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The life history and population dynamics of the prairie vole (microtus orchrogaster) on the Cumberland Plateau in Middle Tennessee

Roger Emerson Deitrick

To the Graduate Council:

I am submitting herewith a thesis written by Roger Emerson Deitrick entitled "The life history and population dynamics of the prairie vole (microtus orchrogaster) on the Cumberland Plateau in Middle Tennessee." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

Ralph W. Dimmick, Major Professor

We have read this thesis and recommend its acceptance:

Michael R. Pelton, James T. Tanner

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

May 15, 1970

To the Graduate Council:

I am submitting herewith a thesis written by Roger Emerson Deitrick entitled " The Life History and Population Dynamics of the Prairie Vole (Microtus ochrogaster) on the Cumberland Plateau in Middle Tennessee." I recommend that it be accepted for nine quarter hours of credit in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

Ralph W Dimmick
Major Professor

We have read this thesis
and recommend its acceptance:

Michael R. Pelton

James T. Tanner

Accepted for the Council:

Hilton A. Smith
Vice Chancellor for
Graduate Studies and Research

THE LIFE HISTORY AND POPULATION DYNAMICS OF THE PRAIRIE VOLE (*MICROTUS OCHROGASTER*) ON THE CUMBERLAND PLATEAU IN MIDDLE TENNESSEE

A Thesis

Presented to

the Graduate Council of

The University of Tennessee

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

Roger Emerson Deitrick

June 1970

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Facilities and financial support for this study were provided through a cooperative effort by the Department of Forestry, The University of Tennessee and the Hiwassee Land Company, Calhoun, Tennessee.

ABSTRACT

The study was conducted on a 28-acre pinetum located near Crossville, Tennessee, on the Cumberland Plateau. The objectives of this study were: (1) to determine the density and structure of the population of prairie voles (Microtus ochrogaster) on the study area, and (2) to relate indirect sign to population densities of prairie voles.

Six one-acre plots were established on the pinetum and a live-trapping program was initiated to obtain data for describing the populations. Amounts of indirect sign were obtained from twenty circular plots, two feet in diameter, that were randomly established on each of the plots periodically during the course of study. Field work was begun in December, 1967, and concluded in May, 1969.

Population densities varied greatly during the period of study and ranged from 10.00 to 122.50 voles per acre. Variations in density were closely related to the breeding activities of individuals and a highly significant correlation was observed between the percent of adults in breeding condition and fluctuations in population numbers.

Seasonal changes in population structure varied with fluctuations in density. Males outnumbered females in most samples and were especially dominant during periods of high levels of sexual activity. The percentages of the different age classes varied during the period of study. Notable increases in the percentage of juveniles were observed following rises in population density after peaks in breeding activity.

The average home range size for voles during the study was 0.082

of an acre and no differences in home range size existed between males and females. The overlapping of home ranges was common throughout the study area.

The most characteristic sign of vole activity was their systems of runways and tunnels that were utilized by more than one vole at a time. Voles in this study were most active at night.

A seasonal variation in weight was observed; mean weights of adults and subadults decreased significantly during the winter months of the study. Voles kept in captivity exhibited growth rates of one gram per day to an age of one month and 0.5 grams per day thereafter, until growth rates leveled off as adulthood was reached. The life spans of all voles were less than one year ($\bar{x}$ = 139.69 days). A highly significant difference was noted between the mean life span for males (129.62 days) and females (155.05 days).

Fleas and lice were the most common parasitic arthropods of the prairie vole in this study. Ticks were less common but were most prevalent on juvenile voles. Examination of blood smears yielded no evidence of parasitic infestation.

The percentage of fresh sign found in twenty random samples that were periodically established throughout the study area was a reliable estimate of the relative abundance of the prairie vole. The frequency of fresh sign, such as runways, droppings, and evidence of feeding activity, was significantly related to mean population densities.

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CHAPTER I

INTRODUCTION

The prairie vole (*Microtus ochrogaster*) has been the object of intensive study throughout most of its range. Major contributions on the species have come from Kansas by Fitch (1957), Jameson (1947), and Martin (1956). Relatively little information concerning the prairie vole in Tennessee has been accumulated heretofore; until 1910, trapping efforts failed to establish the presence of the species within the state. Since then several specimens have been recorded in the northwest portion of the state. Recent records indicate that the prairie vole has extended its range southward and eastward in Tennessee to the eastern rim of the Cumberland Plateau in middle Tennessee and southwardly probably to the southern border of the state (Dimmick, 1969) (Fig. 1). It is also found in suitable habitats in the central part of North America. It has been recorded from Edmonton, Alberta, in the northwest, southward to Chesapeake, Ohio, and in the southwest as far as Fort Reno, Oklahoma (Burt and Grossenheider, 1964; Jameson, 1947).

Following the prairie vole's range extension in Tennessee, the species has become a serious economic problem to large pulp and paper companies throughout the state. The feeding activities of the vole have resulted in extreme damage to several thousand acres of Virginia pine (*Pinus virginiana*) on the Cumberland Plateau. The most severe damage has been in the form of girdling the base of the stems and/or roots of three to five year old pine trees.

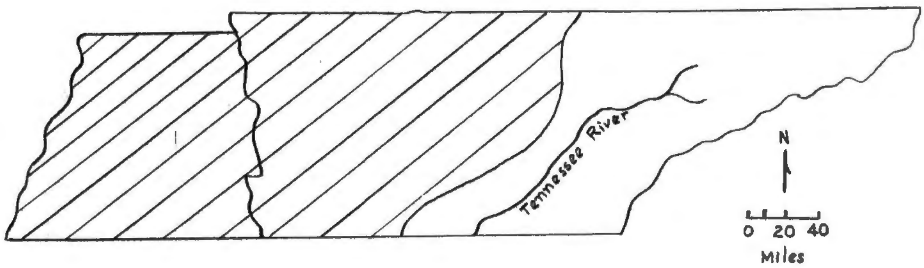

Figure 1. The distribution of Microtus ochrogaster in Tennessee (Dimmick, 1969).

The prairie vole can be separated from other voles in its range by a combination of several factors. Prairie voles are best identified by their short legs and tail, small eyes and ears, and grayish to dark brown and fulvous pelage. The shorter tail and the fulvous or cinnamon ventor of the prairie vole will assist in identification when it occurs with the meadow vole (*M. pennsylvanicus*). Prairie voles may be separated from pine voles (*M. pinetorum*), with which they are sometimes found, by the larger eyes, less auburn pelage, and longer tail.

The prairie vole is an extremely secretive animal and is semi-fossorial. It spends most of its time in an elaborate system of tunnels and surface runways that are well hidden in dense grass cover. Because of its abundance in certain areas, this vole exerts a great influence on the quantity and composition of the vegetation by feeding and burrowing, and is an important item in food chains which sustain many other mammals, reptiles and birds (Martin, 1956).

The major objectives of this study were: (1) to determine the density and structure of the population of prairie voles on the study plots, and (2) to relate indirect sign, such as runways, nests, and evidence of feeding activities, to population densities of prairie voles. This research was a cooperative study, supported by Hiwassee Land Company, Calhoun, Tennessee, and The University of Tennessee, Forestry Department.

CHAPTER II

DESCRIPTION OF THE STUDY AREA

Location

This study was conducted on a pinetum located approximately five air miles southwest of Crossville in Cumberland County, Tennessee. Cumberland County occupies 675.5 square miles in the central part of Tennessee and is situated almost entirely on the Cumberland Plateau (Matzek, 1950).

Topography

Cumberland County is characterized by comparatively smooth land for about half the area, but in the eastern and southwestern portions of the county, stream dissection has cut valleys 100 to 400 feet deep. The elevation of the county ranges from somewhat less than 1,000 feet at Sequatchie Valley in the south to slightly more than 3,000 feet at Hinch Mountain, about a mile distant. Practically all the area is well drained, with three-fourths of the county draining into the Tennessee River and the remaining portion into the Cumberland River (Matzek, 1950).

The study area is a 28-acre rectangular plot completely surrounded by a sand and gravel service road. It is bounded on the north by a young loblolly pine (*P. taeda*) stand and a six acre lake, and on the south by a young stand of white pine (*P. strobus*). A mature hardwood forest constitutes the eastern boundary while the western portion of the study area is bounded by fields that are mowed periodically.

The entire area is on a gently rolling north facing slope with only a twenty foot change in elevation anywhere on the area. Within the area are three ponds ranging in size from less than one-half acre to over one and a half acres.

Climate

The climate of Cumberland County is temperate and continental with short, moderate winters and mild summers. Long frost free periods and a uniformly distributed, moderately high annual precipitation make the area well suited for general farming. Temperature extremes of 103° F to - 18° F have been recorded, but these occur infrequently. The mean annual temperature is 55.6° F with the mean seasonal temperature of 38.7° F in the winter and 72.1° F in the summer. The mean annual precipitation is 54.19 inches, with the wettest month being March (5.92 inches) and the driest month being October (3.17 inches). Generally, precipitation is highest in the summer and lowest in the fall (Matzek, 1950).

During the 1967 to 1969 period that this study was conducted, temperature extremes were 96° F on August 23, 1968, and -4° F on January 5, 1969 (U. S. Weather Bureau, 1967, 1968, and 1969) (Table 1). The average frost free period is 179 days, extending from April 18 to October 14 (Matzek, 1950).

Soil

Most of the soils of the county are uniform in color, texture, structure, natural fertility, and parent material. About 95 percent of them have formed from weathered material of sandstone and shale. In more than 95 percent of the county the soils are low in content of phosphate,

Table 1. Temperature and precipitation data (recorded at the Crossville airport) for the period in which this study was conducted (U. S. Weather Bureau, 1967-1969).

Year	Month	Mean Temp	Departure From Mean	Total Precipitation	Departure From Mean
1967	Dec	42.0	2.8	7.82	1.43
1968	Jan	34.0	-4.7	5.12	0.71
	Feb	27.9	-10.1	0.92	-4.55
	Mar	46.0	-0.7	6.62	0.45
	Apr	55.9	-0.2	5.30	1.66
	May	61.1	-3.2	3.79	0.65
	June	69.8	-1.5	1.81	-2.18
	July	72.9	-1.0	2.30	-1.33
	Aug	74.4	0.4	1.20	-1.10
	Sept	64.5	-3.1	2.04	-1.53
	Oct	55.6	-2.0	2.27	0.50
	Nov	44.9	-0.4	3.06	-0.25
	Dec	34.2	-5.0	4.06	-1.01
1969	Jan	33.5	-5.2	5.41	-0.96
	Feb	36.3	-2.8	5.29	0.46
	Mar	38.0	-8.0	2.38	-2.73
	Apr	57.3	1.4	5.27	1.33
	May	63.0	-1.1	5.13	2.03

lime, and organic matter necessary to proper plant growth. The texture of the soils is prevailing fine, about 88 percent being fine sandy loam (Matzek, 1950).

Vegetation

The study area is a six year old pinetum consisting of three species of pine of approximately equal acreages. The eastern one-third of the area consists of shortleaf pine (P. echinata), the middle one-third is made up of Virginia pine, while the remaining western one-third is loblolly pine. These trees were hand planted and in most cases were spaced six feet apart.

A few hardwoods are present but mainly in the form of small sprouts and saplings. Several grasses (Panicum sp., Setaria sp., Sorgum sp., Triodia sp.) and broomsedge (Andropogan virginicus) constitute the major ground cover and are quite dense throughout most of the area, providing excellent habitat for the prairie vole (Fig. 2).

Briars (Rubus sp.) are also common and in some areas the growth is dense enough to make access virtually impossible. Closely associated with these briar thickets is Japanese honeysuckle (Lonicera japonica) forming dense mats of ground cover.

Dense growths of spike rush (Eleocharis obtusa) are associated with the three ponds on the area and a continually wet drainage located in the center of the Virginia pine portion of the pinetum.

Figure 2. The general habitat type which is prevalent over a majority of the study area, March 15, 1968.

CHAPTER III

METHODS

Trapping program

Two square one-acre plots were set up in each of the three divisions of the pinetum. Within each of these six acres 49 permanent numbered stations were located in a grid pattern with 30 foot intervals between each station. This interval was believed to provide the best possible trapping efficiency (Martin, 1956).

Live traps (Sherman type) were used as a means for sampling the vole populations of this area. Live trapping was chosen over other methods as it gives a more reliable picture of the population allowing the investigator to better determine the size and structure of the population and to observe the activities of individuals (Blair, 1948; Cockrum, 1947; Stickle, 1946).

Each trap was placed inside a metal shelter and cotton batting was placed in one end of the trap. This provided insulation against the cold and greatly reduced the chances of trap mortality. Martin (1956), in a study in Kansas, reported that preventing trap mortality in the summer can be more difficult than in the winter. Placing traps in shaded areas, covering them with vegetation and running traps early in the morning reduces these losses.

Two bait mixtures were used with equal success. Peanut butter was the basic constituent of the bait with either oatmeal or cracked corn added. This mixture was found easy to apply, readily taken and an adequate energy supply that would enable captive voles to maintain body temperatures needed to survive during the winter (Howard, 1951). Martin (1956) found that death of voles in traps in the winter was a result of wet nesting material and a lack of food. To prevent mortality due to wetness in winter, all traps were placed facing down slope whenever possible to keep water from running into the unprotected end of the trap.

Each baited trap was then set perpendicular to a runway (Fig. 3) and operated at intervals of no greater than 30 days. Each trapping session lasted at least three consecutive days as recommended by Chitty and Kempson (1949) who found that there was a gradual increase in the number of captures per day for the first two or three days with a tendency for the number of captures to level off the remainder of the trapping period.

Captured animals were examined to determine their age and sex. Each prairie vole was assigned to one of three age classes (juvenile, subadult or adult) principally on the basis of weight, but partly on various stages of molt as described by Jameson (1947) and Hatfield (1935). The reproductive status of individuals was determined by examinations of external sex organs. Other than dissection, the only indication of the reproductive status of males was the degree to which testes weredescended into the scrotum. Jameson (1947) states that the testes of the prairie vole descend into the scrotum in the breeding season, but also observed that many specimens with retracted testes were found to be fecund. The criteria for females consisted of the condition of the vaginal aperture, i.e. perforate or imperforate; the presence or

Figure 3. The position of a Sherman live trap at a trapping station on the study area, March 15, 1968.

Note the well used prairie vole runway (center, l. to r.) and the metal container used as insulation.

absence of lactation, and obvious pregnancy (Fitch, 1957).

Blood was taken from captured animals to be examined for parasites. Samples were obtained by snipping off the tip of the tail and placing a small drop of blood on a slide. Smears were made in the field using Wright's stain and examined in the laboratory.

The general physical condition of the voles was also recorded. This description included such items as the presence and general extent of external parasites. Other pertinent data such as weight and location of capture were recorded on file cards which were kept for each capture.

Newly captured voles were marked by the toe-clipping method as described by Mosby (1963) and released back into the runway or at the point of capture.

Indirect sign

Twenty circular plots, two feet in diameter, were randomly established on each of the one acre plots. This was done four times per year and all signs of vole activity found in these samples were recorded. "Sign" included such items as runways, nests, food caches, droppings and piles of grass cuttings left in the runways after feeding.

References

References used in this study for the identification of plants and animals included: H. L. Blomquist and H. J. Oosting's A Guide to the Spring Flora of the Piedmont (1959); W. M. Harlow and E. S. Harrar's Textbook of Dendrology (1958); A. C. Chandler and C. P. Read's Introduction to Parasitology (1965); W. H. Burt and R. P. Grossenheider's A Field Guide to the Mammals (1964).

CHAPTER IV

RESULTS AND DISCUSSION

I. POPULATION DENSITY AND STRUCTURE

Population densities were ascertained on the study area by means of the live-trapping program and expressed in terms of individuals per acre. Population numbers were estimated by the frequency of capture method proposed by Eberhardt (1969):

$$\hat{N} = \frac{r(s - 1)}{s - r}$$

Where:

$\hat{N}$ = estimate of population size

r = total number of individuals

s = total number of captures

This method was chosen over the conventional capture-recapture methods such as the Lincoln Index and Schnabel method because of several reasons. These latter methods assume that captures take place randomly with constant, equal probilities of capture, and neither losses or recruitment take place during the period of study. These basic assumptions are rarely met (Eberhardt, 1969). Under these assumptions, the above mentioned methods expect to follow the binomial or the Poisson distribution. One of the characteristics of the Poisson distribution is that its mean and variance are equal (Li, 1957). Examination of the data presented in this study revealed a highly significant difference ($P < 0.01$) between the mean population density ($\bar{x}$ = 55.89 voles per acre) for all sampling areas and the variance (s^2= 341.90).

Estimates of population numbers for this study were based on a total of 1155 captures and 385 recaptures.

Population density

The number of voles fluctuated greatly during the 18 month period for which data were available (Fig. 4). Examples of selected trapping periods and sample sizes used to obtain density estimates are presented in Table 2. The highest density (122.50 individuals per acre) occurred in the Virginia pine plots in November, 1968, and was based on a total of 28 captures and 8 recaptures. The lowest density (10.00 voles per acre) was recorded in the loblolly pine plots in May, 1969, in a sample of four captures and one recapture. The highest densities for the entire period of study occurred in the Virginia pine section ($\bar{x}$ = 76.30 voles per acre). This estimate was based on 550 captures and 184 recaptures. The lowest densities (based on 276 captures and 99 recaptures) occurred in the shortleaf pine section of the study area ($\bar{x}$ = 44.14 voles per acre). A mean of 50.67 individuals per acre was found in a sample 337 captures and 110 recaptures in the loblolly pine section of the area.

Although the total number of individuals varied on the study area, there were definite similarities between all the sampling plots. With only small exceptions, the population fluctuations of each plot were identical. All areas reached peak densities in April, 1968, and again in October and November of the same year, followed by a gradual decrease in numbers for the remainder of the study (Fig. 4).

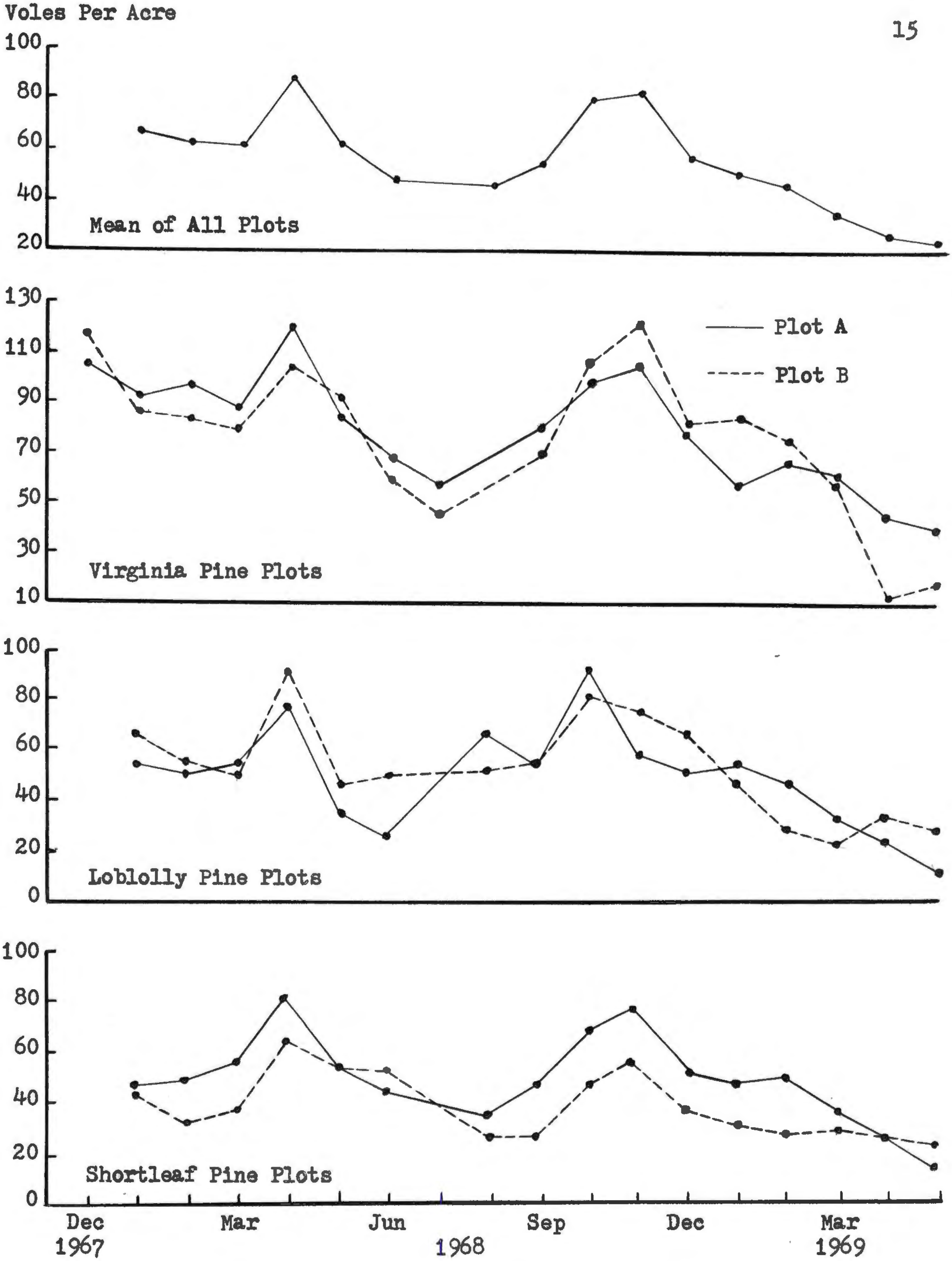

Figure 4. Variations in the density of voles on the six plots in the study area and the mean of these densities.

Table 2. The sample size and population estimates for the six one-acre plots on the study area during four trapping periods.

Trapping Period		Sampling Plots						Mean Density
		Virginia Pine		Loblolly Pine		Shortleaf Pine		
		A	B	A	B	A	B	
April	Total Captures (s)	17	23	14	15	10	13	
	Total Individuals (r)	15	19	12	13	9	11	
1968	Population Estimate ($\hat{N}$)	120.00	104.50	78.00	91.00	81.00	66.00	90.08
June	Total Captures (s)	19	20	9	14	11	12	
	Total Individuals (r)	15	15	7	11	9	10	
1968	Population Estimate ($\hat{N}$)	67.50	57.00	28.00	47.66	45.00	55.00	50.03
Nov.	Total Captures (s)	23	36	15	17	14	15	
	Total Individuals (r)	19	28	12	14	12	12	
1968	Population Estimate ($\hat{N}$)	104.00	122.50	56.00	74.66	78.00	56.00	81.94
May	Total Captures (s)	13	7	5	11	7	8	
	Total Individuals (r)	10	5	4	8	5	6	
1969	Population Estimate ($\hat{N}$)	40.00	15.00	10.00	26.66	15.00	21.00	21.27

There are few records of density of *M. ochrogaster* in the literature, Martin (1956) reported densities ranging from 25.2 to 145.8 individuals per acre of prairie voles in northeastern Kansas. Population densities for the meadow vole (*M. pennsylvanicus*) reported in the literature include 160 to 230 voles per acre (Hamilton, 1937) and 29.8 individuals per acre (Blair, 1948). Van Vleck (1969), in a three year study, noted densities ranging from five to 48 individuals per acre for meadow voles in Vermont.

Density and breeding activities

The reproductive activity of voles captured in this study was measured in terms of the percent of 770 adult individuals of both sexes that were in breeding condition.

This study indicated that there is sexual activity throughout every month of the year, but its incidence varies greatly from one season to another (Fig. 5). Reproductive activity began a definite increase in the winter of 1968 and peaked in March and April, with approximately 60 percent of the 82 adults being in breeding condition. The highest percentage of sexually active adults (86.96 percent) occurred during a second peak in breeding activity in September, 1968, in a sample of 48 adult voles. Following this peak was a rapid decrease in breeding activity until mid-winter when the decrease became more gradual.

A pattern of seasonal variation in population densities coincided with these different levels of breeding activity. There was a highly significant ($P < 0.01$) correlation between the percent of adults in breeding condition and the fluctuations in population densities on the

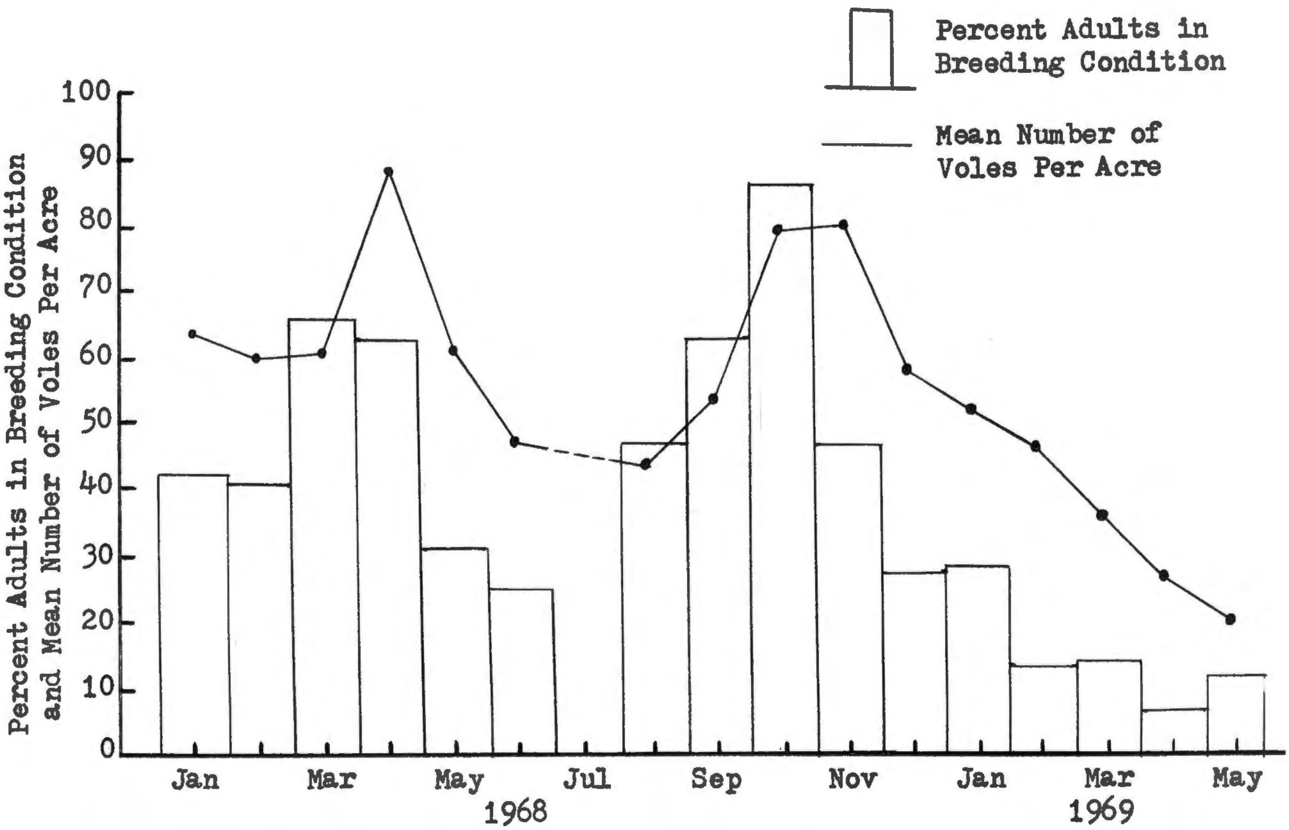

Figure 5. Seasonal changes in the density of voles in relation to the level of breeding activity on the study area.

study area (r = 0.76). A higher correlation (r = 0.96) existed between density and reproductive activity of the previous month. As mentioned before, the highest population densities were reached in April 1968 and again in the October and November, 1968, period. These early spring and fall peaks in population densities on the study plots followed periods of high levels of breeding activity. The low annual densities in the summer months of 1968 and those toward the conclusion of the study occurred when there was a depression in breeding activity.

The pattern of reproductive activity that occurred on the study plots was dissimilar to patterns for voles elsewhere in their range. Summer peaks in breeding seem to be the rule for the several species of Microtus that are found in the United States (Blair, 1940; Hamilton, 1937; Fitch, 1957). Martin (1956) found that the critical factor influencing reproductive activity seems to be the supply of food and cover in the form of new, actively growing grasses that are plentiful during the spring and summer months. The second peak in breeding activity during this study began when food and cover were abundant and increased until October when it began a rapid decline. The decline occurred simultaneously with the disappearance of grasses at the onset of winter. Bailey (1924) reported that a reduction in either the quantity or quality of food had a depressing effect on reproduction. Conversely, the first rise in sexual activity that occurred on the Cumberland Plateau was at a time when food was scarce and declined into the spring months as grasses began to appear. There were no unusual weather conditions or preseasonal growth of grasses evident at this time to satisfactorily explain this peak in reproductive activity.

Population structure

During the course of this study 599 males, 534 females, and 22 unknown voles were captured. The percentage of males in most of the samples was greater than 50 percent (Fig. 6). Only once, in April, 1969, did the percentage of males in the samples from the study area drop below that level and then it was only 48.57 percent (17 males, 18 females). The highest percentage of males in a single sample was 62.50 percent (5 males and 3 females) from the shortleaf pine plots in December, 1968. The low point for one sample, also from the shortleaf pine area, was 40.00 percent (2 males and 3 females) in August, 1968. The percentage of males in all samples taken was 52.86 percent.

Reasons for the imbalance in sex ratios found on the study area and the extent to which sex ratios in samples were affected by trapping procedure was not completely determined. One possibility was that the greater wandering tendency of males (Blair, 1940; Hamilton, 1937) may have increased their chances of capture. This difference in habits between the sexes may have attributed to distorted sex ratios in samples obtained by live-trapping. Seasonal peaks in population densities and breeding activity occurred in the March-April-May, 1968, period and the September-October-November, 1968, period as did the peaks in percentages of males. The low ratio of females during these periods was probably due to a greater number of females tending litters and the confined movements of females in late stages of pregnancy.

A total of 770 adults, 194 subadults, 185 juveniles, and six voles of unknown age was captured during this study. The percentage of

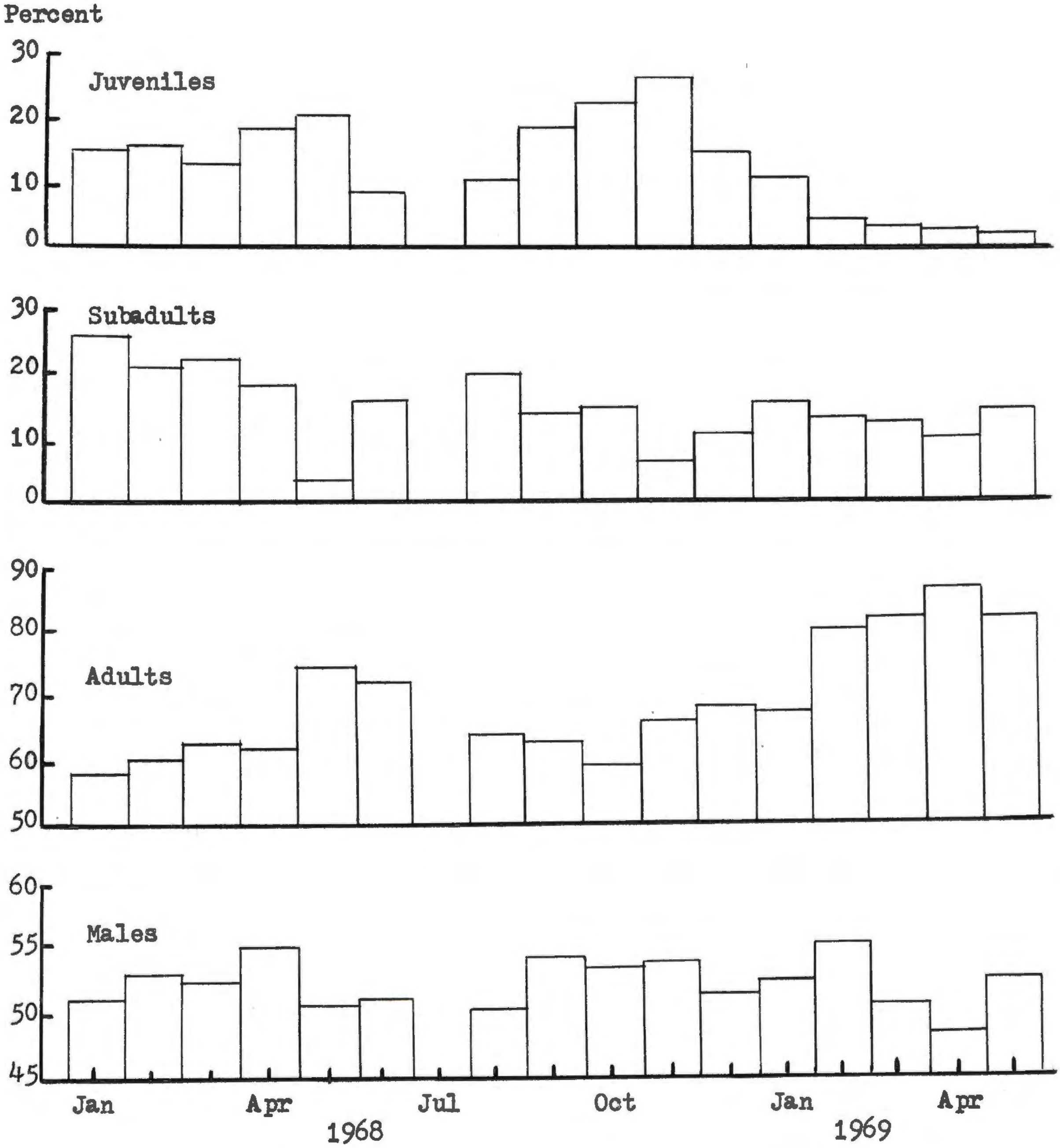

Figure 6. Monthly variations in the percentages of juveniles, subadults, adults, and males in samples from the three study plots.

the different age classes present on the study area varied seasonally (Fig. 6). May, 1968, and March, April, and May 1969, were the months when the adult fraction of the population was highest. Low points in adult populations were found at the beginning of the study and during the September-October-November, 1968, period when they constituted a relatively small portion of the population (Fig. 6). Low levels of juveniles occurred during the summer and concluding months of the study. Subadults also constituted a small portion of the population but their numbers seemed to be more stable than those of the adults and juveniles (Fig. 6). The percentages of the different age classes in the combined sample were: Adults, 66.67 percent; subadults, 16.79 percent; juveniles, 16.54 percent.

Seasonal changes in the population structure varied with fluctuations in population densities. As expected, the rise in the percentages of juveniles in the population followed the increase of mean population densities. At these times more new individuals were added to the population from increased breeding activity (Fig. 7).

II. HOME RANGE AND ACTIVITIES

Much attention has been given to measuring home range and activities of small mammals. Due to the secretive and often nocturnal habits of small mammals, most studies have utilized indirect methods, primarily live-trapping techniques. Some of the more recent studies have utilized radioisotopes to investigate home range, movements, and the general ecology of several small mammals (Ambrose, 1969; Godfrey, 1954; Kaye, 1961; Miller, 1957).

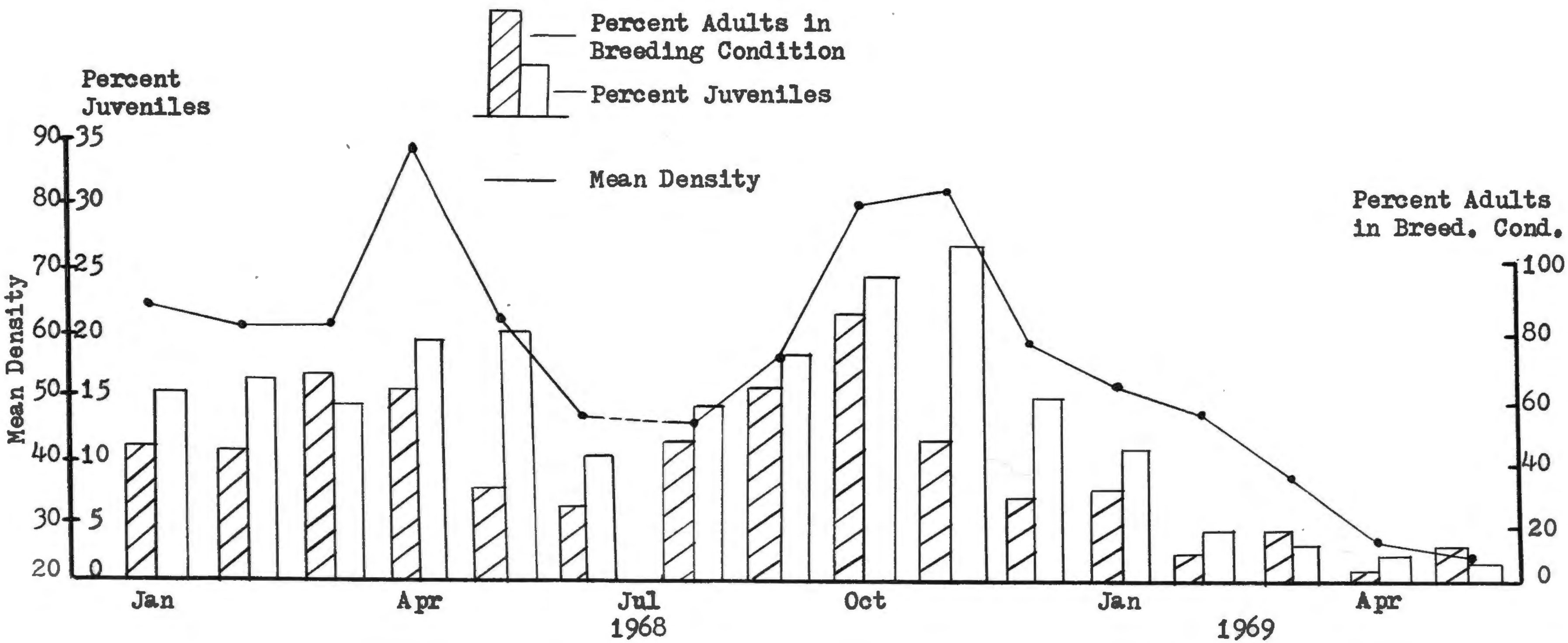

Figure 7. Fluctuations of the percent of juveniles in the population in relation to mean density and breeding activity.

Home range

The validity of live-trapping methods for accurately determining home ranges has been challenged by a number of authors (Ambrose, 1969; Hayne, 1950; VanVleck, 1969). Ambrose (1969) in a study in Kentucky compared trap-revealed and isotope-revealed home ranges of *M. pennsylvanicus*. His study indicated that home ranges determined by the isotope method reflect more accurately the true situation than did those ascertained from the live-trapping methods described by Stickel (1954). The ranges in this study were calculated according to the method described by Blair (1940). Only those individuals that were recaptured at three or more trap sites were used to estimate home ranges. These calculated ranges approximate the actual areas used by individuals over a long period of time and are considered useful for comparison with other ranges calculated by similar methods. Those individuals whose ranges were found on the edge of the trap grid, and juveniles were excluded from calculation of home ranges. The majority of the trapping sessions for this study lasted three or four days each month. For this reason the data needed to plot monthly home ranges or to detect a shift in ranges are not available.

A total of 50 voles were recaptured a sufficient number of times to calculate home ranges. The largest home range was 0.124 of an acre used by a male in the Virginia pine plots and was calculated on the basis of seven captures over a period of four months. The largest range for a female was 0.114 acres for a vole caught four times in October and November, 1968, in the loblolly pine plots. The smallest range (0.041 acres) was that of a female captured five times in the shortleaf pine sampling plots during a three month period. No other individuals exhibited ranges of such small size, except for juveniles that were all recaptured at the point of original capture. The mean home range for all individuals was 0.082 $\pm$ 0.008 of an acre ($P < 0.01$). The variation in size and shape of home ranges observed in this study are represented in Figure 8.

Few records concerning the size of home ranges for the prairie vole were found in the literature. Harvey and Barbour (1965) reported ranges for *M. ochrogaster* that varied from 0.02 to 0.18 acres and Martin (1956) recorded home ranges varying from 0.02 to 0.28 of an acre for prairie voles in Kansas. Estimation of the size of reported home ranges for *M. pennsylvanicus* varied greatly. Hayne (1950) found ranges as large as 0.77 acres, while Getz (1961) reported confined ranges of 0.04 of an acre. Hamilton (1937) concluded that the average range of the meadow vole was about 0.15 of an acre.

Significant differences between the size of home range for males and females were not observed in this study. The mean home range size for 21 males was 0.082 $\pm$ 0.009 of an acre, while the average range for 29 females was 0.080 $\pm$ 0.015 acres ($P < 0.01$). Martin (1956) found this to be the case when he observed that the mean monthly range for both sexes was 0.09 of an acre. Other investigators have reported significant differences in home ranges between male and female meadow voles. Male dominance in home range size seems to be the rule for this species (Ambrose, 1969; Blair, 1940; Van Vleck, 1969).

The prairie voles in this study showed no objection to sharing their areas and overlapping of home ranges was frequently observed. The

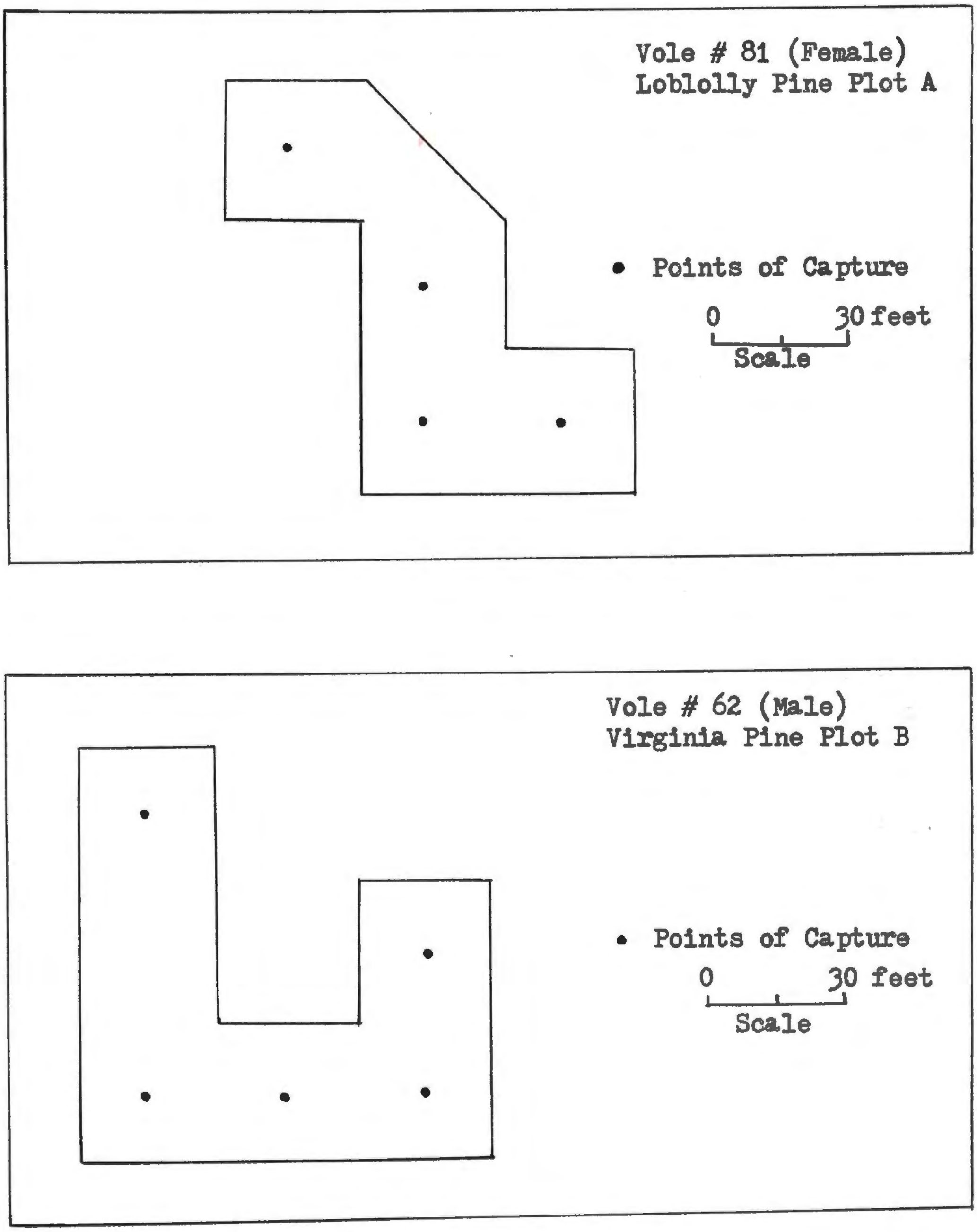

Figure 8. Maps showing the variations in size and shape of two home ranges that were observed on the study plots.

mapping of the home ranges of individuals captured during the same time period further demonstrated home range overlap (Fig. 9).

Activity

From occasional changes in the time of tending traps and by running trap lines at night a few times, this investigator gained the impression the M. ochrogaster was primarily nocturnal. Relatively few individuals were caught during the daylight hours, especially in the summer months. In colder weather there seemed to be an increase in daytime activities. Calhoun (1945) also found this to be the case and concluded that prairie voles were mainly nocturnal with peak activity being reached between sunset and midnight and again just before dawn.

Observations by other investigators on the activity patterns of the several species of Microtus varied greatly. Hamilton (1937) reported that M. pennsylvanicus was more active in the daytime. Martin (1956) found that M. ochrogaster was seldom captured in the hours of darkness, while Davis (1933), working with M. agrestis, and Hatfield (1935), working with M. californicus, both found voles to be more nocturnal than diurnal.

Runways and nests

One of the most characteristic signs of prairie voles on the area was their systems of surface runways and underground tunnels. Typical runway systems observed in this study consisted of long meandering paths and several shorter branches (Fig. 10). Surface runways were almost always well hidden under a dense mat of grass cover, but in some instances were

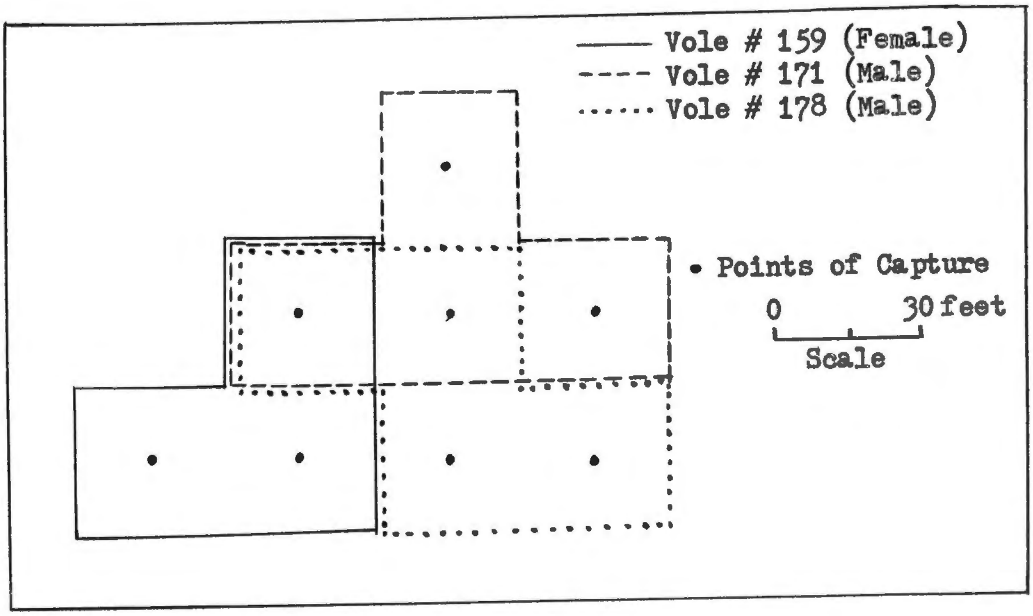

Figure 9. The overlapping ranges of voles captured during the October-November-December 1968, period in the northeast portion of Virginia pine plot A.

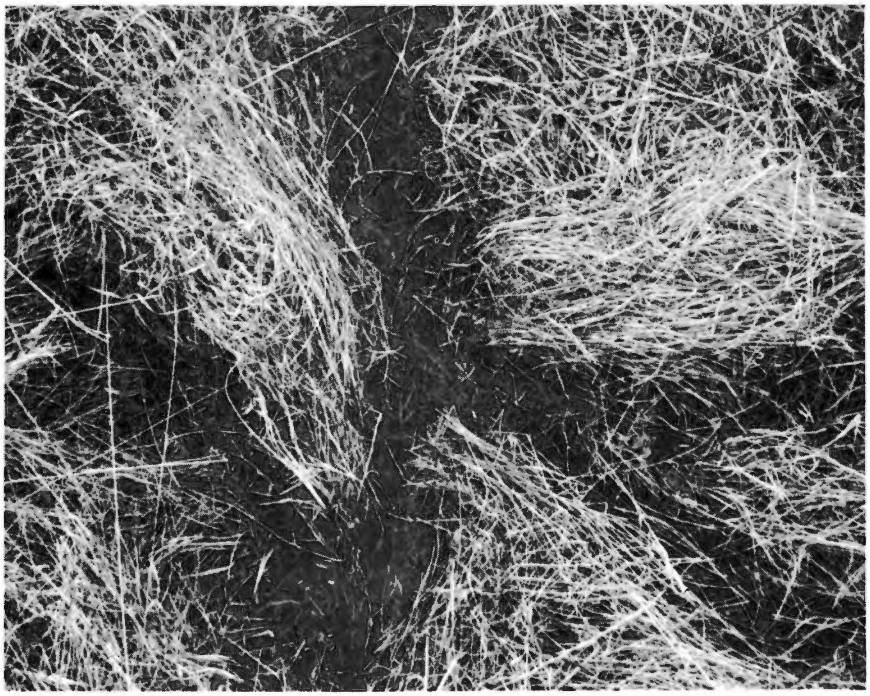

Figure 10. A portion of a runway system in the Virginia pine sampling area.

The grass cover has been pulled back to expose the main runway (center, top to bottom) with the two shorter branches (l. and r.), March 15, 1968.

in full view where grasses and debris were scarce. The majority of the runways were only slightly cut into the ground, but some runways were deep ruts devoid of vegetation due to heavy use. Some runways disappeared briefly into tunnels, while others ended at the entrance of a nest (Fig. 11).

The number of voles using any single runway system at one time was not determined. One system that was mapped included one trap station in which five individuals were captured within a two month period. Another system encompassed two trap sites where four voles were captured during one three-day trap session. Martin (1956) observed as many as four adult voles (three males and one female) using the same runway system.

During the course of this study four underground nests were excavated to determine their extent and uses. Typically, each burrow consisted of a single chamber usually three to six inches below the surface and up to 12 inches in diameter. Fisher (1945) reported none deeper than five inches in central Missouri. All of the nests were lined with dried grass that almost completely filled the burrow. Besides cover and protection, these chambers were probably used for delivering and nursing litters. One food cache was found within a nest and consisted of one Solanum sp. berry and several shoots of freshly cut grass.

III. SIZE, GROWTH RATES, AND LIFE SPANS

Live-trapping, more than any other technique, allows the investigator to follow closely the life history of an animal as small and secretive as the prairie vole. Weights and approximate ages were recorded

Figure 11. A portion of a runway in the loblolly pine section of the study area ending at the entrance to an underground nest, March 15, 1968.

each time an individual was captured, providing some insight into the growth and longevity of the prairie vole.

Size

The mean weight of 550 adult voles examined during the period of study was 42.82 ± 1.44 grams (Table 3). Weights of this age class ranged from 38.50 to 51.00 grams. The largest weight recorded for a subadult was 37.00 grams and the smallest was 21.00 grams. The mean weight of 120 subadults was 31.61 ± 2.52 grams. Weights for a sample of 85 juveniles varied from a low of 17.00 grams to a high of 32.50 grams, with a mean of 22.17 ± 4.42 grams. Other workers reported similar mean weights for adult prairie voles, but greater variations in weights. Jameson (1947), for example, reported a mean weight of 44 grams and a range of 38 to 73 grams for a sample of 50 adult voles. Martin (1956) reported a similar mean (43.78 grams) and a variation of 25 to 73 grams.

During the winter months of this study a notable reduction in the mean weights of voles was recorded (Table 3). Further examination of seasonal mean weights of each age class at the 99 percent level of probability showed a significant difference between the summer and the winter mean weights of adults and subadults. No seasonal difference was observed for juveniles in the sample (Table 4). The drop in mean weight of the two age classes can probably be attributed to the reduction in quantity and quality of their normal diet.

Table 3. Seasonal changes in the weight of voles captured during the course of this study.

Season	Mean Weight in Grams		
	Adult	Subadult	Juvenile
Summer	44.74 ± 2.28	33.86 ± 3.51	22.26 ± 4.64
Fall	43.66 ± 1.95	32.21 ± 3.18	22.68 ± 4.48
Winter	40.08 ± 1.67	28.91 ± 2.89	21.75 ± 4.59
Spring	42.78 ± 2.08	31.53 ± 2.77	21.99 ± 4.54
Total	42.82 ± 1.44	31.61 ± 2.52	22.17 ± 4.42

Table 4. Results of Duncan's new multiple range test for seasonal differences in the mean weights of prairie voles observed during the study.*

Age	Mean Weight in Grams			
	Winter	Spring	Fall	Summer
Adults	40.08	42.78	43.66	44.74
Subad.	28.91	31.53	32.21	33.86
Juvs.	21.75	21.99	22.26	22.68

* Underlining represents no significant difference at the 99 percent level of probability.

Growth rate

Few reports on the rate of growth for *M. ochrogaster* were found in the literature. The limited data presented here were secured primarily from observations of juveniles trapped in the field and kept in captivity in the laboratory. The young voles gained approximately one gram per day up to an age of one month and approximately 0.5 of a gram per day from an age of one month until the individual approaches adulthood. A single litter born in captivity exhibited growth rates of approximately 0.5 of a gram per day up to an age of one month. There seemed to be no difference between the sexes in rates of growth. These observations are substantiated by reports on prairie voles by Martin (1956) and on *M. californicus* by Hatfield (1935) and Selle (1928).

Longevity

The life spans of voles on the area could not be determined accurately since no individual was captured at birth and continually recaptured throughout the period of study. The method used to determine approximate life spans was to estimate ages of voles captured the first time and add to this the time elapsed between original and final capture. Jameson (1947) reported that at the age of three to four weeks a molt occurs in which juvenile pelage is replaced by subadult pelage. A second molt occurs when the prairie vole is between eight and twelve weeks old and is the means by which adult pelage replaces the subadult pelage. Hatfield (1935) found these same two molts to occur in captive *M. californicus*. Observations made by Fitch (1957) indicate that juvenile prairie voles have matured enough in 14 to 20 days to leave the nest and become vulnerable to capture. The following observations are adjusted estimates of ages that are based on the total time elapsed between original and final capture.

The estimated life spans of all voles studied were less than one year. Leslie and Ransom (1940), Hamilton (1937) and Fitch (1957) also found that most voles lived less than one year. The life span of voles on the study area varied greatly. The shortest time (61 days) was that of a female subadult captured eight times in the loblolly pine sampling area, and the longest life span (297 days) was exhibited by another female captured eight times in the Virginia pine sampling area. The mean life span of 343 individuals was 139.69 ± 20.41 days.

The literature yielded few observations on the differences in longevity with respect to sex. Getz (1965) reported that a male vole survived 35 months and a female 27 months in captivity. This study indicated a longer life span for females. A highly significant difference ($P < 0.01$) was observed between the mean life span for a sample of 175 males (129.62 ± 25.80 days) and the mean life span for 172 females (155.05 ± 48.79 days).

IV. PARASITES

The pelage of prairie voles, as well as other small mammals, forms a habitat for many different kinds of parasitic arthropods (Jameson, 1947). The presence of external parasite infestation was recorded for 775 individuals captured in this study as part of the records of the general physical condition of the voles. Selected specimens were taken for identification.

External parasites were found on every vole examined during the entire period of study. The most common parasitic arthropod was the flea (Siphonaptera), which was observed on all individuals examined. Fleas also commonly occupied the several underground nests that were examined where they could easily infest young voles. This would indicate that the prairie vole is host to this parasite throughout its life time. Lice (Anoplura) were also common parasites of prairie voles; 47 percent of the voles examined were infested with lice. Ticks (Ixodoidea) were less common. Only eight individuals were observed harboring this parasite and seven of these voles were juveniles. In each case the ticks were found clinging to the head of the voles near the ears. Mohr and Stumpf (1964a) also found ticks to be most prevalent on juvenile individuals and attributed it to the young being less adept at self-cleansing.

Other external parasites reported to infest voles were mites (Jameson, 1947) and chiggers (Mohr and Stumpf, 1964b). Botflies of the genus Cuterebra were found to infest the meadow vole by Clough (1965).

Examination of blood smears taken by clipping the tip of the tail of 208 voles showed no evidence of parasitic infestation. More thorough investigation and an improvement in field techniques for obtaining blood smears is needed before any conclusions can be drawn. Chandler and Read (1965) state that fleas are the prime transmitters of several blood parasites and serve as intermediate hosts of certain tapeworms. This would seem to indicate that voles harboring the number of fleas as those observed in this study would also be host to blood and intestinal parasites.

V. INDIRECT SIGN AND DENSITY RELATIONSHIPS

Complete counts of small mammals, such as the prairie vole, are impractical since most mammals are shy and adept at keeping out of sight. The method most widely utilized for obtaining population numbers is that of live-trapping animals. This method is time consuming and requires a great amount of labor and expense. Since actual counts are impractical and live-trapping is difficult, it would be very useful if some method could be found for securing a measure of relative abundance and several such methods have been suggested. Hayne and Thompson (1965) found that the counting of amounts of sign, such as grass cuttings and droppings, in a 1/100 meter square plot was a meaningful estimate of microtine abundance. Using the disturbance of a bait line as an index, Griffenius (1939) was able to detect variations in population density for M. pennsylvanicus. Similar methods for estimating populations from indirect sign have been reported by Dice (1930) and Taylor (1930).

The index used in this study to relate vole sign to population density was the frequency of fresh sign observed in twenty circular plots, two feet in diameter, randomly established four times per year on each of the six one-acre plots. As discussed earlier, perhaps the most characteristic sign of the presence and activity of prairie voles is their runway systems. Runways soon disappear when not used regularly, and their presence and status should be a reliable index of population density. Another characteristic sign of vole activity is piles of grass cuttings left in the runways after feeding. The droppings left in runways served as additional evidence of vole presence. Since the droppings were prone to rapid desiccation fresh pellets indicated recent passage of an individual. Any one or a combination of these signs, expressed as a percent of fresh sign observed in the twenty circular plots established periodically on the study area, served as a basis for estimating relative abundance.

The percent of plots containing fresh sign varied throughout the period of study. The smallest amounts of fresh sign (15.00 percent) occurred in the loblolly and shortleaf pine plots in May, 1969. The greatest amount (75.00 percent) occurred on the Virginia pine plots in April, 1968. Percentages for all areas for each sampling period ranged from 70.00 percent in April, 1968, to 24.50 percent in May, 1969.

A comparison of the percent of plots containing fresh sign with mean population densities indicated a significant correlation existed between these variables ($P < 0.01$, $r = 0.94$) (Fig. 12). These results suggest that a good estimate of the relative abundance of prairie voles on a given area can be made from indirect sign.

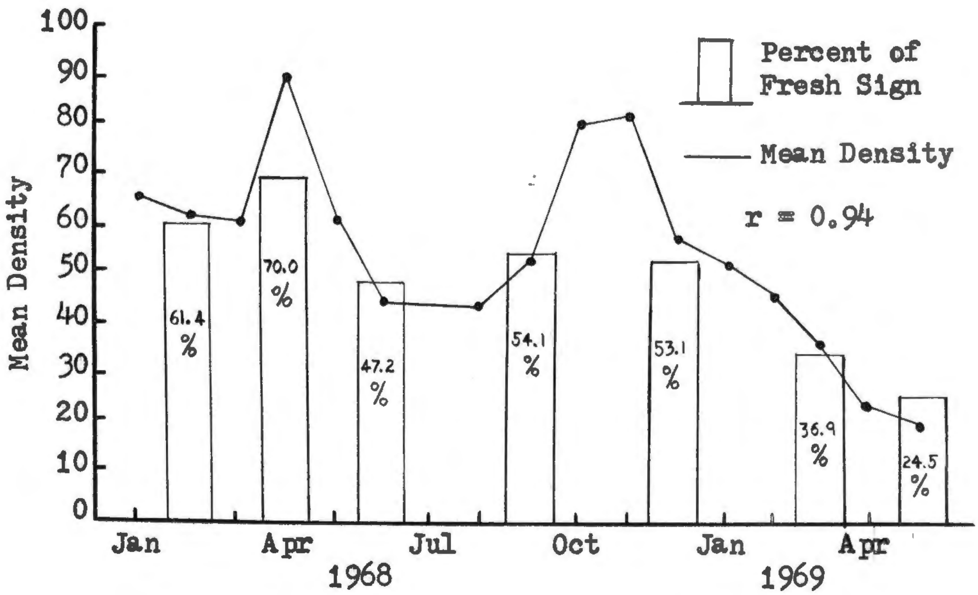

Figure 12. Variations in the percent of plots containing fresh sign at different times throughout the period of study in relation to the seasonal variation in mean population densities.

CHAPTER V

SUMMARY AND CONCLUSIONS

The objectives of this study were: (1) to determine the density and structure of a population of prairie voles, and (2) to determine the relationship between indirect sign and population densities of prairie voles. The study was initiated in the fall of 1967, and was terminated in the spring of 1969.

The study area was a 28 acre pinetum consisting of approximately equal acreages of loblolly, shortleaf, and Virginia pine. The study area was located five air miles southwest of Crossville in Cumberland County, Tennessee.

Six one-acre plots were established on the pinetum and data for describing the populations were obtained by a live-trapping program. Insulated traps were set in a 30 foot grid pattern and operated at regular intervals throughout the study. Captured voles were marked and examined to determine sex, age, breeding condition, weight, and general physical condition. The percent of fresh prairie vole sign observed in twenty random samples taken periodically in each of the six study plots was used as an index for relating indirect sign to population densities.

Population densities varied greatly during the period of study and ranged from a low of 10.00 individuals per acre to a high of 122.50 voles per acre. Peak densities were reached in April, 1968, and again in October and November of the same year and gradually decreased toward the conclusion of the study. The breeding activity of voles on the study area was closely related to variations in population densities. A highly significant correlation existed between the percent of adults in breeding condition and population density. The early spring and fall peaks in density followed periods of high levels of breeding activity. The low annual densities in the summer months of 1968 and those at the conclusion of the study occurred when there was little sexual activity such as perforate females and males with descended testes.

The number of males exceeded the number of females in almost every month of the study. The percent of males in all samples was 52.86 percent and ranged from 40.00 to 62.50 percent. The observed imbalance in sex ratios was partially attributed to the greater wandering tendencies of males resulting in increased trap vulnerability. The especially low numbers of females observed during periods of increased breeding activity and density peaks were probably due to the restricted movements of individuals in late stages of pregnancy and tending litters.

Adults constituted 66.67 percent, subadults 16.79 percent, and juveniles 16.54 percent of the combined samples. Changes in population age structure varied with fluctuations in population densities. Increases in the percentages of juveniles followed rises in densities as more new individuals were added to the population after periods of increased breeding activity.

Calculated home ranges for the prairie vole in this study varied in size and shape. The smallest range was 0.041 of an acre and the largest was 0.124 of an acre, with a mean of all home ranges being 0.082 of an acre. No significant difference in home range size was observed between the sexes. The average home range for males was 0.082 of an acre, while the mean for females was 0.080 acres. Frequent overlapping of ranges was common throughout the study.

Observations made during this study suggest that vole activity is most prevalent during the hours of darkness. A slight increase in daytime activity was noted in the winter months of the study period.

The most characteristic sign of prairie vole activity was the presence of their systems of surface runways and subterranean tunnels. The runways typically consisted of long paths with several shorter branches and varied in size and extent. Runways often encompassed trap stations where several individuals were captured, indicating that the systems were utilized by more than one vole.

The mean weight of voles observed during this study was: 42.82 grams for adults, 31.61 grams for subadults, and 22.17 grams for juveniles. Seasonal variation in weights was observed; a significant decrease in mean weights of adults and subadults occurred in the winter months as normal foods became scarce.

Individuals observed in the laboratory showed growth rates of approximately one gram per day to an age of one month and 0.5 of a gram per day thereafter until growth leveled off as the individual reached adulthood. No difference in the growth rates of males and females was noted.

The life spans of all voles studied were less than one year, with a mean life span of 139.69 days. A highly significant difference was observed between the mean life span for males (129.62 days) and the mean life span for females (155.05 days).

The pelage of prairie voles harbored several kinds of parasitic arthropods. The most common parasites were fleas (Siphonaptera) and lice (Anoplura). The least common parasite was the tick (Ixodoidea), which was most prevalent on juveniles that were less adept at self-cleansing. Examination of blood smears showed no evidence of parasitic infestation.

Results of this investigation indicate that an accurate estimate of the relative abundance of prairie voles on a given area can be made from indirect sign. The percent of samples containing fresh vole sign was significantly related to mean population densities.

LITERATURE CITED

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Ambrose, H.W. 1969. A comparison of *Microtus pennsylvanicus* home ranges as determined by isotope and live trap methods. Amer. Midland Nat. 81:535-555.

Bailey, V. 1924. Breeding, feeding and other life habits of meadow mice. Jour. Agric. Res. 27:523-536.

Blair, W.F. 1940. Home ranges and populations of the meadow vole in southern Michigan. Jour. Wildl. Mgmt. 4:149-161.

__________ 1948. Population density, life span and mortality rates of small mammals in the bluegrass meadow and bluegrass field association of southern Michigan. Amer. Midland Nat. 40:395-419.

Blomquist, H.L. and H.J. Oosting. 1959. A guide to the Spring and Early Summer Flora of the Piedmont, North Carolina. Seeman Printery, Inc., Durham, N.Carolina. 181p.

Burt, W.H. and R.P. Grossenheider. 1964. A Field Guide to the Mammals. Houghton Mifflin Co., Boston, Mass. 284p.

Calhoun, J.B. 1945. Activity rhythm of the rodents *Microtus ochrogaster* and *Sigmodon hispidus hispidus*. Ecol. 26:251-273.

Chandler, A.C. and C.P. Read. 1965. Introduction to Parasitology. John Wiley and Sons, Inc., New York. 822p.

Chitty, D. and D.A. Kempson. 1949. Prebaiting small mammals and a new design of live trap. Ecol. 30:536-542.

Clough, G.C. 1965. Physiological effect of botfly parasitism on meadow voles. Ecol. 46:344-346.

Cockrum, E.L. 1947. Effectiveness of live traps vs. snap traps. Jour. Mamm. 28:186.

Davis, D.H. 1933. Rhythmic activity in the short-tailed vole, *Microtus*. Jour. Animal Ecol. 2:232-238.

Dice, L.R. 1930. Methods of indicating the abundance of mammals. Jour. Mamm. 12:376-381.

Dimmick, R.W. 1969. The distribution of *Microtus ochrogaster* in Tennessee. Jour. Mamm. 50:126.

Eberhardt, L.L. 1969. Population estimates from recapture frequencies. Jour. Wildl. Mgmt. 33:28-39.

Fisher, H.S. 1945. Notes on the voles of central Missouri. Jour. Mamm. 26:435-437.

Fitch, H.S. 1957. Aspects of reproduction and development in the prairie vole (*Microtus*). Univ. Kans. Publ., Mus. Nat. Hist. 10:129-161.

Getz, L.L. 1961. Home ranges, territoriality, and movement of the meadow vole. Jour. Mamm. 42:24-36.

__________ 1965. Longevity of two captive prairie voles. Jour. Mamm. 46:514.

Godfrey, G.K. 1954. Tracing field voles (*Microtus agrestis*) with a Geiger-Muller counter. Ecol. 35:5-10.

Griffenius, R.F. 1939. A method for determining the relative abundance of *Microtus pennsylvanicus*. Jour. Wildl. Mgmt. 3:199-200.

Hamilton, W.J. 1937. Growth and life span of the field mouse. Amer. Nat. 71:500-507.

Harvey, J.J. and R.W. Barbour. 1965. Home range of *Microtus ochrogaster* determined by a modified minimum area method. Jour. Mamm. 46:398-402.

Harlow, W.M. and E.S. Harrar. 1958. Textbook of Dendrology. McGraw-Hill Book Co., Inc., New York. 561p.

Hatfield, D.M. 1935. A natural history of *Microtus californicus*. Jour. Mamm. 16:261-271.

Hayne, D.M. 1950. Apparent home range of *Microtus* in relation to distance between traps. Jour. Mamm. 31:26-39.

Hayne, D.M. and D.Q. Thompson. 1965. Methods for estimating microtine abundance. Trans. 30th N. Amer. Wildl. Conf. p. 393-400.

Howard, W.E. 1951. Relation between low temperatures and available food to survival of small rodents. Jour. Mamm. 32:300-312.

Jameson, E.W. 1947. Natural history of the prairie vole. Univ. Kans. Publ., Mus. Nat. Hist. 1:125-151.

Kaye, S.V. 1961. Movements of harvest mice tagged with gold-198. Jour. Mamm. 42:323-337.

Leslie, P.H. and R.M. Ransom. 1940. The mortality, fertility, and rate of natural increase of the vole (Microtus agrestis) as observed in the laboratory. Jour. Animal Ecol. 9:27-51.

Li, Jerome C.R. 1957. Introduction to Statistical Inference. Edward Brothers, Inc., Ann Arbor, Michigan. 553p.

Martin, E.P. 1956. A population study of the prairie vole (Microtus ochrogaster) in northeastern Kansas. Univ. Kans. Publ., Mus. Nat. Hist. 8:361-416.

Matzek, B.L. 1950. Soil Survey in Cumberland County, Tennessee. U.S. Dept. of Agr. Soil survey series 1938, No. 25. 107p.

Miller, L.S. 1957. Tracing vole movements by radioactive excretory products. Ecol. 38:132-136.

Mohr, C.O. and W.A. Stumpf. 1964a. Relation of tick and chigger infestation to home areas of California meadow mice. Jour. Med. Entomol. 1:73-77.

__________ 1964b. Louse and chigger infestation as related to host size and home ranges of small mammals. Trans. 29th N. Amer. Wildl. Conf. p. 181-195.

Mosby, H.S. (ed.) 1963. Wildlife Investigational Techniques. Edward Brothers, Inc., Ann Arbor, Michigan. 411p.

Selle, R.M. 1928. Microtus californicus in captivity. Jour. Mamm. 9:93-98.

Stickel, L.F. 1946. Experimental analysis of methods of measuring small mammal populations. Jour. Wildl. Mgmt. 10:150-159.

__________ 1954. A comparison of certain methods of measuring ranges of small mammals. Jour. Mamm. 35:1-15.

Taylor, W.P. 1930. Methods of determining rodent pressure on the range. Ecol. 11:523-542.

U. S. Weather Bureau, Climatological Data, U.S. Dept. Comm. Annual Summary, 1967, 1968, 1969. Vols. 72, 73, 74.

Van Vleck, D.B. 1969. Standardization of Microtus home range calculation. Jour. Mamm. 50:69-80.

VITA

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