AN INVESTIGATION OF AN ANNUAL CYCLE OF A POPULATION OF WHITE-FOOTED MICE (PEROMYSCUS LEUCOPUS) IN MONTGOMERY COUNTY, TENNESSEE

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AN INVESTIGATION OF AN ANNUAL CYCLE OF A POPULATION OF WHITE-FOOTED MICE (*PEROMYSCUS LEUCOPUS*) IN MONTGOMERY COUNTY, TENNESSEE

An Abstract

Presented to

the Graduate Council of

Austin Peay State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

James Moroni

May 1971

ABSTRACT

A study of the annual cycle and various factors involved in the regulation of a white-footed mouse population was conducted on the Austin Peay State University farm.

The population was found to be a high but apparently stable condition during the spring and early summer months of the study. Population pressures at this time forced a reduction in home range size and caused some members to inhabit marginal habitats.

Habitat selection seemed to be correlated with protective cover as movement of the population followed foliation in the spring and defoliation in the fall.

A severe population decline, beginning in July and ending in September, was apparently the result of high ecological density and decreasing environmental favorability.

Following the decline, population parameters indicated that much of the stress situations had been relieved and the population was again approaching stability.

AN INVESTIGATION OF AN ANNUAL CYCLE OF A POPULATION OF WHITE-FOOTED MICE (*PEROMYSCUS LEUCOPUS*) IN MONTGOMERY COUNTY, TENNESSEE

A Thesis

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May 1971

To the Graduate Council:

I am submitting herewith a Thesis written by James Moroni entitled "An Investigation of an Annual Cycle of a Population of White-Footed Mice (Peromyscus leucopus) in Montgomery County, Tennessee." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Biology.

Marvin M. Provo
Major Professor

We have read this thesis and recommend its acceptance:

Floyd M. Ford
Second Committee Member

E. W. Chester
Third Committee Member

Accepted for the Council:

Wayne E. Stamper
Dean of the Graduate School

LIST OF FIGURES

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TABLE OF CONTENTS

LIST OF TABLES

INTRODUCTION

Various regulating factors apply to all mammals occurring in natural situations. To gain a fuller understanding of the importance and operation of these influences a detailed study of a wild population over an extended period of time is desirable.

The white-footed mouse (*Peromyscus leucopus*) lends itself extremely well to this type of investigation. These mice are readily captured, withstand handling and trap confinement well, and are usually numerous enough so that data from several animals may be obtained during the same season or trapping interval. They also range relatively short distances and are fairly well limited to distinct habitat types.

Several other species of small mammals such as the prairie vole (*Microtus ochrogaster*) are also found in similar and adjoining habitats with the white-footed mouse and offer the advantage of making observations concerning sympatric species.

The objective of this extended study of these animals was the measurement of various population parameters as well as the evaluation of the roles of factors such as intraspecific competition, interspecific competition, habitat selection and use of various cover types, and patterns of aggregation in the regulation of this small rodent population. The intraspecific and interspecific competition lent itself well to investigation in a laboratory situation, while the remainder of the study was conducted in a field situation. The knowledge gained about the functioning of various regulating factors affecting these small mammal populations might well be applied, within limits, to other mammalian populations with similar ecological requirements.

LITERATURE REVIEW

The life history and ecology of the white-footed mouse has been studied extensively by many investigators. Burt (1940) has reported extensively on the life cycle of this mouse as well as discussing the importance of such concepts as home range (1943) and territoriality (1949). Social habits, as well as those aspects of the life history that are related to this, have been investigated by Nicholson (1941), while Snyder (1956) has reported survival rates, longevity, and population fluctuation. Stickel (1960, 1954, and 1946) has reported extensively on home range size, live trapping, and their evaluation. The more recent literature seems to have become more specific in nature. The ecology of the mouse has been investigated by Brown (1964) and Klein (1960). Gentry and Odum (1957) and Howard (1951) have discussed the influence of weather and low temperature on the activities of small rodents while Pruitt (1959) investigated microclimate relations. Habitat relationships and orientation and distribution have been reported on by various authors (Hirth, 1959; Turner and Stains, 1967; Whitaker, 1967; Wirtz and Pearson, 1960; and Verts, 1957). Intraspecific and interspecific studies have been made by Bradshaw (1965), Getz (1969), and King (1957). Predation has been discussed by Pearson (1964) and Metzgar (1967). Effects of live trapping and responses to traps have been studied by Fitch (1954), Sealander, Griffin, DeCosta and Jester (1958), and Sheppe (1967).

DESCRIPTION OF THE STUDY AREA

The study area was located on the Austin Peay State University farm approximately three miles east of Clarksville, Montgomery County, Tennessee. This region is located on the western section of the Highland Rim and is characterized by rolling hills within the Western Mesophytic Forest area (Braun, 1950).

The study area itself was located on the top and south facing slope of a small hill. Bounding the area on the north was a grove of cultivated white pines (*Pinus strobus*); on the east was a pasture which continued around the southern edge of the study area; the southwest and the west were bordered by an oak (*Quercus*)-hickory (*Carya*) woodland. A fence row demarcated the line between study field and pasture on the east and south. All habitats adjacent to the study area were considered unsuitable except for the extreme southwest and west. These habitats were woodland but they contained a scarcity of undergrowth and debris (such as logs, stumps, and fallen limbs) from which the mice might derive protection and nesting sites (Burt, 1940). Therefore, for all practical purposes, the study area was isolated by surrounding areas of unsuitable habitats for the white-footed mouse (Brown, 1964; Burt, 1940; and Klein, 1960).

The area (Figure 1) enclosed by the surrounding habitats contained approximately 2.25 acres and was 510 feet long at its greatest length and 255 feet wide at its greatest width. The northern and eastern borders were in a straight line. About 150 feet from the eastern border, the southern border began an inward curve to a point about 90 feet from the pines on the north border; much of the western border was delimited by this rounded curve. The geometric arrangement of the study area outline gave the impression of a lopsided right triangle.

There was a 6-12 percent slope from north to south on the study area and 50-75 percent of the topsoil had eroded in the past. The soil of the area was Baxter soil which is deep, reddish clay subsoil and contains a large amount of chert.

The area was in pasture for many years prior to 1954 when corn was planted. After only one year of cropping the area was returned to pasture until 1963 when it was fenced off and cultivated shrubs were planted. Since that time the area has been used as a nursery for the University's landscaping program. Since the planting of the shrubs no mowing has been done on the area and the only disruption has been periodic transplanting of the shrubs.

Table I lists the cultivated plants that are located on the study area.

Three general regions of vegetation are contained within the study area (Figure 1). Rimming the southern and

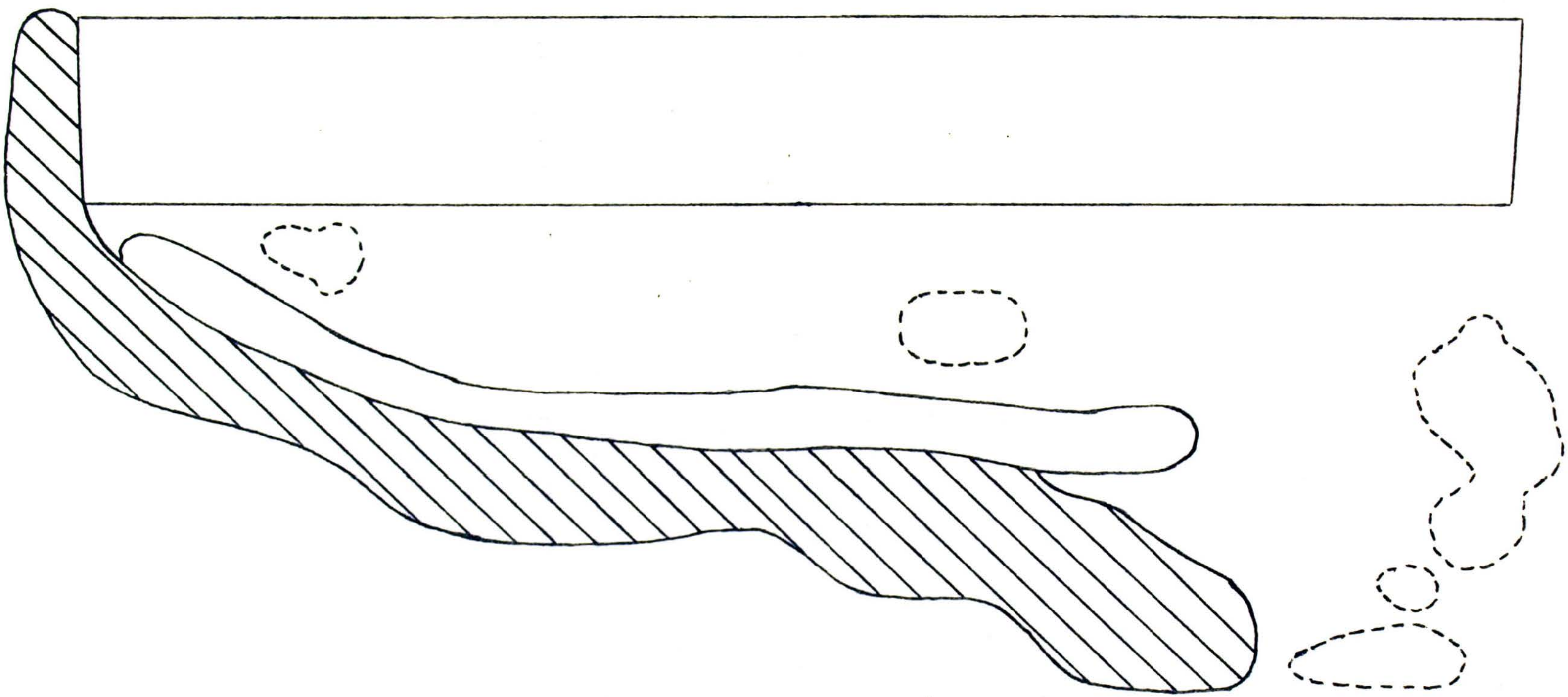

FIGURE 1. Map of the Study Area.

Diagonal lines indicate Honeysuckle and Briars.
Broken lines indicate areas of encroaching briars.
Solid lines enclose Cultivated Shrubs.
Open area in the middle is grass region.

TABLE I. Cultivated Plants on the Study Area

Common Name	Scientific Name
Thunberg Spirea	*Spiraea thunberg*
Van Houetti Spirea	*Spiraea vanhouetti*
Glossy Abelia	*Abelia grandiflora*
Red Leaf Barberry	*Berberis zhunbergii atropurperus*
Sweet Shrub	*Calycanthus floridus*
P. G. Hydrangea	*Hydrangea paniculata grandiflora*
Forsythia	*Forsythia intermedia*
Red Weigela	*Weigela florida*
Flowering Quince	*Chaenomeles lagengria*
Snowball	*Viburnum macrocephalum sterile*
Deutzia	*Deutzia scabra*
Mock Orange	*Philadelphus coronarius*
Flowering Crab	*Malus* sp.
Silver Maple	*Acer saccharinium*
Sugar Maple	*Acer saccharum*
White Birch	*Betula papyrifera*

western boundary was a region of very dense honeysuckle (Lonicera japonica) and briars (Rubus spp.). This region was about 530 feet long and averaged 45 feet in width. There were 18,000 square feet contained within this type habitat. Due to the great amount of overhead and side protective cover afforded in this habitat, it was deemed suitable for mouse occupancy throughout the year.

Alongside the honeysuckle and briars and bordering the north boundary (separated from the pines by only 10 feet in some instances) were two areas containing the cultivated shrubs. The northern area, next to the pines, was 450 feet long and averaged 60 feet wide. The second area, next to the honeysuckle and briars, was 360 feet long and about 15 feet wide. The height of the shrubs in both areas varied from three to eight feet. The two areas combined contained 30,318 square feet. This area offered suitable protection to the mice only after spring foliation had taken place and until the leaves had fallen off in late fall.

During the late spring, summer, and early fall both the honeysuckle and briar regions and the cultivated shrubs region offered suitable habitat for the mice. This was a combined area of 48,318 square feet. During the remainder of the year only the honeysuckle and briar region was suitable for the mice.

Between the two parts of the shrub region and extending back to the eastern border was a third region of fescue grass (*Festuca* spp.). The eastern part of this final region contained some parts with briars but these were not nearly so dense or had the addition of the honeysuckle vines as the first region. Interspersed within this area were various old-field plants such as horse nettle (*Solanum carolinense*), plantain (*Plantage rugelli* and *P. lanceolata*), and goldenrod (*Solidago* spp.), which were found in their greatest concentrations in the eastern section of this region (although still very much dominated by *Festuca*). Lespedeza (*Lespedeza* spp.) was found throughout the area. In the eastern part of this area two rows of mock orange (*Philadelphus coronarius*) saplings had been planted. The western part of the area had two small isolated and sparsely numbered patches of briars and several sumac (*Rhus* spp.), silver maple (*Acer saccharinium*), sugar maple (*A. saccharum*), and white birch (*Betula papyrifera*). The area contained in this third type of region was 46,631 square feet. This region was at no time during the year considered a suitable mouse habitat, although it was excellent for the population of prairie voles that inhabited this area.

METHODS AND MATERIALS

Laboratory Methods

A laboratory phase of the study was conducted to determine the extent of intraspecific behavior within the groups of white-footed mice and the relation of inter-specific behavior when populations of the two largest species (i.e. the white-footed mice and the prairie voles) were in contact.

All animals used in the experiment were wild trapped individuals captured from the Clarksville, Tennessee and Painton, Missouri areas. Five male and two female prairie voles and six male and three female white-footed mice were used. All males were separated immediately upon capture from other males of both species. The animals were kept in cages in an area providing the least possible disturbance and yet providing enough exposure as to accustom the animals to the presence of humans. Food, water, and nesting material were provided ad libitum. The animals used in the tests remained in cages long enough to become accustomed to laboratory conditions, were in good health, and were sexually mature.

All cages were constructed of 1/4 inch hardware cloth. Holding cages were 12 x 6 x 6 inches in size. One male or one male and one female of the same species occupied a single cage. A large cage, designated the nest cage, was used in the tests concerning nesting segregation. The nest cage was 36 x 12 x 10 inches. The third type of cage, the test cage, was used for the aggressive behavior tests. It was 18 x 6 x 6 inches in dimensions and contained a solid sliding partition midway in the cage.

Tests concerning intraspecific behavior were conducted first. This was done to avoid a possible traumatic experience for the animals when they were placed in the test cage with the other species and to ensure better results since the mice and voles would be expected to come in contact with members of their own species more frequently than with those of the other species in a natural situation.

The animals were taken from their holding cages and marked by spotting appropriate patterns on their bodies or ringing their tail with fingernail polish. This was later found to be unnecessary because such familiarity with the animals developed as to enable the identification of each individual by its physical appearance.

The animals were placed in the test cage, one on each side of the partition, and left separated long enough for them to calm down. This was signified by the absence of any frantic running or jumping and their huddling in a corner or quietly exploring the cage; about one minute was required to obtain this state. The partition was then removed and the reactions of the individuals observed and recorded. The animals were left together long enough to ascertain which individual tended to be dominant, but not long enough to allow a definite dominant-submissive relationship to develop. Five minute test encounters were used. All males were tested in a round-robin fashion with at least 20 minutes time elapsed between tests involving the same individual. The animals were separated when necessary to prevent serious injury. This same procedure was followed for the interspecific behavior tests.

Behavior tests were conducted at night, with the aid of a red light, and during the day to determine if the time of encounter was of influence involving the tests with the nocturnal mice and the diurnal voles.

During all tests the investigator sat quietly alongside the test cage and recorded the data. All data were collected by the same investigator to avoid discrepancies in the interpretation of the reactions.

Behavioral reactions were divided into ten categories. These categories were threats, approaches, attacks, fighting, avoidance, defensive position, retaliation, fraternizing, sniffing and no conclusive reaction. Threats, approaches, and attacks were grouped under a larger heading of aggressive reactions and the total recessive reactions were those under avoidance, defensive position, and retaliation. The descriptions of each categorized reaction were the same as those used by Clarke (1956), Krebs (1970), and Wirtz and Pearson (1960).

A second test involved the nesting habits of the animals. Two groups of male-female paired animals were introduced into the nest cage and allowed to reassociate themselves at will in their nesting habits.

Nesting material was evenly distributed throughout the nest cage and two sources of ample food and water were located within the cage. Notes were taken on the reactions of the animals upon their introduction into the nest cage and then the nesting position of the animals was periodically later noted. Both intraspecific and interspecific reactions were observed in this experiment.

Vegetative Analysis

A survey of the vegetation present was conducted at the beginning of the study and on a seasonal basis thereafter. Identification of the plants on the study area was made through the use of the field guide by Blomquist and Oosting (1959). Factors studied were the dominants within the study area, the amount of overhead and side protective cover, the patterns of the plant community, and the change in the protective cover with the seasons. The sample quadrat method outlined by Smith (1966) was employed to determine the dominant vegetation.

An estimate of the overhead protective cover afforded by the various vegetation types was obtained by holding a meter square frame over randomly selected areas and estimating the percentage of the ground surface that could be observed. The meter square frame was held at a height of three feet in all areas except in the tall cultivated shrubs. In this type of habitat the overhead cover was estimated by crawling under the vegetation and looking up through the foliage.

An estimate of the side cover was made by placing one side of the meter square frame on the ground and determining the percentage of the enclosed square covered by the vegetation.

Live Trapping Methods

A thirty foot grid pattern of live traps, randomly set, was used in this investigation. The study area was measured off into eight rows with the first row beginning in the extreme northeast corner of the study field. The first trap station of the first row was placed in the interval of the grid pattern (thirty feet) from the fence row bounding the pasture on the east and the pine grove on the north.

The eight rows ran in an east-west direction and paralleled each other in a north-south direction; the rows were lettered A through H. Each row contained a certain number of sequentially numbered trap stations; rows A, B, and C each contained 16 trap stations; D and E had 15 each; F had 13; G contained nine; and H had five trap stations. This gave a total of 105 trap stations within the study area.

The measurement of the study area was made using one-hundred-foot steel tape measure. At each thirty foot grid intersection, the site of a trap station, a white tag, used as a permanent marker, was attached to some form of permanent vegetation at the site. If no such vegetation was available then a wooden stake was driven into the ground at the appropriate position and the tag was attached to it. Each tag was labeled with the correct row letter and trap station number.

The area within the grid pattern was calculated to give the original area of the study field and, after the inclusive boundary strip advised by Stickel (1946), a fifteen foot border (one-half the distance of the grid spacing) was added around the trap perimeter to obtain the adjusted area.

Monthly trapping was begun during February 1970 and continued until mid-February 1971. The first month was used to capture and mark as many individuals as possible. Each trap period consisted of five trap nights. The entire area was trapped in two weeks as insufficient numbers of traps were available to cover the entire study field in one setting.

Traps were usually set late on Sunday afternoons and taken in on Friday afternoon of the same week. The remainder of the area was then set the next Sunday and the trap period concluded at the end of this five day period. The trap period usually consisted of the middle two weeks of each month.

One trap was placed at each site indicated by the markers. These traps were placed within a two foot radius of the markers to provide for consistency of sampling. The traps used were either single catch Sherman live traps with outside dimensions of 3 1/4 x 3 1/4 x 9 inches or single catch Havahart live traps with outside dimensions of 3 1/4 x 3 x 10 inches. The use of these two types of traps was in a random fashion to aid in eliminating any bias due to trap preference on the animals' part.

Traps were baited with a mixture of scratch feed and peanut butter. The scratch feed consisted of cracked and broken corn kernels and soybeans along with seed of various field plants. Ample bait was provided at all times. Fresh bait was applied after captures and as needed, especially during the warmer months when bait-pilfering insects and the growth of mold necessitated frequent replenishment of the bait. No deterrent to the insects was added to the bait. During the cooler months a small amount of fresh bait was added about once a week.

A small wad of cotton batting was placed in each trap for the dual purpose of providing warmth for the animals in the winter and to aid in calming them at other times. Fresh batting was added after captures or when required.

Cardboard sunshelters were placed over the traps during the summer to aid in preventing overheating of the traps.

Periodic perimeter trapping was conducted to determine the movement of marked animals into and out of the study area. This perimeter trapping employed the use of the same grid pattern as used on the study area but was only two rows deep. The first row of traps was set approximately 90 feet from the last line of traps on the study area. The lines trapped in this perimeter sampling were along the northern and western borders of the study area; the southern and eastern sections were not sampled because of the unsuitable habitat provided by overgrazed pasture in the adjacent field. Trapping was conducted for three nights, usually after every second trap period. During the September-October intertrap period, extensive perimeter trapping was conducted in an effort to locate the mice which had apparently moved from the study area. During this time the perimeter was trapped for two consecutive weeks.

The animals were identified by the use of guides by Blair, Blair, Brodkorb, Cagle, and Moore (1968) and Burt and Grossenheider (1964). The date and trap station position was noted with each capture. The animal was removed from the trap and placed in a holding cone. This cone was constructed of wires attached to form a cone and with a heavy cloth sleeve fashioned to the large end. The cloth sleeve was large enough to fit over the end of the traps. By opening the back end of the trap and blowing into the front end, the animal usually entered the cone. Once inside the cone the animals were examined, weighed, marked and released.

Each animal was examined to determine its sex and breeding condition. Records were kept as to the abdominal or scrotal position of the testis of the males and of the condition of the vulva and nipples of the females. Males were considered mature and in breeding condition if the testis were in a scrotal position. Females were considered to be in breeding condition if the vulva was open and/or swollen. Lactating females could be identified by the enlarged and darkened appearance of the nipples. Pregnant females could usually be identified by the enlarged nipples, which were lighter in color than those of the lactating ones, and generally by their more rounded body contour. All animals were examined for general health, parasites, injuries, pelage change, and age.

The mice were divided into two age groups: juveniles were designated as all mice captured that were still in the gray juvenile pelage or had not yet completed the pelage change to the adult coloration. Adults were those mice in adult pelage. Estimation of age used in determination of the breeding season followed methods described by Gottschang (1956).

All animals were marked by toe clipping with the use of manicure scissors after the method used by Provo (1962). When marked in this way the animal suffered very little bleeding and there were no signs of detrimental effects on any of the recaptured individuals.

A triple beam Ohaus balance, accurate to the nearest 0.1 gram was employed to weigh the animals. The holding cone containing the animal was weighed, then the animal was released and the cone reweighed. The difference between the two weights gave the weight of the animal.

Notes were collected concerning the reactions of the individual upon release. These notes provided information as to whether the animal seemed confused or lost when released or if it seemed to know where it was in relation to a hiding place or nest. This behavior of the mouse was used in determining whether the animal was a migrant or a resident. The stations were checked for captures and to ascertain if each trap was in proper working order early in the morning and late in the afternoons. If the same animal was captured two successive nights in the same trap, that trap was closed for a 24 hour period to prevent the acquisition of the "trap habit" by the animal. The data taken from the second capture of the animal was discarded.

Daily observations were made during the trap periods on the climatic conditions and changes in ground cover provided by the vegetation. Complete weather information for the general locality was obtained from the United States Air Force Weather Detachment stationed at Fort Campbell, Kentucky.

Methods of Calculation

The total area within the study area and the various habitat types were found by measurement of the external borders of each and calculating the square footage of each area.

Trapping efficiency based on the comparison of actual catch with the possible catch for mice known to be on the study field and for the length of time between first and last captures were based on the method used by Snyder (1956). Trapping efficiency for the sexes used the same method with the only change being the separation of the individuals into groups by sex.

Mice estimated to be on the study field each month and season were tabulated using the method employed by Snyder (1956). Capture records of all individuals were entered on a table similar to that used by Snyder (1956). Tabulations of mice per acre using the original and adjusted areas were the method used by Stickel (1946). Ecological density was then estimated to illustrate the high population density within the study area. Sex ratios and age structure of the population, both monthly and seasonally, were determined from trapping records.

Longevity was estimated by using the age at completion of pelage change as described by Gottschang (1956) and adding this time to the average length of time adult mice were known to have been on the study area. The length of time spent on the study area was shown for each individual using a system modified from that of Burt (1940). First and last captures were recorded by x; o denoted a period in which an individual was not captured but had been taken in periods both before and after; a solid line designated the time the individual was known to be on the study area; and a broken line delimited periods the individual was assumed to be on the study field.

Recruitment and disappearance rates, as termed and used by Provo (1962), were expressed as percentages of the total population on a seasonal basis. These rates were calculated for the population as a whole as well as for sex. Graphic representation of these rates was plotted.

Home ranges, as defined by Burt (1940), were figured using the exclusive boundary strip method used by Ambrose (1969) and Van Gleck (1969). Average home range size of all individuals captured three or more times per month and per season were recorded.

Habitat selection and use of various cover types were demonstrated in three ways. The total number of mice captured in each habitat and the total captures of mice in each habitat were recorded in bar graphs. The individual center of activity for each animal was found using the method described by Cockrum (1962). These centers of activity were then combined to give a monthly center of activity and combining these gave a seasonal center of activity for the population. Shift of home range was also used to emphasize seasonal shift.

Weather influence was plotted on a graph showing the average monthly high and low temperatures as well as the total captures each month. The total monthly captures were also plotted against the monthly precipitation.

RESULTS

Intraspecific Behavior

A total of ten intraspecific behavior tests were conducted for the male white-footed mice. The mice had a total of 235 reactions for an average of 23.5 per trial.

Intraspecific encounters (Table II) indicated a definite dominance ranking among the mice. This dominance ranking among the white-footed mice was further emphasized with the result of the nesting study. When two groups of male-female paired mice were introduced into the nest cage, one of the males always dominated the other. The dominant male nested with the two females, often occupying the top position of a pyramid shaped huddle formation. The submissive male either huddled alone in one corner or, when allowed in the nest, occupied a peripheral position in the huddle formation.

Interspecific Behavior

A total of 56 interspecific behavior tests were conducted between the white-footed mice and the prairie voles resulting in 1,231 contact reactions or an average of 21.9 reactions per trial. Of the total tests, 31 were conducted at night and 25 during the day. The night tests resulted in 564 reactions with an average of 18.0 per trial. The day tests had a total of 667 reactions averaging 26.4 per trial.

TABLE II. Results of Intraspecific Encounters. Figures represent the percentage each reaction is of the total reactions.

Mouse	Aggressive: Threat	Aggressive: Approach	Aggressive: Attack	Aggressive: Fight	Recessive: Avoid	Recessive: Defense Position	Recessive: Retaliate	Fraternize	Sniff	No Reaction	Total Reactions
		34.0				45.3					
0	11.3	22.7	--	--	36.3	9.0	--	4.5	9.0	6.8	44
		42.5				27.7					
1	1.6	37.7	3.2	4.9	3.2	19.6	4.9	1.6	22.9	--	61
		54.1				18.6					
2	10.4	35.4	8.3	10.4	8.3	4.1	6.2	--	2.0	14.5	48
		39.2				42.9					
3	--	39.2	--	1.9	21.5	15.6	5.8	3.9	9.8	1.9	51
		12.9				67.6					
4	--	12.9	--	--	61.2	--	6.4	3.2	6.4	9.6	31

The results of the night tests (Table III) revealed the prairie voles recorded twice as many aggressive reactions as did the mice. The percentage of approaches was approximately equal for both species, however, the voles combined threats and attacks with their approaches much more often than did the mice. A great difference was recorded in the recessive behavior of the animals as over one half of all reactions of the mice were of a recessive nature. The recessive behavior of the voles in response to the mice was minimal and most of these reactions were in the smaller category of retaliations. There was no substantial difference in the categories of fraternizing and sniffing, while there was a difference in the no conclusive reaction category. The voles paid no attention to the presence of the mice a greater percentage of the time than did the mice in the reverse sense.

Day testing (Table III) further demarcated the more aggressive tendencies of the voles. The voles increased their percentage of aggressive reactions by a greater percentage of approaches and attacks, while their percentage of threat reactions decreased. The recessive activity of the voles also decreased by nearly one half. The recessive behavior of the mice increased greatly with the percentage in the category of avoidance nearly doubling, while the percentage in the category of defensive position and retaliation both dropped. This seems to indicate that the mice preferred to take immediate flight from the voles rather

TABLE III. Results of Day and Night Interspecific Encounters. Figures represent the percentage each reaction is of the total reactions.

Animal	Threat	Approach	Attack	Fight	Avoid	Defense Position	Retaliate	Fraternize	Sniff	No Reaction	Total Reactions
	Aggressive				Recessive						
Night Test											
		36.4				57.8					
Mice	2.2	32.0	2.2	0.2	37.2	12.6	8.0	0.2	1.4	3.4	349
		72.7				8.7					
Voles	21.1	37.2	14.4	1.3	2.7	--	6.0	0.4	2.7	13.4	215
Day Test											
		24.1				74.5					
Mice	--	23.5	0.6	--	61.7	6.4	6.4	--	0.3	0.9	327
		92.8				4.8					
Voles	12.0	41.4	39.4	--	0.2	0.2	4.4	--	0.5	1.4	340

than make any antagonistic action. The percentage of aggressive responses of the mice lessened proportionately.

The voles evidenced a decidedly greater activity during the day tests as witnessed by 340 reactions in 25 tests during the day as opposed to 215 reactions in 31 tests at night. A significant increase was recorded in their total percentage of aggressive activity.

The comparison of the aggressive and recessive columns of the total results for the interspecific behavior test (Table IV) indicates the clearly more aggressive tendency of the prairie vole in relation to the white-footed mouse. Little difference could be ascertained from the last three columns.

The interspecific nesting study demonstrated positive reactions. Almost immediately upon the introduction of the animals into the nest cage, the voles attacked the mice and chased them around the cage. This activity continued with only momentary pauses for an hour. The voles then went to one corner and started to construct a nest. Periodically, the male vole would run to the distal corner of the cage where the mice were huddled and attack them, then he would return to the female vole and the nest building activity. The female vole tended to remain at the nest site, once its construction had begun, throughout the duration of the test. With each approach by the vole, the mice would frantically run away. Little actual fighting was observed as the mice were usually quick enough to avoid the voles.

TABLE IV. Total Interspecific Encounter Data. Figures represent the percentage each reaction is of the total reactions.

Animal	Aggressive	Fight	Recessive	Fraternizing	Sniffing	No Reaction	Total Reactions
Mice	30.6	0.14	63.0	0.14	0.88	2.21	676
Voles	85.2	0.54	6.5	0.18	1.44	6.12	555

Occasionally a mouse would be caught in a corner and fighting would ensue until the mouse was able to escape. This activity continued throughout the length of the test.

During the first night the voles moved all the nesting material into one corner of the cage and constructed their nest. The mice huddled in a far corner and were denied any nesting material at all.

Two separate groups of four individuals each were tested in this manner and the results were identical in both cases, with the exception of one mouse actually being killed by the voles in the second test group. It is not known if the physical violence from contact with the voles or exhaustion from the constant harassment by the voles was responsible for this death. Upon examination the mouse had some wounds on his nose, ears, feet, and tail, evidencing the amount of physical abuse encountered.

After two days the animals were separated to avoid any further deaths among the mice as the aggressive activity of the voles had not abated and some of the mice had visible wounds on them.

Evaluation of Trapping Methods

Varying numbers of trap nights were used early in the field study to determine a suitable length of time to leave the traps in the field. Periods of less than five trap nights yielded a low number of captures while a longer period of time produced excessive recaptures. Five trap nights per station per month was found to be a suitable number; this number was also found to be suitable by Blair (1942) and Snyder (1956).

A comparison of the actual catch with the possible catch of marked mice for each period during the study (Table V) shows both the monthly and the total trapping efficiency. The total trapping efficiency of 84 percent agreed with Burt's (1940) statement that nearly 100 percent of the population of white-footed mice can be taken. Monthly trapping efficiency remained high (80-100 percent) throughout the study except for September and January.

Table VI shows the comparison of actual catch with the possible catch for mice grouped according to the number of weeks between first and last captures. These data indicated that mice known to be present on the study area for extended periods of time were just as likely to be captured as mice present for a much shorter length of time. These results agreed with those of Snyder (1956), although the efficiency for the present study was considerably higher, the relation in weeks between captures was very close.

The trapping efficiency of adult mice according to sex revealed only slight differences with the males having a higher efficiency (95 percent) than the females (80 percent).

Periodic perimeter trapping revealed only two captures, both during the September-October intertrap period

TABLE V. Comparison of Actual Catch (Left Column) with Possible Catch (Right Column) of Marked Mice for Each Trap Period During the Study. First and Last Captures Indicated by X.

Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Total
X	1 1	1 1	1 1	1 1	1 1	1 1	0 1	1 1	1 1	1 1	1 1	X	10-11
X	2 2	2 2	2 2	2 2	2 2	X							10-10
X	1 1	0 1	1 1	1 1	X								3-4
X	1 1	1 1	1 1	X									3-3
X	1 1	1 1	X										2-2
			X	0 1	X								0-1
						X	0 1	1 1	1 1	1 1	0 1	X	3-5
									X	1 1	0 1	X	1-2
	6 6	5 6	5 5	4 5	3 3	1 1	0 2	2 2	2 2	3 3	1 3		32-38
	100%	83%	100%	80%	100%	100%	0%	100%	100%	100%	33%		84.21%

TABLE VI. Comparison of Actual Catch with Possible Catch for Mice Grouped According to Number of Weeks Between First and Last Captures.

	Number of weeks between first and last captures						
	1-8	9-12	13-16	17-20	21-24	25-28	49-52
Number of mice in group	2	1	2	1	2	2	1
Actual Catch	2	0	3	3	6	10	10
Possible Catch	2	1	4	3	8	10	11
Efficiency	100%	0%	75%	100%	75%	100%	90.9%

and only one of these individuals was captured previously (one time) on the study area. The other individual was taken only once.

Population Density

Population densities on a monthly and seasonal basis (Table VII) were estimated using the method employed by Snyder (1956) and Burt (1940).

The estimated population density was high during the spring and early summer months when compared with the work of others (Burt, 1940; Snyder, 1956; and Stickel, 1960). The high population density was followed by a sharp decline in the late summer and early fall months after which an equilibrium was established and continued into the winter months. Using estimations of population numbers on a monthly basis (Table VII) the population low occurred during October. However, these results may reflect changes in trapping success rather than a population decline.

Table VIII shows the months the individuals were actually captured and the number of captures of each animal each month. This data shows a reduction in the number of mice and the number of captures in August and a complete trapping failure during September. Also there is a build up of numbers of mice following the September period until the January and February 1971 periods (Table VIII). Heavy snow in February may have decreased the movement of some individuals and it also covered the traps, making them

TABLE VII. Total Number of Mice Estimated to be Present on the Study Area each Period.

Period	Male	Female	Total
Spring	7	6	13
March	4	6	10
April	5	6	11
May	6	3	9
Summer	7	4	11
June	7	3	10
July	7	3	10
Aug	6	2	8
Fall	4	2	6
Sept	3	1	4
Oct	1	2	3
Nov	2	2	4
Winter	3	2	5
Dec	3	2	5
Jan	3	2	5
Feb	2	2	4

TABLE VIII. Trap Record of Each Mouse Captured. ■ designates first and last captures; o denotes a period the individual was not captured; x^1-x designates a capture, the exponent signifies the number of captures.

Ind	Sex	Feb	Mar	Apr	May	Ju	Jly	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Total
1	male-ad	■^{2}	x^1	x^1	x^4	x^3	x^1	■^{3}							7^{15}
2	female-ad	■^{3}	x^1	x^4	x^2	■^{3}									5^{13}
3	male-ad	■^{2}													1^2
4	male-ad	■^{1}	x^3	x^2	x^1	x^1	x^2	x^2	o	x^4	x^1	x^3	x^3	■^{1}	12^{24}
5	female-ad	■^{4}	x^1	x^3	■^{3}										4^{11}
6	male-ad	■^{3}	x^1	x^2	x^3	x^2	x^1	■^{1}							7^{13}
7	female-ad	■^{1}	x^1	o	x^3	x^1	■^{1}								5^7
8	female-ad		■^{1}												1^1
9	female-ad		■^{1}												1^1
10	female-juv		■^{1}												1^1
11	male-juv				■^{5}	■^{1}									2^6
12	male-juv				■^{1}	o	■^{3}								2^4
13	male-ad					■^{3}	■^{1}								2^4
14	male-ad						■^{1}								1^1

TABLE VIII. (Continued).

15	female-ad							a^1	o	x^6	x^4	x^3	a^1		5^{15}
16	male-ad									a^1	perimeter trapping-pines				1^1
17	female-ad										a^1	x^1	o	a^1	3^3
19	male-juv											a^3			1^3
20	male-juv												a^1		1^1
Captures		16	11	12	22	14	10	7	0	10	6	10	5	2	126
Mice		7	9	5	8	7	7	4	0	2	3	4	3	2	19

unavailable for several days. The two mice captured during the February 1971 period were both found dead in their snow-buried traps.

The crude population density was shown when the number of mice per acre per month and season were tabulated (Table IX). Both the original area (the area within the grid pattern) and the adjusted area (the area within the grid pattern plus a fifteen foot border around the grid) were used in these calculations.

The number of mice per acre as indicated by this method gave crude densities within the ranges reported by Burt (1940), Snyder (1956), and Stickel (1960). However, the studies by these persons were apparently conducted in a location in which the entire area was suitable habitat. Odum (1959) refers to ecological density as the numbers of organisms per unit of habitat space. When this estimate is made the density is high and variable as seasonal changes cause crowding (Table X).

Sex Ratio and Age Structure

Monthly and seasonal sex ratios, based on actual captures and using all animals taken during each period (Table XI), shows a greater number of males beginning in late spring and continuing until the end of the summer. These results were found to differ from those of Burt (1940), Hirth (1959), Nicholson (1941), and Snyder (1956), who reported close to a 50-50 sex ratio in their studies. This deviation may have been the result of greater activity,

TABLE IX. Crude Density of Mice Estimated to be on the Study Area each Period.

Period	Number/Acre	
	Original Area	Adjusted Area
Spring	7.67	5.96
Mar	5.91	4.58
April	6.49	5.05
May	5.31	4.13
Summer	6.49	5.04
June	5.91	4.58
July	5.91	4.58
Aug	4.72	3.67
Fall	3.54	2.75
Sept	2.36	1.83
Oct	1.77	1.37
Nov	2.36	1.83
Winter	2.95	2.29
Dec	2.95	2.29
Jan	2.95	2.29
Feb	2.36	1.83

TABLE X. Ecological Density of Mice Estimated to be on the Study Area Each Month.

Period	Number-Acre	Habitat
Mar	24.39	Honeysuckle-Briars
Apr	9.918	Honeysuckle-Briars & Shrubs
May	8.12	"
June	9.02	"
July	9.02	"
Aug	7.21	"
Sept	5.75	"
Oct	7.26	Honeysuckle-Briars
Nov	9.69	"
Dec	12.11	"
Jan	12.11	"
Feb	9.69	"

TABLE XI. Sex Ratio for Each Period

Period	Sex Ratio
Spring	5:6
Mar	3:6
April	3:2
May	5:3
Summer	7:3
June	5:2
July	6:1
Aug	3:1
Fall	1:2
Sept	0:0
Oct	1:1
Nov	1:2
Winter	3:2
Dec	1:1
Jan	2:1
Feb	1:1

increasing the chances of the males being more trap-prone during periods of heightened breeding activity.

Age structure indicates the tendency toward an increase in old individuals in the population. The early data shows a deviation from that reported by Hirth (1959) and Verts (1957), who reported nearly 50 percent of the populations in their studies were juveniles. In this study the juveniles never composed more than 40 percent of the population and were usually much less. No juveniles were recorded from June until December, at which time they constituted 33 percent of the population. The large proportion of old individuals during the summer may have been a factor in the population decline at this time (Odum, 1959).

Breeding Season

The first juvenile was captured during the March trapping period giving evidence of a mid-January birth. After this initial capture, juveniles were taken in May, June, December, and January trap periods indicating birth times of March, April, October, and November, respectively.

Longevity

The average longevity of the adult population on the study area after their first capture was 4.5 months. Extremes were one mouse being captured during all of the 13 trap periods, except September, and four mice, each captured during one trap period. All adult mice captured were assumed to be at least 65 days old at first capture because of complete adult pelage. This figure, added to the average length of time an animal was on the study area, resulted in an average longevity of 6.8 months. Juveniles were captured on the study area for a much shorter time. Only one was taken in more than one trap period.

Table XII summarizes the length of time each animal was on the study area.

Recruitment and Disappearance Rates

Recruitment and disappearance rates were calculated on a seasonal basis. The table for these rates (Table XIII) indicated a fairly stable population during the spring season. Beginning in July and continuing through August the population experienced an increasing disappearance rate which resulted in a seasonal total disappearance rate of 80 percent, as opposed to only a 30 percent recruitment rate. During the fall the recruitment remained near the rate it had been for the prior two seasons, but the disappearance rate dropped to zero percent. The winter season indicated a return to a stable condition as recruitment and disappearance tended to balance each other.

The disappearance rates for males at the close of the summer was higher than that of the females. Other than this disparity, no real difference according to sex was indicated. In general, the recruitment tended to remain very stable throughout the year with population declines being associated with increased disappearance rates.

TABLE XII. Summary of the Length of Time Each Animal was on the Study Area. X denotes first and last captures; o designates a period an animal was not captured; solid line indicates the time an animal was present; broken line denotes the time an animal was estimated to be present.

Ind	Sex	Feb	Mar	Apr	May	Ju	Jly	Aug	Sept	Oct	Nov	Dec	Jan	Feb
1	male-ad	x-- ___	___	___	___	___	___	x---	---					
2	female-ad	x ___	___	___	___	x---	--							
3	male-ad	x---	---											
4	male-ad	x ___	___	___	___	___	___	___	o ___	___	___	___	___	x
5	female-ad	x ___	___	___	x---	--								
6	male-ad	x ___	___	___	___	___	___	x---	---					
7	female-ad	x ___	___	o ___	___	___	x---	--						
8	female-ad	----	---x--	--										
9	female-ad	----	---x--	--										
10	female-juv	----	---x--	--										
11	male-juv			-----	x ___	x---	--							
12	male-juv			-----	x ___	o ___	x---	-						
13	male-ad				-----	x ___	x---	-						

TABLE XII. (Continued)

14	female-ad	------x-----
15	female-ad	------x___o________________________x-------
17	female-ad	-----x____________o_______x
19	male-juv	-----x------
20	male-juv	-------o-------

TABLE XIII. Recruitment and Disappearance Rates for Each Season

Season	Mice Present			Recruitment			Disappearance		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
Spring	5	6	11	2	1	3	-	4	4
				Male	2/5=40.0%		Male	0/5=0.0%	
				Female	1/6=16.6%		Female	4/6=66.6%	
				Total	3/11=27.2%		Total	4/11=36.3%	
Summer	7	3	10	2	1	3	6	2	8
				Male	2/7=28.5%		Male	6/7=85.7%	
				Female	1/3=33.3%		Female	2/3=66.6%	
				Total	3/10=30.0%		Total	8/10=80.0%	
Fall	1	2	3	-	1	1	-	-	-
				Male	0/1=0.0%				
				Female	1/2=50.0%				
				Total	1/3=33.3%		Total	=0.0%	
Winter	3	2	5	2	-	2	2	1	3
				Male	2/3=66.6%		Male	2/3=66.6%	
				Female	0/2=0.0%		Female	1/2=50.0%	
				Total	2/5=40.0%		Total	3/5=60.0%	

In reviewing the year as a whole, it can be seen that the two rates were nearly stable during the spring, followed by a severe disappearance during the summer. This decline was followed by a gradual population build-up in the fall, and with equilibrium being established during the winter.

Weather Influence

The total number of captures for the months of March through January, an index for activity, were compared with the average monthly maximum and minimum temperatures (Figure 2). Results of this comparison indicate a decreasing activity with increase of temperature. The minimum temperature appeared to be more important than the maximum. Activity was high until the minimum temperature reached the 60° Fahrenheit mark. At this point the capture total steadily declined with the rise in minimal temperature until this temperature had been lowered to well below 60° (47° Fahrenheit).

The average number of captures per individual per month also showed a corresponding decline with increase in daily temperature.

Activity, as evidenced by the number of captures per night, was greatest when the sky was overcast and after a change in the weather had been stabilized. Rain reduced the activity as did clear moonlight nights.

The amount of precipitation appeared also to be a factor in influencing activity. The activity of the mice

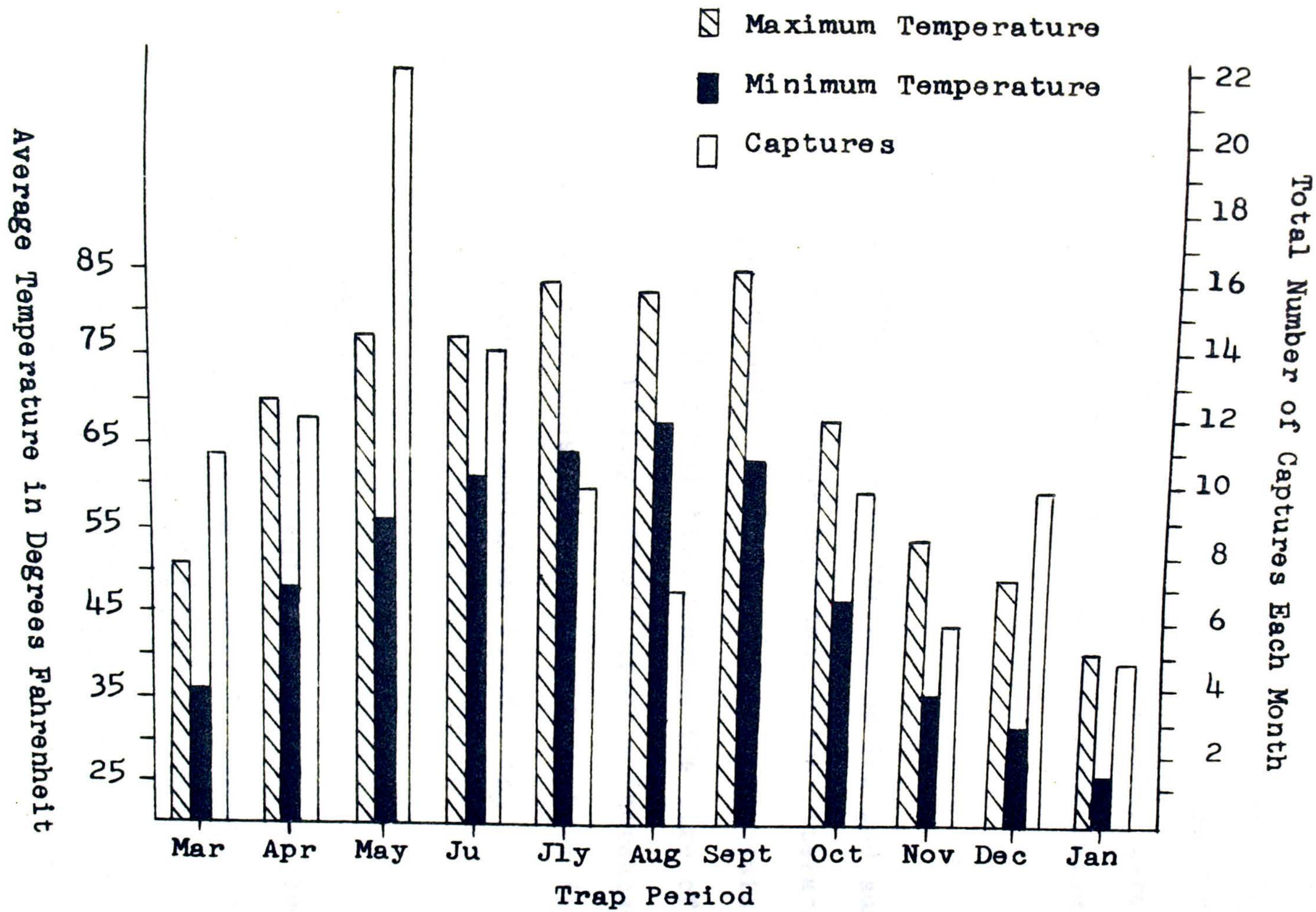

FIGURE 2. Average Monthly Maximum and Minimum Temperatures Compared with Total Captures.

seemed to be reduced at both periods of excessive dryness and heavy rainfall (Figure 3). It should be noted that during August most of the rainfall was during the first eight days of the month and was in two major rains (2.82 inches of a total of 3.18 for the month), so except for this period the months of July, August, and September were very dry and also had the highest temperatures, both maximum and minimum.

Home Range Size

Average home range size for the spring and summer months were below the average reported in the literature. This is the case on both a monthly and seasonal basis (Figure 4). After the population decline the size of the home ranges of the remaining animals greatly increased to a point comparable to those sizes reported by Burt (1940), Howell (1954), Redman and Sealander (1958), and Stickel (1960).

Patterns of Aggregation

Home ranges of males tended to overlap one another although these overlap areas were small in comparison with the rest of their total home ranges.

The home ranges of the females commonly were overlapped by those of the males in her vicinity, but no overlap was found between females, although sometimes the ranges would adjoin. These findings were in agreement with those of Burt (1940), Redman and Sealander (1958), and Stickel (1960).

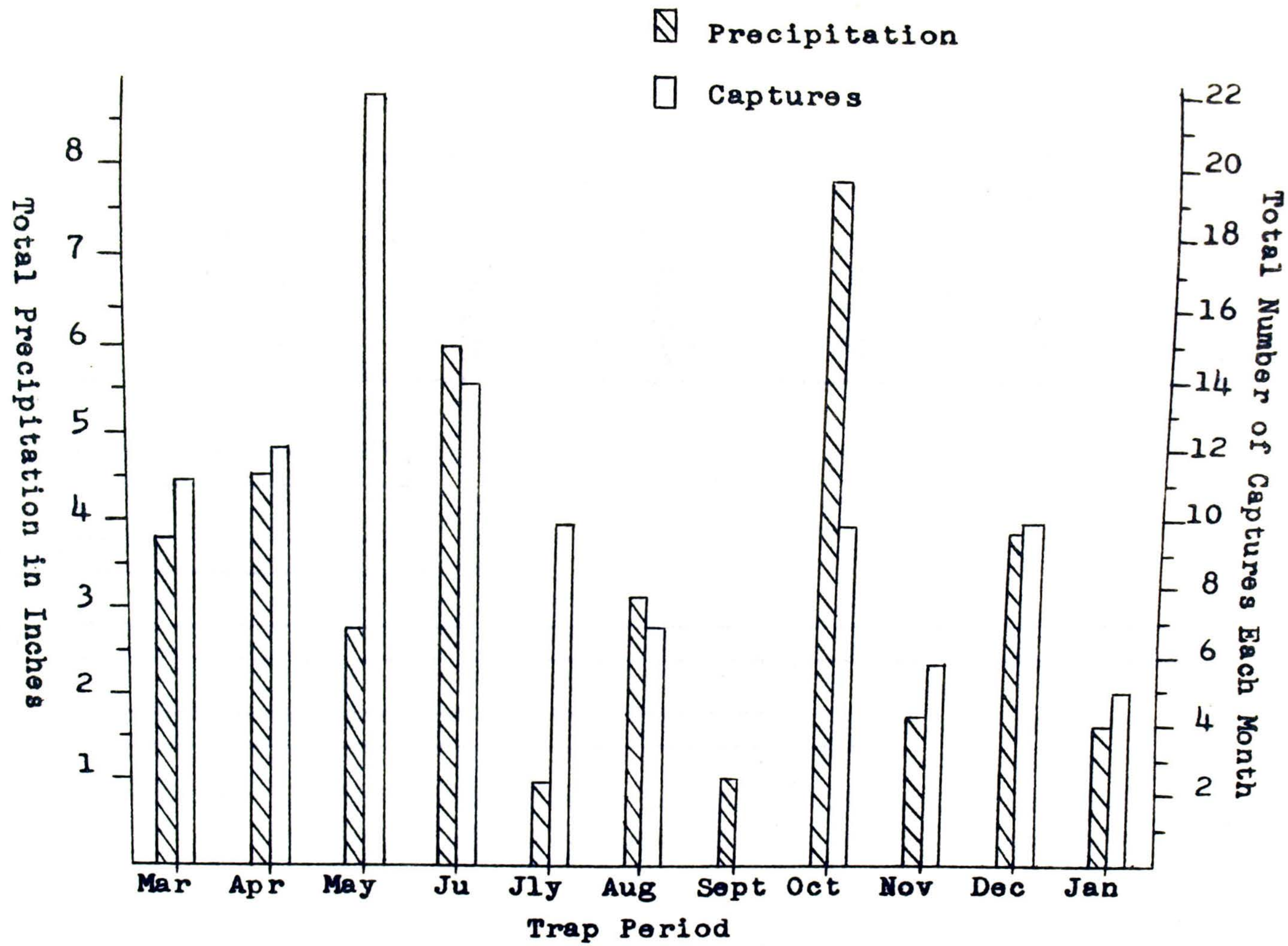

FIGURE 3. Total Monthly Precipitation Compared With Total Captures.

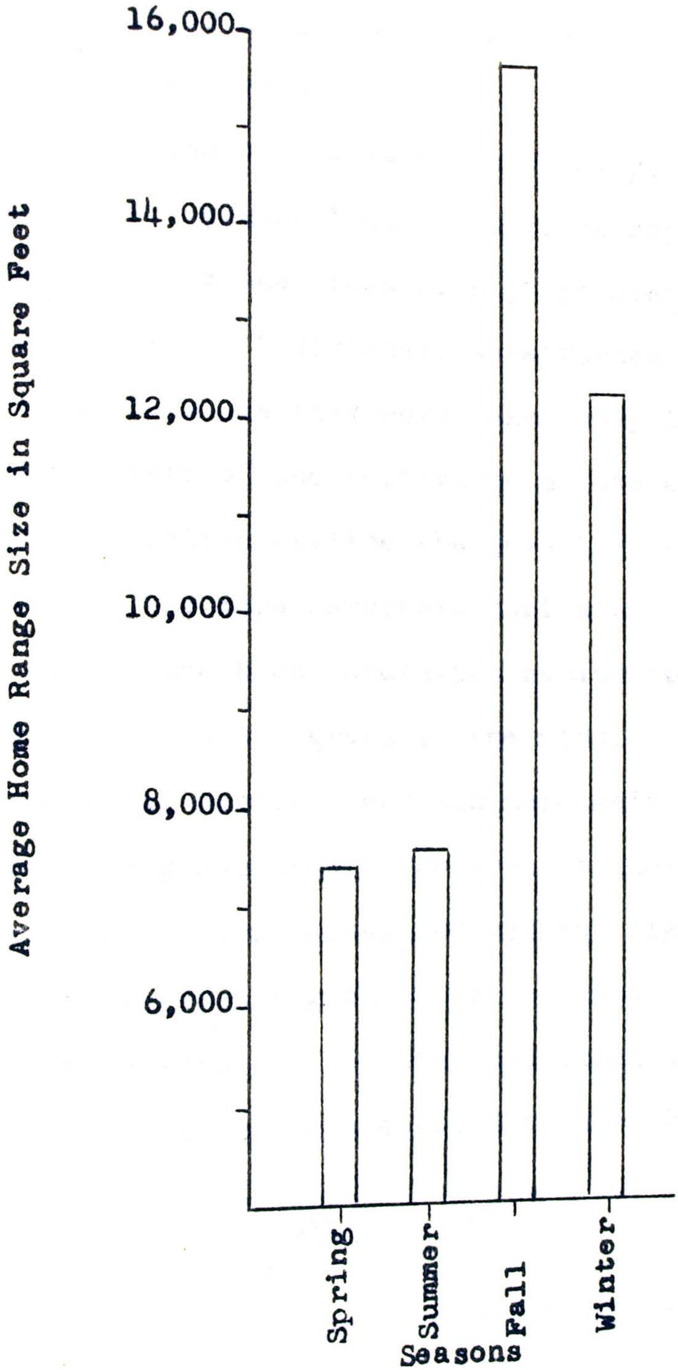

FIGURE 4. Average Home Range Size Each Season.

When the home ranges of the females were plotted on a seasonal basis a slight amount of overlapping was apparent. This may, however, be the result of varying activity over the length of a season and the abandonment of parts or all of home ranges by an individual, thus opening it up for occupancy by a new mouse.

Population pressures may have exerted a force on the patterns of aggregations. Locations mapped for juveniles taken during the times of high population seem to indicate that these individuals were forced to occupy less suitable habitats, as they were taken only in the very outermost borders of the cultivated shrubs and in the grass. After the population decline the juveniles captured were found only in the more favorable habitats.

During the high population period two adult mice were taken only in the grass in the middle of the western part of marginal habitat, and two more made regular excursions into the grass area. The area of these captures was almost entirely fescue grass and was not like the eastern section of the grass region which contained many old-field successional plants. After the population decline no mice were taken in this western section of the grass region.

Habitat Selection and Seasonal Use of Various Cover Types

Data indicate a preference of habitats containing suitable protective cover. Results of the percentage of protective cover analysis indicated the area of honeysuckle and briars contained suitable cover in both an overhead and side concealment throughout the year. The area of cultivated shrubs permitted suitable overhead cover from mid-spring until early fall. Side cover was densest during the late spring, after that defoliation of the lower regions of the shrubs would not allow visual concealment, but the numbers of stems could afford escape protection throughout the year. Defoliation during the fall and winter would allow visual observation from both an overhead and side manner.

Figure 5 shows the number of individuals captured in the areas of habitat for each month. A definite shift in habitat preference can be followed from late winter (February 1970) through the end of the summer (August). The fall and winter months show an equal capture ratio except for November and January. This perhaps indicates a decreasing supply of food and increased activity in a greater diversity of habitats.

Figure 6 shows the total number of captures in each of the habitats. These data indicate the areas of preferred activity when an individual may be captured in both habitats during the same trap period. These data also show the shift in habitat preference as patterns of aggregation are changed.

Shift of habitat preference was further indicated by the change of home range location. Most of the mice shifted their ranges over a matter of a few feet when moving

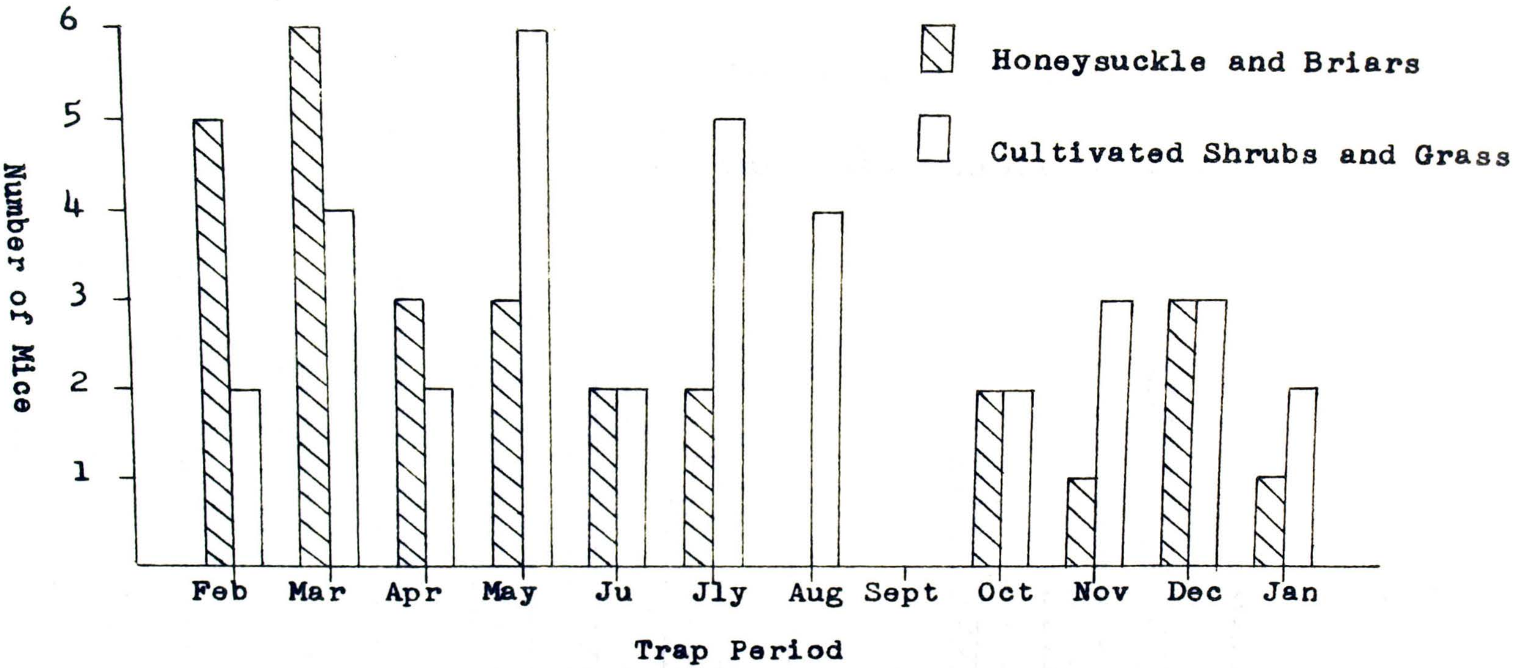

FIGURE 5. Number of Mice Captured in Major Habitats per Month

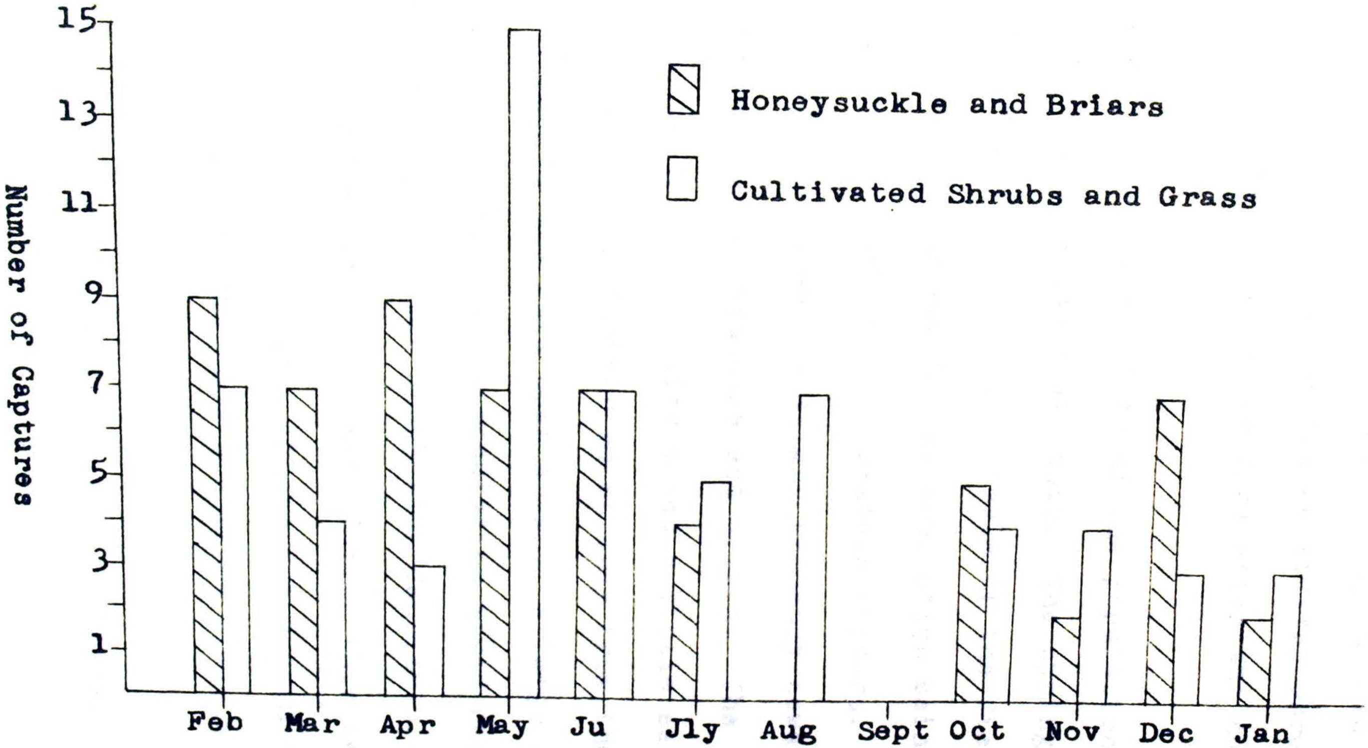

FIGURE 6. Total Number of Captures in Major Habitats per Month.

from one habitat to another but a great shift was recorded for mouse number one-male, who was captured several times in the western sector of the study in the honeysuckle and briars early during the study. Once foliation was well established this individual moved its range across the study area to the northeast corner in the cultivated shrubs and remained there until his disappearance after the August trap period.

Figure 7 plots the shifts of the population's center of activity on a seasonal basis. The spring center of activity appeared to be in the middle of the field, however, this was influenced by the population being spread along the northern, southern, and western borders. The center of activity does show a slight tendency toward the western areas and the honeysuckle and briars. The summer season had the center of activity moved a little east and south indicating a still further shift away from the honeysuckle and briars to the more open areas. A large shift occurred during the fall as the population moved back to the western regions. A lower population density with resulting greater freedom of movement during this season may be responsible for this change. The winter season again showed the shift back to the more protected areas of the study area.

Figure 8 plots the monthly shift in center of activity and serves to better illustrate the mobility of the population.

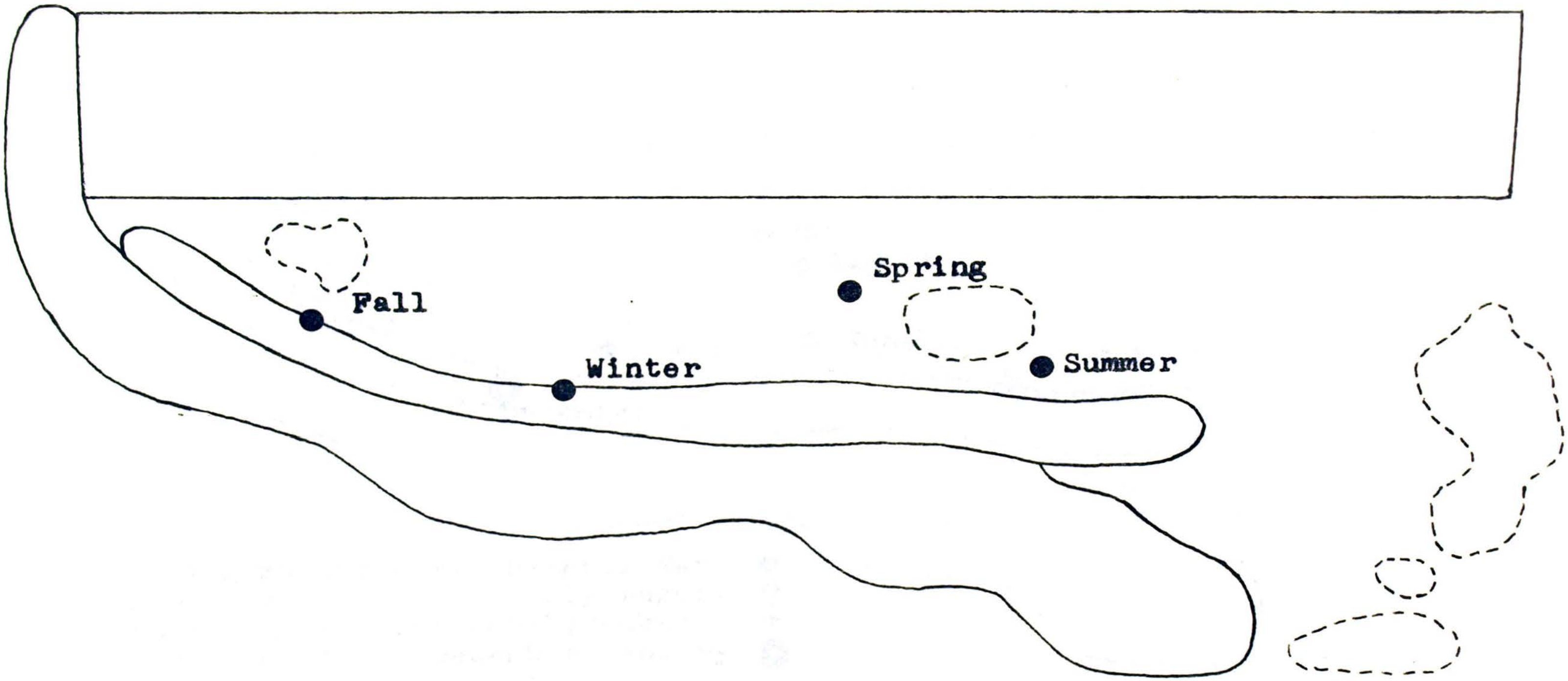

FIGURE 7. Population Center of Activity for Each Season.

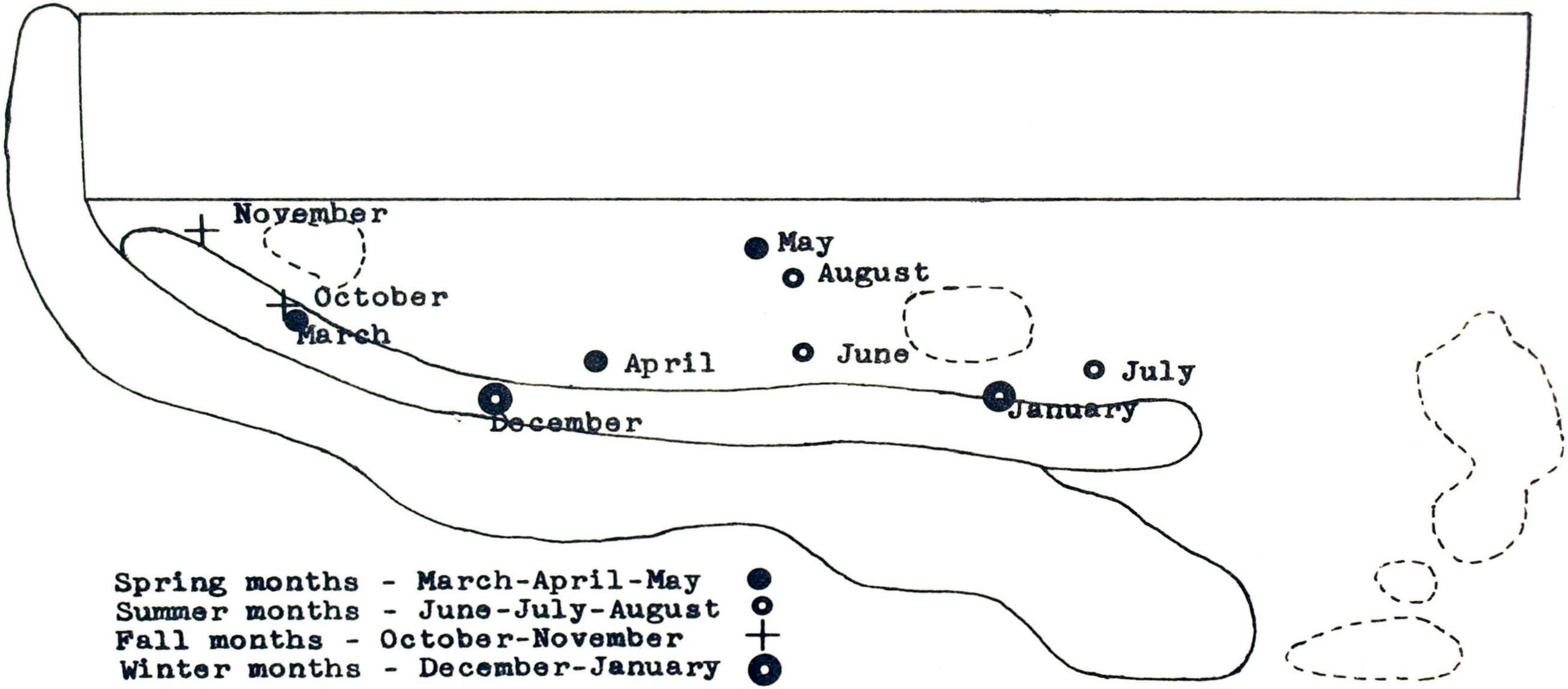

FIGURE 8. Population Center of Activity on a Monthly Basis.

Habitat selection is undoubtedly related to population pressures. This is possibly shown by the home ranges of two mice during the early months of the study, which were found in the grass while others made regular excursions into this region. Since this region is unsuitable habitat at all times it is reasonable to believe that the less dominant members were forced into it by population pressure. Following the population reduction no mice were trapped in this region.

Other Species Encountered on the Study Area

Various other species of small mammals were captured on the study area.

The prairie vole (Microtus ochrogaster) was captured in the grass area. This species comprised the largest population on the study area other than the white-footed mice. Voles were taken from February 1970 through May, when the population became untrappable. No further captures were recorded until October. After this time members were trapped every period until the close of the study.

All the voles were confined to their preferred habitats (Barbour, 1963; Dice, 1922; Findley, 1954; and Getz, 1962). Insufficient data was collected, both concerning number of individuals and numbers of capture of each individual, for any in-depth evaluation of the prairie vole population.

Several deer mice (*Peromyscus maniculatus*) were captured throughout the study. These animals were taken in the more open regions of the study area in accordance with their preferred habitats (Brown, 1964; Dice, 1922; Klein, 1960; and Whitaker, 1967). Insufficient data collected concerning this species negated the possibility of any population parameters being determined except for possible breeding season. Juvenile deer mice were taken during the winter season which perhaps indicates that they breed throughout the year in this locality.

One harvest mouse (*Reithrodontymus humulis*) was recorded in the cultivated shrubs next to the pines during the March trap period.

One golden mouse (*Ochrotomys nuttalli*) was found dead in a trap in the honeysuckles next to the wooded area in the southwest corner of the study area.

Short-tailed shrews (*Blarina brevicauda*) were recorded on three occasions, twice in the southern part of the study area and once in the grass.

Natural predators seen on the study area included the red fox (*Vulpes fulva*), raccoon (*Procyon lotor*), opossum (*Didelphis marsupialis*), feral house cat (*Felis domestica*), black rat snake (*Elaphe obsoleta*), loggerhead shrike (*Lanius ludovicianus*), red-tailed hawk (*Buteo jamaicensis*), red-shouldered hawk (*B. lineatus*), and great horned owl (*Bubo virginianus*).

DISCUSSION

From the intraspecific tests conducted it is indicated that the white-footed mice maintain a rather rigid framework of social hierarchy among males. This social hierarchy seemed to be arrived at with little in the way of overt physical violence.

Brown (1964) reported that in his nesting studies the submissive males were often killed. Although no such deaths were observed in this investigation, the submissive males were harassed and forced to occupy a peripheral nesting position in relation to the dominant male and the females.

This rigid framework of social hierarchy evidenced by the mice may be the result of their being sexual competitors and territorial animals (Bradshaw, 1965; and Burt, 1940).

Interspecific tests between the mice and the prairie voles were conducted to determine if the reason no mice were taken in the grass close to the vole population was primarily because less dominant members of the mouse population were forced, by population pressures, into this area or if interspecific aggression from the voles was significant enough to exclude the mice.

Since the prairie vole is primarily a diurnal herbivore which shows a decided preference for dry, grassy, upland situations (Barbour, 1963; Dice, 1922; Findley, 1954; and Getz, 1962), populations do not normally occur with white-footed mice; Whitaker (1957) reported he found them occurring together as often as would be expected by chance.

This testing indicated that the prairie voles were much more aggressive in relationships with the white-footed mice. During the night tests the mice recorded more aggressive responses than they did during the day but these still amounted to only one half of those recorded by the voles. The voles showed a marked increase in aggressive tendencies during the day testing, their normal activity period, over what they had displayed at night. The mice responded to this increase in aggression on the voles' part with a correspondent increase in their recessive activity. This might suggest that activity period had an influence on the behavioral patterns of these species.

Nesting segregation was positive on the voles' part as they drove the mice to the furthest corner of the nest cage and denied them any nesting material. One mouse was actually killed as a result of the aggressive actions of the prairie voles.

It is possible that interspecific aggression displayed by the voles could exclude the mice from habitats in which they both might occur. This was especially evidenced by the continued attacks by the voles during the nesting study and the day light behavior test. However, this probably would not be a major factor in the habitat segregation of these animals. Other factors, such as their habitat preferences, food habits, and activity patterns would more than likely serve as more effective barriers to the co-existence of these species under natural conditions.

The use of live traps has been critized for hampering the activity of the animals, giving false readings due to a higher possible encounter with traps nearest the nest, and producing the possible effect of an "after-trap" response in which the mice expand their ranges spontaneously and excessively. Work by Sheppe (1967) with tracking by the use of smoked kymograph paper has shown that the mice normally move throughout at least one half of their home range before entering any trap or shelter and the more distal traps are just as likely to be entered as those near the nest. Sealander (1958) reported that mice make a thorough investigation of the trap before entering. These results seem to minimize the first two criticisms to the live trapping method of sampling. The third criticism is of a more serious nature to the validity of the method. Since Sheppe (1967) has shown that mice often roam a much greater distance than normal on nights immediately after their release, however, Sheppe also stated that a large number of the records may have been made in the daylight immediately after the release of the animal.

The resolution of the problem of any "after-trap" response was to eliminate any capture data of distances greater than the length of the average home range when the animal returned to the area of his previous capture after a long distance excursion. Long movement followed by the individual remaining in the new area may be considered a permanent shift of home range and data was kept and utilized.

Live trapping, as a method of studying populations, has given good results when checked with tracking, trailing, and other methods (Stickel, 1965) and should reveal acceptably accurate information concerning the population of many small rodents.

Burt (1940) has stated that by sampling an area larger than the normal home range of an animal, a reasonable estimate can be made of the size of the home range and more accurate population numbers can be ascertained. Burt (1940) also stated that the white-footed mouse readily enters traps to obtain the bait and by using an appropriate grid pattern for several days and trapping the area at periodic intervals nearly 100 percent of the population can be captured. Also, by not closing the traps after captures a degree of utilization of different parts of the range can be obtained (Redman and Sealander, 1958).

A grid pattern of 30 feet has been employed by various investigators in their sampling of small mammal populations (Getz, 1961; Provo, 1962; Sheppe, 1967; Stickel, 1954; and Verts, 1957). This distance seemed to give a reasonable estimate of activity ranges in this study.

The method of calculating trapping efficiency gives only the chance of recapturing, in a given period, a marked mouse known to be present both before and after the period. Calculating the chance of capturing a new mouse is difficult to determine because the number of unmarked mice on the study area at any given time is not known. Snyder (1956) and Metzgar (1967) stated that immigrants and juveniles seeking home ranges must travel over greater distances than resident mice and therefore come in contact with a greater number of traps. It seems reasonable to assume that the efficiency of capture of all mice on the study area is actually higher than that calculated for the marked mice.

Age measured in length of time spent on the study field does not seem to influence the efficiency of trapping since the animals known to have been present for extended lengths of time were captured just as readily as those present for only a few weeks.

Males entered traps slightly more readily than did females. This may be partially explained by the greater wandering and aggressiveness on the part of the males (Burt, 1940; and Hirth, 1959).

The population numbers of this study were estimated to be from eight to 11 individuals present from February 1970 through June. The population density then began to decline in July 1970 and reached a low in September.

Following this decline the numbers then began to increase until the mid-winter season. Data indicate that this build-up was the combined result of increased immigration and natality.

The crude population density, until the decline in September, appear to be within the ranges reported by Burt (1940), Snyder (1956), and Stickel (1960). This data is deceptive since in the studies by these people the entire study area was apparently suitable habitat during any one period. The ecological densities of this investigation were high throughout the study. The high ecological density figure following the population decline was the result of the smaller area of suitable habitat. The difference in the densities can be seen by comparing the data from the early months of the study with that of the later months (Table VII, page 35).

Deviation in the normal 50-50 sex ratio of the population was apparent in the summer season. This could be the result of the greater activity and aggressiveness of the males during peak breeding activity and the lessened activity of the females at this time (Burt, 1940; Hirth, 1959; Nicholson, 1941; Odum, 1959; and Verts, 1957). However, since the white-footed mouse readily enters traps it seems a fair assumption that a greater preponderance of males were present on the study area during this time.

Davis and Golley (1963), in reference to mammalian populations in general, stated that altered adult sex ratios may be brought back into balance by other factors, such as immigration and natality. Since the white-footed mouse is a polygynous animal, this abnormality seems not to be an important factor in the population cycle of the mice being studied in this investigation, especially when considering that Burt (1940) stated that the normal home range of the female is about one-fourth an acre with a maximum of four females to an acre. On this basis the small area of suitable habitat was saturated with females even during the summer season when maximum discrepancy in sex ratio was apparent.

After the population decline the sex ratio neared a 50-50 appearance.

The age structure of the population, until the decline, indicated that less than the usual amount of juveniles were present (Hirth, 1959; and Verts, 1957), although the discrepancy was not great. Perhaps more important was the fact that juveniles were taken on the study area for a much shorter time than the average length of time an adult was present. This might be expected as juveniles are forced to migrate and are subject to heavy predation (Burt, 1940; Nicholson, 1941; Metzgar, 1967; and Wecker, 1963).

This tendency toward an old population may have had important consequences in the population decline (Odum, 1959) when stress situations of high population pressure combined with developing unfavorable weather conditions culminated in a population crash in September.

The average longevity of the mice on the study area was 6.8 months with extremes of some individuals being taken throughout the entire study, except for the September trap period. This longevity data agrees favorably with that of Snyder (1956) when she figured the longevity of the mice on her study area under a higher mortality standard which would coincide with the greatly increased disappearance rate for the summer season of this study.

Burt (1940) and Snyder (1956) reported that a few individuals may live over a year and on rare occasions approach two years in the wild. This study was for 13 months and only one individual was known to have been alive throughout the study.

The white-footed mouse appears to breed throughout the year in this locality. Burt and Grossenheider (1964) and Hirth (1959) reported that the white-footed mouse is a seasonal breeder in the northern part of its range and may breed throughout the year in the southern part. Burt (1940) and Hirth (1959) have indicated two peak reproductive phases, April and October, for the mouse in the northern part of the range. The few juveniles taken during this study yielded insufficient data to determine any reproductive peaks in the apparent year round breeding season of this population.

The average home range size per individual was smaller than that reported by Burt (1940), Howell (1954), and Stickel (1960) until after the population decline when the individual average home range size increased to nearly that of the above literature. No difference could be found in the size of the home ranges on a sexual basis and too few juveniles were taken to gather any information about their home range.

The small size of the home ranges during the first part of the study was apparently due to the crowding conditions of the high population density. After this stress was somewhat relieved, the small area of suitable habitat may have been a factor in keeping the home ranges slightly smaller than that reported by others.

Woods and woods' edges are the typical habitat of the white-footed mouse (Brown, 1964; Dice, 1922; Klein, 1960; and Nicholson, 1941). In this study the preferred habitat seemed to be correlated with the amount of protective cover. This would be expected since the method of escape for these small mammals is through flight and concealment (Kavanau, 1968). These habitats also offer a more abundant food supply for the granivorous white-footed mouse.

The home ranges are not static devices, but may become mobile under differing conditions (Turner and Stains, 1967). The mice of this study usually moved their home ranges over small distances but on one occasion a mouse moved the entire length of the field to establish a new home range.

Season movement may give the population an advantage of great foraging area, nesting area, and protective areas.

During the winter period activity fluctuated in the available habitats. Since the adult white-footed mouse requires about six grams of food per day under normal conditions (Verme, 1957), this fluctuation could possibly be the result of a shortening food supply, forcing the animals into a greater diversity of habitats.

Internal population pressures are an important factor in determining the extent to which a species occupies the more favorable portions of its environment and high densities may force individuals out of the preferred habitats (Klein, 1960; and Wecker, 1963). Evidence of these observations were shown during the early months of high population when pressures apparently forced several mice to make regular excursions into the grass region in the central and western parts of the area; two mice were captured exclusively within this region.

With decreasing population, no mice were captured exclusively within this region for the remainder of the study. Some were taken in the region of encroaching briars and goldenrod in the eastern part of the grass area. Activity in this area may have been due to the lessening food supply during the winter season and the association with the goldenrod habitat found by Wirtz and Pearson (1960).

Recruitment rates for the population was rather stable throughout the study suggesting that this rate may be relatively constant and indicating a steady influx of new members to the population. A higher proportion of these new individuals were males, perhaps indicating a greater wandering tendency of the males.

The disappearance rate appears to effect both sexes equally. However, this rate for the summer season was higher for the males since a greater number of males were present on the study area at this time.

The two rates were similar during the spring indicating the population, though high, was in a stable situation. During the summer a sharp increase in disappearance correlated with the population decline.

The steady rate of recruitment continued into the fall season, while the disappearance rate dropped to zero, demonstrating the gradual build-up of the population.

With the winter season, the rates again stabilized indicating the population was leveling off. The accidental deaths during the snow of February 1971 shifted the rates in the direction of disappearance resulting in an unnatural balance. The first two months of the winter indicated a more natural balance.

Gentry and Odum (1957) have stated that weather has a marked effect upon the activities of small mammals, as evidenced by the number of captures. Results of this investigation indicate that overcast nights appeared to favor greater activity than did clear nights, while activity was greater on nights with drizzling rain over nights which had a substantial rainfall, even though this rain may have been for a short duration. On nights of climate change (e.g. frontal activity) and for one or two nights thereafter, activity was reduced. These findings were in agreement with those of Gentry and Odum (1957) and Hirth (1959).

Activity of the population declined as the temperature increased. The minimum temperature seemed to be the more important as the activity of the mice remained high when average high temperatures were similar (May and June). A sharp decrease in activity appeared when the average minimum temperature reached around 60° Fahrenheit and continued to decline until the average minimum temperature fell below 50° Fahrenheit.

Minimum temperatures are, perhaps, more influential than maximum because these are normally night temperatures which is the activity period of the nocturnal mice. Low minimum temperatures appeared not to discourage activity as these mice do thrive when sufficient food and nesting material are available (Howard, 1951). High temperatures can be endured, although several small rodents apparently lack sufficient cooling systems (Dice, 1922; and Howard, 1951). The summer temperatures, especially the minimum temperatures, did not approach critical levels for survival but apparently were high enough to lessen activity.

The driest period of the year was also during this period. The Baxter soil, containing large amounts of chert, may have allowed rapid drainage of the moisture that was available. The dryness combined with the highest temperatures, both maximum and minimum, may have had substantial effect on the population decline which was taking place at this time.

The population decline does not seem to be responsible for the decline in activity as the average number of captures per individual per month also declined.

Perhaps another explanation for this decline in activity is that the decline may have been in trap response rather than in activity. Abundance of invertebrates and plant food in summer may lower bait acceptance resulting in a lowered activity as indicated by trapping whereas, in actuality, there may have been no activity decrease at all (Fitch, 1954).

The question of the relation between temperature and activity patterns seems to be one warranting further investigation.

The white-footed mouse population maintained a stable number during the first five months of this study. During this time stress of high population density forced some, apparently the more submissive and juveniles, to occupy marginal habitat. Average home range size was also reduced. When spring foliation had progressed enough to allow more of the study area to be utilized a shifting of the population occurred relieving the high density situation slightly.

In addition to the high density, this population was subjected to an unbalanced sex ratio in favor of the males. This, however, was probably important only in regard to the intraspecific contacts with other males, as the available area of suitable habitat was saturated with females (Burt, 1940). Perhaps more important was the tendency toward an old population (Odum, 1959). Recruitment, which remained constant throughout most of the study, was apparently insufficient to relieve this situation.

During the summer season a population decline began, culminating during September. Various factors may be attributed to this decline, although all are hypothetical. The tendency toward old age of this population may have resulted in too few animals available to replace the natural disappearance of animals due to various factors, such as predation. The stress situation of high population density combined with the decreasing favorability of the weather (the study area received the highest temperatures and the lowest amount of rainfall during this time), may have forced the possible emigration away from these situations (Pruitt, 1959). Perhaps indicating this emigration was the capture of one previously marked mouse in the woods northwest of the study area during the September-October intertrap period and the reappearance of this mouse on the study area along with another individual which had been present both before and after the September period.

The stress of the weather situation may be reflected in the fact that during the September period the only animal recorded was a short-tailed shrew captured in the grass region. Since shrews are usually confined to habitats of moist soil with a thick layer of ground debris (Burt, 1940; and Pruitt, 1959), this capture, in totally unsuitable habitat, may indicate the extreme conditions operating in the study area during this time.

Following this population decline the numbers of mice slowly began to build up. Because of fewer numbers of mice present, the average home range expanded with the individuals occupying previously vacant portions of suitable habitat. It is doubtful if the interspecific interactions with the prairie voles played a major part in excluding the mice from the grass region. The sex ratio and age structure of the population assumed a more favorable appearance and the recruitment and disappearance rates tended to stabilize as the numbers increased. These factors seem to indicate a return to a stable population.

SUMMARY

A thirteen month study was conducted on a population of white-footed mice located in an old-field situation on the Austin Peay State University farm.

This population was found to have an abnormally high ecological density during the early months of the study. High population pressures apparently forced a reduction of home range size and forced some of the members of the population, apparently the more submissive and the juveniles, to inhabit less suitable habitats of the area.

Habitat selection seemed to be correlated with protective cover as movement of the population accorded with the increase of foliation in the spring and with the decrease in the fall.

A decline in numbers began in July culminating in September when no mice were taken on the study area.

This decline appears to have been the result of a diversity of factors. A tendency toward old age of the population may have had an important influence, although the disproportionate sex ratio in favor of the males probably was not a major factor in this decline. Perhaps of greatest importance to this decline was the high temperatures, both maximum and minimum, combined with low amounts of rainfall may have forced the mice to migrate from the hot and dry conditions prevailing during this period.

After this population decline the mice present returned to the more suitable areas of habitats (reduced population pressures seemed more important than inter-specific strife in this movement) and the average home range increased.

Measurable population parameters seemed to indicate that the population was returning to a stable condition.

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