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A NUMERICAL AND SPATIAL STUDY OF THE MEADOW VOLE, *MICROTUS PENNSYLVANICUS*

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
Margaret Higgins Bowker
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APPROVAL SHEET

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

This study was an attempt to measure whether social interactions among Meadow Voles, Microtus pennsylvanicus, determine spacing within the population. A population of voles was live-trapped on a three-acre field near Williamsburg, Virginia from September through November, 1969; and from March through May, 1970. Resident voles were removed from the study area for five days and then released back into the field.

Appearance of new voles and movements of remaining voles did not increase significantly during the absence of residents. Possibly voles do not respond to vacancies either at the low densities experienced in this study, or with the short time period of five days. Voles occurred in a few highly active sites. The small home ranges and lack of long movements possibly indicate an attachment to a specific home site as the important factor in spacing of voles.

The population rose during the fall of 1969, and then declined to six known living animals in the spring of 1970. The proportion of juveniles in the spring population was low and then dropped to zero; whereas the increasing fall population averaged fifty percent juveniles. Recruitment of juveniles did not occur even though the percentage of females reproducing remained constant during the population decline.

Weight losses by individual male voles were significant, and data indicated that females lost weight and juveniles failed to gain weight. These weight losses and low fat deposits of dead voles occurred between March 12 and April 15. After April 15, heavy fat deposits increased significantly, and females appeared to gain weight.

Weight losses of individual voles, absence of recruitment of juveniles, and high trap mortality appear responsible for the population decline. These data may support Chitty's hypothesis that deterioration in the quality of a population results in declines.

A NUMERICAL AND SPATIAL STUDY
OF THE MEADOW VOLE,
MICROTUS PENNSYLVANICUS

INTRODUCTION

Spacing of small mammals is believed by many to be determined and maintained by intraspecific interactions (Calhoun and Webb, 1953; Fisler, 1962; Robinson and Falls, 1965; Van Vleck, 1968; Watts, 1970; Metzgar, 1971). Experiments in which resident animals were removed from an area show that new animals swiftly established themselves in the vacated areas (Blair, 1940; Calhoun and Webb, 1953; Stickel, 1946; Krebs, 1966; Van Vleck, 1968). Calhoun (1963) postulated that animals space themselves evenly over the available habitat and thus maximize utilization of the area and minimize encounters with neighbors. Residents maintain this spacing by either avoiding neighbors' signals or equalizing neighbors' signals from all directions. Removal of this signal, postulated by Calhoun to be vocal, allows neighbors and wandering non-residents to invade and remain in the vacated area.

This experiment was designed to test whether the presence of established residents influences the spacing of other animals of the same species. The meadow vole, Microtus pennsylvanicus, the most abundant small mammal in the study area, was chosen for this study. Resident voles were removed for five days and movement of remaining resident voles and appearance of new voles noted. An increase in these two measurements during the absence of residents would indicate that an intraspecific interaction or avoidance does maintain the spacing within a population.

MATERIALS AND METHODS

The Study Area

The study area was an old field located south of the city of Williamsburg, Virginia at the Laboratory of Endocrinology and Population Ecology of the College of William and Mary. An aspect survey of the vegetation made on June 18, 1970, with the help of Dr. S. Ware revealed that vegetation different from that in the field bordered most of the field and so isolated the study area. Figure 1 represents the study area with the grid lines and vegetation sub-areas.

Along the east border, the edge of a woods, were wild black cherry, (*Prunus serotina* Ehrh.), hackberry (*Celtis occidentalis* L.), and tree of heaven (*Ailanthus altissima* (Miller) Swingle). From grid lines I to O, tree of heaven, with wild grape vine (*Vitis baileyana* Munson) entwined, was especially numerous. At the south and west these same species bordered the area. From lines A to F, a row of small trees and shrubs of hackberry, wild cherry, and tree of heaven formed the west border. From J to U, pokeweed (*Phytolacca americana* L.) formed a margin line just in front of an increased downward slope. The whole field sloped downward toward this drop off beyond the west boundary.

The northern end had no well-defined boundary, and the field vegetation continued beyond line U. A large clump of tree of heaven and a honeysuckle patch (*Lonicera japonica* Thunberg) provided a partial boundary.

The study area could be divided into sub-areas of uniform vegetation, labeled in Figure 1. Area 1 was predominantly vetch (*Vicia villosa* Roth) and wild grape vine. Fleabane (*Erigeron annus* (L.) Persoon and *E. strigosus* Muhl. ex. Willd.), orchard grass (*Dactylis glomerata* L.), and goldenrod (*Solidago* sp.) were scattered throughout this area. The wild grape was tangled over the other vegetation, providing extensive coverage.

Vetch dominated area 2, west of area 1. Orchard grass and goldenrod occurred in scattered clumps. Some wild carrot (*Daucus carota* L.) was scattered throughout, but fleabane was absent. A patch of pokeweed and one of honeysuckle, labeled on the map, occurred next to this area.

Vetch also dominated area 3. Goldenrod, fleabane, and aster (*Aster* sp.) were distributed throughout in clumps. Isolated patches of honeysuckle, Johnson grass (*Sorghum halapense* (L.) Persoon) and tree of heaven broke up the uniformity of the area.

A large hackberry tree stood at the junction of areas 3, 4, and 5. Area 4 was predominantly vetch and fleabane with patches of goldenrod and orchard grass. A single row of hackberry, hickory (*Carya* sp.), sycamore (*Platamnus occidentalis* L.), tree of heaven, and wild grape formed a partial boundary along line N at 12 and 13.

The remainder of the field, area 5, was fairly uniform. Vetch was most numerous, followed by fleabane, and goldenrod. Generally, these species were mixed, though patches several yards in diameter did occur where one species predominated. Beginning at line J, chicory (*Cichorium intybus* L.) occurred mixed with the other species. At the southern end of the field, the open area narrowed and large patches of honeysuckle predominated.

A large amount of aster occurred with the dominating vetch, fleabane, and goldenrod in area 6.

The old field was once cultivated but has been wild for many years. The college removes trees and topsoil occasionally, but primarily from an adjacent area. Aside from a few hunters in the fall and a bird banding study along the periphery, the area was undisturbed during the study.

Field Procedures

Trapping continued intermittently from June, 1969 through May, 1970. The preliminary trapping in June with 30 Sherman live traps revealed the presence of *Mus musculus*, *Blarina brevicauda*, and *Peromyscus leucopus* populations in the field. No *Microtus* spp. occurred in traps until the fall of 1969.

In July, 1969, I set up a three acre grid, conforming in shape to the open area of the field. I chose a ten meter trap interval because previous studies with *M. pennsylvanicus* (Getz, 1961b; Hayne, 1950) suggested that this spacing increased the likelihood of catching more of the population. White metal posts marked the stations and single traps were placed in a radius of six feet from each marker, in a runway under the vegetation if possible. I sampled this area using 176 traps throughout the study.

The traps were built in the shop of the Department of Biology of the College of William and Mary. The single entrance live trap measured 25.5 x 7 x 7.5 cm., and the gravity fall door and lock ordinarily resulted in only single captures. A screen covered the opposite end, the floor and treadle were of wood, and the sides of aluminum. This wooden floor reduced heat conduction from the animals in the winter. A square of roofing material covered each trap to reduce heat conduction and maintain a more constant environment in the trap in summer and winter. Peanut butter, rolled oats, corn, and laboratory mouse food were tried for bait. Laboratory food was chosen as all appeared equally effective. The dry pellets, the D & G Research Animal Laboratory Diet, measured 3/4 x 3/4 x 1/4 inches. Each trap was baited with four to five pellets. Cotton was placed in the back of all traps when the outside temperature began dropping in November and was retained through May trapping.

The grid was trapped with Sherman live traps in August and September. The gravity lock traps were used for all subsequent trapping in the fall of 1969 and spring 1970.

I inspected, reset, and rebaited all traps once a day beginning at 7:00 hr. and usually finishing by 9:30 hr. With the help of Patti Staples, I checked traps again at 17:00 hr. in March 1970, in order to reduce mortality in the traps from excessive cold. After March 25, 1970, the evening inspections were discontinued as few animals were found during the evening inspections. All evening captures counted as captures on the following morning in the analysis, and a morning capture of the same animal following an evening capture was discounted. This data is therefore comparable to data from single daily inspections.

A captured animal was transferred to a plastic bag and held at the back of the neck for examination. For each animal, I recorded the species, sex, date, and site of capture. The condition of the vagina, either perforate or imperforate, pregnancy by palpation, and lactation were recorded for females. The position of the testes, scrotal or abdominal, was recorded for the males. I weighed every new animal, all dead animals, and all animals used in the experiments described later. Most recaptured animals were weighed more than once during the experiment. Each individual was numbered by a toe removal system, with a separate sequence for each species. Only one animal is known to have lost additional toes between the fall and spring, so this system of marking appeared accurate. All dead animals were autopsied and preserved in formalin.

Each morning I noted general weather information: rainfall, cloud cover, wind, the maximum and minimum temperatures of the past 24 hours, and the current temperature from a thermometer at a height of five feet above ground under trees at the edge of the area.

Predators and scavengers at first posed a great problem to the trapping success. These animals turned over traps, removed bait, and sprang traps. In the early fall, an average of 56 (31.8%) traps were disturbed every night. Two types of disturbance occurred: a row by row checking of the traps and removal of bait, and a more random disturbance. The latter was believed to be a predator checking for mice as bloody traps, bitten mice, or pieces of mice were sometimes found. The number of experimental animals removed by predators from the live traps is an unknown but possibly important mortality factor. On October 8, 1969, seven #1 steel traps were set in highly disturbed areas, and five more were added October 14. The traps were shifted to different sites frequently. In March, 1970, five conibear traps were added. The total number of animals caught in the steel traps and removed were: 9 raccoon (*Procyon lotor*), 9 opossum (*Didelphis marsupialis*), 3 skunk (*Mephitis mephitis*), 1 woodchuck (*Marmota monax*), 1 gray fox (*Urocyon cinereoargenteus*), and 4 wild domestic cats (*Felis domestica*). Other animals seen which may have preyed on the experimental animals were black snakes and king snakes. Disturbance dropped to 16.7 traps per night (9.5%) in the fall and 10.45 traps per night (5.9%) in the spring after steel traps began removing or discouraging predators and scavengers.

Experimental Manipulation

The experimental manipulation consisted of removing resident voles, *Microtus pennsylvanicus*, from the field to see if the resulting vacancies affected movement and invasion by other voles.

I defined a resident as any vole caught at least once before removal was begun. Any vole first caught on day one of the removal period was regarded as a resident and was removed on subsequent captures.

Each replication required 15 trap nights for completion (Figure 2). An afternoon, night, and the following morning trap records constituted one trap night. Trap nights 1-5 consisted of trapping, marking, and releasing, giving five nights of continuous trapping. After the fifth night, and for four additional nights, all captured residents were replaced in the traps and carried into the laboratory. While in the laboratory, the animals were placed separately in plastic cages, without physical or visual contact with other voles. Wood shavings, water and food (a combination of laboratory pellets, carrots, apples and lettuce) were available in the cages at all times. This resulted in five trap night records, nights 6-10, when residents were absent. In the evening before trap night 11, each resident was released at the site from which it had been removed. Trap nights 11-15 provided five additional nights of trapping when the residents were present, and completed the fifteen-day experiment. Three removal sequences were run, March 22 - April 5, April 6 - April 20, and May 7 - May 21, 1970.

Trapping periods were also established to obtain records of vole movement and invasion without any treatment affect. These consisted of a sequence of fifteen trap nights on the same field with no removal of residents. Two sequences of trapping without removal were run. The first was March 12 - March 26, before any experimental trapping; and the second was April 22 - May 6, 1970, between removals two and three. These fifteen-day control periods could therefore be compared to the fifteen-day treatment periods.

RESULTS

General Results

Five species occurred repeatedly in the traps; *Blarina brevicauda*, *Microtus pennsylvanicus*, *Microtus pinetorum*, *Mus musculus*, and *Peromyscus leucopus* (Table 1). The study area also supported a large *Sylvilagus floridanus* population.

Large *Mus* and *Blarina* populations occurred on the area in the fall of 1969. A total of 195 *Mus* and 128 *Blarina* individuals were trapped from August through November, 1969. The *Microtus* spp. did not appear until October, and then the *M. pennsylvanicus* and *M. pinetorum* populations increased through November when the trapping ended. I recorded *M. pinetorum* and *Peromyscus leucopus* throughout the spring. *P. leucopus* was trapped mainly in the peripheral wooded areas.

Trapping in March revealed low *Mus* and *Microtus pinetorum* populations, and a high *Microtus pennsylvanicus* population. For this reason *Microtus pennsylvanicus*, the meadow vole, was chosen as the experimental animal.

In the spring, 1970, 106 meadow voles were captured a total of 418 times. Individuals of other species occurred 552 times, or an average of 6.27 captures per night. Of the 176 traps set every night, an average of 8.82 were disturbed, and 6.27 used by other species; hence, 160.91 traps were available to the vole population on each of 90 nights. For 13,472.9 trap nights the trapping success of M. pennsylvanicus was 0.786%.

I recorded 66 females, 39 males, and one individual of unknown sex (Figure 3), a sex ratio significantly different from 1:1 ($X^2 = 6.44$, $P<0.025$). All males had disappeared by May 12, and after April 15, no more than two were recorded during any five-day interval.

Of the 106 voles, 44 or 41.5% died in the traps. An unknown number of animals were killed in traps by predators.

Fall Data, 1969

A few results from the fall, 1969, trapping appear pertinent to this analysis. However, no fall data are included in the spatial and experimental results.

From August through November, 1969, 53 M. pennsylvanicus individuals were recorded. Fifty of these appeared in November (Figure 4).

The age distribution of the population shows a large juvenile class. In November, in five-day intervals, juveniles made up 66.7%, 37.5%, 18.8%, 47.0%, and 75.0% of the known living population. Juveniles, therefore, averaged 49.0% of the November vole population (Figure 4).

Demographic Results, Spring 1970

Figure 4 illustrates the total vole population known to be alive at successive five-day intervals. Animals, not captured during a five-day interval but captured later, were counted as part of the population. The graph shows that the known population increased until March 21, 1970, to a high of 47 animals. Thereafter, the population declined steadily to a low of six known living animals at the end of May when trapping ceased.

The number of juveniles appearing in traps declined steadily to zero after March 31 (Figure 4). No female weighing 22 grams or less was ever found with a perforate vagina. Voles weighing 22 grams or less were considered juveniles, agreeing with the age designation by weight of Krebs, Keller, and Tamarin (1969). Testes position in the *M. pennsylvanicus* male was unreliable as a criterion for age. Ten juveniles or 21.3% of the population, the largest percentage and number of juveniles known to be alive at any interval, occurred during the population high at the end of March. Until April 15, when they disappeared, juveniles made up an average of 14.7% of the total known population.

Reproductive Condition

All mature females were classed as reproductive by the presence of embryos, uterine scars, pregnancy as determined by palpation or lactation. Non-reproductive females lacked these signs. The percentage of females which were reproductive was calculated for three 25-day intervals (Figure 5). A female judged reproductive in one interval was considered reproductive in all previous intervals. The percentage of reproductive females in the three intervals was 61.4%, 52.9% and 57.9%. This change in percentage of reproductive females was not significant by a chi-square (contingency table) test.

Trap Mortality

Figure 6 graphs the number of voles dead in the traps each five-day interval. This number, added to the number dead from all previous trapping, gives the curve of cumulative dead. The total number of voles known to be alive, the population curve, plus cumulative dead from previous intervals results in the uppermost curve of the graph. This curve represents the total vole population which theoretically could have existed with no trapping mortality. This number increased until the period of the recorded population high on March 27-31. The curve then stays almost constant until it begins to fall steadily on May 2.

Body Weights

A significant weight loss ($P<0.05$) by adult male voles occurred in March and April (Table 2). All males, weighed more than once, lost an average of 8.22 grams, with the largest loss being 33.4 grams and the only gain by any male 0.2 grams. Females, not pregnant at either weighing, were also tested. Animals with uterine scars were not used in this analysis; however, the chance of error in determining pregnancy by palpation is still high. The average female weight loss was 2.38 grams, significant only at $0.1<P<0.2$ by the Wilcoxon signed rank test. However, the three females weighed after the steepest population decline, April 15, gained large amounts, 12.7 and 4.9 grams, or lost an insignificant amount, 0.9 grams. Weight loss by the females before April 15 was significant ($P<0.02$).

Females, pregnant at the second weighing only, gained an average of 1.9 grams. The average juvenile weight gain was 3.12

grams over 11.8 days (Table 2). Three of the five juveniles, all less than 22 grams on the first weighing, lost 5.4 grams and 0.9 grams or gained an insignificant amount, 1.9 grams. Two juveniles gained 7.7 grams and 12.6 grams, respectively. Periodically, the Ohaus Dial-O-Gram scale was checked against known weights and was found to maintain a high accuracy.

Fat Analysis

Fat deposits of all dead and preserved voles were visually examined, and two categories of amounts of fat noted. Some animals had fat deposits only in the intestinal mesentery, whereas others had heavy mesenteric fat and subcutaneous fat. Results showed that 18 of 26 voles dying by April 15 had only mesenteric fat. After April 15, seven of eight voles had heavy mesenteric and subcutaneous fat. The proportion of voles with heavy fat deposits after April 15 was significantly higher, by a chi-square test, than before April 15 ($P<0.01$.).

Spatial Results

The spatial analysis includes all data from March through May, 1970, and excludes all data from the fall, 1969.

Thirty-nine males were captured 132 times, an average of 3.385 captures per animal. Sixty-six females, captured a total of 286 times, averaged 4.333 captures per animal. The frequency of recapture (Table 3) did not differ between males and females at the 0.05 level of significance. Fourteen females were captured more than six times, accounting for 154 or 53% of the 286 captures. Three males were captured more than six times, 49 or 37% of the

132 captures. Many voles died in the traps after repeated captures.

Table 4 lists the number of different traps visited by the voles which were caught more than once. Female voles visited 2.26 different traps on the average, males 2.40 different traps. Male and female voles did not differ significantly in the number of different traps which they visited.

Localization

In order to test whether one sex localized more than the other, the proportion of captures in which each animal was caught in the same trap on successive captures was calculated. Voles captured once only could not be used in this analysis. Females exhibited a higher proportion of successive captures in the same trap (0.52) than did males (0.41), although this difference was not significant.

Home Range

Home range size was measured by the minimum area method, as described by Brown (1962), for all voles with three or more captures (Figure 7). A high proportion of the males, 58.3% and females, 59.4% occurred in only one or two traps and so had no measurable home range. Twenty-five percent of males and 31.25% of females had home ranges of 1-100 square meters, so that 83.3% of males and 90.65% of the females had home ranges less than or equal to one square trap interval, 100 square meters. The difference in home range size between males and females was not significant.

Range Length

Range length, the greatest distance between two capture sites, was measured for all animals with two or more captures, including single location captures (Figure 8). Fifty percent of males ranged from 0-15 meters and 66% of females had range lengths of 0-15 meters. Since 10 meters is one trap interval and 14.14 meters is one diagonal trap interval, 50% or more of all voles captured two or more times ranged no farther than one trap interval. A higher percentage of males (50%) than females (34%) had range lengths greater than 15 meters, though comparison using a 2 x 2 contingency table did not find this significant.

Range length was determined at high and low population densities for all females. Figure 9 shows that 7 of 31 females, 22.5%, ranged beyond 15 meters when population density was high from March 12 to April 10. At the low densities, from April 22 to May 21, a greater percentage, 28.7%, of females ranged beyond 15 meters. The higher percentage of females with range lengths greater than 15 meters at the lower population densities was not significant by 2 x 2 contingency test.

Experimental Manipulation

Three separate removal experiments, each lasting 15 days, were conducted with voles in the spring. The animals removed, the residents not removed but appearing later, capture sites, day of removal, and new animals on the plot were the raw data collected. These data were analyzed to see if the removal or absence of voles had an effect on population spacing and movement.

For each experiment, the numbers of animals caught when residents were present, days 1-5 and days 11-15, were totaled. This was compared to the numbers of new animals caught when residents were absent, days 6-10 (Table 5); with the null hypothesis being that no difference in numbers of new animals, or invaders, would occur. The expected ratio of invaders is 1:2 since a five-day period is being compared to a ten-day period. A test for heterogeneity between experiments was not significant, hence the three removal experiments were pooled. The data analyzed, by a chi-square test, show that the presence or absence of residents had no differential effect on the number of animals which entered traps for the first time.

For each animal a center of activity, as defined by Hayne (1949), was calculated from all captures during days 1-5 and a second center of activity from all captures during days 11-15. The distance between these two points, the change in center of activity, was then calculated. Table 6 lists the numbers of animals and the mean change in centers of activity for two categories of residents. Residents appearing in traps during days 5-9 were removed from the field into the laboratory and are called removed residents. Those voles not appearing during days 5-9 but trapped later were therefore not removed and are called unremoved residents.

Two control periods of 15 days of trapping were run from March 12 - March 26 and April 22 - May 15. No resident voles were removed during each control period. The same shifts in centers of activity were calculated for residents captured during days 1-5 and 11-15.

The shifts in center of activity measurements of each type of resident did not differ over the three replications, and so were pooled. The shifts in centers of activity of removed residents did not differ significantly from the calculated shifts of controls. Residents, not removed from the field, also showed no significant difference in shifts of their centers of activity when compared to controls. However, the average shifts of both removed residents, 8.55 meters, and unremoved residents, 7.37 meters, were longer than the average shifts by controls, 5.92 meters.

Another analysis (Table 7) tested whether residents shifted greater distances due to the absence of other voles. The distance between the center of activity in trap nights 1-5 and the removal site was calculated for all removed residents. Voles removed on the first day of removal, and thus trapped while all residents were present, were not included in this test. Control measurements consisted of the distances between centers of activity in trap nights 1-5 and the first capture site in trap nights 6-10 for voles captured during the two 15-day control periods. Results of homogeneity tests again permitted pooling over the three removal trials. The removed residents did not shift greater distances by a t-test than did controls ($T = 1.32$, $P<0.1$), though the mean shift of the residents, 7.04 meters, was larger than controls, 3.56 meters.

Another calculation tested whether voles caught during the removal period tended to move into or toward spaces vacated by removed residents. The distance between the removal site of a vole and the closest trap in the home range of a previously removed vole of the same sex was calculated. This value was subtracted from another distance measurement between these two voles based on home range calculations from the previous ten days. This measurement was the distance from the closest trap in the home range of the vole being removed to the closest trap in the home range of the previously removed resident. This difference between two nearest neighbor measurements should indicate whether voles move toward the vacated area of the nearest removed vole of the same sex. Results, pooled over the three replications, show that two females moved toward a vacuity, 14 stayed in the same location, four moved away. Two males moved toward a vacated area, four did not move, three moved away. A chi-square test showed that females moved toward a vacated area less than expected by chance ($P<0.025$, $X^2 = 5.31$), and that male movement toward or not toward a vacancy did not differ from chance.

DISCUSSION

Demographic Results

The Microtus sp. are known for large fluctuations in population density, though the causes behind these fluctuations are still unknown (Frank, 1957; Keller and Krebs, 1970). In this study, I followed a population of voles through nine months on a three-acre area. The population was very low in August and September when only one vole was trapped. By November the population was rapidly increasing. Many juveniles were recorded, accounting for 29 of the 53 trapped voles. The population was not trapped from December through February; however, in March, trapping revealed that the population level was high and was breeding. The number of voles recorded in traps decreased steadily from April to the end of May when the study was terminated.

Significantly more females than males were recorded in this study. Krebs (1966) found that female M. californicus survival was higher than male survival during the breeding season, and that mortality was often sex selective, with male M. pennsylvanicus having highly variable survival rates (Krebs, Keller, and Tamarin, 1969). Van Vleck (1968) trapped more female meadow voles in Sherman live traps and equal numbers of both sexes in snap traps, and postulated a sex bias for live traps.

The sex ratio did not differ from 1:1 in live trapping studies of M. pennsylvanicus (Blair, 1940; Getz, 1960) and M. ochrogaster (Yang, Krebs, Keller, 1970).

In my study, females tended to be captured more times per animal than males, possibly indicating a live trap bias for females. I think an unequal survival of the sexes rather than a live trap bias might better explain the complete absence of males after May 25.

The cause of the population decline is unknown though many factors, alone or combined, could have contributed to the crash. An obvious cause would be the high trap mortality recorded in this study. Getz (1961a) recorded a trap mortality of 6.6% and Van Vleck (1968), using two-week periods of live trapping on a moving grid, a 10% mortality. Krebs, Keller, and Tamarin (1969) live trapped two days every other week with very few trap deaths. Of the voles I marked in the fall 58.5% died in traps, and 41.5% died in the spring, an unusually high mortality. Voles often died after many successive captures. The voles did not eat the bait, and frequently urinated on the cotton provided for warmth.

These other workers had interrupted trapping designs, whereas my design required continuous trapping over three months. However, the percentage of voles dying in traps was higher in the fall, and the population density continued to increase. Therefore, I conclude that the continuous trapping design may have increased mortality, but did not cause the spring population decline.

It is unlikely that emigration of voles caused the population decline. Natural boundaries of differing vegetation surrounded the field on three sides, with only 70 meters of the northern edge having no natural boundary. Movement through these boundaries, while not impossible, was probably reduced. Trapping outside the study area to the west yielded no *M. pennsylvanicus* in May. No voles made movements of longer than 40 meters, and more than half ranged no farther than 10 meters. I found that *M. pennsylvanicus* tended to stay in a small area, conclusions also reached by Getz (1961b) and Hamilton (1937). Getz (1960), Krebs (1966), and Krebs and Delong (1965), all working with *M. californicus*, believed that mortality and not emigration accounted for losses. Krebs, Keller, and Tamarin (1969) suggested that emigration is necessary to regulate vole populations and that dispersal is associated with periods of high loss. However, Getz (1961b) reported that most subadults stay in the nest area near their mother. Myers and Krebs (1971) found that a higher percentage of males than females dispersed, a possible explanation for lower male survival. However, this dispersal was associated with periods of population increase. Mortality, not dispersal, was the important factor during population declines. On the basis of data from these studies, I believe the population decline was the result of mortality and not emigration.

The number of voles killed by predators is an unknown and possibly important factor in the population decline. Removal of predators reduced the trap disturbance; however, another large animal usually moved into the vacated area. This sustained appearance of animals onto the study area indicated a high level of predators and predation pressure. Feral cats were observed hunting in the field and were very difficult to remove. No stomach analyses of the removed predators were done. Pearson (1971) measured predation pressure on M. californicus populations, and found pressure to be heaviest during the decline. A predator sustained itself on a less preferred prey species, and so maintained heavy pressure on the low vole population. He concluded that predators accentuate and possibly cause microtine cycles.

Shrew (Blarina brevecauda) predation on nestling M. pennsylvanicus may be important to the vole population (Barbehenn, 1958). Eadie (1952) found that M. pennsylvanicus failed to reach a high level for six years when the Blarina population remained high. This could explain the lack of juveniles in the declining spring population. However, 60 shrews were recorded in October and November when the population increased and many juveniles appeared. Only 16 shrews were recorded in the spring.

Predation pressure, in numbers removed and trap disturbance, was as high in the fall as in the spring. However, the fall population continued to grow and the spring population declined in density. Therefore, the effect of predators on the vole population remains unknown but possibly significant.

A decline to zero of the juvenile age group occurred in the spring (Figure 4). In November, while the population increased, juveniles averaged 49.0% of the known population. However, in the early spring only 14.7% of the vole population were juveniles, with the highest percentage of juveniles being only 21.3%. No juveniles were trapped from April 15 through the termination of trapping on May 26.

The cause of the juvenile class disappearance is unknown. A change in natality apparently did not cause the disappearance of juveniles as reproduction continued and remained at a constant rate during the spring. Emigration by the young also appeared unlikely. A heavy mortality of this class may best explain the observed decline of juveniles. This juvenile mortality may be a highly important factor in the decline of the entire vole population.

Addition of all trap deaths to all known living voles resulted in a straight line curve (Figure 6) or theoretically stable population. If new voles had replaced the dead voles, the curve would have continued upward. Reproduction should have supplied an overabundance of individuals to replace vacancies in the population. A lack of the surplus juveniles reduced recruitment into the population and possibly resulted in the population decline.

Reproduction and pregnancy rates were independent of density in studies by Krebs and Delong (1965) and Krebs (1966). Juvenile survival and recruitment, though highly variable (Krebs, 1966), were not low during population declines (Krebs and Delong, 1965; Krebs, Keller, and Tamarin, 1969). Blair (1940) calculated that a high mortality and not dispersal accounted for 65% of the young meadow voles never being seen. Getz (1960) assumed that 88% of the young he calculated had been born did not appear in traps and were dead. Golley (1961) reported that mortality was higher for the 11-20 gram weight class.

Keller and Krebs (1970) found no indication that pregnancy rates increased during population increases of _M. pennsylvanicus_, hence reproductive changes probably did not cause population fluctuations.

Hoffman (1958) found that natality changes did not account for population fluctuations of M. montanus. However, during peak density years, weanling and juvenile mortality was low, and at times of a population crash very few weanling and juvenile animals appeared. This lack of recruitment resulted in a later shortage of mature reproductive voles for juveniles did not fill the vacancies in the older classes. Hoffman postulated that high juvenile mortality, followed by lowered recruitment and breeding in the population, caused the population decline.

A statistically significant weight loss by individual male voles was found during the spring of the present study. Females also appeared to lose weight, and three of five juveniles lost or gained insignificant amounts. Lack (1954) proposed food shortage as a cause of Microtus declines, and suggested that his population may have been deprived of food as the field vegetation grew. By May of the present study, the green vegetation had grown off the ground, leaving dried brown stalks at ground level. However, fat reserves were found in the animals of this population, with a higher proportion of voles having heavy fat deposits after April 15 than before. Food was not apparently a limiting factor.

Barbehenn (1955) found that individual M. pennsylvanicus weights depended on time of weighing and length of confinement. One male lost 5.0 grams after 13 hours in a trap. Barbehenn believed a weight fluctuation of 10% to be insignificant unless the majority of the population reacted in the same manner.

Voles stopped growing at lower weights in declining populations (Krebs, Keller, and Tamarin, 1969). The large size voles occurred only in increasing and peak populations.

Batzli and Pitelka (1971) found that vole fat reserves declined during the breeding season. Voles ate grasses and leaves but switched to seeds after the grasses died. The authors postulated that this food switch may have caused nutritional deficiencies in the voles.

The weight losses before April 15 of the males and females and insignificant weight gains by juveniles in the present study appear real and not an artifact of the study as suggested by Barbehenn (1955). The average weight loss by males was 18.9% of the average body weight of 43.5 grams. However, the apparent weight gains and increase in fat deposits after April 15 indicated food was not limiting. This weight loss by individual voles may be important in the population decline.

The spring decline of the M. pennsylvanicus population occurred along with a high trap mortality, apparent high predation pressure, low juvenile survival and recruitment, and weight loss by individual voles. Chitty (1960) hypothesized that indefinite increase in population size is prevented by a deterioration in quality of the population. As quality and viability of a population change, the susceptibility of individuals to the usual mortality factors increases. The high trap mortality, absence of juveniles, and individual weight losses may indicate a decreased viability of the voles. Decreased viability of the population and predation possibly contributed to the population decline.

Spatial Results

Females tended to stay in the same area and travel over less area than males though these tendencies were slight and insignificant. Females averaged more captures per animal than males, but entered fewer different traps than males. The localization test revealed that females tended to enter the same trap on successive captures more frequently than males.

More females than males had home ranges of 100 square meters or less and a higher percentage of females than males ranged no farther than one trap interval. Though all statistically insignificant, these comparisons suggest that the female *M. pennsylvanicus* is more sedentary than the male. The male shifted more often, wandered farther, entered more different traps, and was caught less frequently.

The data also revealed that *M. pennsylvanicus* had very restricted home ranges. A large percentage of males (83%) and females (90%) had home ranges of one square trap interval, 100 square meters, or less. More than half of all voles moved no farther than one neighboring trap. Apparently, *M. pennsylvanicus* has a small home area and remains on this area over a long time. The vole appears to make few if any movements outside this area.

Female voles also appeared to have larger range lengths at a low population density.

That male *M. pennsylvanicus* had larger home ranges than females was found by Getz (1961b), Hamilton (1937), and Hayne

(1950). Golley (1961) found that males moved more than females during the breeding season but females more than males in the winter. Krebs (1966) with *M. californicus* found males moving longer distances than females during the breeding season with no difference in other seasons.

The home range of *M. pennsylvanicus* was reported by Hamilton (1937) seldom to exceed one fifteenth of an acre. Getz (1961b) and Van Vleck (1968) found that the vole remained in the same home range over a long time. *M. californicus* remained on a very restricted area, often for a lifetime according to Fisler (1962), Krebs (1966), and Pearson (1960). *M. californicus* primarily stayed within a five-foot radius of its home (Pearson, 1971).

Others have found that density affected spatial characteristics of a population. Working with *M. pennsylvanicus* in a marsh, Getz (1961b) found home range size decreasing as density increased. However, temperature had a greater affect than density on home range size. As density decreased, Krebs (1966) reported that male *M. californicus* moved more frequently but that females moved greater distances.

Trap Response

The *M. pennsylvanicus* occurred in a few highly active areas of my study site. For females, 16.5% of the traps recorded 72.7% of the females and 72.1% of all female captures. Four and one-half percent of the traps caught 52.6% of the males and 54.9% of all male captures. This suggests that voles congregated in favorable areas and did not space themselves evenly over the area. Getz (1961b) also found clumped centers of activity of M. pennsylvanicus, with vacant areas in between. Blair (1940) and Getz (1961b) each reported that home ranges of male voles broadly overlapped, with female areas overlapping less. Pearson (1960) recorded nine M. californicus individuals using the same runway. Getz (1961a) believed the local distribution of voles was determined primarily by the type of vegetation and food. Therefore, interaction with neighbors may be a less important factor in the spatial dynamics of voles.

Experimental Manipulation

This experiment attempted to test whether presence and awareness of neighbors in a Microtus pennsylvanicus population influenced spatial dynamics of the population. I removed resident voles from the area, to determine if their absence increased immigration and longer and more frequent movements of the remaining voles.

Results showed no significant difference in invasion or movement when residents were absent or present. However, mean changes in centers of activity (Table 6) do indicate a tendency for shifting to occur in response to removal. Residents left on the field shifted centers of activity 7.37 meters, and residents removed and returned to the area shifted 8.55 meters. Controls shifted 5.93 meters. During the removal period of days 6-10, voles were captured an average of 7.04 meters from the previous center of activity in days 1-5. However, controls were found in days 6-10 an average of only 3.56 meters from the center of activity in days 1-5 (Table 7). The number of new animals captured during the removal period was no different from the number appearing when residents were present.

Other workers have found a response to removal of animals. In a trapping experiment with *M. pennsylvanicus*, Blair (1940) noticed that other voles took the places of missing residents. Krebs (1966) also recorded a heavy immigration of *M. californicus* into a depleted vole population. Calhoun and Webb (1953) were unable to decimate a community of *Peromyscus*, *Cleithrionomys*, *Blarina*, and *Sorex* by snap-trapping. The number of animals removed each day remained constant indicating a steady invasion of neighboring animals into the vacated areas. They theorized that an animal moves away from neighbors into areas of least density, where avoidance stimuli are lowest. Also, an animal may be conditioned to a pattern of perception of neighbors, and then shift its home range to restore an altered pattern. By removing adult male *Cleithrionomys gapperi*, Watts (1970) captured juveniles at earlier ages than in control areas with adults present. He suggested that the resident males restricted activity of the juveniles. Stickle (1946) recorded home ranges of *Peromyscus leucopus* and then for 35 days snap-trapped a central acre of the 17-acre area. Invasion into the vacated area occurred from all directions, with animals closest to the snapped area moving in first. Removal of residents in the central area appeared the stimulus for invasion by others, as no inward movement occurred before the snap-trapping. Van Vleck (1968) removed *M. pennsylvanicus* in a study patterned after that of Stickle (1946). More voles moved into the vacated center from high density areas, so that movement appeared density dependent. Therefore, the presence of established adults appeared to most workers to discourage invasion by wandering adults and juveniles and to discourage movement by neighboring established adults.

Metzgar (1971) found that *Peromyscus leucopus* established home ranges exclusive of those of the same sex. At high densities, the ranges remained constant in size and occupied the entire study plot. No female immigrants settled on the plot once this saturation density was reached. Therefore, Metzgar postulated that female *Peromyscus leucopus* populations are regulated by social and spatial behaviors, an intolerance toward others of the same sex, and maintenance of a constant home range size.

Robinson and Falls (1965) found that *M. pennsylvanicus* returned home when displaced, and postulated that a social intolerance toward the displaced animal stimulated its return. In another homing experiment, displaced *M. californicus* sometimes established home ranges at unoccupied release sites but always moved away from previously occupied sites (Fisler, 1962). Fisler postulated that intraspecific competition in unknown territory stimulated the animals' return. Finding a suitable living area, not necessarily a familiar area, was the stronger motivation.

These investigators believed that social stimuli determined the spatial patterns in a population. However, removing neighbors, and supposedly removing the social stimuli of these neighbors, did not significantly alter the spatial characteristics of *M. pennsylvanicus* in my study. Van Vleck (1968) suggested that below a density of 14-20 voles per acre voles do not respond to their neighbors' proximity. In Metzgar's study (1971) immigrant woodmice settled successfully at all densities below saturation density. Possibly the M. pennsylvanicus population was two sparse for animals to detect presence or absence of neighbors, or the population never reached the saturation density at which space was limiting.

The meadow voles occurred at high activity sites with unoccupied areas between. The removal possibly did not sufficiently alter the social patterns because of this non-uniform distribution of animals.

An animal may contact its neighbor directly or by its signs; urination sites, defecation sites, food, nest, vocalization (Calhoun, 1963). Though Calhoun believed the signal was vocal, the eyes and ears of M. pennsylvanicus are very reduced in size. If the spacing of the meadow vole relies instead on chemical signals then the sign would persist longer. Possibly the five-day removal period was too short to allow perception of the vacancies. The slightly longer average shifts found during the removal period may represent the beginnings of movement into vacated areas.

The home range may represent more than an area of minimum social contact to the vole. Microtus spp. sometimes remain on a small home range for a lifetime. M. californicus remained on its home range even during high winds, rain, and high tides (Fisler, 1961). A homing study by Griffo (1961) revealed the strong attachment of Peromyscus gossypinus to its home area. Mice released outside the home area, after being confined in the laboratory for 32 to 87 days, returned to the home area and remained. Those homing avoided traps outside the home area, and so responded differently to objects within and out of the home range. The home range appeared to satisfy physical needs such as food, nest, mate, and cover; and also psychological needs. The home range was an area of familiarity and displacement of the animal appeared to stimulate its return. Even after a long absence, the ability to return to the home range remained strong.

Possibly in the present study, an attachment to the familiar area rather than a repulsion from neighbors reduced wandering in the *M. pennsylvanicus* population.

TABLES AND FIGURES

TABLE I

SPECIES TRAPPED ON THE STUDY AREA

Species	Aug. I2 - Sept. I3 24 nights	Oct. 4 - Nov. 26 47 nights	Mar. I2 - May 26 76 nights	Totals
Blarina brevicauda	68	60	I6	I44
Microtus pennsylvanicus	I	52	I06	I59
Microtus pinetorum	4	42	3I	77
Mus musculus	59	I36	I0	205
Peromyscus leucopus	20	26	44	90

TABLE 2

WEIGHT LOSSES BY INDIVIDUAL VOLES

	First Weight	Second Weight	Weight Change	Days Between Weighings	Dates
Males					
	27.3	22.8	-4.5	59	3/12-5/10
	68.5	35.1	-33.4	9	3/12-3/21
	45.0	42.7	-2.3	17	3/13-3/20
	33.8	30.0	-3.7	13	3/14-3/27
	62.7	50.3	-12.4	10	3/17-3/31
	45.1	45.3	0.2	7	3/21-3/28
	46.9	36.1	-10.8	13	3/24-4/6
	44.4	38.4	-6.0	2	3/24-3/26
	38.9	32.6	-6.3	9	3/28-4/6
	22.8	19.8	-3.0	13	3/14-3/27
$\bar{X}$ =	43.54	35.2	-8.22		$P<0.05$
Females, not pregnant at either weighing					
	40.8	39.2	-1.5	5	3/12-3/17
	45.1	40.8	-4.3	16	3/12-3/28
	38.6	34.4	-4.2	17	3/13-3/30
	35.1	33.8	-1.3	14	3/13-3/27
	32.0	25.6	-6.4	32	3/13-4/12
	27.3	30.0	2.7	14	3/14-3/28
	33.5	26.5	-7.0	21	3/20-4/10
	48.3	31.4	-16.9	19	3/22-4/10
	27.8	21.4	-6.4	13	3/29-4/11
			$\bar{X}$ = -5.03		$P<0.02$
	35.2	34.3	-0.9	28	4/15-5/13
	26.3	39.0	12.7	18	4/25-5/13
	37.6	42.5	4.9	4	4/28-5/2
$\bar{X}$ =	35.63	33.24	-2.38		$0.1<P<0.2$

	First Weight	Second Weight	Weight Change	Days Between Weighings	Dates
Females, pregnant at second weighing					
	31.1	24.3	-6.8	12	3/12-3/24
	43.0	30.1	-12.9	8	3/12-3/20
	40.8	30.2	-10.6	12	3/12-3/24
	42.8	40.5	-2.3	13	3/13-3/26
	41.0	45.5	4.5	22	3/19-4/10
	44.5	45.7	1.2	6	3/22-3/28
	47.2	60.8	13.6	32	3/22-4/23
	33.3	34.5	1.2	2	3/24-3/26
	39.1	32.7	-6.4	7	3/24-3/31
	35.7	46.5	10.8	15	3/27-4/11
	38.6	45.4	6.8	33	4/7-5/10
	23.3	41.1	17.8	40	4/16-5/26
	68.4	75.9	7.5	5	4/26-5/1
	$\overline{X}$ = 40.68	42.55	1.88		P = NS
Juveniles, less than 22 grams at first weighing					
	12.4	20.1	7.7	17	3/20-4/6
	19.7	14.3	-5.4	6	3/29-4/4
	16.8	18.4	1.6	13	3/26-4/8
	19.2	31.8	12.6	14	3/31-4/14
	18.0	17.1	-0.9	9	4/2-4/11
	$\overline{X}$ = 17.22	20.34	3.12		P = NS

TABLE 3

RECAPTURE FREQUENCY OF MALES AND FEMALES

Number of Captures	1	2	3	4	5	6	7	8	9	10	11	12	18	19	31	$\bar{X}$
Males	18	8	1	1	5	3			2						1	3.385
Females	16	15	7	6	6	2	1	1	5	1	2	2	1	1		4.333

TABLE 4

NUMBERS OF DIFFERENT TRAPS USED BY ANIMALS CAUGHT MORE THAN ONCE

Number of traps	1	2	3	4	5	6	$\overline{X}$
Males	4	10	4	2	1		2.40
Females	12	21	11	5		1	2.26

TABLE 5

APPEARANCE OF UNMARKED VOLES

	Trap Nights 1-5	Trap Nights 11-15	Trap Nights 6-10
Resident Voles	Present	Present	Absent
Experiment 1	20	6	13
Experiment 2	1	2	3
Experiment 3	1	1	0
Totals	22	9	16

TABLE 6

DISTANCE BETWEEN CENTER OF ACTIVITY IN TRAP NIGHTS 1-5 AND TRAP NIGHTS 11-15

	Controls	Removed Residents	Unremoved Residents
Removal #1	4.713	2.5	10.0
	14.142	5.0	18.027
	20.0	0.0	20.0
	7.071	0.0	0.0
	0.0	8.944	0.0
	0.0	20.0	
	14.906	5.0	
	0.0	22.36	
	0.0	0.0	
	10.0	25.0	
	0.0	14.142	
	0.0	22.36	
	0.0	7.452	
		14.142	
		14.142	
		7.071	
		10.0	
		0.0	
		22.36	
Removal #2	2.0	7.5	0.0
	6.008	20.0	0.0
	7.071	7.071	14.142
	6.667	0.0	4.711
	0.0	0.0	0.0
	20.0	10.0	
		22.36	
		0.0	
		14.142	
		0.0	
		0.0	

	Controls	Removed Residents	Unremoved Residents
Removal #3		0.0 0.0 0.0	14.142
N	13	33	11
$\overline{X}$	6.958	8.548	7.366
S^2	48.818	74.147	65.038

TABLE 7

DISTANCE BETWEEN CENTER OF ACTIVITY DAYS 1-5 AND REMOVAL SITE DAYS 6-10 AFTER REMOVAL BEGUN

	Controls	Residents Removed	
Removal #1	9.427	0.0	0.0
	5.0	0.0	22.360
	7.071	10.0	0.0
	10.0	0.0	0.0
	0.0	0.0	25.0
	17.950	0.0	22.360
	0.0	0.0	31.622
	0.0	5.0	0.0
	7.452	0.0	0.0
	0.0	10.0	14.142
	0.0	0.0	14.142
Removal #2	0.0	0.0	20.0
	0.0	0.0	14.142
	0.0	14.142	0.0
	0.0	0.0	0.0
	0.0	28.284	0.0
		22.360	
Removal #3		7.071	0.0
		0.0	0.0
N	16	37	
$\overline{X}$	3.566	7.044	

FIGURE I

STUDY AREA AND TRAPPING GRID. EACH TRAPPING STATION SPACED TEN METERS APART

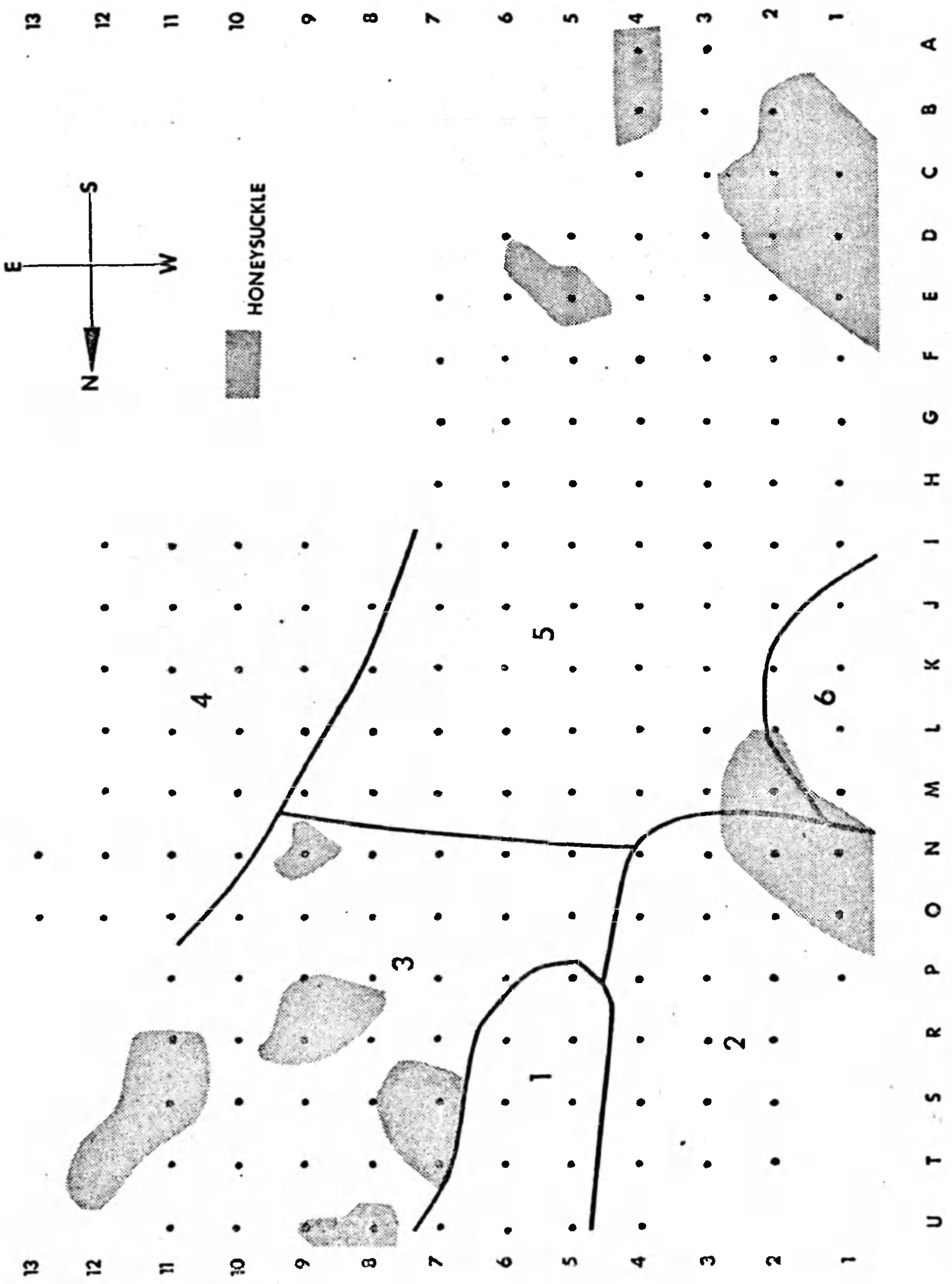


FIGURE 2

EXPERIMENTAL MANIPULATION. AN AFTERNOON, NIGHT, AND THE FOLLOWING MORNING CAPTURES CORRESPONDED TO ONE TRAP NIGHT

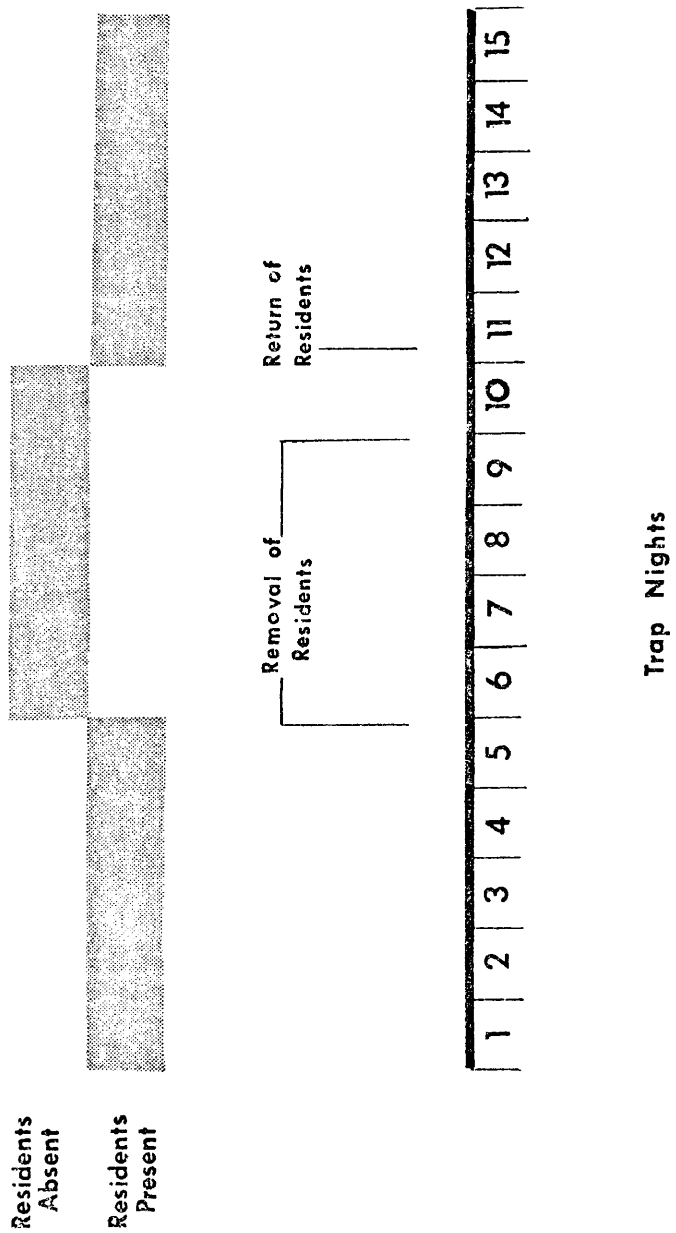


FIGURE 3

NUMBERS OF INDIVIDUAL MALE AND FEMALE *M. PENNSYLVANICUS* KNOWN TO HAVE BEEN ALIVE ON THE STUDY AREA, SPRING, 1970

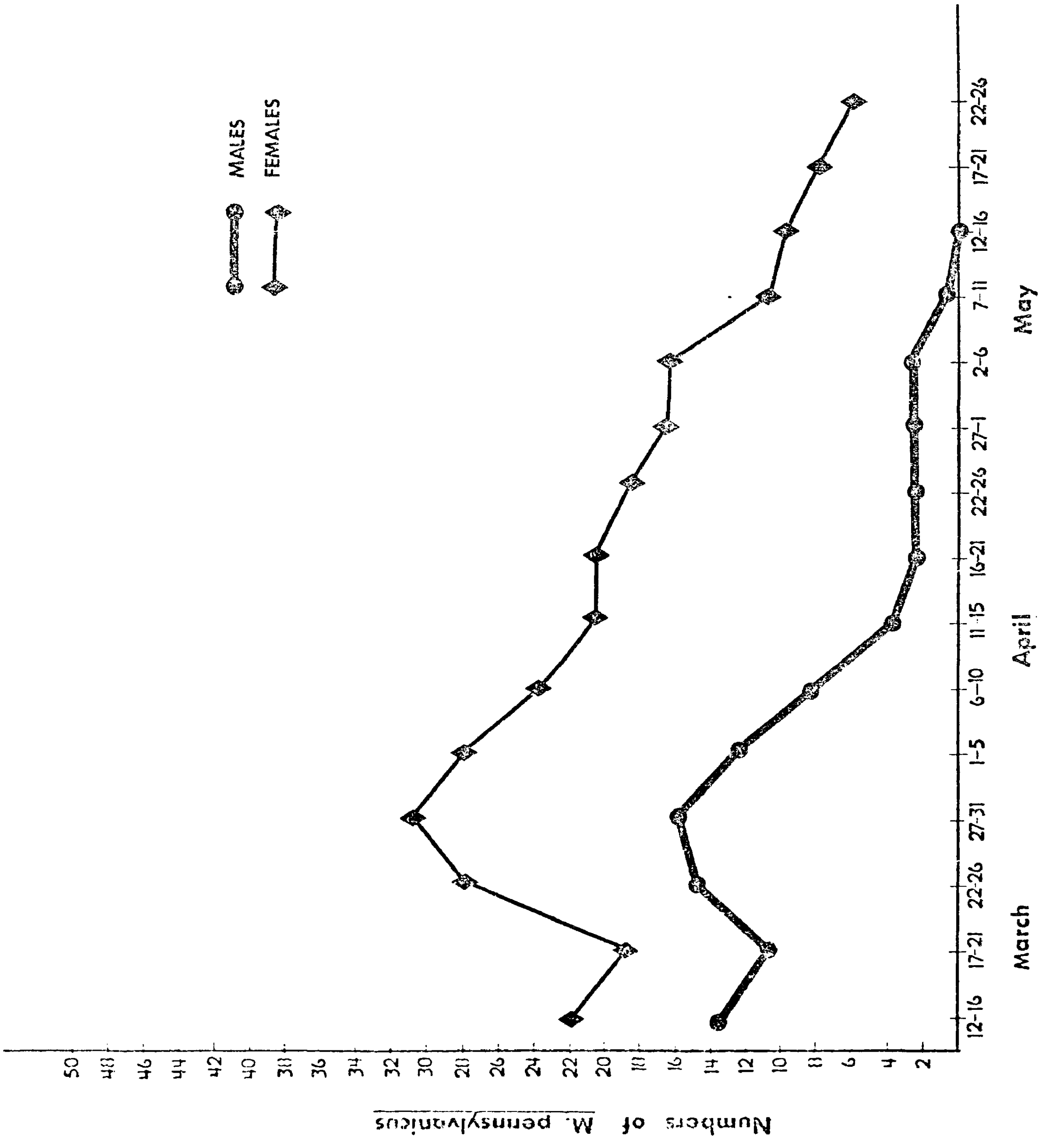


FIGURE 4

TOTAL NUMBERS OF M. PENNSYLVANICUS KNOWN TO HAVE BEEN ALIVE ON THE STUDY AREA, FALL, 1969 AND SPRING, 1970

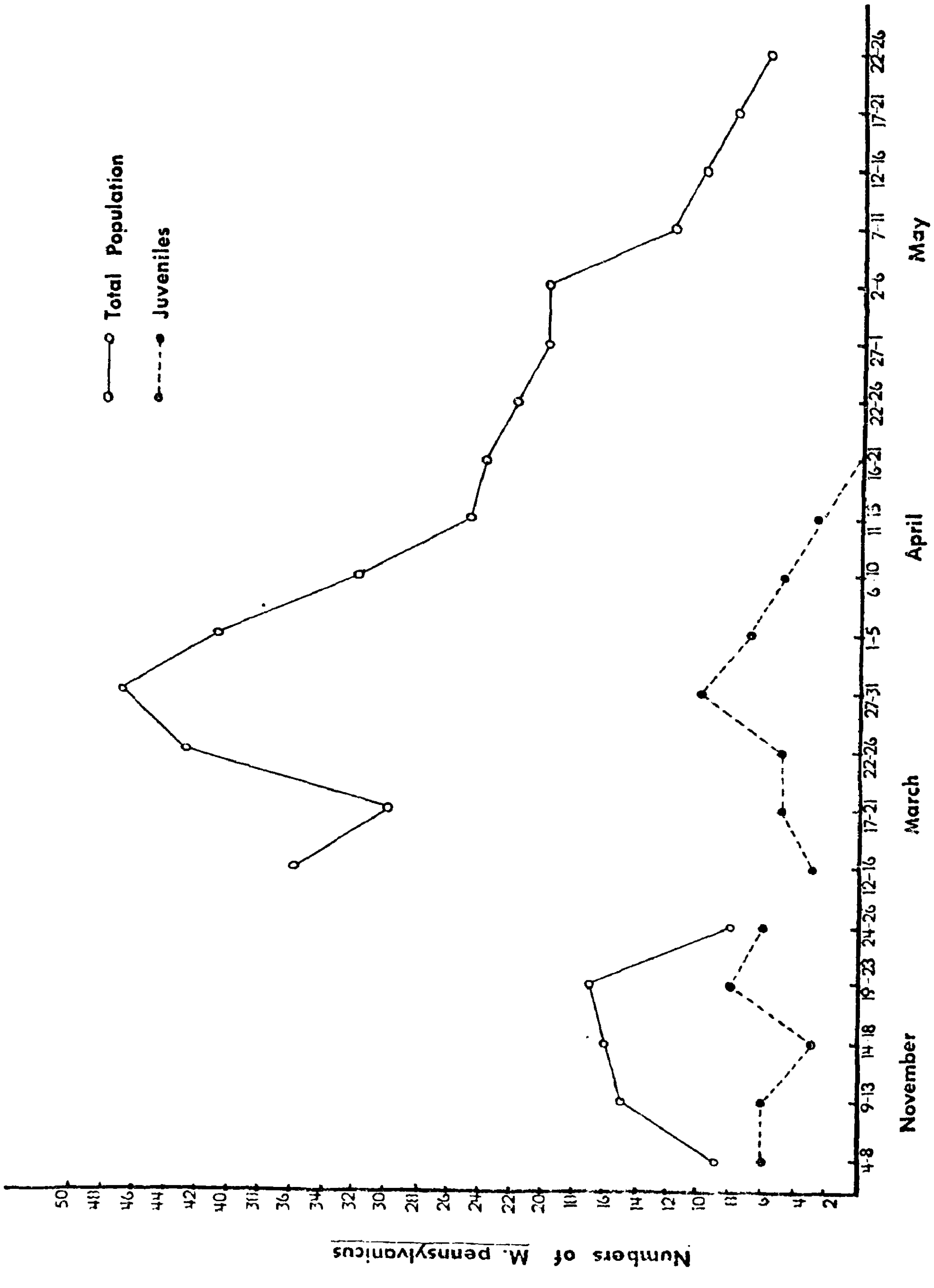


FIGURE 5

PERCENTAGES OF FEMALES, IN THREE 25 DAY INTERVALS, WITH SIGNS OF BEING REPRODUCTIVE

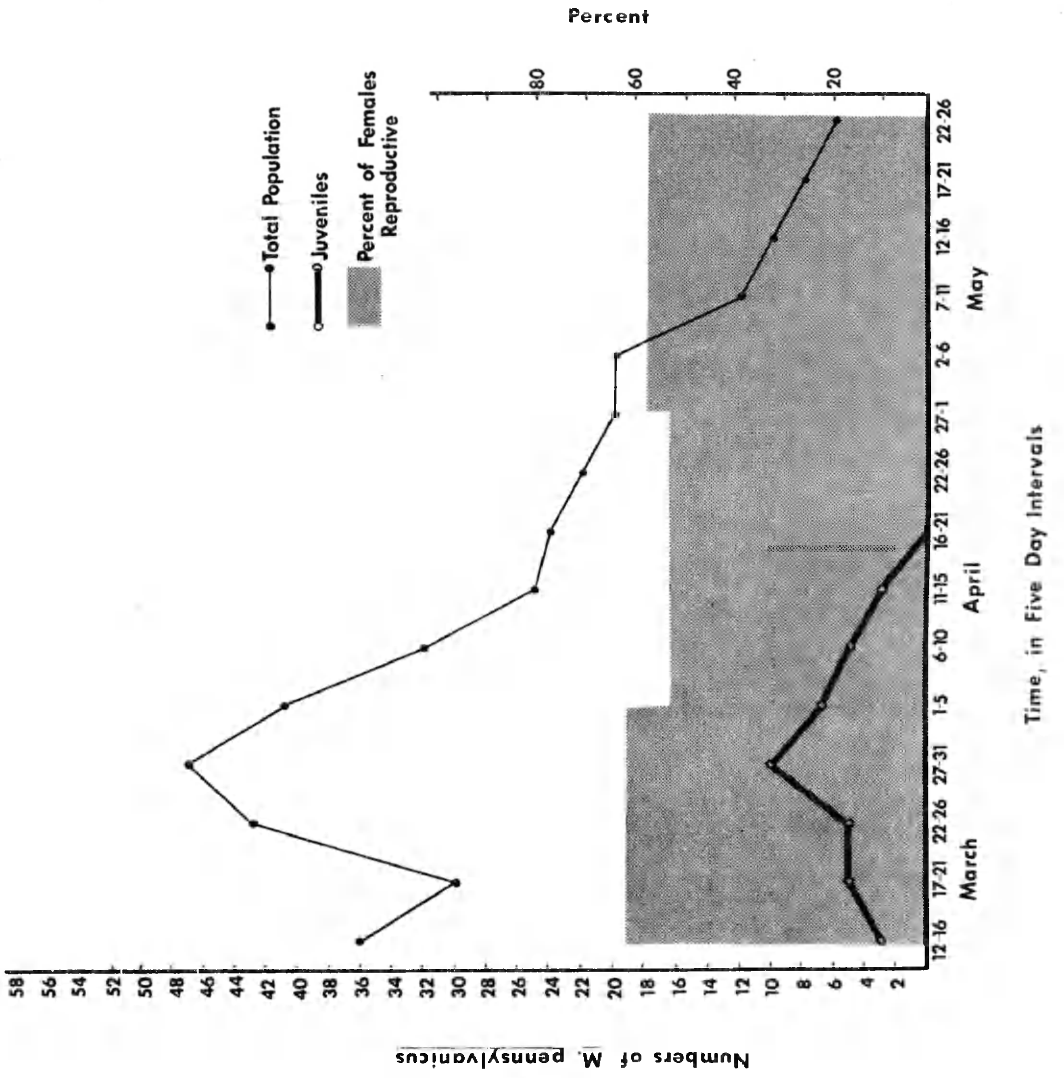


FIGURE 6

TRAP MORTALITY AND POPULATION DECLINE OF M. PENNSYLVANICUS

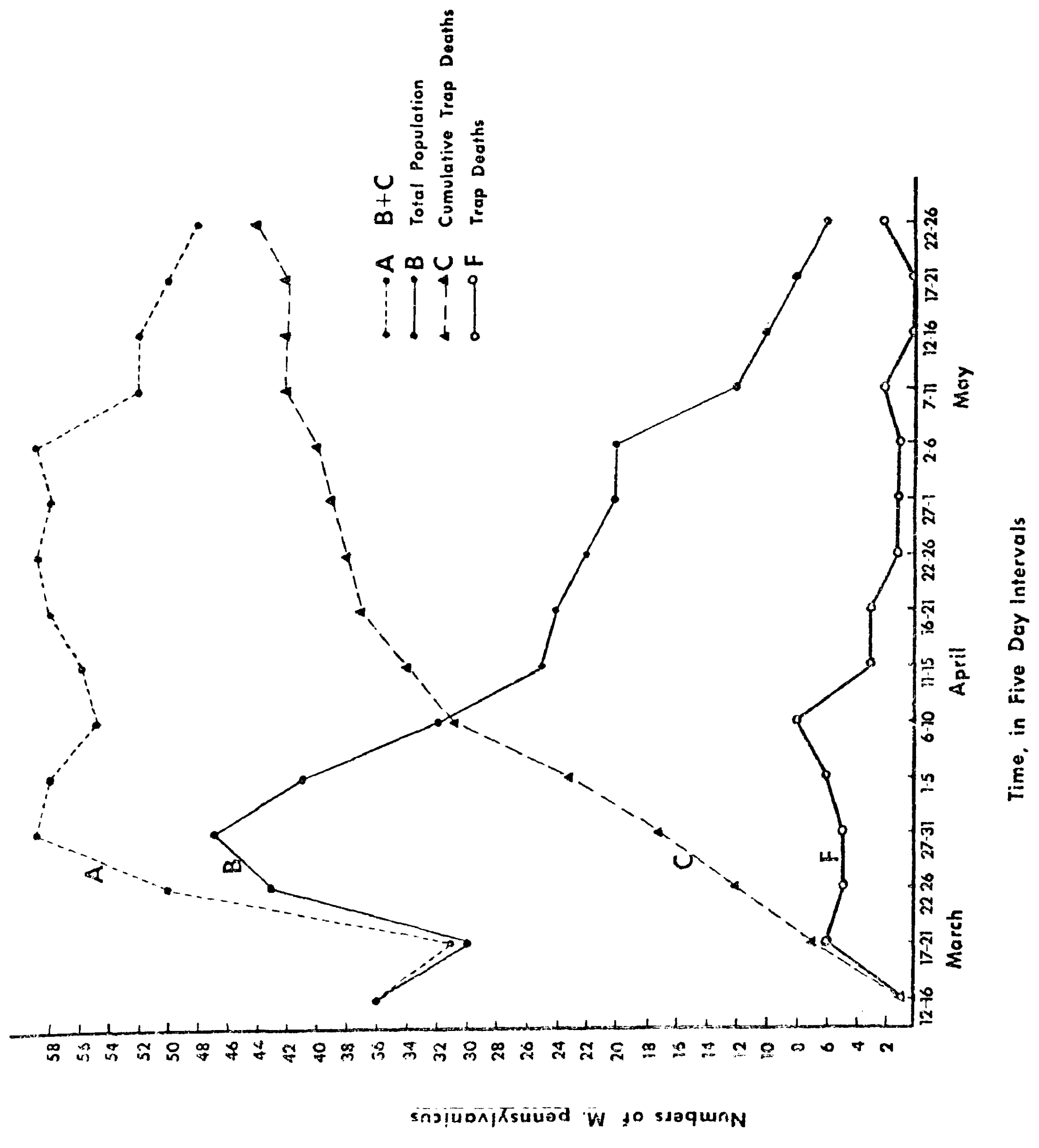


FIGURE 7

HOME RANGE SIZE OF ALL VOLES CAPTURED THREE OR MORE TIMES

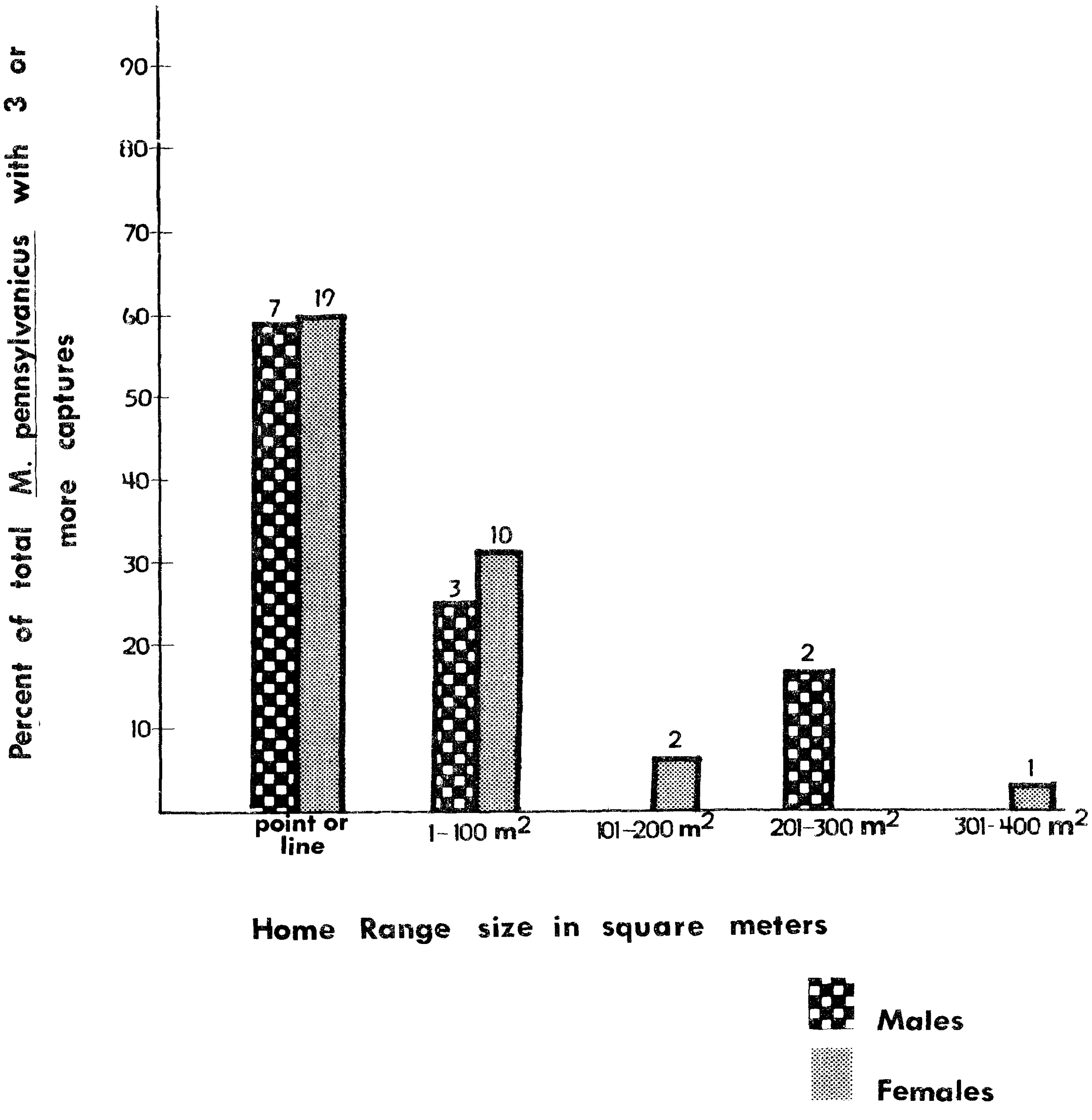


FIGURE 8

RANGE LENGTH OF ALL VOLES CAPTURED TWO OR MORE TIMES

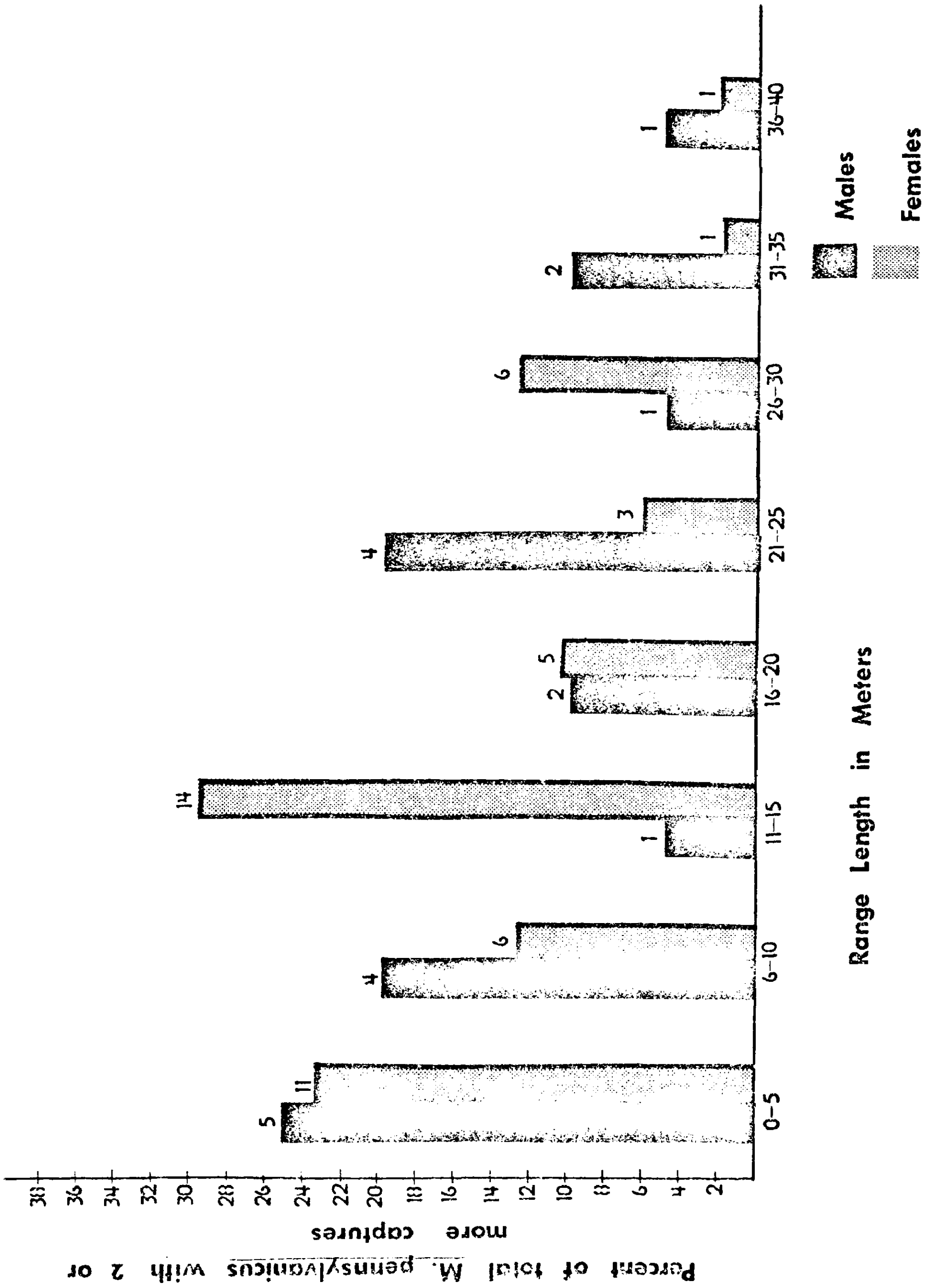


FIGURE 9

COMPARAISON OF RANGE LENGTHS OF FEMALES AT HIGH AND LOW POPULATION DENSITIES

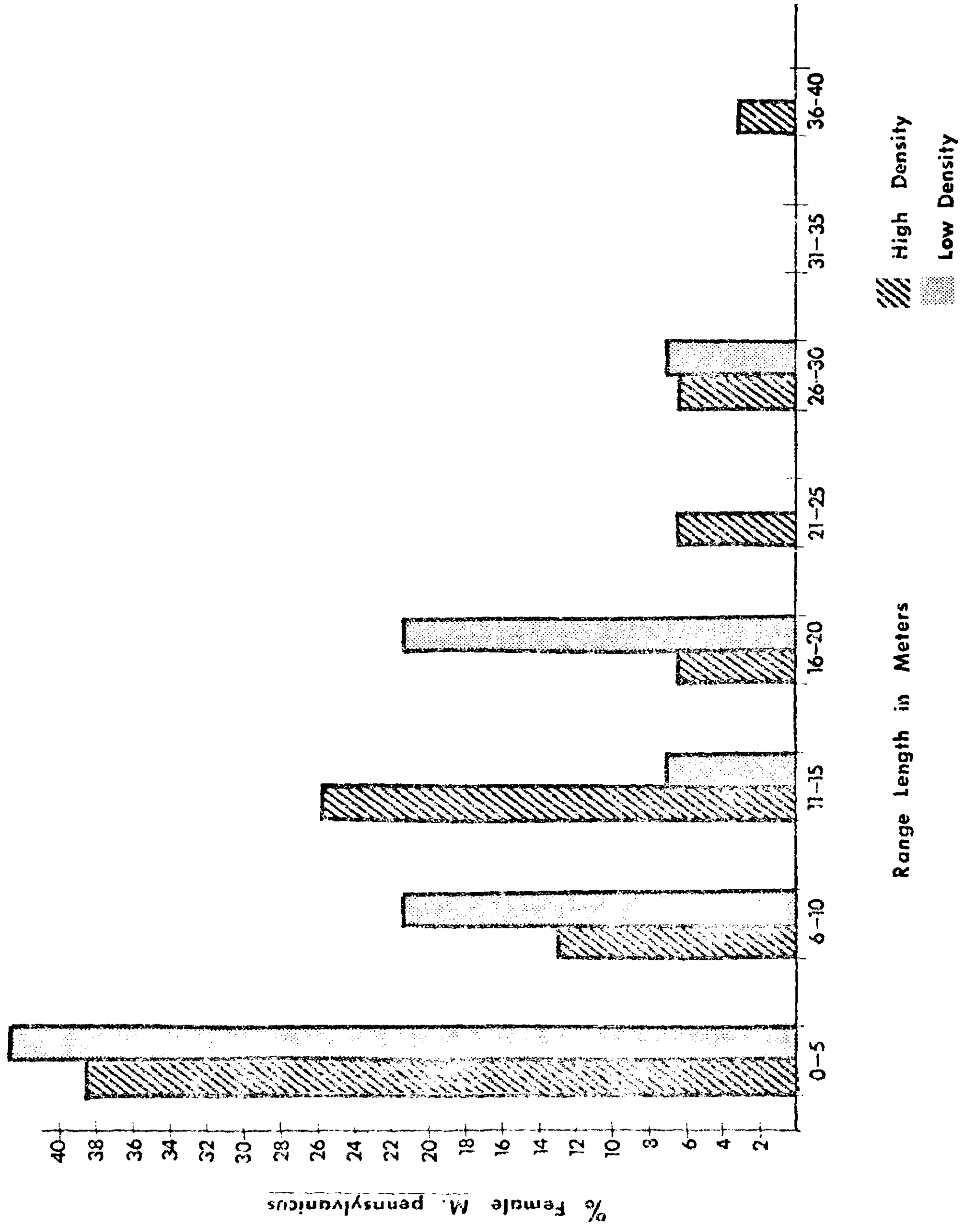


FIGURE IO

STUDY AREA, FALL, I969

FIGURE II

STUDY AREA, SPRING, 1970

FIGURE I2

A TRAPPING STATION IN A RUNWAY UNDER THE VEGETATION

FIGURE I3

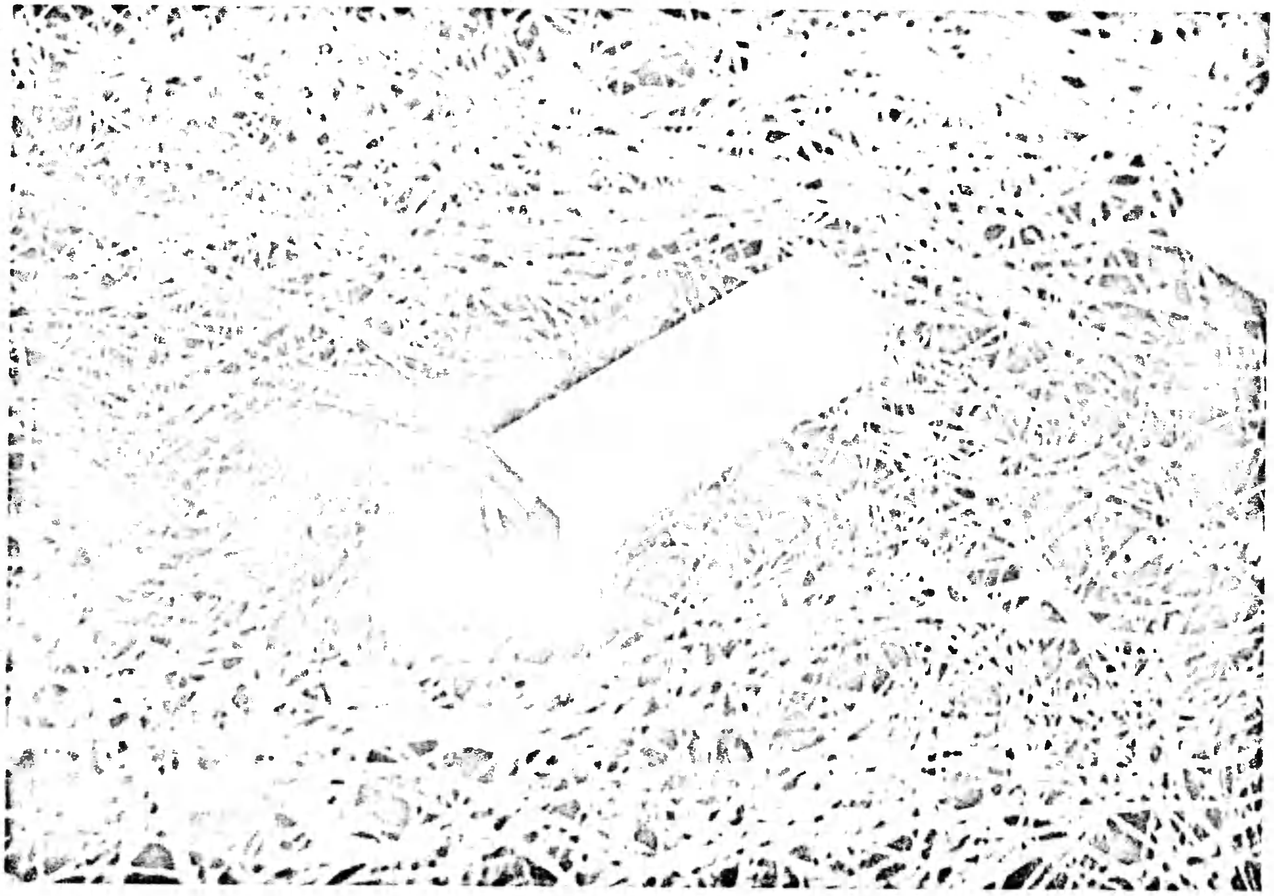
WEIGHING TECHNIQUE FOR ALL NEW, REMOVED, AND DEAD VOLES

FIGURE I4

MAINTENANCE OF VOLES IN THE LABORATORY DURING REMOVAL

FIGURE I5

RELEASE OF VOLES ON TRAP NIGHT ELEVEN AT THE PREVIOUS SITE OF CAPTURE



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