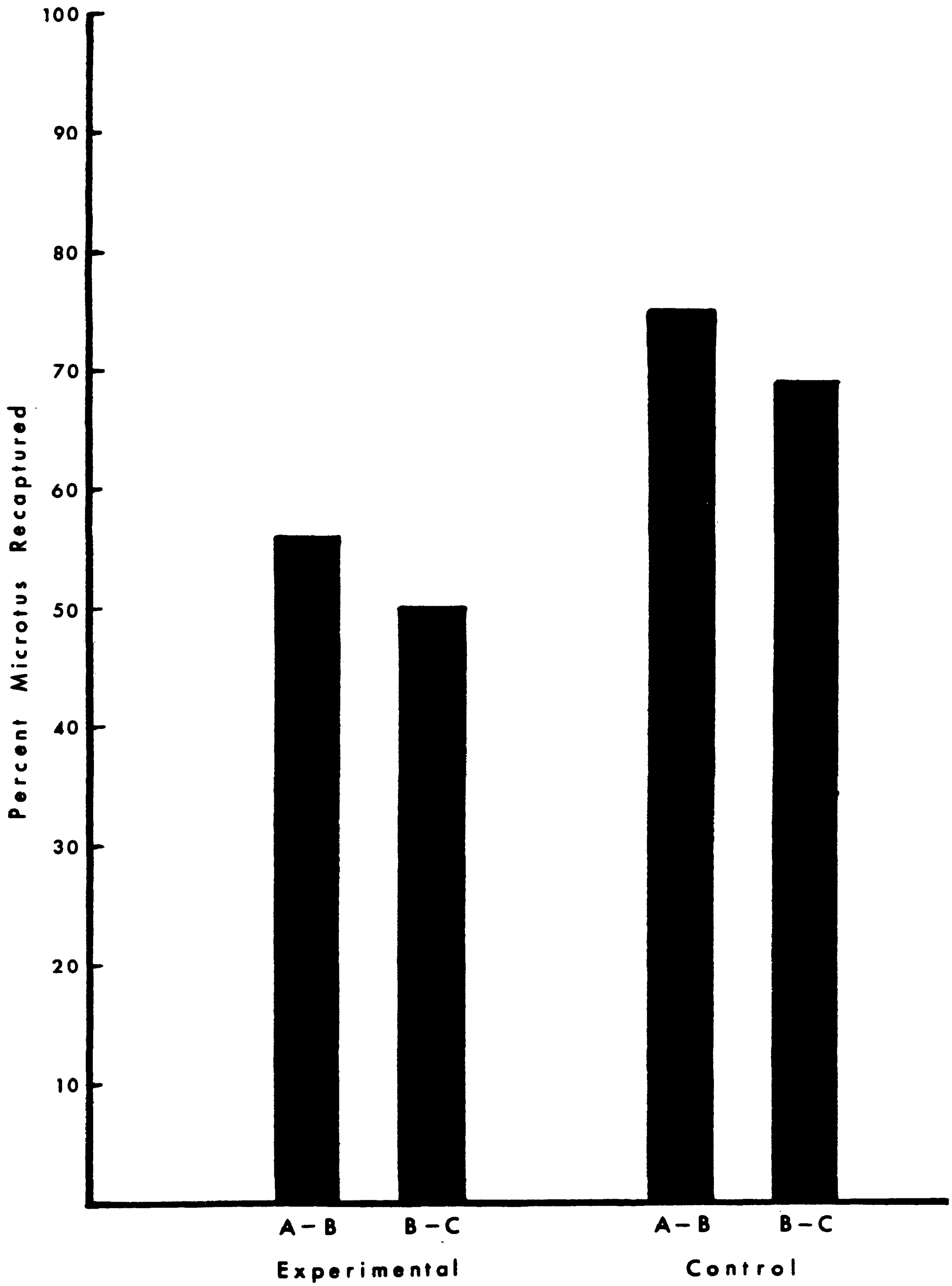
Eleven voles were trapped on the control plot during Trapping Period D (Table II). This number is similar to the number present on the control plot the previous spring (Table II). Only one of these animals, an adult male, was eartagged from the previous year (initial capture 14 August) and was also one of the animals captured occasionally on the experimental plot during August and September, 1979. It was not caught on the burned area in 1980.

Survival (recapture) rates were used to make comparisons between pre-burn and post-burn populations on both plots. From comparing the population of voles on the control plot in all three trapping periods in 1979, it can be seen that population turnover was similar before and after the burn; 75% of the original marked animals from Period A were recaptured in Period B, while 68% of the voles captured during the second period were recaptured in Period C (Fig. 5).

Examination of the 13 voles caught on the control after the burn in Trapping Period C (Table II) reveals three important facts; (1) the voles present were not the result of an influx of juveniles since no new juveniles were trapped; (2) ten of the Microtus had been trapped on the control plot prior to the burn (77% were recaptures); and (3) only one of these animals was a known emigrant from the experimental plot. These facts indicate that the fire had no noticable effect on the vole population on the control plot.

Although survival of experimental voles was 26% less than those on the control plot after the fire, this same difference in survival rates (25%) occurred before the burn (Fig. 5); perhaps the reason for

Fig. 5. Survival rates (percent animals recaptured) of *Microtus pennsylvanicus* between successive Trapping Periods A and B, and B and C in 1979 for experimental and control plots. Burn occurred between Periods B and C.



100
90
80
70
60
50
40
30
20
10
Percent Microtus Recaptured
A – B
B – C
A – B
B – C
Experimental
Control

this is due to higher predation on the experimental plot in general because one edge ran along the road where more large predators may travel.

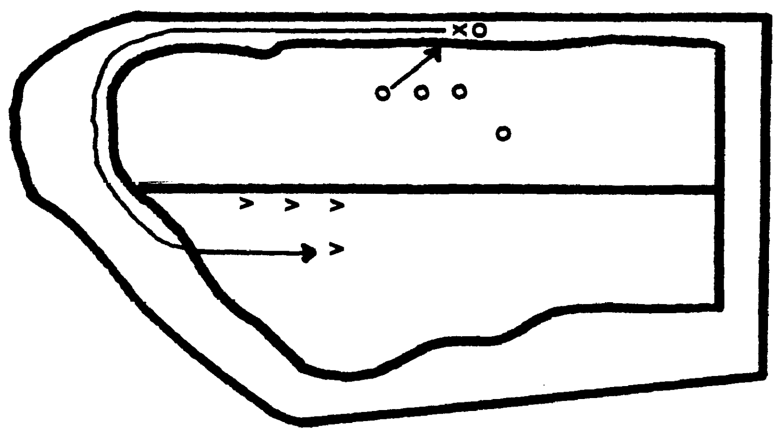
The recapture of voles on the experimental plot was slightly less between Periods B and C (after the burn) than between Periods A and B before the fire, but this slight decrease was matched by a similar drop (11% versus 9%) on the control plot. One might suspect that this similar drop was a result of the loss of the same animals which had home ranges including portions of both plots. If voles that inhabited both plots are not included in the analysis, the same trend is seen with an even greater drop on the control plot. Although voles were absent from the burned area for awhile, comparisons of survival rates suggest that most survived the burn and just moved into a new area (see below).

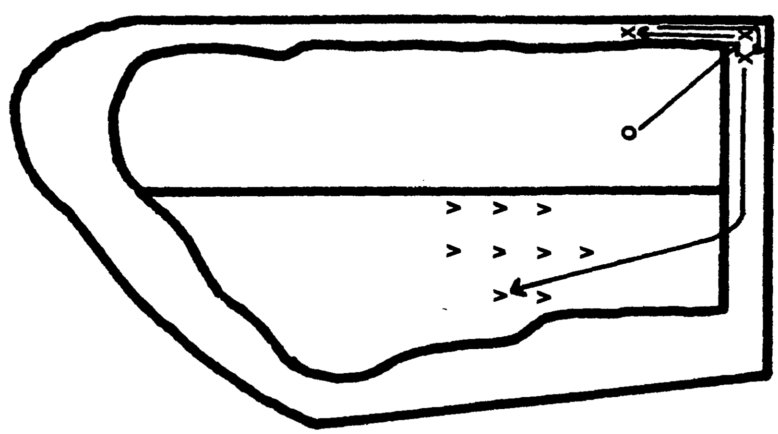
If trapping records for individuals are examined, chronologies showing the emigration pattern of several animals trapped on the experimental plot before the fire can be established. Live trapping in the perimeter around the experimental plot during the first few days after the burn yielded five animals that had been trapped only on the experimental plot prior to the fire. One of these animals emigrated to the control plot and established a home range there within the fifteen day trapping period subsequent to the burn. Three other voles trapped exclusively on the burned area prior to the fire emigrated around the perimeter to establish home ranges on the control plot during the first five weeks following the burn (Fig. 6). Three other voles, which initially had home ranges that included portions of both plots, were captured only on the control plot after the fire (Fig. 7). The emigration of voles from the burned area to the unburned area together with the lack of evidence of direct mortality indicates that mortality due to the controlled burn was low, if any.

Effects on age and sex distribution.--No effect of fire on age and sex distribution is evident from the data that were collected. On the control plot, the only change in age distribution that occurred in the three trapping periods of 1979 was an increase in the number of juveniles captured; the number of adults and subadults stayed relatively the same (Table V). Although juveniles were not captured during the first period, once they were caught starting at the beginning of Trapping Period B, their numbers remained fairly stable, even following the fire. In Trapping Period A, males outnumbered females five to three (Table V). This relationship changed during the second period when four more females than males were trapped. In the third trapping period, the number of females continued to exceed the number of males. Age distribution and the proportion of males to females on the experimental plot followed a similar pattern to that seen on the control in Trapping Periods A and B. In Periods C and D there were too few captures to make age and sex comparisons.

Effects on reproduction.--No effect of fire on reproductive activity of either males or females is evident from the data that were collected. With the exception of one adult, all *Microtus* adult and subadult males were reproductively active (testes were in the scrotal

Fig. 6. Emigration pattern of three voles from their original home ranges on the experimental plot (o) around the perimeters (x⟶x) to the control plot where new home ranges (v) were established following the burn.





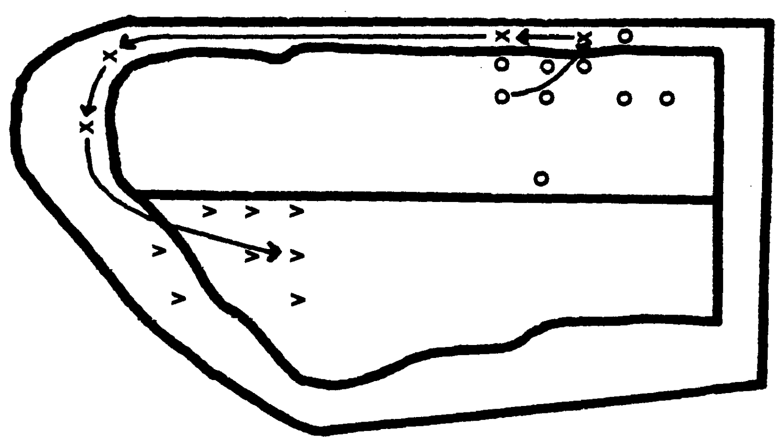
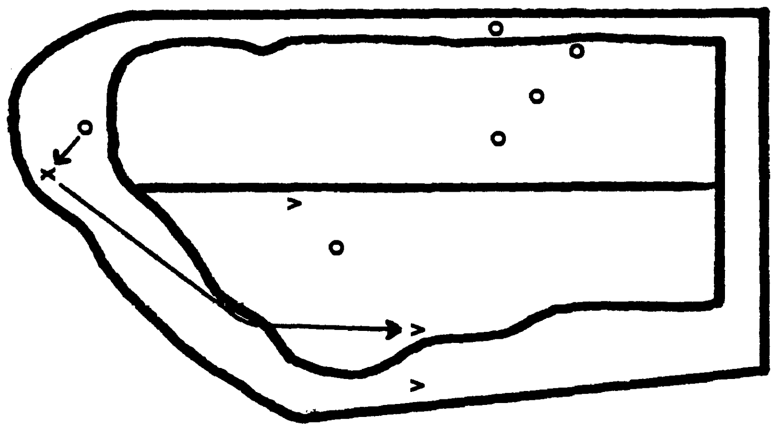
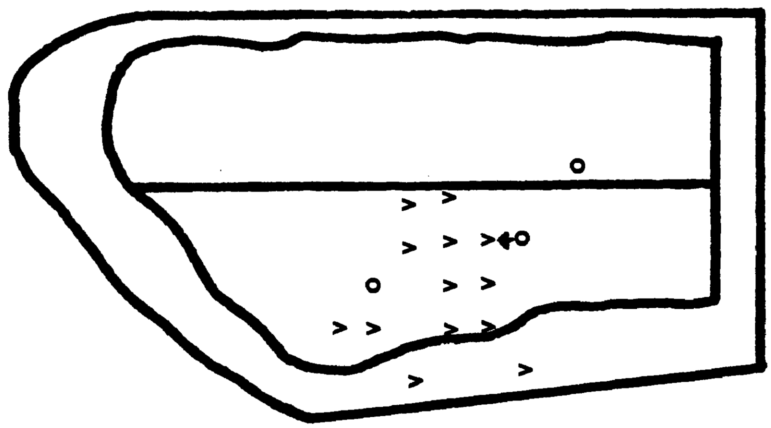


Fig. 7. Movement of home ranges of three voles whose original home ranges (o) were located on both the experimental and control plots before the burn to new home ranges (v) located on the control plot after the burn. The only capture of a vole in the wooded area, that occurred five hours after the burn, is indicated by the (x).





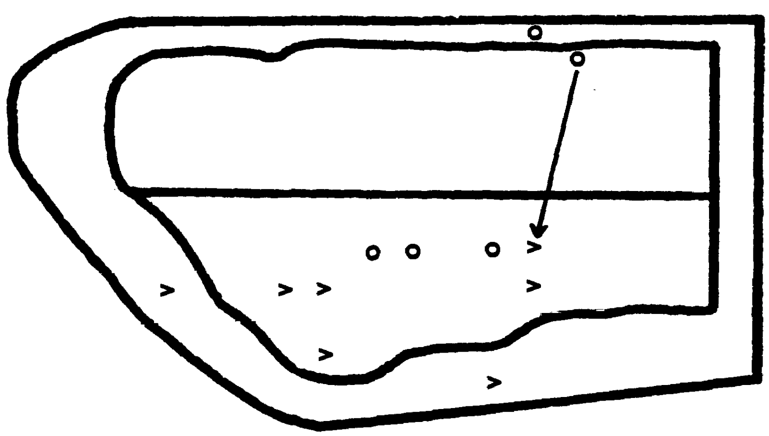


Table V. Number of *Microtus pennsylvanicus* of each sex and age class present on experimental and control plots during Trapping Periods A, B, and C in 1979, and D in 1980.

Age Sex	Trapping Period							
	A April 14-28		B April 30-May 14		C May 15-29		D April 28-May 12	
	Exp.	Con.	Exp.	Con.	Exp.	Con.	Exp.	Con.
Adults								
Males	6	4	3	4	0	5	1	5
Females	3	1	4	2	1	2	0	1
Subadults								
Males	3	1	0	0	0	1	1	0
Females	6	2	4	3	0	1	0	1
Juveniles								
Males	0	0	2	2	0	0	0	3
Females	0	0	3	5	0	4	0	1
Totals	18	8	16	16	1	13	2	11

position) when trapping was initiated in April 1979; by the end of Trapping Period A all males were apparently active. Most remained with testes in the scrotal condition until the conclusion of trapping in 1979, although a few became non-reproductive by the end of September. No difference in male reproductive activity was evident between the two plots, and no difference could be noted as a result of the fire. Males that emigrated from the experimental plot to the control plot after the burn remained reproductive. In the spring of 1980, all adult and subadult males were scrotal before trapping was concluded. During both years of trapping, some precocious juvenile males became scrotal before attaining subadult weight, a few at weights as low as 17 g.

Near-term pregnant females were first trapped on 28 April 1979. However, reproductive activity must have occurred several weeks earlier since juveniles were captured on 1 May. Females that were obviously pregnant and new juveniles were subsequently trapped throughout 1979, with one pregnant adult found as late as 19 October and a new juvenile trapped 20 October. Of five pregnant females trapped before the burn, four were captured on the experimental plot; only one subadult was caught on the control plot. In the first three months following the fire, numerous pregnant females were recorded on the control plot. Between 15 August and 20 October, pregnant voles were trapped on both plots. In the spring of 1980, no females were captured on the burned plot; of the three found on the unburned plot, one was obviously pregnant.

Several voles were recorded as being pregnant more than once during the course of this study. Two females had four recorded pregnancies. One was first trapped as a lactating subadult on the control plot two days after the burn; as an adult, she was recorded pregnant four times during succeeding captures on the control plot. The other was an adult first recorded pregnant early in Trapping Period A on the experimental plot. Two days after the fire she was caught on the control, again pregnant; the fire apparently had no effect on this pregnancy. Another female that was initially trapped as a juvenile on the experimental plot prior to the burn was recorded as pregnant twice on the unburned area post-burn; she was pregnant a third time when captured on the burned plot on 29 September. Two voles actually delivered litters in traps; one subadult delivered six pups on the experimental plot before the fire; one adult delivered four pups on the control plot on 29 September.

Peromyscus leucopus (white-footed mouse)

Although there were never high numbers of P. leucopus on either the experimental or control plot, a few individuals were trapped on the experimental plot during Trapping Periods A and B prior to the burn (Table III). Immediately following the fire during Trapping Period C, no white-footed mice were captured on the experimental plot; one juvenile was caught on the control plot during this interval.

Examination of the population of P. leucopus established in the wooded area on the study site showed that the size of the population increased continuously through all three trapping periods, including after the burn (Table III); part of this increase in size can be attributed to continually increasing numbers of juveniles (Table VI). Survival rates for white-footed mice were fairly high; 75% of tagged animals from Trapping Period A were recaptured in Trapping Period B. Recapture rates actually increased following the burn in Period C to 94%. These increases in population size and in survival of animals indicate that the fire had no major effect on the population of P. leucopus except for the immediate response of avoidance of the burned area.

Spot trapping during the months of June through October showed a continued increase in population size of white-footed mice. As the size increased, individuals were again occasionally caught on the experimental plot and on the control plot (Table III and Fig. 8). By the spring of 1980, the population had decreased, dropping back to the size it was in Period B before the burn, with only occasional captures occurring on the experimental plot and none on the control. Only one adult trapped on the burned area had been captured in the north perimeter during the fall of 1979.

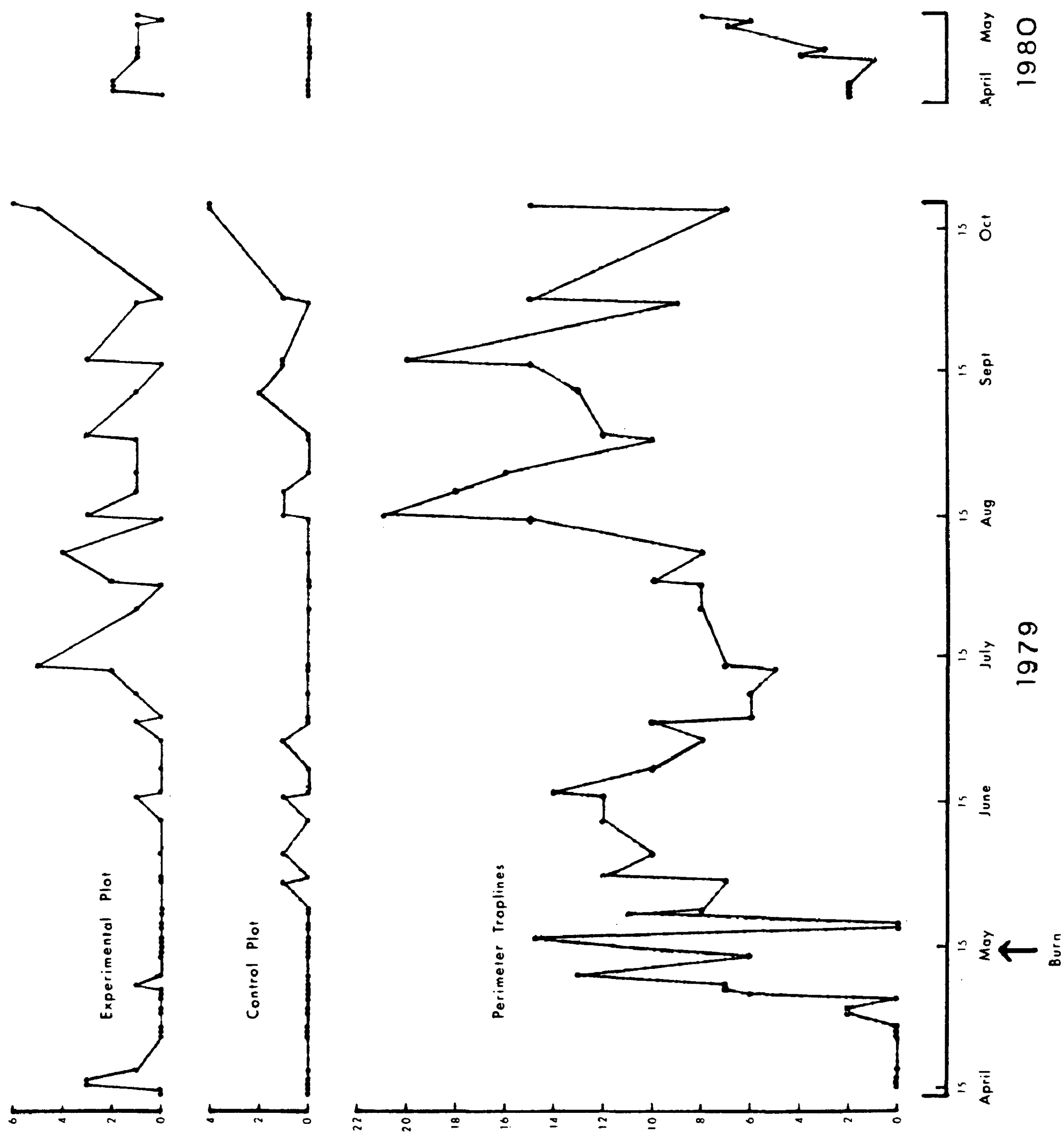
Peromyscus maniculatus (deer mouse)

No deer mice were trapped on either the experimental or control plot before the burn. One animal, an adult, was captured before the fire; it was trapped once in the middle of Trapping Period B in the southernmost trap on the east perimeter trapline and then never recaptured (Fig. 9). For the first week after the fire no deer mice were caught on the burned area. Then nine days following the burn

Table VI. Number of _Peromyscus leucopus_ of each sex and age class present on experimental and control plots and on perimeter traplines during Trapping Periods A, B, and C, and spot trapping (ST) in 1979, and Trapping Period D in 1980.

Age / Sex	Trapping Period: A, April 14-28			B, April 30-May 14			C, May 15-29			ST, June 4-Oct. 20			D, April 28-May 12		
	Exp.	Con.	Per.	Exp.	Con.	Per.	Exp.	Con.	Per.	Exp.	Con.	Per.	Exp.	Con.	Per.
Adults															
Males	2	0	0	0	0	6	0	0	7	8	3	24	1	0	7
Females	2	0	0	1	0	5	0	0	6	6	4	11	1	0	2
Subadults															
Males	0	0	0	0	0	0	0	0	0	4	1	12	0	0	0
Females	0	0	0	0	0	0	0	0	0	2	3	9	0	0	0
Juveniles															
Males	0	0	0	0	0	4	0	1	8	2	1	8	0	0	0
Females	0	0	0	0	0	1	0	0	3	6	1	10	0	0	2
Totals	4	0	0	1	0	16	0	1	24	28	13	74	2	0	11

Fig. 8. Daily capture of *Peromyscus leucopus* on experimental and control plots and on perimeter traplines from 14 April to 20 October, 1979, and from 25 April to 12 May, 1980.



Experimental Plot
Control Plot
Perimeter Traplines
Number of Individuals
April
May
June
July
Aug
Sept
Oct
15
Burn
1979
1980

P. maniculatus suddenly began to invade the burned plot. At this time grasses on the burned area averaged 11 cm in height and 15% vegetative cover (Fig. 2). The number of mice increased through the end of Trapping Period C on into June and then remained relatively stable until the middle of August when it began to decline. No deer mice were captured after 1 September (Fig. 9). There were no captures of P. maniculatus on the control plot at any time during trapping in 1979 (Table III).

By the spring of 1980 the population of deer mice had increased again on the experimental plot (Table III) and was significantly higher than the population on the control plot where only one juvenile was captured ($P < 0.05$, Table VII). All of these captures were on the southern one-third of the plot where grasses were shorter and where there was less vegetative cover and litter.

Since there were no Peromyscus maniculatus on the experimental or control plots prior to the burn, the invasion of only the burned area by deer mice shortly after the fire appears to be a positive response to changes resulting from the fire.

Reithrodontomys megalotis (western harvest mouse)

Only five R. megalotis were captured on the study area before the burn in Trapping Periods A and B, two on the control plot and three on the experimental plot (Table III). After the burn, harvest mice were not captured anywhere until 13 July. From 13 July to 14 August, six individuals were trapped on the control plot and on the south perimeter and southern end of the west perimeter traplines, but still none were

Fig. 9. Daily capture of *Peromyscus maniculatus* on experimental and control plots and on perimeter traplines from 14 April to 12 October, 1979, and from 25 April to 12 May, 1980.

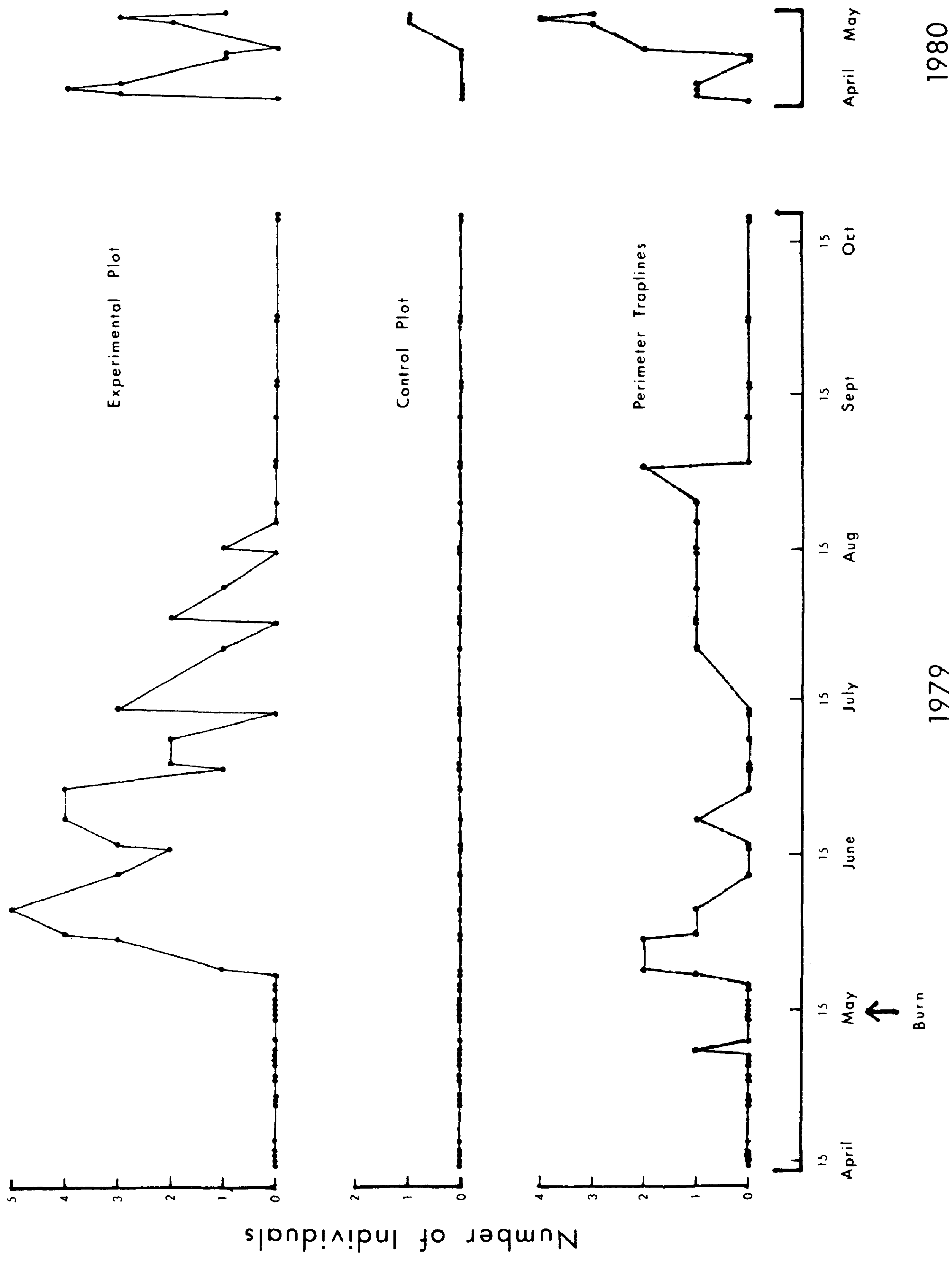

Number of Individuals
Experimental Plot
Control Plot
Perimeter Traplines
0
1
2
3
4
5
15
April
May
June
July
Aug
Sept
Oct
Burn
1979
1980

Table VII. Daily capture rates of <u>Peromyscus</u> <u>maniculatus</u> for experimental and control plots and perimeter traplines during Trapping Periods A through D.

Trapping Day	A April 14-28			B April 30-May 14			C May 15-29			D April 28-May 12		
	Con.	Exp.	Per.	Con.	Exp.	Per.	Con.	Exp.	Per.	Con.	Exp.	Per.
1	0	0	0	0	0	0	0	0	0	0	4	1
2	0	0	0	0	0	0	0	0	0	0	3	1
3	0	0	0	0	0	0	0	0	0	0	1	0
4	0	0	0	0	0	0	0	0	0	0	1	0
5	0	0	0	0	0	1	0	0	1	0	0	2
6	0	0	0	0	0	0	0	1	2	1	2	3
7	0	0	0	0	0	0	0	3	2	1	3	4
8	0	0	0	0	0	0	0	4	1	1	1	3
Mean	0	0	0	0	0	0.1	0	1.0	0.8	0.4	1.9	1.8
<u>t</u> value*						1.00		1.76	0.55		3.00	0.19
<u>P</u> value						>0.10		>0.10	>0.10		<0.05	>0.10

*Paired <u>t</u>-test

found on the burned plot. On 15 August, 93 days after the burn, harvest mice began to reappear on the experimental plot (Fig. 10). Numbers of mice on the burned plot increased slightly until 1 September and then remained stable through October, at which time trapping was concluded for 1979. While harvest mice were increasing on the experimental plot, captures decreased on the control plot and in the perimeters.

In Trapping Period D, the number of harvest mice trapped on the experimental plot had increased over the number caught during spot trapping in 1979 (Table III), and was significantly higher than the number trapped on the control plot ($\underline{P} < 0.005$, Table VIII).

Spermophilus tridecemlineatus (thirteen-lined ground squirrel)

During my entire study, eleven S. tridecemlineatus were captured (Table I). Before the fire, four thirteen-lined ground squirrels were trapped on the west and south perimeter traplines, and two were caught on the control plot. Immediately after the burn, Trapping Period C, the number of ground squirrels caught in these areas were three and one respectively (Table III). No S. tridecemlineatus was captured on the experimental plot prior to burning; however, two were trapped on the burn 45 days following the fire. In fact, two days after the burn, a freshly dug burrow was noted among the ashes on the south end of the burned plot. Captures of thirteen-lined ground squirrels decreased everywhere on the study area during spot trapping through October.

The 1980 population of S. tridecemlineatus was almost equal in numbers to the pre-burn population of 1979, with most of the captures

Fig. 10. Daily capture of *Reithrodontomys megalotis* on experimental and control plots and on perimeter traplines from 14 April to 20 October, 1979, and from 25 April to 12 May, 1980.

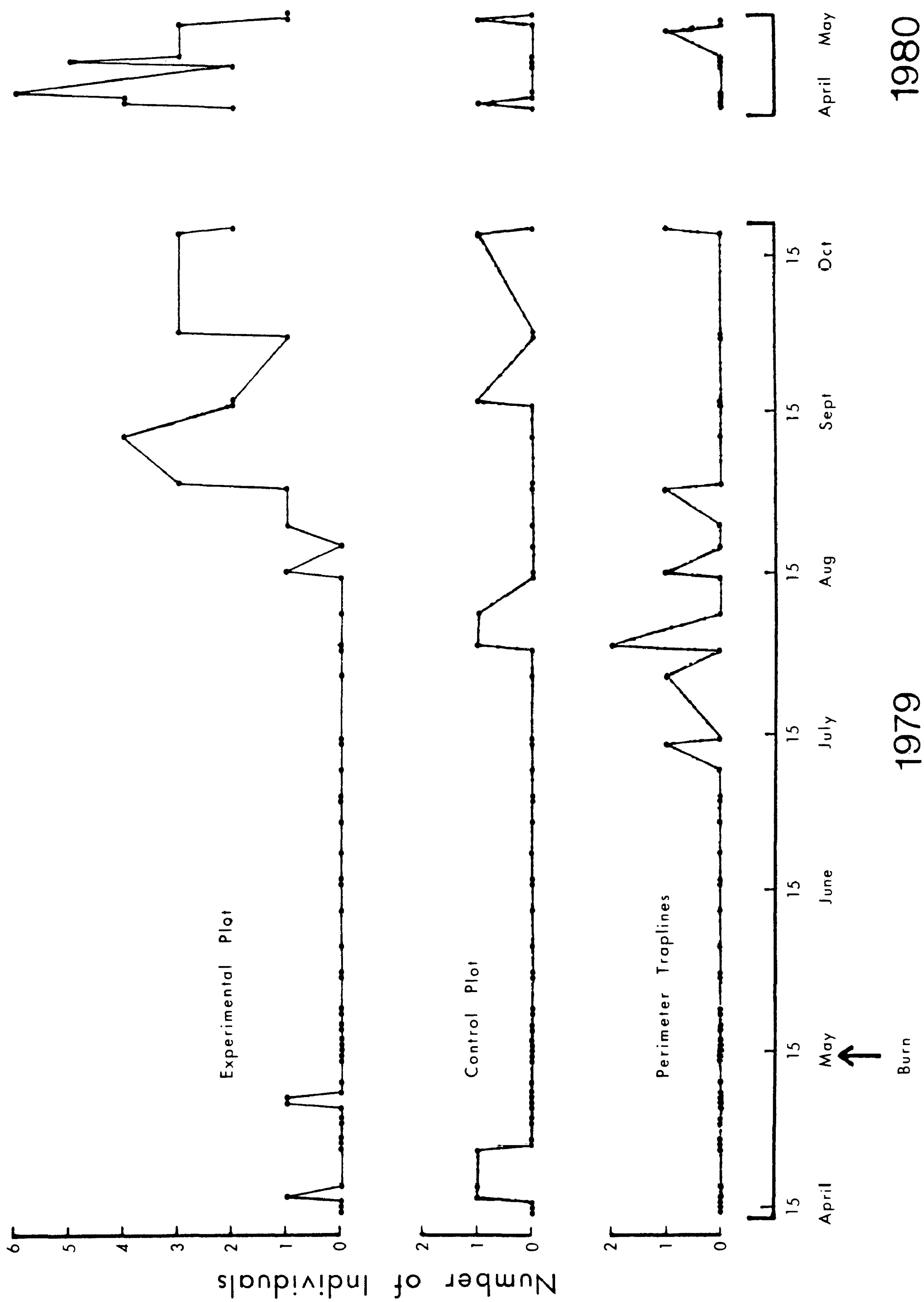

Number of Individuals
Experimental Plot
Control Plot
Perimeter Traplines
April
May
June
July
Aug
Sept
Oct
15
Burn
1979
1980
0
1
2
3
4
5
6

Table VIII. Daily capture rates of *Reithrodontomys megalotis* for experimental and control plots and perimeter traplines during Trapping Periods A through D.

Trapping Day	Trapping Period A April 14-28			B April 30-May 14			C May 15-29			D April 28-May 12		
	Con.	Exp.	Per.	Con.	Exp.	Per.	Con.	Exp.	Per.	Con.	Exp.	Per.
1	0	0	0	0	0	0	0	0	0	1	4	0
2	0	0	0	0	0	0	0	0	0	0	4	0
3	0	0	0	0	1	0	0	0	0	0	6	0
4	1	1	0	0	1	0	0	0	0	0	2	0
5	1	0	0	0	0	0	0	0	0	0	5	0
6	1	0	0	0	0	0	0	0	0	0	3	1
7	0	0	0	0	0	0	0	0	0	0	3	0
8	0	0	0	0	0	0	0	0	0	1	1	0
Mean	0.4	0.1	0	0	0.3	0	0	0	0	0.3	3.5	0.1
t value*	1.53	1.00		1.53	1.53					5.02	5.67	
P value	>0.10	>0.10		>0.10	>0.10					<0.005	<0.005	

*Paired *t*-test

again occurring in the south perimeter trapline.

Shrews

Although no *Sorex cinereus* (masked shrews) were trapped on the experimental plot before the burn, one was captured on the burned area four months after the fire (Table III). *Blarina brevicauda* (short-tailed shrews) were never captured on the experimental plot, either before or after the controlled burn (Table III). Trap mortality was high for *Sorex*; although two more *Blarina* died than *Sorex*, masked shrews had the highest percentage of captured animals die while in traps (Table I).

Mus musculus (house mouse)

Although *M. musculus* were not captured anywhere on the study site before the burn, four were trapped on the experimental plot three and one-half months after the fire; they were never recaptured (Table III).

Mustela nivalis (least weasel)

Four least weasels were caught on the experimental plot during the first week of trapping in 1979. They were never recaptured, and no other weasels were caught anywhere during the rest of the study (Table III). The lack of subsequent captures was probably due to trap avoidance.

Zapus hudsonius (meadow jumping mouse)

Two *Z. hudsonius* were trapped during this study; one was taken on the south end of the experimental plot three months following the burn, and the other was captured in May, 1980, in the brome perimeter next to the woods (Table III). Neither was recaptured.

Perognathus flavescens (plains pocket mouse)

Only one pocket mouse, a female, was captured during this study; it was taken on the experimental plot three and one-half months after burning (Table III).

Spermophilus franklinii (Franklin's ground squirrel)

Only one S. franklinii was trapped during this study; it was caught on the burned plot three and one-half months following the fire (Table III).

Habitat Separation

The study area consisted of four major types of habitat. The wooded area was divided into two habitats based upon the type of understory -- brush or smooth brome. The open tallgrass of the experimental and control plots was the third type, while the portions of the brome waterways that were not covered by a canopy of trees was the fourth type of habitat.

All captures and recaptures were examined to determine the habitat frequented most often by each species in this study. Before and after the burn habitat separation between species tended to follow patterns described by Jones (1964) (Table IX). Microtus pennsylvanicus was most abundant in moist, lowland areas having dense vegetative cover and litter accumulation and was decidedly more common in open grass than grass covered by a canopy of trees. Peromyscus leucopus was captured primarily in the woods and only rarely caught in open grass. Conversely, P. maniculatus inhabited open grasslands and was never trapped in the woods or even in grass with a tree canopy.

Table IX. Number of captures (including recaptures) per 100 trapnights for all species trapped from 14 April 1979 to 12 May 1980 in the four major habitat types.

Species	Open Grass		Woods	
	Tallgrass	Brome	Brome	Brush
Microtus pennsylvanicus	6.4	5.3	3.8	0.2
Peromyscus leucopus	1.1	1.2	24.1	32.0
Peromyscus maniculatus	1.0	2.2	0.0	0.0
Reithrodontomys megalotis	1.0	0.3	0.0	0.0
Spermophilus tridecemlineatus	0.4	1.1	0.0	0.0
Blarina brevicauda	0.2	0.3	1.2	0.0
Sorex cinereus	0.1	0.1	0.2	0.2
Mus musculus	0.1	0.0	0.0	0.0
Mustela nivalis	0.1	0.0	0.0	0.0
Zapus hudsonius	tr.*	0.0	0.1	0.0
Perognathus flavescens	tr.*	0.0	0.0	0.0
Spermophilus franklinii	tr.*	0.0	0.0	0.0

*Trace (tr.) <0.05

Reithrodontomys megalotis was similarly abundant in open grass and never caught under trees. *Spermophilus tridecemlineatus* favored drier sites, usually those with a relatively low percentage of vegetative cover. *Blarina brevicauda* was trapped most frequently in moist, lowland areas, particularly next to waterways, that had a dense litter layer. *Sorex cinereus* usually favor moist habitats (Jones, 1964), but captures of masked shrews were scattered all over the study site making it impossible to discern any pattern. Captures of all other species were too infrequent to determine habitat preferences.

DISCUSSION

Evidence indicates that the total absence of mammals from the burned area immediately following the fire was primarily due to emigration to adjacent grassy areas; fire-induced mortality and increased predation most likely played a minor role if any. Although no casualties were noted during the search following the burn, it is possible that some mammals perished in their burrows after taking refuge from the fire. For example, some animals may have died of suffocation due to the decrease in O_2 (Bendell, 1974). Because the highest temperatures produced in grassland fires occur well above ground and underground temperatures rarely reach lethal levels (Howard et al., 1959; Vogl, 1974), numbers of deaths resulting from heat should have been fairly low.

Any animal active on the burn plot immediately after the fire would have been completely exposed to predators due to elimination of vegetative cover. This probably would be an important factor when burns destroy large areas, and resident animals cannot immediately find cover. In my situation, it would appear that when the animals finally ventured out of their burrows after the burn, they immediately headed for the protective cover provided by the adjacent perimeters and the control plot. Thus, if they immediately emigrated (as was indicated by the capture of voles in the perimeters the very next day), predation on the burned area would have been low except for the short period of time it took for them to get to the perimeters.

Predation, reduced cover, availability of food, and competition are the four factors that appear to explain the population shifts observed in this study. Increased predation on the burned plot always could have played a role in slowing down reinvasion of this area; however, the impact of predation could not be determined in this study. Two predators, the least weasel and the short-tailed shrew, were trapped on the study area and others were observed on or near the study site -- great horned owls (Bubo virginianus) and domestic cats and dogs. Predation-proof plots could be utilized to determine the impact of predation in future studies.

When discussing the reduction of cover caused by the fire, two aspects must be considered: the reduction in vegetative cover, and the destruction of the litter layer. Different species utilize vegetative cover and litter in different ways, and their response to the reduction of cover seems to reflect this.

Voles responded negatively to the destruction of both vegetative cover and litter by emigrating from the burned area. Voles nest both below ground in burrows and above ground in shallow depressions; thus individuals nesting above ground would require vegetative cover for protection of nests. Voles did not return to the experimental plot until vegetation attained maximum cover. But even under these conditions, the density of voles remained relatively low and none established home ranges exclusively on the burned plot. Apparently, dense vegetative cover alone did not satisfy the habitat requirements of the voles -- the missing element was probably surface litter. Under the thick vegetation there were still large bare patches of ground so that any animals active in these areas would be exposed to predators like weasels. Tester and Marshall (1961) reported a high positive correlation between meadow voles and litter depth. Meadow voles are diurnally active, and make surface runs beneath the litter layer. Throughout my study, I noted that immediately upon release voles would burrow under the litter and disappear from view. Even though some litter had accumulated one year after the fire, it was relatively sparse compared to the accumulation present on the control plot, and the low density of voles indicated that it still was not enough to fulfill their habitat requirements. The lack of surface litter has been cited in several studies as the key factor which keeps Microtus from establishing home ranges on burned plots for extended periods (Cook, 1959; Schramm, 1970; Moreth and Schramm, 1973).

Other studies have found that short-tailed shrews also respond negatively to the destruction of litter by fires (Springer and Schramm, 1972). However, although short-tailed shrews were trapped on the control plot, they were not captured on the experimental plot either before or after the burn in my study.

Although deer mice and harvest mice both responded positively to the new habitat created by the fire, deer mice quickly invaded the burned area while harvest mice did not enter until much later. The reason for this difference is probably related to how each species utilizes vegetative cover. Deer mice appeared to thrive in the post-fire habitat where vegetation was sparse and where surface litter was low. Under these conditions, numbers of mice increased until vegetative cover reached a maximum, and then began to decline. These findings agree with past studies. Tester and Marshall (1961), for example, found that deer mice were not observed where there was heavy litter accumulation, and LoBue and Darnell (1959) reported that as vegetative height and cover increased, populations of deer mice decreased. The sparseness of the vegetation may provide greater ease of locomotion, partially accounting for their response. Unlike voles, deer mice were never observed to burrow under litter after being released. Also, because deer mice nest in burrows and are nocturnal animals, dense vegetation is not necessary to provide cover for nest sites. The fact that deer mice were captured all over the burn plot for the first few months after the fire while grasses were sparse but were caught only on the sparsely vegetated and unlittered south end one year after the burn lends further credence to these ideas.

Harvest mice did not return to the experimental plot until vegetative cover was maximal. However, unlike deer mice, harvest mice are ground nesters and require clumps of grass in which to build their nests; their prolonged avoidance of the area, thus, possibly was due to the need for dense vegetation for nesting habits. The amount of litter did not seem to be an important factor in distribution of harvest mice; they were captured in areas devoid of litter as well as in areas which had a heavy litter accumulation.

Although the white-footed mouse was the most common species of small mammal in this study, it was captured primarily in the woods, and most were not directly affected by the fire. The slightly larger number of captures on the burned area that occurred after the fire may be attributed to an increase in population size in the wooded area forcing some mice, mostly immature ones, into suboptimal habitat. I think the reason they moved onto the burned area and not the control plot was because of the sparse vegetation and lack of litter. Springer and Schramm (1972) found that white-footed mice thrived in recently burned areas and observed that white-footed mice reached highest densities in places with no litter. They suggested that white-footed mice prefer unlittered areas for ease of locomotion. This is supported by my observation that all white-footed mice remained above litter when released. Similarly, Springer and Schramm (1972) and Schramm (1970) suggested that ease of locomotion was the reason for an increase in meadow jumping mice noted following fires. However, only one meadow jumping mouse was captured on the burned plot in my study.

Thirteen-lined ground squirrels also appeared to react favorably to the reduction of vegetative cover on the experimental plot after the fire. While they were trapped only in the sparsely vegetated perimeters before the burn, they appeared on the experimental plot after the fire. Similarly, the only Franklin's ground squirrel caught was on the burned area a few months after the fire.

The availability of each type of food utilized by the resident mammals is another factor that must be taken into consideration when discussing population changes. Voles are primarily grazers, and thus the initial emigration could have been suspected as a response to the destruction of their food (Bock and Bock, 1978). New growth of grasses, however, was present on the burn for twelve weeks before voles reinvaded; so I do not believe that insufficient food was the reason for their prolonged absence from the plot. On the other hand, most of the other resident species are primarily granivores, and while fire destroys vegetation, seeds lying on the ground usually survive (Ahlgren, 1966; Daubenmire, 1968). In fact, the removal of thick vegetation and litter might make fallen seeds easier for the granivores to find. This, combined with other changes in the habitat, possibly explains the attraction of deer mice to the burned area so quickly following the fire and also may have been involved in the appearance of white-footed mice and the one pocket mouse on the burned area. However, the delayed reappearance of harvest mice on the burned plot indicates that greater accessibility of seeds alone does not explain the attraction to harvest mice, thus indicating that a combination of factors was involved.

Although it is evident that vegetational changes were involved in the responses of the animals, the factor of competition also must be considered. An inverse relationship in density between some species can be seen if population trends are followed. There were no deer mice present on the experimental plot prior to the burn but nine days after the fire, while voles were absent, deer mice invaded and apparently established home ranges. When voles began to reappear on the plot, deer mice rapidly disappeared. The following spring, both species were caught on the experimental plot; however, voles were captured only on the lowland north end while deer mice were trapped only on the south end, on the slope, where vegetation was more sparse.

A similar inverse relationship can be seen between voles and harvest mice. When high numbers of voles were present on both plots before the burn, the population of harvest mice was very low. Although harvest mice did not reenter the burn site immediately after the fire while voles were absent, this delay was most probably caused by the need for clumps of vegetation to meet their nesting requirements, as discussed above. Thirteen weeks after burning, both harvest mice and voles appeared on the burned plot at the same time, but harvest mice increased in number and established home ranges while voles did not. This situation persisted through the end of trapping in 1980. The initial low density of deer mice and harvest mice may have been due to the presence of more aggressive voles. Removal studies are needed to measure the impact of competition.

The possibility of competition between the two granivorous species, deer mice and harvest mice, also must be considered. The first time that deer mice established home ranges on the burned plot was during the three month absence of harvest mice. After harvest mice began to reappear on the plot, deer mice quickly disappeared. Although both species were caught on the burned area one year later, harvest mice were captured mainly on the lowland north end while deer mice were trapped on the sparsely vegetated south end. Again, removal studies are needed to measure the impact of competition.

CONCLUSIONS

Controlled fires that are used to manage grasslands generally are not destructive to wildlife. The immediate post-fire environment confronts resident fauna with radical changes in vegetative cover, litter depth, food availability, predation rates, and competition. These factors may have positive or negative effects on various species. The results of my study indicate that the fire seemed to "benefit" more species of mammals than it "harmed".

Even the one species that responded negatively to the fire, the meadow vole, may actually "benefit" in the long term. Studies have shown that fires increase not only species diversity, but also the productivity of most grassland vegetation, in terms of biomass and seed production (Vogl, 1967; Daubenmire, 1968; Vogl, 1974). This means that the carrying capacity of the habitat is increased in terms of food, and therefore could be able to support greater numbers of animals than the original habitat, if food is a main limiting factor. If space is a main limiting factor, some species may respond to conditions of high productivity by reducing the size of their home ranges and thus increasing the number of individuals that area can support.

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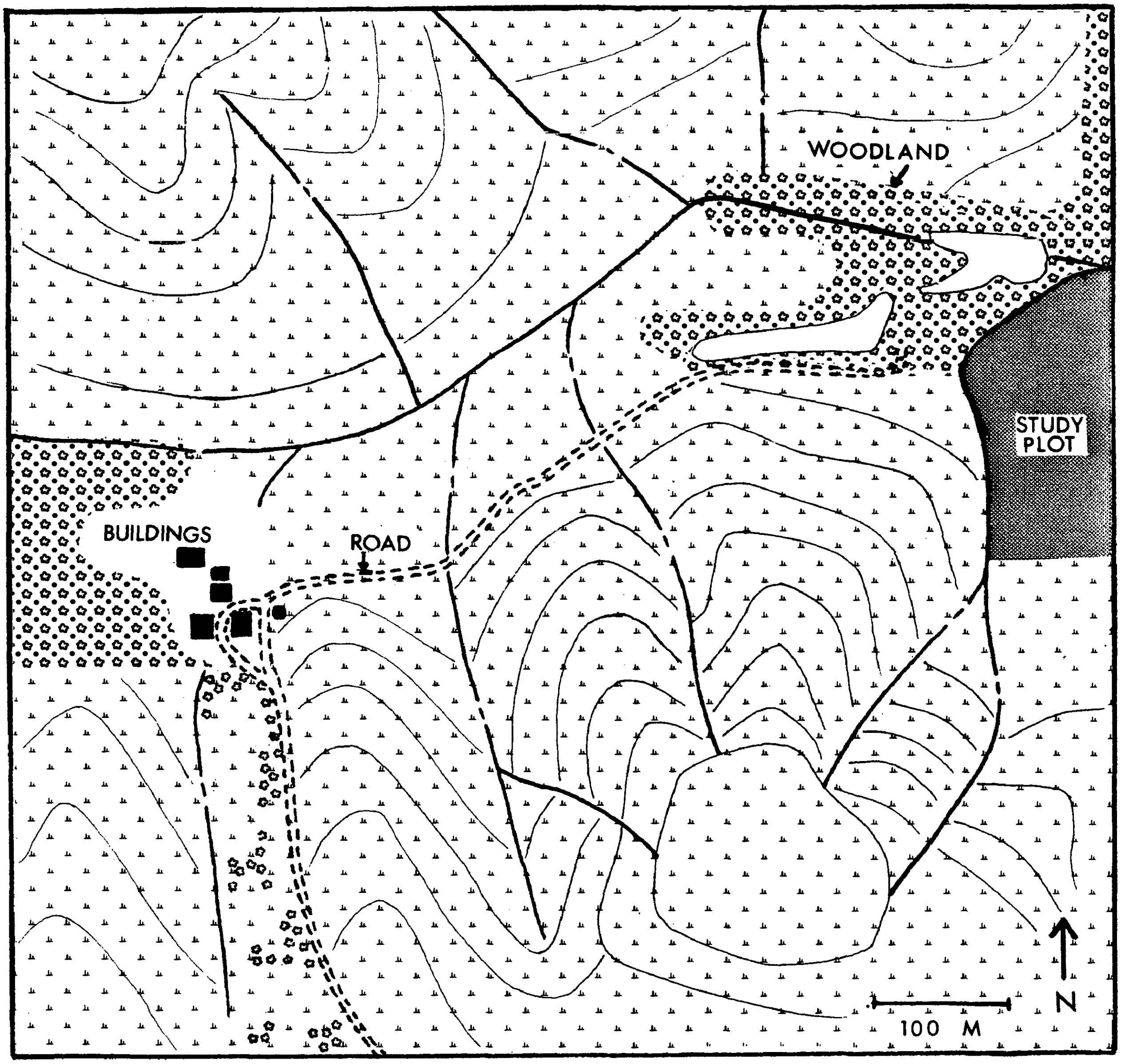
APPENDIX



Location of the study area on Allwine Prairie Preserve.