DENSITY CORRELATED MOVEMENTS
OF FOUR SMALL MAMMAL SPECIES

A Thesis

Presented to

The Faculty of the Department of Biology

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

By

Martin Lloyd Prather

1973

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Master of Arts

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ACKNOWLEDGMENTS

This study owes much to the stimulating guidance of Dr. C. Richard Terman who influenced the course of my thinking throughout. I appreciate the help of Dr. Stewart Ware in determining the vegetational composition of the study field. I am indebted to Drs. Mitchell A. Byrd, Garnett R. Brooks and Stewart Ware for critically reviewing the manuscript. I am especially grateful to my wife, Pat, for her assistance and patience throughout the study.

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ABSTRACT

This experiment was designed to measure and compare movements of *Microtus pennsylvanicus*, *Microtus pinetorum*, *Mus musculus* and *Peromyscus leucopus* in response to increased density. Individuals of these species were removed from one-half of the three acre study field (plot B) during a seven night removal period. Following this period the removed animals were released in the center of the other half of the field (plot A) and their movements were noted by live-trapping for the next seven days (return period). Four replications of this manipulation plus two control periods were conducted over four months.

The *Peromyscus leucopus* population was the largest and most stable of the four species. Individuals of this species were captured a significantly greater number of times and had significantly fewer nights between captures than the other three species. The population levels of the other three species were too low in most cases for the data to be analyzed.

Introduction of *P. leucopus* into plot A caused a significant decrease in the number and proportion of new animals captured there during the return period and a significant increase in the proportion of plot A residents disappearing during the return period. These responses occurred even though only three of the released mice were subsequently captured in plot A and 58 per cent of them returned to plot B by the second night after release. The cues involved in producing these responses are discussed.

No response to the removal of *P. leucopus* individuals from plot B was noted.

Sixty-five per cent of 20 *P. leucopus* individuals released in plot A homed (returned to within 14.3 m. of the site from which they were removed). Seventy-four per cent of the animals which homed did so by the second night after they were released.

Nine instances of long intervals between captures ($\bar{x}$=120 calendar days) of individual *M. pennsylvanicus* suggest these voles were present during the summer on the area and yet were not trapped.

DENSITY CORRELATED MOVEMENTS

OF FOUR SMALL MAMMAL SPECIES

INTRODUCTION

Small mammal populations exhibit varied responses to changing densities. Some population and individual attributes affected by density change are home range size (Batzli, 1968; Getz, 1961; Stickle and Warbach, 1960), mortality (Calhoun, 1948; Chitty, 1960; Davis and Christian, 1956; Getz, 1960; Krebs, 1966; Murray, 1965; Snyder, 1956), natality (Beer and MacLeod, 1966; Golley, 1961; Krebs and Delong, 1965; Lidicker, 1966), body weights (Krebs and Delong, 1965), activity (Pearson, 1953; Orr, 1959; Ambrose, 1973), aggression, and dispersal (as discussed below).

Responses to density changes have been studied either in populations with naturally occuring density fluctuations or by experimentally manipulating density. Cropping or removal of animals and introduction of animals are methods used artificially to alter densities.

The present study examines dispersal movements in four small mammal species by utilizing removal and transfer techniques. Two types of dispersal are recognized by Howard (1960): innate dispersal is a density independent, genetically controlled movement at puberty and environmental dispersal is a density dependent response to environmental factors. This experiment is concerned specifically with density dependent, thus environmental dispersal as defined by Howard.

Previous studies have shown that removal of small mammals from an area typically results in immigration into the vacated area (Blair, 1940; Calhoun and Webb, 1953; Krebs, 1970; Krebs, Keller and Tamarin, 1969; Stickle, 1946; Smyth, 1968). In addition, the rate of resettling of these vacated areas is directly related to the density of the surrounding populations (Andrzejewski and Wroclawek, 1962; Myers and Krebs, 1971; Van Vleck, 1968). Introduction of animals into an area may increase the tendency of residents to disperse to outer areas (Blair, 1940; Calhoun, 1948; Davis and Christian, 1956; Orr, 1959).

Non-manipulative studies of naturally fluctuating populations also indicate an association between density and dispersal (Ambrose, 1973; Gentry, 1968; Grant, 1971; Metzgar, 1971; Pearson, 1953; Snyder, 1956). Myers and Krebs (1971) report a significantly greater emigration from local populations during the increase phase of a population cycle than during the peak phase or decreasing phase.

Increased aggression during population growth has been noted by Brown (1953), Christian (1971), Krebs (1970), Myers and Krebs (1971), Sadleir (1965) and Southwick (1955). These studies led to a postulate that dispersal is the factor regulating density in these populations and may reflect behavioral changes (Getz, 1972; Healey, 1967; Krebs, 1970; Lidicker, 1962; Metzgar, 1971; Strecker, 1954).

The densities of populations of small mammals in nature vary widely due to numerous factors. These differences may be partially explained by differential sensitivity of species to density changes. This differential sensitivity may in turn be attributed to the relative ability of individuals of different species to perceive epideictic cues - cues signaling density changes (Wynne-Edwards, 1965). The data from a previous study on the same experimental area show that three species of small mammals exhibited varying degrees of awareness of a partially depleted population (Staples, 1972). Mus musculus indicated a greater perception of this depletion than did Microtus pinetorum which in turn showed a response greater than that of Microtus pennsylvanicus.

I designed this experiment to ascertain whether the differential responses shown by the species in Staples' study are due to the difference in their densities. The basic objectives of this experiment were: (1) to measure movements in response to different degrees of increased density; (2) to compare the relative responses of Microtus pennsylvanicus, Mus musculus, Microtus pinetorum, and Peromyscus leucopus to these changes in density.

MATERIALS AND METHODS

The study field is located adjacent to the Laboratory of Endocrinology and Population Ecology of the College of William and Mary and is approximately 3.3 acres in area. It is an old field community bordered on three sides by wooded areas. This area was divided into two approximately equal sized plots, plot A (1.6 acres) and plot B (1.7 acres) (Figure 1). The plots appeared similar in all respects. During a preliminary trapping period, approximately equal numbers of individuals of each species were caught on the two plots.

The vegetational composition of the field was estimated along the lines of the trapping grid and is illustrated in Figure 2. Vegetation was grouped into seven categories to describe the field:

1) Medium and tall grasses: *Sorghum halapense* (L.) Pers. (Johnson grass); *Dactylis glomerata* (L.) (Orchard grass); *Erigeron* sp. (Fleabane); *Solidago* sp. (Goldenrod).
2) Short grass and low forbs: *Cynodon dactylon* (L.) Pers. (Bermuda grass); *Vicia* sp. (Vetch).
3) Tall forbs: *Aster* sp. (Aster); *Solidago* sp. (Goldenrod); *Phytolacca americana* L. (Pokeweed);

Figure 1. The experimental field indicating plot A, plot B, the release site, and grid notation.

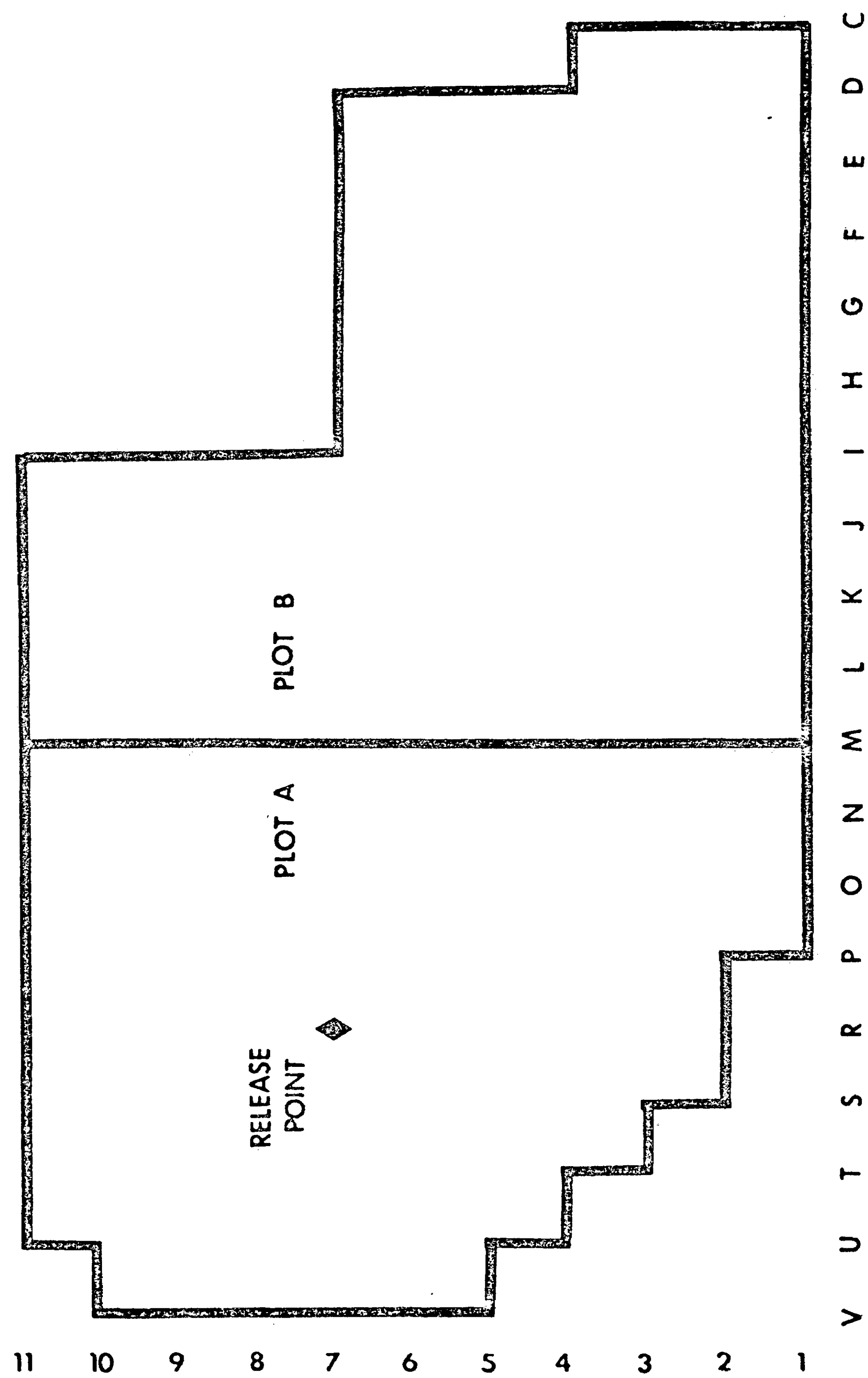

PLOT A
PLOT B
RELEASE POINT
C D E F G H I J K L M N O P R S T U V
1 2 3 4 5 6 7 8 9 10 11

Figure 2: Vegetational Distribution of the Study Field

Key

Medium and tall grasses . . . . . .
(Johnson grass; Orchard grass;
Goldenrod; Erigeron)

Short grass and low forbs .
(Bermuda grass; Vetch)

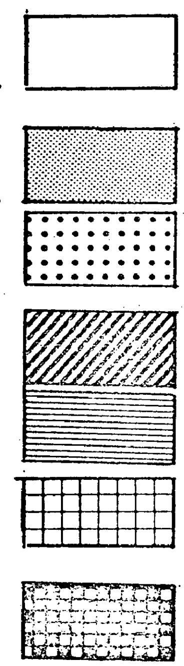
Tall forbs . . . .
(Aster; Goldenrod; Pokeweed;
Thistle; Erigeron)

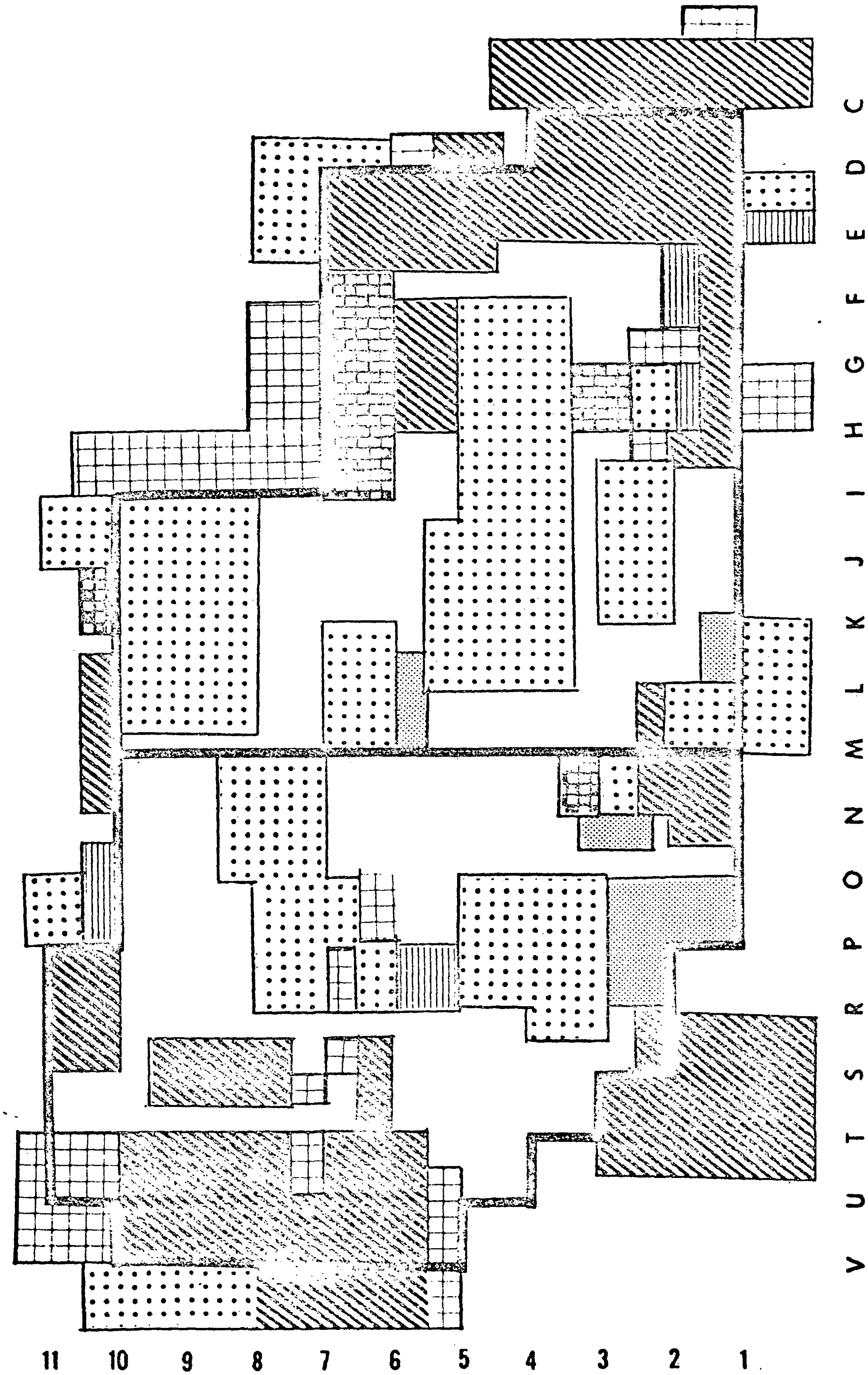
Honeysuckle . . .

Vines . . . .
(Grapevine; Poison Ivy)

Trees . . . .
(Hackberry; Tree of Heaven; Black
Cherry; Honey Locust; Eastern Red Cedar)

Shrubs. . . . .
(Elderberry; Blackberry)




C D E F G H I J K L M N O P R S T U V
11 10 9 8 7 6 5 4 3 2 1

Cirsium sp. (Thistle); *Erigeron* sp. (Fleabane).

4) Honeysuckle: *Lonicera japonica* Thubb.

5) Vines: *Vitis* sp. (Grapevine); *Rhus radicans* L. (Poison Ivy).

6) Trees: *Celtis occidentalis* L. (Hackberry); *Ailanthus altissima* (Mill.) Swingle (Tree of Heaven); *Prunus Serotina* Ehrh. (Black Cherry); *Gleditsia triacanthas* L. (Honey Locust); *Juniperus virginiana* L. (Eastern Red Cedar).

7) Shrubs: *Sambucus canadensis* L. (Elderberry); *Rhubus* sp. (Blackberry).

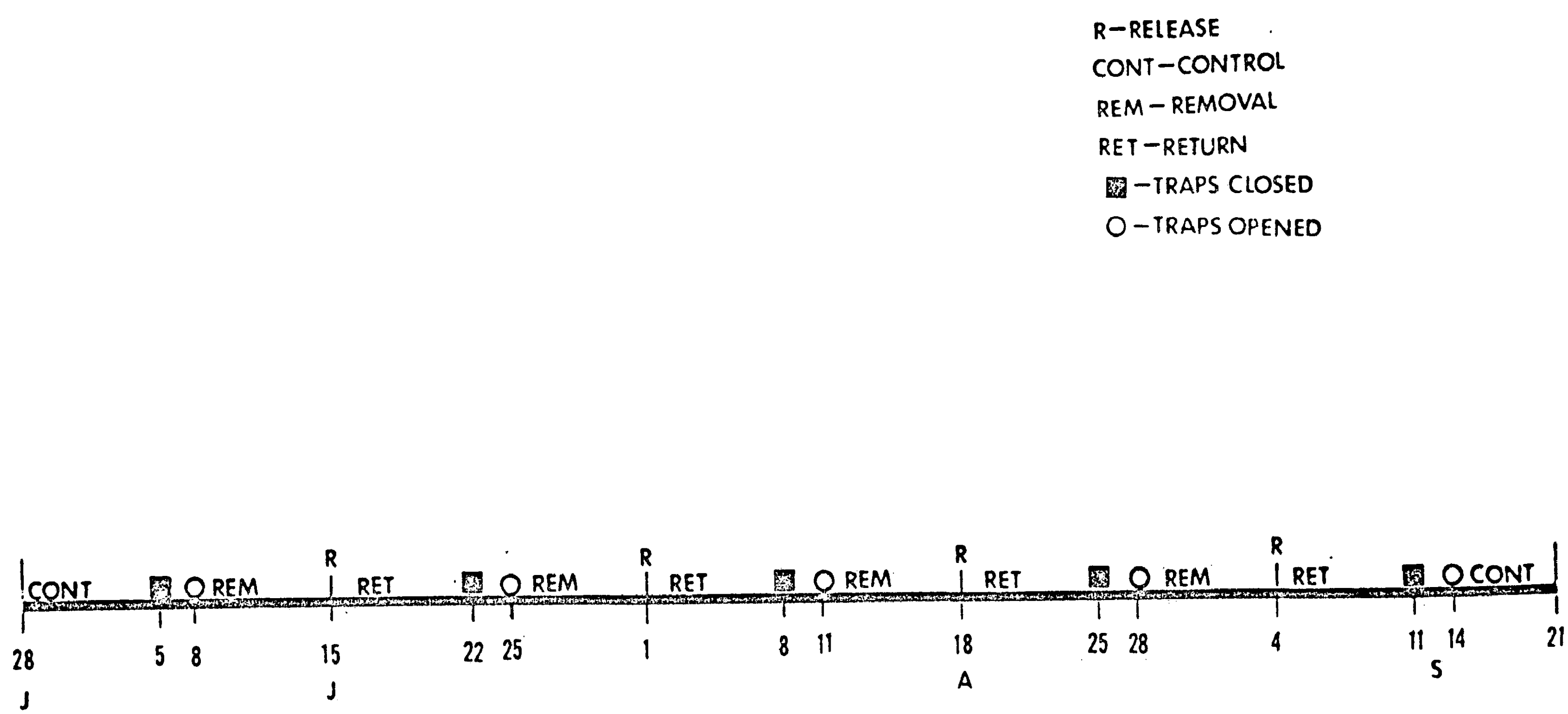
Superimposed upon the field was a 10x10 meter grid of trapping stations. An additional trap station was placed equidistant between each of the 10 meter intervals on the border lines of the field. Each trap station had two traps covered with a 12"x12" piece of roofing that helped reduce temperature fluctuations within the traps. There were 219 trapping stations and 438 traps. Each trap was constructed with a plywood floor, aluminum sides, top and door, and a 1/4" hardware cloth back. The gravity fall door was released by the action of a plywood treadle, activated when the animal crossed the treadle to reach the bait in the back of the trap. The trap dimensions were 25.5 cm. x 7 cm. x 7.5 cm. D&G Laboratory mouse food was used as bait and cotton was placed in the traps during the colder fall and winter months. Bait was replaced daily as necessary and fresh bait added and old discarded every two weeks.

Four species of small mammals: the meadow vole (*Microtus pennsylvanicus*), the pine vole (*Microtus pinetorum*), the house mouse (*Mus musculus*) and the white footed mouse (*Peromyscus leucopus noveboracensis*) were of primary interest in the study. These were marked by toe clipping, sexed, and their reproductive condition and location trapped were noted at each capture. Traps were inspected between six and ten a.m.

The major part of the study was conducted from June 29 to September 21, 1972, including two control periods, of seven nights of trapping each, and four successive replications of the experimental manipulation. The four experimental periods were preceeded by one of the control periods and followed by the other. Between each of the replications and control periods were three nights when the traps were closed. The complete experimental time table is represented in Figure 3.

An experimental manipulation involved 14 nights of trapping. The first seven nights were termed the *removal period* during which all animals caught in plot B were removed, their *removal sites* noted, and then caged individually in the laboratory. One half-hour before sunset on the eighth night of trapping, in each replication, all of the previously captured animals from plot B were released at a central point in plot A, the *release site*. During the final seven nights of each manipulation (the *return period*), all captures were noted.

Figure 3. Experimental time table.


R—RELEASE
CONT—CONTROL
REM—REMOVAL
RET—RETURN
—TRAPS CLOSED
O—TRAPS OPENED
CONT
REM
R
RET
REM
R
RET
REM
R
RET
REM
R
RET
CONT
28
J
5
8
15
J
22
25
1
8
11
18
A
25
28
4
11
14
S
21

RESULTS

Population Description

Table 1 represents the population composition of the four species studied. Age categories were determined by weights based on work by Bendell, 1959; Delong, 1967; Gentry, 1968; Krebs, Keller, and Tamarin, 1969; and Miller, 1969. *Peromyscus leucopus* age categories can also be determined by pelage color: juveniles with grey pelage; subadults with grey pelage being replaced by adult brown pelage; and adults with brown pelage (Bendell, 1959). Weight ranges were *Mus musculus*: 9.5-23.6 g., *Peromyscus leucopus*: 10.2-25.2 g., *Microtus pennsylvanicus*: 24.2-59.4 g., and *Microtus pinetorum*: 16.0-33.4 g. The percentages of males captured were for *Peromyscus leucopus*: 60.8 per cent, *Mus musculus*: 68 per cent, *Microtus pennsylvanicus*: 59 per cent, and *Microtus pinetorum*: 62 per cent. Only the number of *P. leucopus* males differed at the .10 significance level from an expected 50:50 ratio.

The sex, age, and plot composition of the four populations are represented in Figures 4-13. These graphs include not only the two control periods and the four experimental replications described previously but also a preliminary trapping period of four nights and four trapping periods of

TABLE 1: Population Composition

Species	Age	Weight	Males	Females	Total
Mus musculus					
	Juvenile	(<8.0g)	0	0	0
	Subadult	(8.0-12.0g)	3	3	6
	Adult	(>12.0g)	10	3	13
	Undetermined		0	0	0
	Total		13	6	19
Microtus pennsylvanicus					
	Juvenile	(<22.0g)	0	0	0
	Subadult	(22.0-33.0g)	7	3	10
	Adult	(>33.0g)	10	8	18
	Undetermined		0	1	1
	Total		17	12	29
Microtus pinetorum					
	Juvenile	(<16.5g)	2	0	2
	Subadult	(16.5-19.0g)	3	1	4
	Adult	(>19.0g)	21	14	35
	Undetermined		2	2	4
	Total		28	17	45
Peromyscus leucopus					
	Juvenile	(<14.0g)	3	3	6
	Subadult	(14.0-18.0g)	9	9	18
	Adult	(>18.0g)	30	15	45
	Undetermined		0	0	0
	Total		42	27	69

Figure 4. Sex composition of the *Peromyscus leucopus* population. Numbers of different *Peromyscus leucopus* individuals captured per period are indicated at the midpoint of the period.

The abcissa follows a daily time scale except for the final two points which are indicated as being on a different time scale by remaining unconnected.

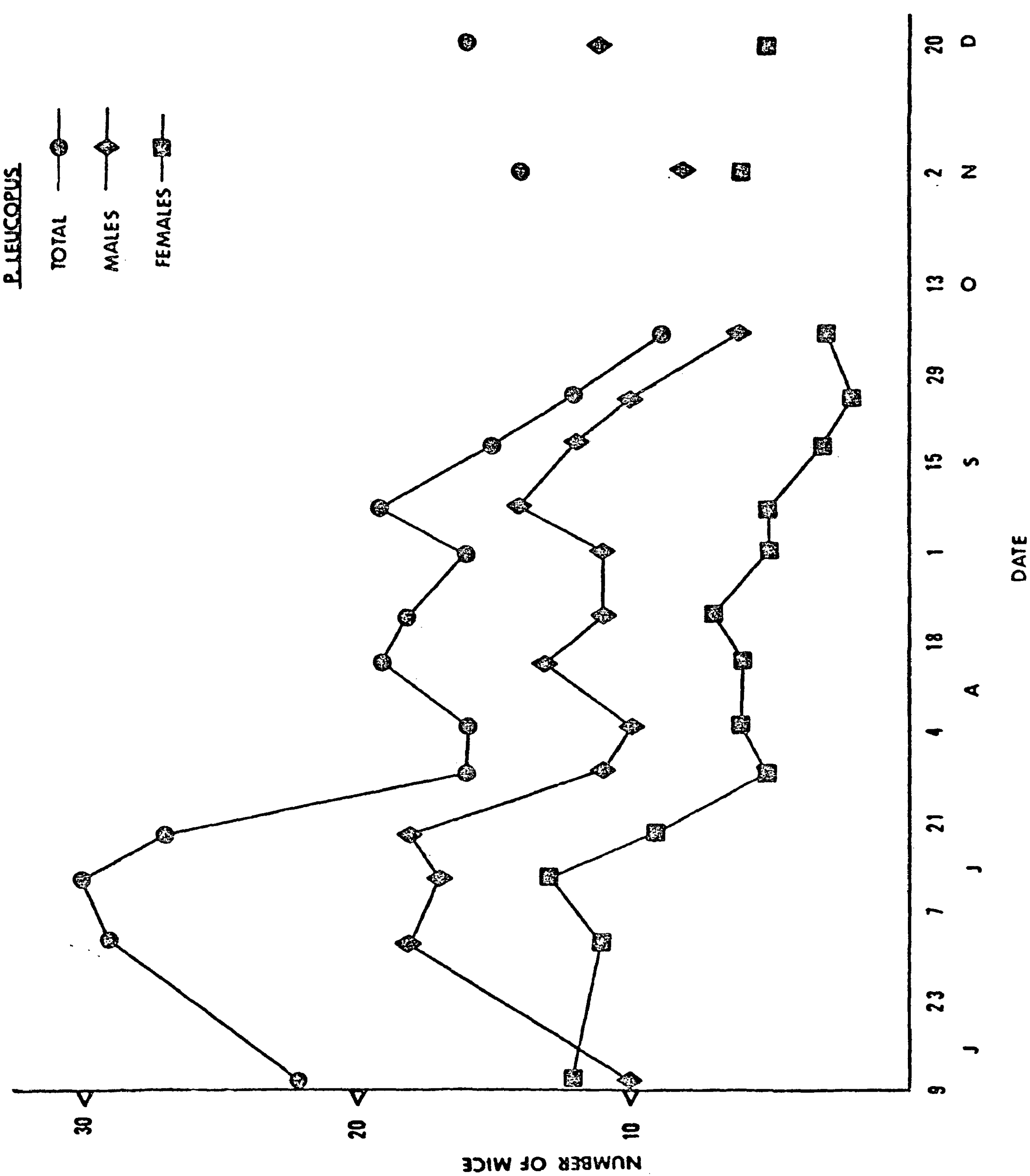

P. LEUCOPUS
TOTAL
MALES
FEMALES
NUMBER OF MICE
10
20
30
DATE
9 J 23 7 J 21 4 A 18 1 15 S 29 13 O 2 N 20 D

Figure 5. Sex composition of the *Microtus pinetorum* population. Numbers of different *Microtus pinetorum* individuals captured per period are indicated at the midpoint of the period.

The abcissa follows a daily time scale except for the final two points which are indicated as being on a different time scale by remaining unconnected.

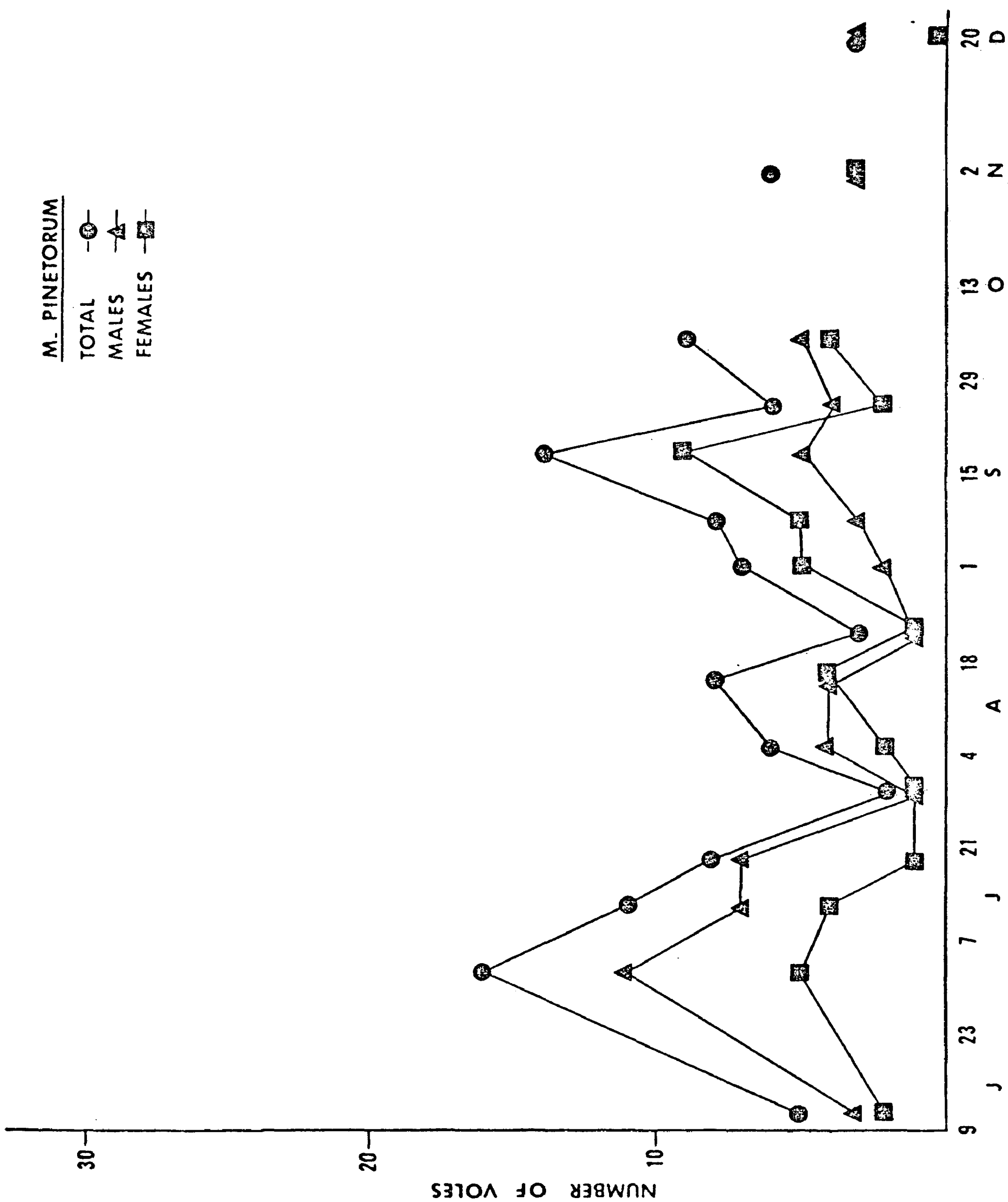

M. PINETORUM
TOTAL
MALES
FEMALES
NUMBER OF VOLES
30
20
10
9
J
23
7
J
21
4
A
18
1
15
S
29
13
O
2
N
20
D
DATE

Figure 6. Sex composition of the *Microtus pennsylvanicus* population. Numbers of different *Microtus pennsylvanicus* individuals captured per period are indicated at the midpoint of the period.

The abcissa follows a daily time scale except for the final two points which are indicated as being on a different time scale by remaining unconnected.

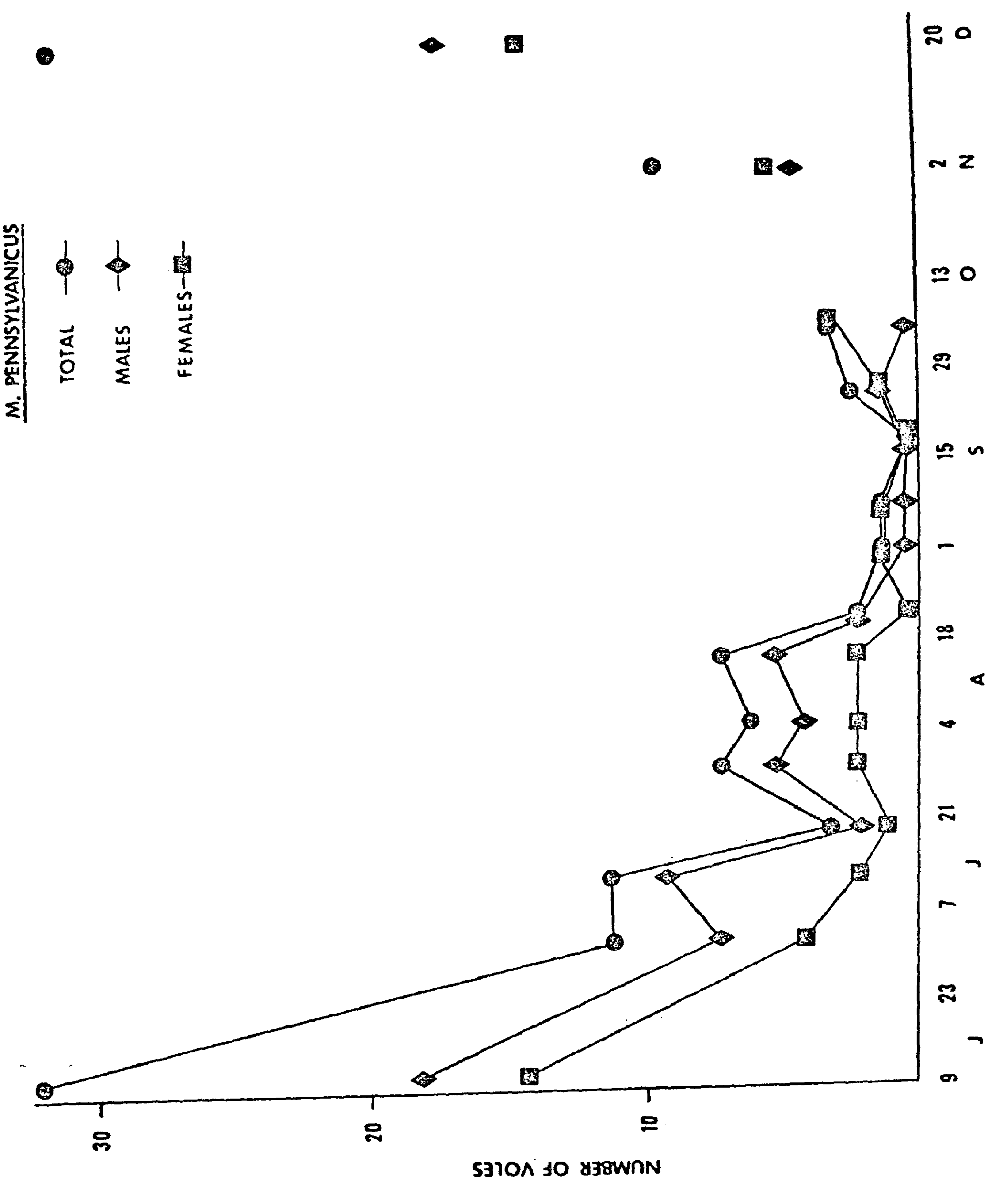

M. PENNSYLVANICUS
TOTAL
MALES
FEMALES
NUMBER OF VOLES
30
20
10
DATE
9
J
23
7
J
21
4
A
18
1
15
S
29
13
O
2
N
20
D

Figure 7. Total *Mus musculus* population expressed in terms of numbers of different individuals captured per period and indicated at the midpoint of the period.

The abcissa follows a daily time scale except for the final two points which are indicated as being on a different time scale by remaining unconnected.

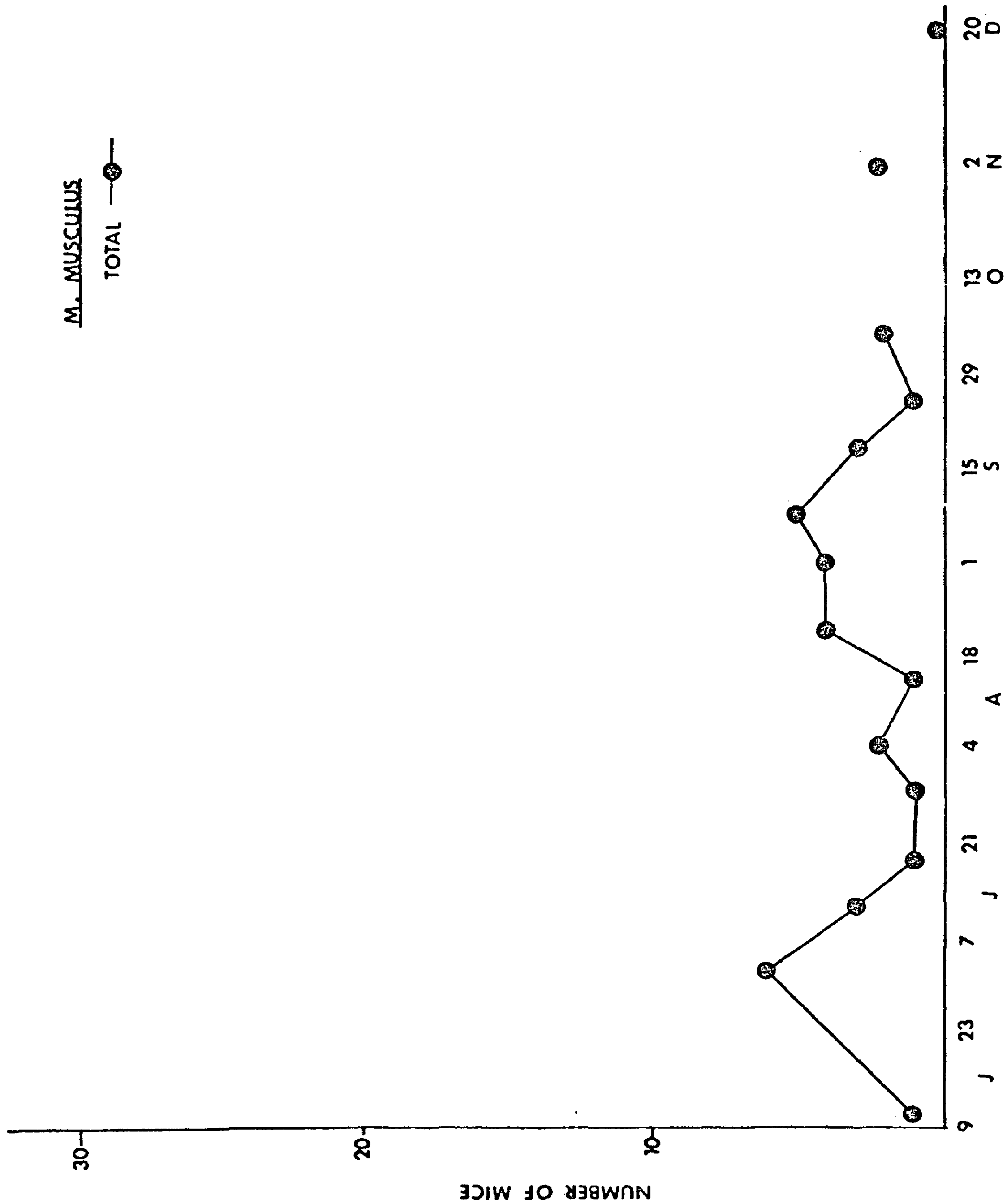

M. MUSCULUS
TOTAL
NUMBER OF MICE
30
20
10
DATE
9
J
23
7
J
21
4
A
18
1
15
S
29
13
O
2
N
20
D

Figure 8. Plot composition of the *Peromyscus leucopus* population. Numbers of different *Peromyscus leucopus* individuals captured per period are indicated at the midpoint of the period.

The abcissa follows a daily time scale except for the final two points which are indicated as being on a different time scale by remaining unconnected.

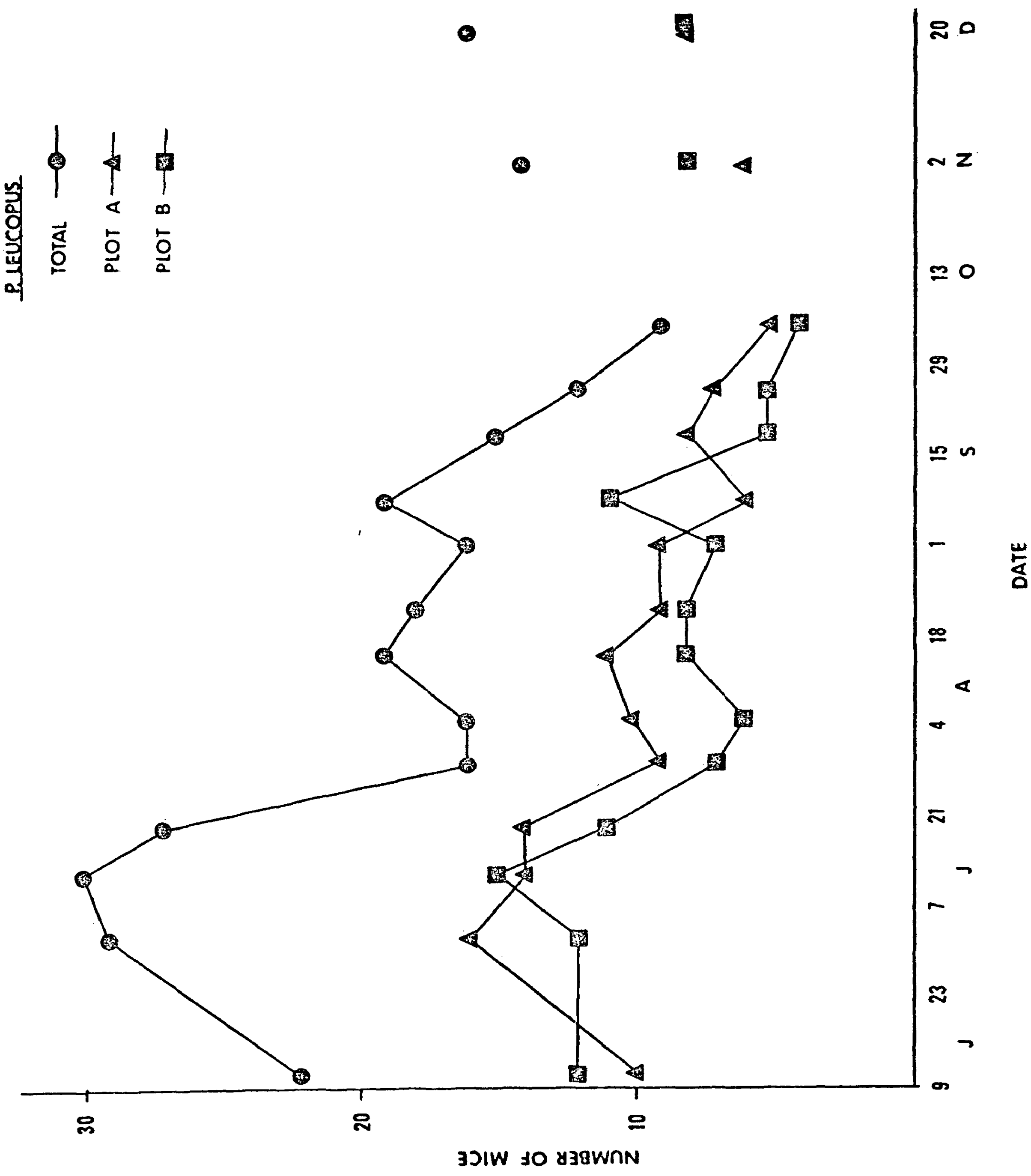

P. LEUCOPUS
TOTAL
PLOT A
PLOT B
NUMBER OF MICE
30
20
10
DATE
9
J
23
7
J
21
4
A
18
1
15
S
29
13
O
2
N
20
D

Figure 9. Plot composition of the Microtus pinetorum population. Numbers of different Microtus pinetorum individuals captured per period are indicated at the midpoint of the period.

The abcissa follows a daily time scale except for the final two points which are indicated as being on a different time scale by remaining unconnected.

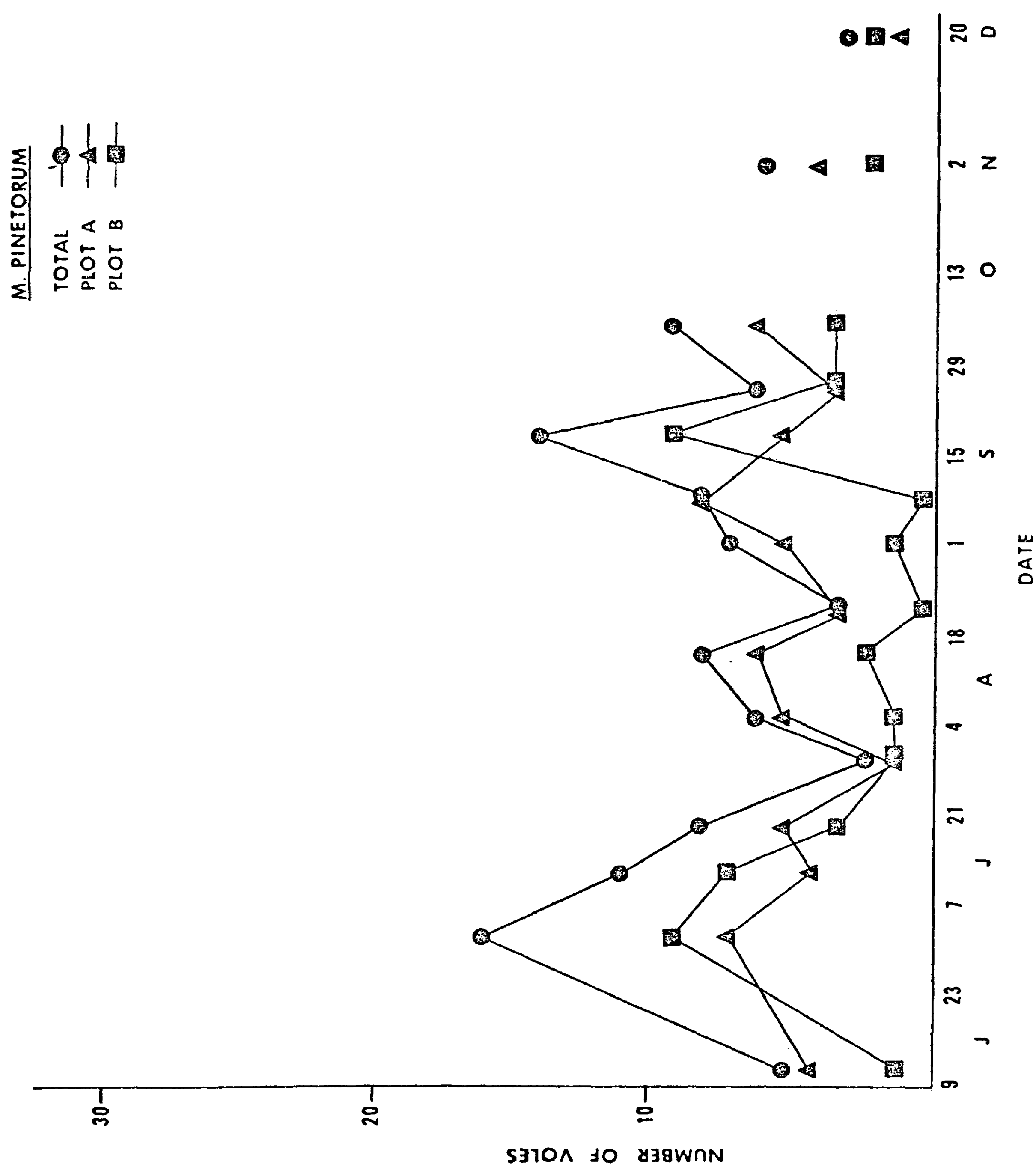

M. PINETORUM
TOTAL
PLOT A
PLOT B
NUMBER OF VOLES
10
20
30
DATE
9
J
23
7
J
21
4
A
18
1
15
S
29
13
O
2
N
20
D

Figure 10. Plot composition of the *Microtus pennsylvanicus* population. Numbers of different *Microtus pennsylvanicus* individuals captured per period are indicated at the midpoint of the period.

The abcissa follows a daily time scale except for the final two points which are indicated as being on a different time scale by remaining unconnected.

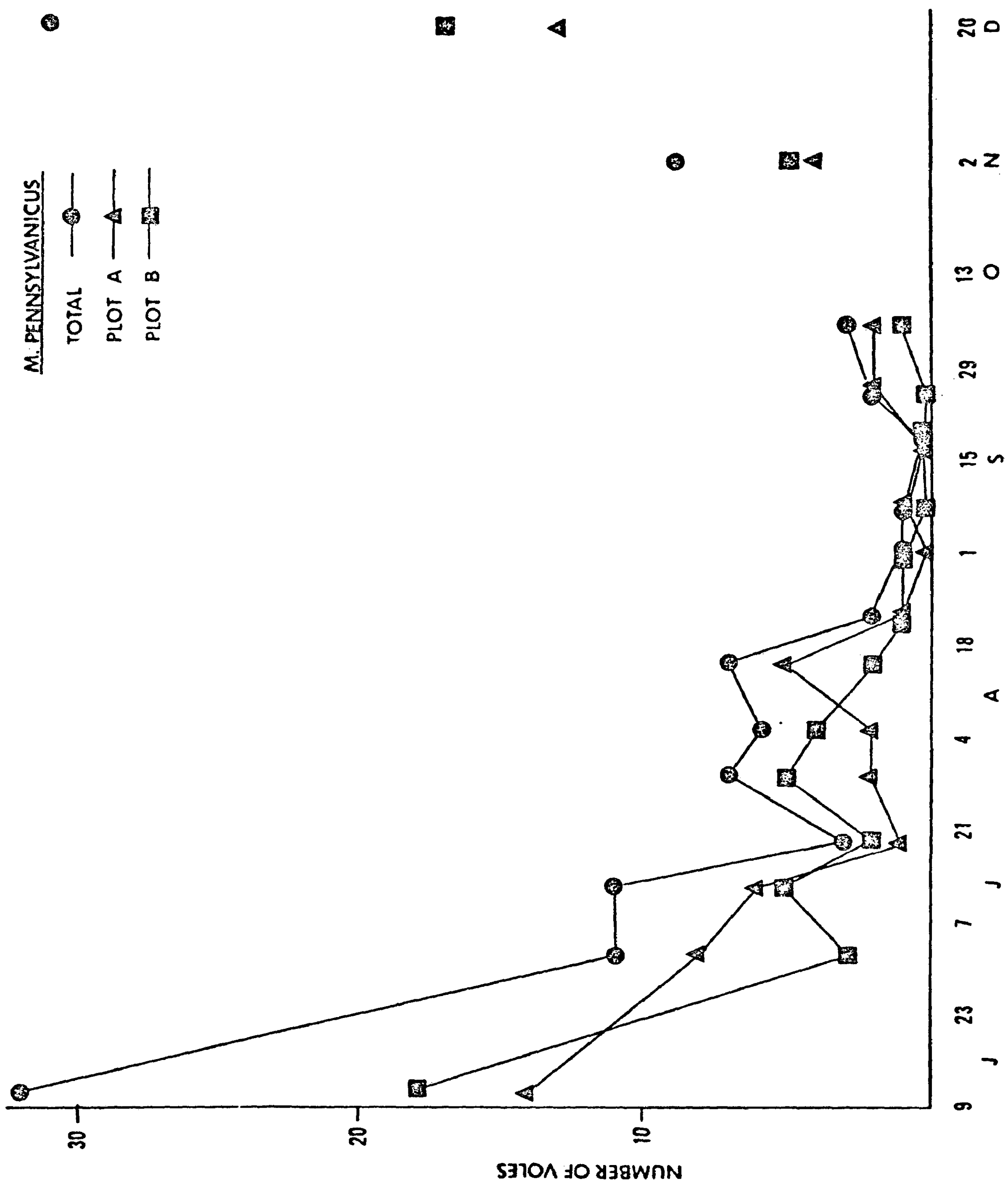

M. PENNSYLVANICUS
TOTAL
PLOT A
PLOT B
NUMBER OF VOLES
30
20
10
DATE
9
J
23
7
J
21
4
A
18
1
15
S
29
13
O
2
N
20
D

Figure 11. Age composition of the *Peromyscus leucopus* population. Numbers of different *Peromyscus leucopus* individuals captured per period are indicated at the midpoint of the period.

The abcissa follows a daily time scale except for the final two points which are indicated as being on a different time scale by remaining unconnected. Unconnected points prior to October 13 indicate rare departures of that class from zero captures.

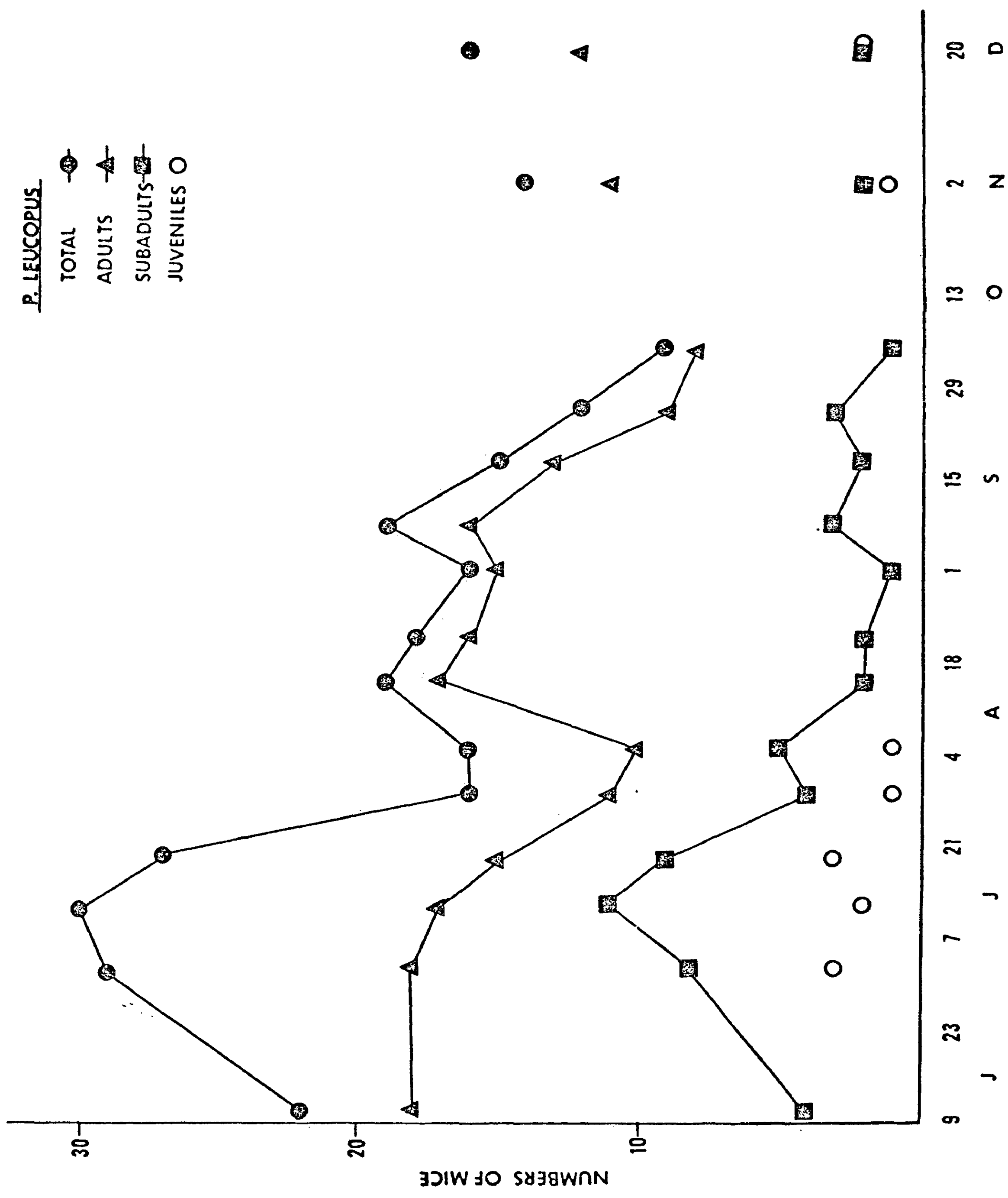

P. LEUCOPUS
TOTAL
ADULTS
SUBADULTS
JUVENILES
NUMBERS OF MICE
30
20
10
9
23
7
21
4
18
1
15
29
13
2
20
J
J
A
S
O
N
D
DATF

Figure 12. Age composition of the *Microtus pinetorum* population. Numbers of different *Microtus pinetorum* individuals captured per period are indicated at the midpoint of the period.

The abcissa follows a daily time scale except for the final two points which are indicated as being on a different time scale by remaining unconnected. Unconnected points prior to October 13 indicate rare departures of that class from zero captures.

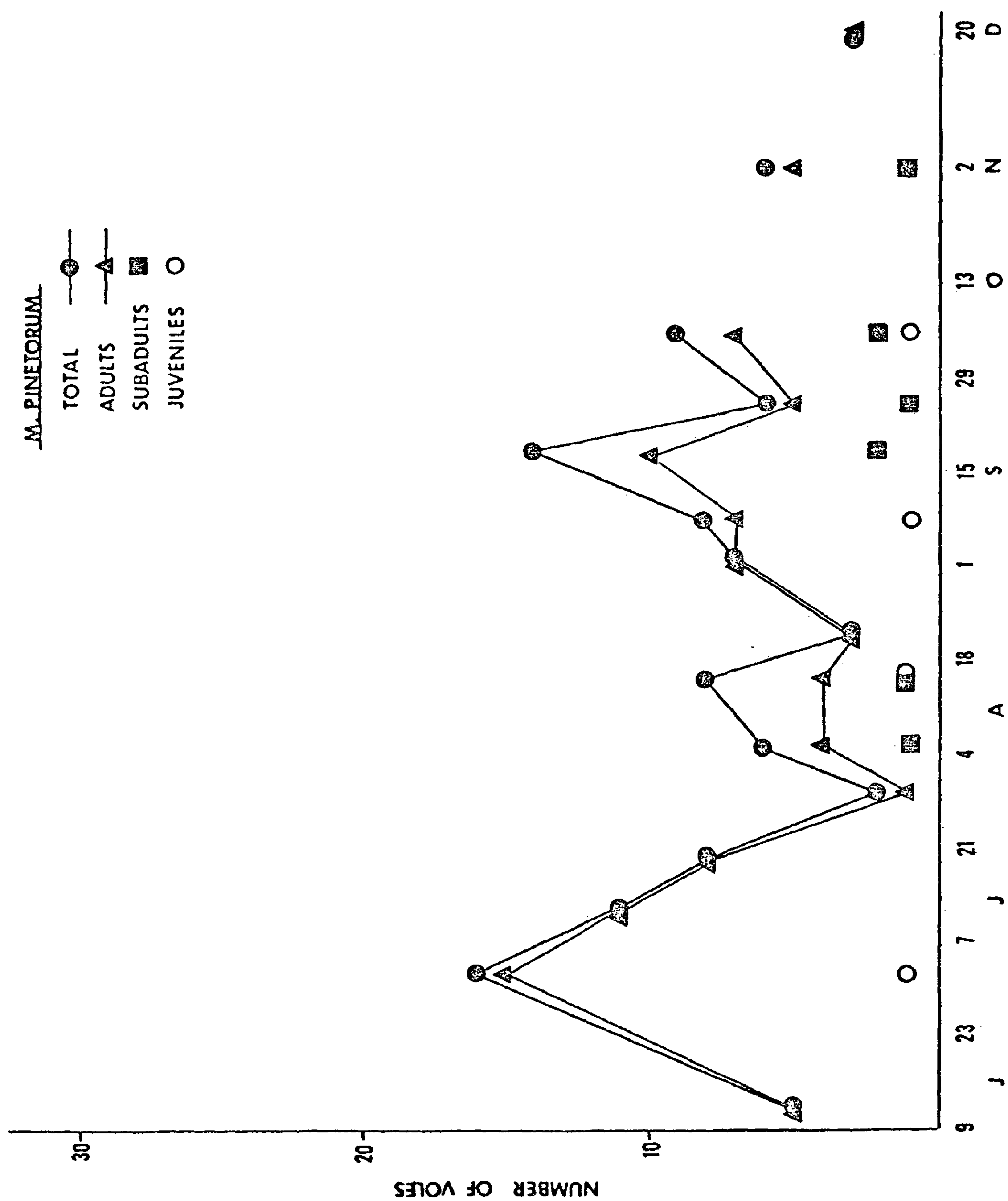
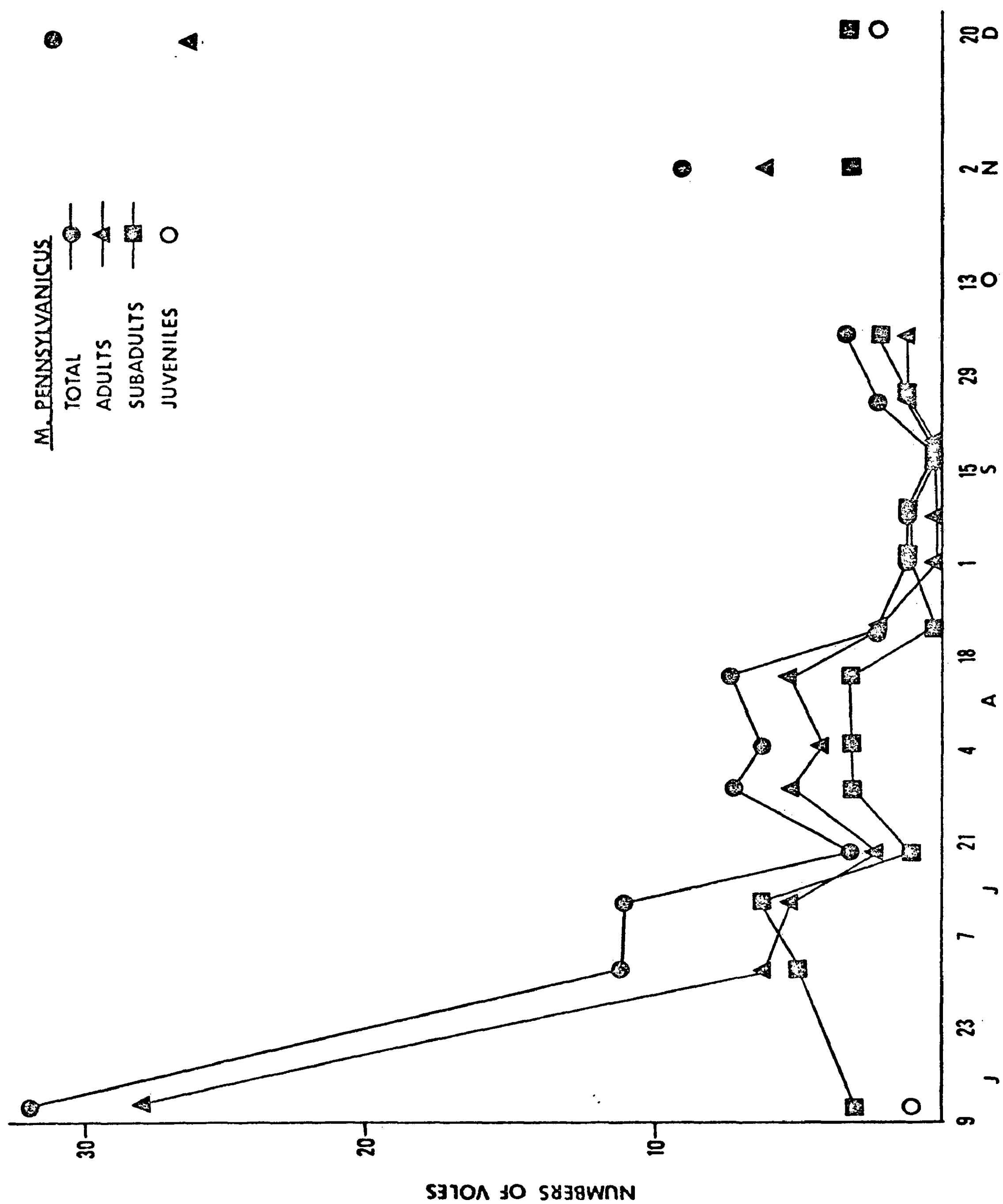

M. PINETORUM
TOTAL
ADULTS
SUBADULTS
JUVENILES
NUMBER OF VOLES
30
20
10
DATE
9
J
23
7
J
21
4
A
18
1
15
S
29
13
O
2
N
20
D

Figure 13. Age composition of the *Microtus pennsylvanicus* population. Numbers of different *Microtus pennsylvanicus* individuals captured per period are indicated at the midpoint of the period.

The abcissa follows a daily time scale except for the final two points which are indicated as being on a different time scale by remaining unconnected. Unconnected points prior to October 13 indicate rare departures of that class from zero captures.


M. PENNSYLVANICUS
TOTAL
ADULTS
SUBADULTS
JUVENILES
NUMBERS OF VOLES
30
20
10
DATE
9
J
23
7
J
21
4
A
18
1
15
S
29
13
O
2
N
20
D

seven nights each following the second control period. The decline in the numbers of M. pennsylvanicus captured per period during the course of the study should be noted. The small size of the Mus musculus population is also apparent. A summary of the trapping results by replication is found in Table 2.

Table 3 shows the number of pregnant and lactating females per period as well as the reproductive rate for each period. The percentage of pregnant and lactating females was used as the reproductive rate. The reproductive rates for the different species over the entire study period were: P. leucopus - .37, M. pinetorum - .167, M. pennsylvanicus - 0, and M. musculus - .182.

Trappability

Various measurements used to estimate the "trappability" (Krebs, Keller and Tamarin, 1969) of each species are represented in Table 4. When all species were compared via "t" tests, Peromyscus leucopus showed a significantly higher mean number of captures per individual and a significantly smaller number of nights between captures per individual ($p<.05$). Note also the large percentage of M. pennsylvanicus and M. musculus which were caught only once (72 per cent and 55 per cent respectively), and the small number of individuals captured for these species. No significant differences between species were shown for the mean number of calendar days between an individual's first and last capture.

TABLE 2: Numbers of Different Males and Females Captured Per Replication

Period	*P. leucopus*			*M. pennsylvanicus*			*M. pinetorum*			*Mus musculus*		
	M.*	F.*	Tot.*	M.	F.	Tot.	M.	F.	Tot.	M.	F.	Tot.
Replication												
1	21	14	35	7	4	11	10	6	16	3	3	6
2	12	7	19	5	4	9	5	3	8	1	1	2
3	12	9	21	6	1	7	6	3	9	2	2	4
4	14	9	23	0	2	2	6	6	12	2	3	5
Control Periods												
1	18	11	29	7	4	11	11	5	16	5	1	6
2	12	3	15	0	0	0	5	9	14	0	3	3

* M.=Males; F.=Females; Tot.=Total

TABLE 3: Numbers of Different Pregnant and Lactating Females Captured Per Replication

Period	*P. leucopus*				*M. pennsylvanicus*				*M. pinetorum*				*Mus musculus*			
	PF*	LF*	Tot.*	RR*	PF	LF	Tot.	RR	PF	LF	Tot.	RR	PF	LF	Tot.	RR
Replication																
1	1	3	4	.29	0	0	0	0	0	0	0	0	0	0	0	0
2	2	3	5	.71	0	0	0	0	1	0	1	.33	0	1	1	1.00
3	0	5	5	.55	0	0	0	0	2	1	3	1.00	2	0	2	1.00
4	1	6	7	.78	0	0	0	0	2	1	3	.50	0	3	3	1.00
Total	4	17	21		0	0	0		5	2	7		2	4	6	
Control Periods																
1	0	2	2	.18	0	0	0	0	1	0	1	.20	1	0	1	1.00
2	0	2	2	.66	0	0	0	0	0	2	2	.22	1	1	2	1.00
Total	0	4	4		0	0	0		1	2	3		2	1	3	
Control Periods & Replications	4	21	25		0	0	0		6	4	10		4	5	9	

* PF=Pregnant Females; LF=Lactating Females; Tot.=Total; RR=Reproductive Rate

TABLE 4: Species Trappability

	SPECIES			
	M. pennsylvanicus	*M. pinetorum*	*P. leucopus*	*Mus musculus*
No. of Individuals Captured	29	45	69	19
Mean of Captures/Individual	2.10	2.97	8.37	2.0
Per Cent Individuals Caught Only Once	72	37	18	55
Mean of Nights Between Captures/Individual	8.78	4.41	1.57	4.14
Per Cent of Individuals Averaging One Night Or Less Between Captures	12.5	30	58	33
No. of Individuals Captured More Than Once	8	27	56	9
Mean of Calendar Days Between First & Last Captures/Individual	33.33	18.0	25.94	18.5

Immigration of New Animals (*Peromyscus leucopus*)

Animals captured were classified in the following ways: a new animal was one captured for the first time during any given removal or return period, whereas, previously caught animals had been captured at least once before on either plot. The number of new and previously caught animals were determined for each return and removal period and then summed over the four experimental replications. These data are presented in Table 5.

Tests of homogeneity were performed on all data to be tested and in all instances except one the data for replications could be justifiably pooled. The proportions of new animals to previously caught animals captured during the removal period in plot A showed significant heterogeneity between replications and thus, were not used in the analysis.

Plots A and B were compared by a Fisher exact probability test with respect to the proportion of new to previously caught animals captured during the return periods. A significantly smaller proportion of new animals were captured on plot A than on plot B during the return periods ($p=.0115$).

The removal and return periods of plot B were compared in terms of the proportions of new to previously caught animals captured. No significant differences between the periods were shown.

The number of new animals captured on plot A and plot B were compared for both the removal and return periods. The

TABLE 5: Immigration of *Peromyscus leucopus* Per Replication

Period	Replicates	Plot A		Plot B		Total	
		New	Previously Caught	New	Previously Caught	New	Previously Caught
Removal	1	4	10	5	10	9	20
	2	0	9	0	7	0	16
	3	7	4	3	5	10	9
	4	2	7	1	6	3	13
	Total	13	30	9	28	22	58
Return	1	0	14	4	7	4	21
	2	2	8	1	5	3	13
	3	1	8	1	7	2	15
	4	0	6	5	6	5	12
	Total	3	36	11	25	14	61
Combined		16	66	20	53	36	119

proportions of new animals captured on plots A and B during the return periods were significantly different than during the removal period ($p=.0288$). The return and removal periods did not differ with respect to the proportion of previously caught animals captured in plot A versus those captured in plot B.

Plots A and B were compared in terms of the proportions of new animals captured in each plot via a Chi-square test based on a 50 per cent probability of capture in either plot. When the captures for the return and removal periods were combined the plots did not differ significantly in the proportions captured compared to that expected. Also no plot differences were significant when the numbers of new animals captured during the removal periods were compared. However, a smaller number of new animals than expected were captured on plot A than on plot B during the return periods ($p<.10$).

Next the return and removal periods were compared for the number of new animals captured. A Chi-square test was again used with an expectancy of 50 per cent captures in each period. With plots A and B combined there were no significant deviations from this expectation. The two periods did not differ from expected with respect to the numbers of new animals captured on plot B only. A significantly smaller number of captures of new animals than expected occurred during the return periods on plot A than during the removal period ($p<.025$).

Immigration (Other Species)

The data on immigration in *Microtus pinetorum* were collected and analyzed in the same manner as were those for *P. leucopus* (Table 6). None of the tests proved significant. The meadow vole and house mouse populations were too small for analysis in this way.

Disappearance of Residents (*Peromyscus leucopus*)

The treatment periods on plot A were compared relative to the frequency of disappearance of residents. Plot B could not be examined in this manner since residents were constantly being removed and released in plot A.

An animal was termed a resident when it was captured for the second time on the same plot. A resident was considered to have disappeared during the period when it was last captured.

A Fisher exact probability test indicated that the return periods had a significantly ($p=.0097$) greater proportion of residents disappearing than did the removal periods. These data are shown in Table 7. Disappearance occurred throughout the seven days of the return periods with three residents disappearing on day one, two on day two, three on day three, one on day four, two on day five, three on day six, and none on day seven.

Plot A was divided into a central and a peripheral area. The peripheral area was encompassed by the border traps and the row of traps nearest to the border. The remainder of

TABLE 6: Immigration of *Microtus pinetorum* Per Replication

Period	Replicates	Plot A		Plot B		Total	
		New	Previously Caught	New	Previously Caught	New	Previously Caught
Removal	1	2	3	3	5	5	8
	2	0	1	1	0	1	1
	3	2	4	2	0	4	4
	4	2	4	1	0	3	4
	Total	6	12	7	5	13	17
Return	1	1	4	0	2	1	6
	2	3	2	0	1	3	3
	3	1	2	0	0	1	2
	4	3	4	1	0	4	4
	Total	8	12	1	3	9	15
Combined		14	24	8	8	22	32

TABLE 7: Disappearance of *Peromyscus leucopus* Residents From Plot A

Period	Replicate	Residents Not Disappearing	Residents Disappearing	Total
Removal	1	11	1	12
	2	8	1	9
	3	7	0	7
	4	6	2	8
	Total	32	4	36
Return	1	9	4	13
	2	5	4	9
	3	3	5	8
	4	7	1	8
	Total	24	14	38

plot A was the central area. For further analysis of disappearance center of activity calculations were utilized to determine whether the residents of plot A resided in the central or peripheral area.

There was no significant difference between the proportions of residents disappearing from the central area and those disappearing from the peripheral area in plot A during either the return or removal periods (Table 8).

A significantly larger proportion of residents (p=.022) disappeared from the periphery of plot A during the return periods than disappeared from the periphery during the removal periods. The central area of plot A showed no differences in disappearance between periods.

No significant differences resulted from a comparison of the proportion of the two sexes disappearing.

Disappearance of Residents (Other Species)

Again, the identical tests were used for *M. pinetorum*, with no differences significant. *Microtus pennsylvanicus* and *M. musculus* were too few to be tested.

Recaptures and Movements of Residents of Plot A (*Peromyscus leucopus*)

The removal and return periods did not differ significantly in terms of the number of recaptures of residents of plot A. The mean number of moves by plot A residents during the return and removal periods were compared and were not significantly different. The distance moved per recapture

TABLE 8: Disappearance of *Peromyscus leucopus* Residents From Central or Peripheral Areas of Plot A

Period	Replicate	Number of Residents Not Disappearing			Number of Residents Disappearing		
		Peripheral	Central	Total	Peripheral	Central	Total
Removal	1	11	0	11	1	0	1
	2	5	2	7	1	0	1
	3	11	0	11	0	0	0
	4	7	0	7	2	0	2
	Total	34	2	36	4	0	4
Return	1	6	3	9	4	0	4
	2	5	1	6	1	2	3
	3	4	0	4	3	2	5
	4	5	0	5	2	0	2
	Total	20	4	24	10	4	14
Combined		54	6	60	14	4	18

for plot A residents was also used to compare the return and removal periods and again no significant differences could be found. The *P. leucopus* residents of plot A moved a mean distance of 20.0 m. per move and those of plot B a mean distance of 20.6 m. per move. Table 9 contains these data.

Homing (*Peromyscus leucopus*)

The homing performance of the animals removed from plot B and released in plot A was analyzed. An animal was considered to have homed when it was captured within a circle with a radius of 14.3 m., the center of which was the removal site. The radius is the distance between diagonally located trapping stations on a 10x10 m. grid. The return to within this distance had to take place within the seven night return period to be regarded as a homing event.

Twenty different individuals were released and 13 (65 per cent) homed. These data are presented in Table 10. Out of 37 releases, 23 or 62 per cent, resulted in homing (Table 11). In 15 or 40.5 per cent of the releases the mouse returned to plot B by the first night while 22 or 59.6 per cent returned to plot B by the second night.

The relationship between the mean number of nights the animals were kept in the laboratory before release (Table 12), and the latency to home (Table 13) was examined via a linear correlation coefficient calculation. No significant correlation was found. Similarly, the mean number of nights the

TABLE 9: Movement & Recaptures of Resident *Peromyscus leucopus* on Plot A

Replicate	Removal			Return			Total		
	Distance Moved (m)	No. of Recaptures	No. of Moves	Distance Moved (m)	No. of Recaptures	No. of Moves	Distance Moved (m)	No. of Recaptures	No. of Moves
1	545.15	42	31	682.42	33	31	1227.57	75	62
2	677.23	33	29	285.53	16	17	962.76	49	46
3	177.29	20	11	208.38	8	6	385.67	28	17
4	82.17	7	3	46.18	7	3	128.35	14	6
Total	1481.84	102	74	1222.51	64	57	2704.35	166	131

TABLE 10: Homing Performance of *Peromyscus leucopus* (Individuals)

	Number of Individuals Transferred	Number Homing at Least Once	Number Returning to Plot B But Not Homing	Number Disappearing	Number Staying in Plot A
	20	13	1	3	3
Per Cent of Total Number of Individuals		65	5	15	15

TABLE 11: Homing Performance of *Peromyscus leucopus* (Transfer Events)

Replicate	Number of Transfers	Number of Animals Homing	Number Returning to Plot B But Not Homing	Number Disappearing	Number Staying in Plot A
1	15	8	1	3	3
2	7	4	1	2	0
3	8	6	2	0	0
4	7	5	1	1	0
Total	37	23	5	6	3
Per Cent of Total Number of Transfers		63	13	16	8

TABLE 12: Frequency Table for the Number of Nights Homing *Peromyscus leucopus* Were Held in Laboratory

Number of Nights in Laboratory	1	2	3	4	5	6	Total
Number of Animals	4	0	2	1	4	12	23
Per Cent of Total	17.4	0	8.7	4.3	17.4	52.2	100

TABLE 13: Frequency Table for the Number of Nights Between Release and Capture at Home Site (*Peromyscus leucopus*)

Number of Nights Before Homing	1	2	3	4	5	6	7	Total
Number of Animals	11	6	2	2	0	2	0	23
Per Cent of Total	47.8	26.1	8.7	8.7	0	8.7	0	100

animals were kept in the laboratory and the accuracy of the homing were not correlated significantly. The accuracy of the homing performance was measured by the distance between the site to which the animal homed and the removal site of an animal.

The distance from the release site to the homing site was used as the homing distance. No significant correlation was found between the mean homing distance and the mean number of nights between release and trapping again. Also the mean distance homed and the accuracy of the homing were not significantly correlated. No significant differences were found between the proportion of the sexes homing.

Homing (Other Species)

The small number of transferred *M. pinetorum*, *M. pennsylvanicus* and *M. musculus* plus their poor recapture record produced little homing information. The mean number of recaptures per manipulation was 3.14 for *P. leucopus*, while only 1.75 for *M. pennsylvanicus*, 0.44 for *M. pinetorum*, and 0.33 for *M. musculus*. The percentages of individuals recaptured were 82 per cent for *P. leucopus*, 63 per cent for *M. pinetorum*, 45 per cent for *M. musculus*, and 28 per cent for *M. pennsylvanicus*.

Eight manipulations of *M. pennsylvanicus* produced four instances of homing (three by the same individual in successive replications), three disappearances, and one animal was caught once in plot A and then disappeared.

Of the nine manipulations of *M. pinetorum* there were five disappearances, three animals were caught in plot A and then disappeared, and one animal disappeared after one capture in plot B.

Two of the three manipulations of *Mus musculus* resulted in disappearance; the other animal disappeared after one capture in plot B.

DISCUSSION

Population Parameters

The *Peromyscus leucopus* population was the most stable of the four populations studied. The numbers of individuals captured per period remained fairly stable with a decrease in the late summer and a return to previous levels by the late fall trapping sessions. Reproductive rates for this species were moderate but stable over the entire study.

Microtus pennsylvanicus exhibited an extreme peak of abundance in the spring preliminary trapping period followed by a precipitous decline in individuals trapped in mid-June. The numbers of individuals captured remained very low through the first week in October with a noticeable increase in November and another peak equal to that in the spring occuring in December. There was no evidence of reproduction throughout the study.

The numbers of *Microtus pinetorum* individuals captured per period were relatively moderate and fluctuated narrowly with moderate peaks occuring in late June and late September. The pine vole population was intermediate in size to the *Peromyscus* population and the low meadow vole and house mouse population. The *Mus musculus* captures stayed very low throughout the experiment. Low reproductive rates were characteristic of the M. pinetorum population while the few M. musculus captured showed high indications of reproduction.

Although not statistically significant at the .05 level, all four species had a higher percentage of males than females.

The extreme decline of the M. pennsylvanicus population during the experimental period and the consistently few captures of M. musculus had detrimental effects on two of the basic objectives of this study. First, it was impossible to determine whether the varying degrees of awareness to a depleted area shown by M. musculus, M. pennsylvanicus and M. pinetorum in Staples' (1972) study is a reflection of their relative densities. Secondly, few valid comparisons of the four species' responses to density changes could be made.

Trappability

Peromyscus leucopus was the most "trappable" of the species studied in this experiment. It demonstrated a significantly larger number of captures per individual and a significantly smaller number of nights between captures. These findings could reflect not only the densities of the species but also of the relative exploratory behavior or activity (Sheppe, 1966). Mus musculus and Microtus pennsylvanicus data were not analyzed in most instances because of the high percentage of individuals of these species which were captured only once, coupled with low population densities throughout the experimental part of this study. Microtus pinetorum was less "trappable" than P. leucopus and had only one capture for 37 per cent of the individuals.

An extreme decline in *M. pennsylvanicus* captures occurred during the summer months. In nine instances individual meadow voles were captured once during the spring or early summer and again much later in the fall trapping sessions with no captures in the intervening period (Table 14). The intervals between these captures were from 40 to 97 nights of trapping and from 51 to 193 calendar days. Six of the nine voles were recaptured within 14.3 m. of their original capture site. These instances suggest that the decline of *M. pennsylvanicus* during the summer may be attributed to the voles leaving the area and then returning in the fall or that they remain on the plot but become less trappable. Krebs, Keller, and Tamarin (1969) studying fenced populations suggested that the trappability of meadow voles declines during the summer and that only 50 per cent of those present could be captured. My data appear to support this suggestion. Reduced trappability might be explained by decreased desirability of the bait due to the emergence of preferable natural foods or increased subterranean activities.

Introduction and Removal

Introduction into plot A produced two significant effects in the movement patterns of *Peromyscus leucopus*. First, the number and proportion of new animals captured during the return period on plot A were significantly smaller than those of the return period on plot B. On plot A a smaller number

TABLE 14: Nine *Microtus pennsylvanicus* Capture Records Showing Long Intervals Between an Early Summer Capture and a Fall Capture

Animal No. & Sex		Number of Nights of Trapping Between Captures	Number of Calendar Days Between Capture	Distance Between Points of Capture
257	Female	96	192	0.0 m
264	Female	97	193	10.0 m
282	Male	80	117	31.6 m
295	Female	52	66	10.0 m
300	Male	85	163	31.6 m
301	Female	70	106	10.0 m
304	Male	64	97	14.3 m
307	Female	59	92	10.0 m
309	Female	40	51	5.0 m

of new animals were captured during the return period than during the removal period. No differences in the number or proportion of new animals captured were found when comparing the two periods for plot B or the two plots during the removal periods. I believe these data indicate that there is a decreased movement of new animals into plot A following introduction of animals during the return period rather than an increased movement into plot B. If the effect was due to an increase in movement into plot B one would expect a difference between the removal and return periods in that plot. Also an increase in movement into plot B would be expected during the removal period rather than the return periods.

The second major effect of introduction of animals was that a greater proportion of plot A residents disappeared during the return period than during the removal period. Introduction thus seems to produce a tendency for residents to emigrate.

Interestingly, these two responses occurred even though the majority of mice that were transferred either homed or disappeared, with only three transferred animals captured on plot A following release. The brief appearance of released animals on plot A produced effects similar to those caused by an increase in density and yet there was no increase in the number of individuals captured on plot A after the animals were released.

It would appear that factors other than a simple increase in the number of animals on the plot is producing the above responses. A question then arises as to the nature of the cue through which the animal detects this change in "density." These epideictic cues could be one of two types in this situation. First, if the cue has a brief duration which corresponds to the length of stay of the released mouse on the plot then either the movement responses (inhibition of immigration or increased emigration) occurs immediately, or the reception of the signal has an effect on the behavior of the plot A mice which persists after the introduced mice leave the plot. Secondly, the signal or cue may remain on the plot and be received by nearby animals after the emitting animals have departed. It is doubtful that the movement responses occur only during the stay of the mouse on plot A since disappearance is distributed evenly throughout the return periods. Also, if the cue is ephemeral, then inhibition of immigration would be expected to be greater on the first days of the return period. Again this does not appear to be so since as many immigrations occurred during the first part of the removal periods as during the latter part. Thus, the effective life of the signal must be long enough to produce these effects throughout the seven night return period while not producing the effects during the removal period.

Orr (1959) reports no difference between the ability of caged or non-caged <u>P. leucopus</u> to produce an increasing tendency to disperse when introduced into a laboratory population. He believes awareness of neighbors exists without direct encounter. Since homing apparently occurred very rapidly in the present experiment it is doubtful that direct encounter between animals yielded the responses noted. The cues must therefore be detectable over a greater distance than possible for tactile or visual stimuli, leaving olfactory or auditory cues as possibilities.

Peromyscus leucopus exhibited no significant movement responses to the depopulated area in plot B. This must be considered to be unique to the conditions present in this situation since many removal experiments produce immigration. The depletion produced may not have been maintained long enough to ellicit a response from the neighboring animals since the displaced mice returned immediately after release. A second possibility exists if there is a constant "hum" of signals between animals in a population as postulated by Calhoun (1963). He believes "a change in the intensity (or frequency) of stimuli emanating from" an area signals a change in the density of that area. Removal would lower the intensity of stimuli coming from an area. Failure to recognize a depleted area may result when the area is so narrow that signals from animals surrounding the removal area prevent a detectable change in the intensity of the stimuli (Calhoun and Webb, 1953). This is a doubtful possibility in the present study since other workers have shown immigration into areas narrower than plot B. A final possibility is that the densities of the surrounding populations were not large enough to cause a noticeable immigration (Andrzejewski and Wroclawek, 1962; Van Vleck, 1968). However, substantial immigration into plot B did occur during both periods.

Microtus pinetorum showed no significant responses to the manipulations. This could indicate a smaller degree of sensitivity to the changes produced or since few *M. pinetorum* were transferred the alterations may not have been noticeable to the other voles. Possibly, the size of the resident population on plot A was too small for the introduction to elicit a response.

Homing

Although this experiment was not designed to study homing, some pertinent homing data resulted. A high percentage of the *P. leucopus* transferred in this experiment homed and of those which homed 73.9 per cent did so by the second day after release. That homing takes place rapidly or not at all is a general characteristic emerging from a variety of experiments with many different species of small mammals. Gentry (1964) found 91 per cent of displaced *Peromyscus polionotus* homed within one night after release. The average homing time was similar from a variety of distances for the meadow and California vole in studies by Robinson and Falls (1965) and Fisler (1962). The majority of displaced *Peromyscus maniculatus* homed within three days (Terman, 1962) and one *P. maniculatus* was observed homing from 300 m. in one hour (Rawson and Hartline, 1964). Fisler

(1966) noted that individual *Reithrodontomys megalotis* homed "quickly" and Griffo (1961) reported that cotton mice exhibit a direct correlation with distance and latency to home.

I could find no significant correlation between the distance displaced and the success or latency of homing. An inverse relationship usually exists between the displacement distance and the percentage of animals successfully homing (Fisler, 1962, 1966; Furrer, 1973; Griffo, 1961; Murie, 1963; Robinson and Falls, 1965; Stickle, 1949). The lack of correlation in my experiment could be due to the relatively short distances of displacement. In other experiments showing a direct relationship between distance and homing success the distances have been substantial: 200-1600 yards for deermice (Murie, 1963), 320-1000 feet for California voles and western harvest mice (Fisler, 1962, 1966), 100-2700 feet for cotton mice (Griffo, 1961). The displacement in my study did not represent a very wide gradient of distances and even the longer distances are probably within the range of familiar terrain for the mice. Furrer (1973) postulates 600 m. as the approximate distance beyond which *P. maniculatus* individuals rarely range.

A majority of workers support the hypothesis that homing takes place primarily by prior knowledge of the terrain and to a minor extent through random wandering (Fisler, 1962; Furrer, 1973). *Microtus pennsylvanicus* individuals from a population with larger home ranges returned in a higher proportion from long distances than meadow voles from a population showing small home ranges, leading Robinson and Falls (1965) to believe that the ones with the larger home ranges had a more extensive knowledge of the terrain and could therefore home more successfully. Griffo (1961) feels homing involves "environmental imprinting" resulting from wanderings of the animal during its lifetime. Others believe that many of the demonstrated instances of homing could not result from the animal's previous contact with the area, therefore a built-in orientation or homing sense must exist (Bovet, 1968; Burt, 1940).

Griffo (1961) found no detrimental effects on homing ability of cotton mice by keeping them in confinement for as much as 12 weeks. Robinson and Falls (1965), however, kept meadow voles through the summer in a two acre enclosure and observed decreased homing success. In this experiment, no significant correlation was noted between the length of time the animals were kept in the laboratory (one to six nights), and their homing performance.

The numbers of *M. pinetorum*, *M. musculus*, and *M. pennsylvanicus* translocated to plot A were too small to analyze for homing responses.

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