AN ABSTRACT OF THE THESIS OF

Jerome Stafford Smith for the Master of Science degree in
(Name) (Degree)

Wildlife Management
(Major)

Date thesis is presented May 14, 1964

Title: Effects of Dispersion and Parent Population Density on Enclosed Populations of *Microtus montanus* (Peale).

Abstract approved [redacted]

This field investigation was designed to further the understanding of the significant influence which parent population density, as well as dispersion, have on the dynamics of enclosed populations of the montane vole, *Microtus montanus* (Peale). The study was conducted in Klamath County, Oregon from June, 1963 to February, 1964. The objectives were to investigate possible effects of parent population density on such characteristics of the ensuing generations as density, reproduction, survival, and movement, and to determine the effects of dispersion on a population. Four one-quarter acre enclosures were used during this study. Two contained voles from a 1962 high parent population density (E 4 and E 6) and two contained voles from a 1962 low parent population density (E 5 and E 7). A means for mice to disperse was provided in two enclosures (E 5 and E 6), one enclosing mice from

a low parent population, the other, mice from a high parent population. All population characteristics were determined by live trapping from three to five days at two to six week intervals.

The enclosed populations had comparable peak densities during December, with the exception of E 4 which was significantly lower than E 7. The ratio of increase was greatest in E 4 and E 6. E 6 supported the largest number of mice and E 4 the smallest. Males were dominant in E 4 and E 7 through most of the study. Females were dominant in E 5 throughout the study and in E 6 until December. E 5 and E 6 supported a larger percentage of young animals then did E 4 or E 7. E 4 had the highest average percent of females perforate, pregnant, and with mammary glands large or lactating; E 6 had the next highest percentages and E 5 and E 7 the smallest. Reproduction stopped in all enclosures after the November trapping period. All enclosures had very good survival through December but poor survival through January. The poor January survival was probably due to the presence of tularemia within the enclosures. E 4 and E 6 had consistently better cohort survival throughout the study than did E 5 and E 7. Juveniles survived best in all enclosures until August, after which time the sub-adults and adults had the better survival rate. E 6 had statistically better mean survival through December than did E 4 or E 7, and through January than either E 5 or E 7. The dispersal ramps captured 2.73 times more animals from E 6 than from E 5. During the study juvenile and sub-adult females and sub-adult and adult males were the only age classes of mice captured in the ramps until November when adult females were first caught. Most sacrificed dispersal males were found to be in breeding condition while only a few of the females had bred. Captures per ramp day were generally density dependent.

Some differences observed in the population characteristics of the four enclosures can be attributed to parent population density and/or dispersion. High parent population density did not adversely affect reproductive potential or the survival of a vole after it had become established in a population. Prenatal mortality and the amount of wounding, an indication of intraspecific strife, was greatest in the enclosure with mice from a high parent population density and where dispersion was not allowed. Where dispersion was allowed recruitment was high, survival was good, and the amount of wounding was low regardless of parent population density. It is suggested that animals from a high parent population are selected for aggressiveness which eventually causes a disruption of the social structure. Dispersal tends to maintain a stable social structure until populations become dense, at which time dispersion is a less effective regulatory mechanism.

EFFECTS OF DISPERSION AND PARENT POPULATION DENSITY ON ENCLOSED POPULATIONS OF *MICROTUS MONTANUS* (PEALE)

by

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A THESIS

submitted to

OREGON STATE UNIVERSITY

in partial fulfillment of
the requirements for the
degree of

MASTER OF SCIENCE

June 1964

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Date thesis is presented May 14, 1964

Typed by Josephine Schuh

ACKNOWLEDGMENTS

Sincere thanks are given to Mr. Edward L. Hansen, Instructor, Department of Fish and Game Management, Oregon State University, for his supervision, guidance and assistance throughout the study. My deepest appreciation is given to Dr. Thomas Scott, Department Head, and Mr. Lee Kuhn, Associate Professor, Department of Fish and Game Management, Oregon State University, for their helpful criticism in the preparation of this thesis. I am also grateful to Mr. Lonnie Belden, Graduate Research Assistant, for his assistance during part of the field work and to Mr. James Munn for the preparation of some figures used in this thesis. Land upon which the enclosures were built was provided by Mr. E. A. Geary, to whom I am very grateful.

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INTRODUCTION

This field investigation was designed to further the understanding of the significant influences which parent population density as well as dispersion have on the dynamics of enclosed populations of the montane vole, *Microtus montanus montanus* (Peale). The field work for this study, began in June, 1963, and terminated in January, 1964, was done on the E. A. Geary Ranch, which is located eight miles Northwest of Klamath Falls, Oregon. The objectives were: 1) to investigate possible effects of the parent population density on such characteristics of ensuing generations as density, reproductive rate, survival, and movement, and 2) to determine the effect of dispersion on a population. During this study four one-quarter-acre enclosures located in optimum vole habitat were used. Two enclosures contained voles from a low 1962 parent population and two contained voles from a high 1962 parent population. A means for mice to disperse was provided in two enclosures, one enclosing mice from a low parent population, the other, mice from a high parent population.

In April, 1958, a research project was started in Klamath County by the Oregon Agricultural Experiment Station through the Department of Fish and Game Management at

Oregon State University. The project was titled, "The Life History of the Meadow Mouse, Microtus montanus in Oregon, with particular reference to factors influencing seasonal and annual population trends". Since October, 1960, the program has received additional support from the U. S. Public Health Service (Research Grant 7758). A primary objective of the investigation was to ascertain a reliable method for predicting population increases of meadow mice. From this objective several secondary aims were derived. Since June, 1961, graduate students have been assigned to these secondary objectives as partial fulfillment of the requirements for advanced degrees. This study is such a phase of the project.

The history of microtine fluctuations and the resulting devastation to man has been recorded since Biblical times. Vole irruptions, with spread of disease and extensive destruction have been common in Europe and Asia for many centuries. Elton (14, p.1-11) cites records of major vole outbreaks in Europe, which occurred at the rate of two or three per century since 1271.

There are only a few records of vole plagues in this country. Elton's (14, p.107-108) account of the 1907 vole outbreak in Humboldt Valley, Nevada, reports that four-fifths of the crops were completely destroyed. Hamilton (18, p.788-789) described the years of mouse abundance in New York during which heavy damage was inflicted to field crops and orchards. Possibly one of the worst outbreaks of meadow mice in North America occurred in the Klamath Basin of Oregon and Northern California beginning in the summer of 1957 and continuing until the spring of 1958. This irruption seriously affected a total of 110,000 acres of cropland in Oregon (31, p.3) with a loss to agriculture of an estimated $2,000,000, (26, p.6).

Population fluctuations of Microtines and other rodents have been investigated for many years and in many places, yet these fluctuations have not been satisfactorily explained. In the past 20 years, some investigators have begun using pens or enclosures in the study of mouse populations. Louch (25, p.701-712) used indoor pens containing *Microtus pennsylvanicus pennsylvanicus* (Ord) in order to test the hypothesis that high population density constitutes a stress factor which may limit population growth. Chitty (6, p.57-67) used indoor pens to "re-examine without prejudging its truth or falsity, the idea that a change in the condition of the individuals may be reflected in the vitality of their descendents". Large open-air concrete cages were used by Clarke (9, p.68) in an investigation to determine if intraspecific strife was the primary cause of population cycles in voles.

It is a biological fact that dispersal of some members of every species at some stage of the life cycle is essential for the existence of that species (20, p.1).

To understand this fact we must ask ourselves three questions: 1) What is dispersal? 2) What causes dispersal? 3) How does dispersal affect the wild population? According to Dice (12, p.338), dispersal is "a regulatory mechanism which operates to maintain uniformity and stability in communities." Kendeigh (23, p. 145) defines dispersal as "the spread of individuals away from their homesites." Dispersal is described by Howard (21, p.152) as "the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate." Dispersal may be caused by factors such as: loss of food supply, loss of homesites, mate selection, territoriality, parental ejection, or crowded conditions. Population pressure, according to Kendeigh (23, p.150), "is doubtless the most potent force inducing dispersal." Howard (21, p.152) describes dispersal as being either innate or environmental. Innate dispersal is when individuals "are predisposed at birth to disperse beyond the confines of their parental home range." Environmental dispersal is "the movement an animal makes away from its birthplace in response to crowded conditions." Howard further states that innate dispersal is independent of density and may be the result of heredity, but environmental dispersal is density dependent, and caused by population pressure. Little information is available on the effects dispersion has upon population density, survival, reproduction, and sex and age composition of wild populations. Howard (20, p.1-52; 21, p.152-160), who studied the dispersal movements of the prairie deer mouse, <u>Peromyscus</u> <u>maniculatis</u> <u>bairdii</u>, (Hoy and Kennicott) points out that innate dispersers 1) increase the spread of new genes 2) create wide outbreeding 3) enable a species to spread its range rapidly as favorable habitats are created 4) permit the species to have a continuous distribution, and 5) help the species quickly to reinvade areas that may have been depopulated by catastrophes such as floods, fires, or man's activities. Howard further states that dispersal traits might be sex-linked, for about two males disperse for each female, and that dispersal takes place only when deer mice reach sexual maturity.

The influence of parent population density on subsequent generations is not well understood or documented. Chitty (8, p.99-113) found that susceptibility to natural hazards increased among generations descended from animals affected by adverse environmental conditions, and that the change in environment, as a necessary antecedent to decline in numbers, is not simply an increase in density, but a change in the nature and frequency of the interactions. He expresses the opinion that it is not known how to observe or quantify these interactions. Chitty (7,p.505-552) also presents the view that the intensity of mutual strife during the breeding season largely predetermines the chances of increased mortality during the following 1-2 years. Clarke (9, p.68-85) studied two populations of *Microtus agrestis* in large, cement, open-air cages. One population started with four times as many animals as the other. The larger initial population (P2) contained only slightly greater maximum numbers in its second year compared to the first year. Breeding began a month earlier in the second year of the lower population (P1) as compared to P2. Also in P2 the fertility and infant survival was much less in the second than in the first breeding season. Agressiveness was more severe in the larger population.

STUDY AREA

The study area is located about eight miles northwest of Klamath Falls, Oregon, on the E. A. Geary Ranch. This ranch consists of 5,000 acres of cropland and pasture under flood-type irrigation. Crops grown are cereal grains of various types and bent grass *Agrostia palustria* (Hudson). The pasture vegetation is predominantly meadow foxtail *Alopecurus pratensis* (L.), bluegrass *Poa pratensis* (L.), and bent grass.

The muck-type soil of the region consists of well decomposed organic material from one to several feet in depth. The substratum is clay. The water table normally fluctuates from a few inches below ground level in winter to about 18 inches below ground level in summer. The study area may be partially flooded in the winter months due to flooding of the surrounding pasture by Mr. Geary, or because of heavy winter precipitation.

Precipitation for this area averages about 14 inches per year. About two inches comes as rain during the months of June, July, August, and September. The remaining 12 inches of moisture is evenly distributed over the following eight months.

The average yearly temperature for Klamath Falls is 48.3° F. The warmest month is July with a mean of 68.7° F and the coldest month is January with a mean temperature of

29.4° F. (30, p.230-236).

During this study, the summer was cooler and the fall warmer than usual, with slightly more precipitation than the 30-year normal. Table I gives a month by month breakdown of averages and departures from normal of the temperatures and precipitation recorded from June, 1963, through January, 1964.

Table I. Average monthly temperature in Fahrenheit degrees, departure from 30-year normal and monthly precipitation in inches recorded at Klamath Falls, Oregon from June, 1963 through January, 1964.

	TEMPERATURE IN DEGREES F.		PRECIPITATION IN INCHES	
MONTH	AVERAGE	DEPARTURE FROM 30-YEAR NORMAL	TOTAL	DEPARTURE FROM 30-YEAR NORMAL
June	57.3	-2.8	1.37	.42
July	62.1	-6.6	.02	-.29
August	64.1	-2.8	.88	.55
September	62.2	1.8	.04	-.56
October	49.2	-0.8	1.25	.10
November	38.0	-0.5	2.11	.50
December	33.2	1.0	.70	-1.51
January	27.8	-1.6	3.83	1.72

METHODS

Four one-quarter-acre enclosures, two with dispersal ramps, two without dispersal ramps, were utilized during this project. Two enclosures contained *Microtus* from a high 1962 parent population and two were stocked with *Microtus* from a low 1962 parent population. Each enclosure was live trapped from three to five days, at intervals of two-six weeks throughout the study. The two dispersal ramps were opened periodically each month through November. The population density, sex and age composition, reproduction, survival, and movement, were determined and compared for the populations within each enclosure. Figure I summarizes the experimental design for this study.

Enclosures

The four enclosures used during this study were constructed during the Spring of 1961. Each enclosure was approximately one-quarter acre in size (104 feet by 104 feet).

Since "mouse proof" enclosures were desired, each enclosure was fenced with 36-inch wide, one-quarter-inch mesh, hardware cloth. This material was buried 18 inches in the ground with the lower six inches turned inward to prevent mice from burrowing beneath the fence. Tar was used on the buried material to prevent rust. To prevent mice from climbing over the fence, aluminum strips were used to cover the

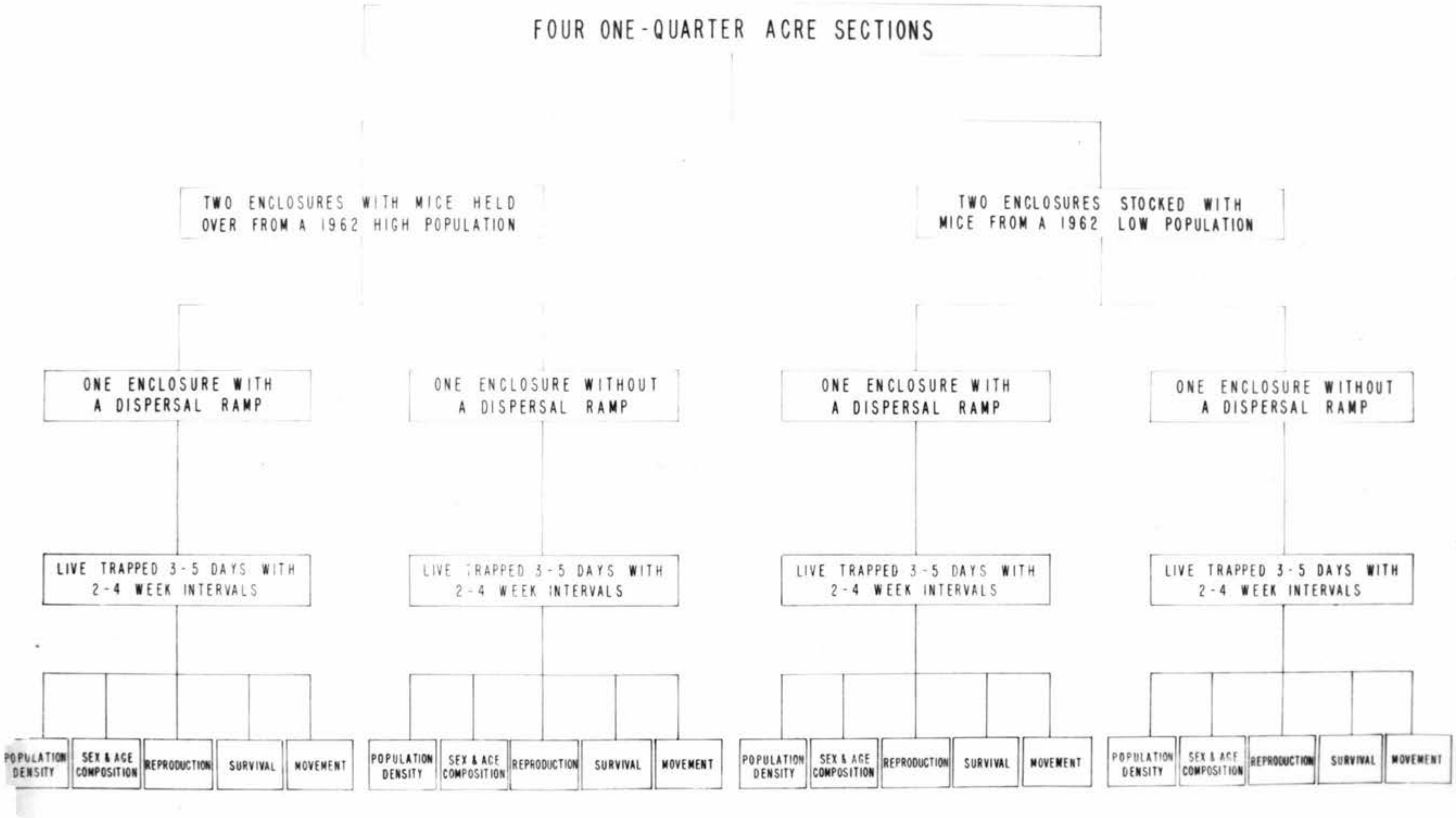

Figure 1. Experimental design for the study.

top six inches of the hardware cloth. The fence was attached to steel posts spaced at 12-foot intervals. Two strands of barbed wire were strung around the top to keep out cattle.

Vegetation within the enclosures was predominantly meadow foxtail, bluegrass, and bent grass. Composition and density of the vegetation at the beginning of the study was approximately the same in each enclosure.

One objective of this study was to determine whether parent population density had any influence on the ensuing generations. To satisfy this objective, the enclosures contained mice from what was believed to be two distinct population phases. The initial density, sex, source, and the 1962 peak density per acre for the mice released in the enclosures is shown in Table 2.

Enclosure five (E 5) and enclosure seven (E 7) were stocked with voles from a low parent population. Prior to the time of stocking, both enclosures were live trapped and all mice were removed. The mice stocked in E 5 and E 7 came from Caledonia-3 pasture, on the E. A. Geary Ranch, which had a July, 1962, peak population of 75 <u>Microtus</u> per acre. On July 31, 1962, this area was poisoned with toxaphene. In September the <u>Microtus</u> density was 20 per acre. This pasture was flooded in October, 1962 and again in January, 1963. Sixteen adult <u>Microtus</u> were live trapped in Caledonia-3 pasture on May 18 and 24, 1963. Eight were placed in E 5 and eight in E 7.

Table 2. Initial density, sex, source, and the 1962 peak density per acre of the parent populations of *Microtus* that were released in the enclosures from May 18, 1963 to June 7, 1963.

Enclosure	Initial Density	Number Males	Number Females	Source	1962 Peak Density Per Acre
MICE FROM A HIGH 1962 PARENT POPULATION					
4	5	2	3	1-E 4 1-E 2 3-E 7	792 480 812
6	5	2	3	1-E 1 2-E 6 2-E 5	420 670 592
MICE STOCKED FROM A LOW 1962 PARENT POPULATION					
5	8	4	4	Caledonia 3	75
7	8	4	4	Caledonia 3	75

Enclosure four(E 4) and enclosure six (E 6) were classed as having voles from a high 1962 parent population. Both enclosures were live trapped June 4-6, 1963. Only one mouse was captured in E 4 and two in E 6; these mice were left in their respective enclosures. To increase the density of the enclosures to a level as comparable as possible with E 5 and E 7, four mice were added to E 4 and three to E 6. These mice came from enclosures stocked in 1962 which had reached peak population densities ranging from 420 to 812 *Microtus* per acre.

During the summer of 1963 the enclosures were irrigated to allow maximum vegetation growth. Water was pumped from a large nearby canal into smaller irrigation ditches within the enclosures.

Three feeding stations were placed in each enclosure on October 23, 1963. Each week during the remainder of the study from 8 to 18 pounds of feed oats were placed at the feeding stations within each enclosure. To provide additional food supplement as well as to provide dry nesting facilities, baled hay was placed in the enclosures during November.

The enclosures were periodically inspected for signs of damage to the fence or for burrows underneath the fence. While examining the fence on August 29, several holes large enough for mice to pass through were discovered. Only one of the holes located in E 5, showed sign of use. Two nights of extensive trapping around the enclosures yielded only one marked mouse. The total number of mice which entered or left the enclosures will never be known. However, based upon results of extensive trapping in and around the enclosures, I believe the number of mice which may have moved is too small to be significant in the conclusions reached.

During this period, several mice which were marked and released in one enclosure were later caught in an adjacent enclosure. In each case the mice were adult males. I inspected the fences but found no holes large enough for a mouse to pass through. It is believed that the mice may have used over-hanging vegetation or deep burrows to cross over or under the barrier. Since the number of mice escaping into another enclosure was very small, I do not believe that this activity affected the accuracy of the findings to any significant degree.

Dispersal Ramps

Prior to the initiation of this study, one dispersal ramp was attached to E 5 and one to E 6. Each ramp was designed to provide a means for the mice to move out of the enclosure, and at the same time provide relatively adverse conditions, thus making it unlikely that any mice other than dispersal mice would use the ramp.

Each dispersal ramp was two feet wide and 16 feet long, and constructed from one-quarter-inch plywood. The first eight feet of the ramp sloped upward at approximately a 25 degree angle. The second eight feet was horizontal. Four 2 X 4 inch wooden posts, three feet high, supported each ramp. Protruding above the plywood floor and surrounding each ramp was 18 inches of one-quarter-inch mesh hardware cloth. The hardware cloth was capped with three inches of tin (Figure 2). Each ramp had a plastic bucket located at one end and directly beneath a 4 X 4 inch opening in the plywood floor. Covering each opening were two tin treadles in a wooden, open-end, shelter box. A mouse would go up the ramp, into the shelter box, step on a

Figure 2. Dispersal ramp.

treadle and fall into the bucket. Movement from each enclosure to its ramp was permitted through a 4 X 20 inch opening in the enclosure fence. When closure of the dispersal ramp was desired, two pieces of tin were bolted together over the opening.

The dispersal ramps were first opened July 1, 1963. They were opened an average of 17 days each month for the months of July, August, September, and October. Due to inclement weather, a factor which may disrupt the pattern of dispersal movement, the ramps were opened only three days in November, not at all in December or in January.

When a mouse was caught in a dispersal ramp, it was removed and placed in captivity. Records kept on each mouse included: sex, age, weight, reproductive status, previous trapping data, and ramp number. Ramp 5 was the dispersal ramp for E 5 and Ramp 6 the ramp for E 6.

Live Trapping

A grid of 41 trap stations was established within each enclosure. In addition to this basic grid, 12 stations were placed around the perimeter within each enclosure, with three stations along each side. For a complete picture of the trap stations and the distance between these stations, refer to Figure 3. Sherman and Longworth live traps were used in each of the four enclosures during this study. The number of traps in each

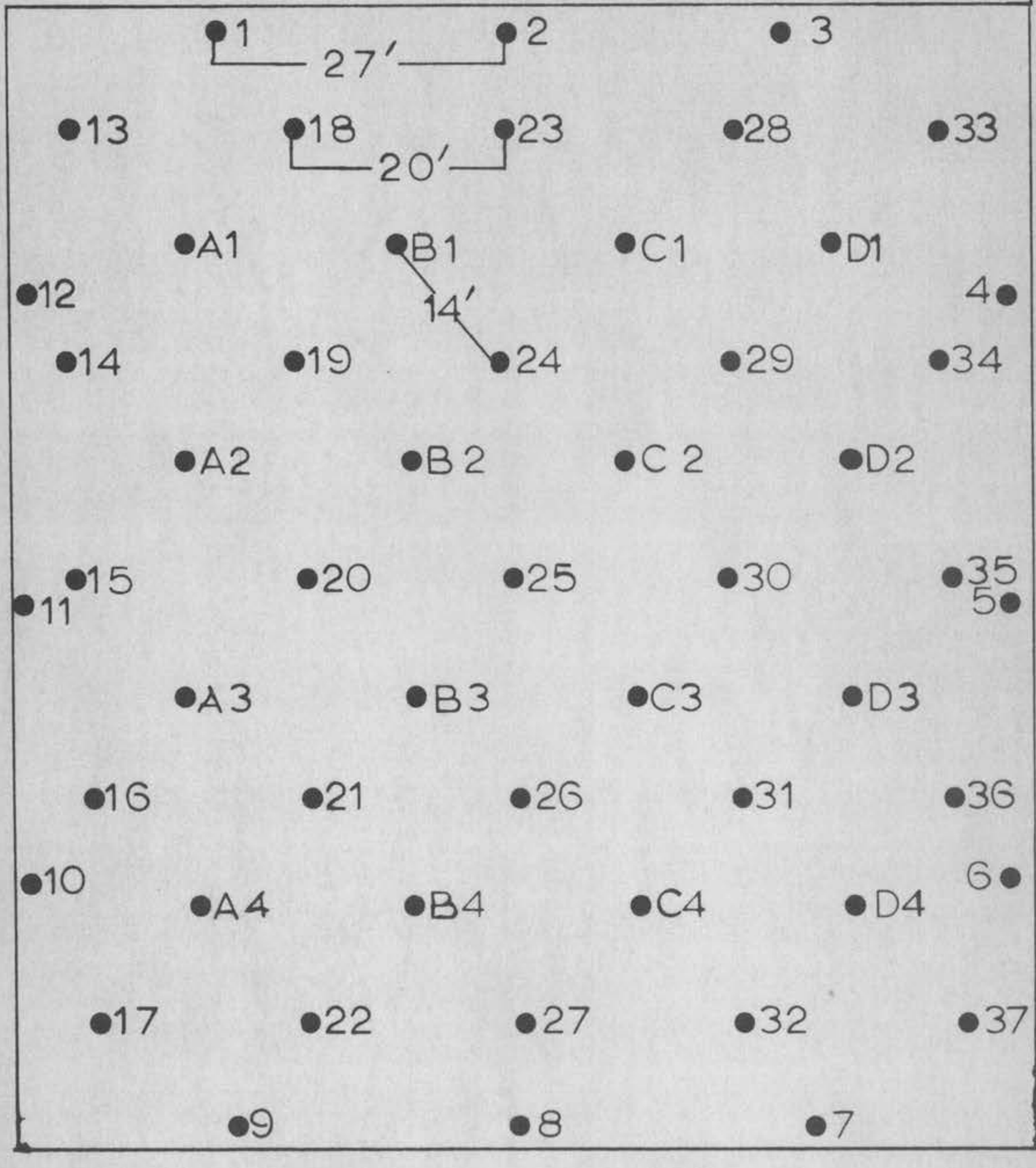

Figure 3. Trapping stations and the distance between stations as used in this study.

enclosure during a trap period was either 37, 53, 65, 74, 78, or 106, depending upon population density.

During this study two enclosures (E 4 & E 6) were live trapped eight times and two enclosures (E 5 & E 7) were live trapped nine times between June, 1963, and January, 1964. Each trap period was from three to five days in length. Each enclosure was live trapped for the first time approximately one month after the initial stocking took place. The time lapse between trap periods varied from two to six weeks.

The live traps were baited with whole oats, set in the evening, and checked the following morning. A complete record was kept on each captured mouse. This record included: location of capture, sex, age, reproductive status, weight, notes on wounds, and signs of disease or abnormalities. Identification of the mice was accomplished by attaching metal, fingerling fish tags to the right ear and toe clipping. Each mouse was weighed on a spring scale calibrated at 10-gram intervals.

Determination of Population Density

The population density of each enclosure per trap period was calculated by the mark and recapture method using the Lincoln index as described by Davis (11, p.17). During each trap period, the last day was considered the recapture day; all other days were marking days.

Confidence limits were calculated at the five percent significance level, as described by Davis (11, p.19).

Determination of Sex and Age Ratios

Sex determination was not difficult except in juveniles and during the non-breeding season. When not obvious, sex was determined by noting the distance between the anus, and penis or clitoris. This distance is considerably greater in males than in females. The sex ratio was calculated on the proportion of males per 100 females.

Age was determined on the basis of size (weight) and pelage (19, p.81, and 13, p.249-254). The mice were classed as juveniles, sub-adults, or adults.

Determination of Reproduction

In *Microtus*, the vaginal orifice becomes perforate as the female becomes mature. This is the case during the actual breeding season. In the winter or non-breeding season, the females, as a rule, have imperforate vaginas. Reproduction for each enclosure was based on the percentage of adult and sub-adult females having: 1) open vulvas - a sign of breeding condition, 2) nipples large or lactating - a sign of recent suckling by young, and 3) palpable pregnancies. Embryos can be readily detected by palpation during the last two-thirds of the 21-day gestation period, when embryo length is from 6-9 mm. Greenwald (17, p. 213) gives a lactation period of 14 days for *Microtus californicus*. Thus, reproductive success can be estimated by comparing the number of lactating females to the number of previously detected pregnancies.

Determination of Survival

The mice captured for the first time during any particular trap period were considered a distinct cohort. These animals were added to the population either by recruitment since the previous trap period, or were present but not captured during the previous trap periods. Minimum survival rates were obtained through analysis of recapture data kept on each mouse. These rates show the percentage of mice from each cohort recaptured during each trap period. The survival rate is calculated only for animals live trapped and does not include mice found dead or those caught in the dispersal ramps.

Determination of Movement

Movement was calculated for each enclosure, by measuring the average distance mice moved between successive captures. The average distance (av. D.) method was described by Brant (2, p.126) as being an index of movement. This measure was used to compare the relative size of movement patterns in the four enclosures and to determine the changes of the patterns that may be related to seasonal changes in density, breeding, parent population density, or dispersal movement. Measurements of distances moved were made on a scale diagram of the trap arrangement. The average distance moved was determined only for animals captured three or more times in a particular trap period.

RESULTS

Trap Period Designation

Due to the high densities obtained in each enclosure, it was not possible to trap all enclosures at one time. To assist in the analysis of the data, the trap periods are designated as shown in Table 3. The trapping dates for the different enclosures may have been close together and still have fallen in different months. When this happened the enclosures were considered to have the same trapping period. An example of the above situation is the September-I trapping period in which E 4 and E 6 were trapped from August 27-29 with E 5 and E 7 being trapped from September 4-6. Unless otherwise noted, all reference to particular trap periods in the following pages are based upon the above-mentioned trap period designations.

Population Density

The population estimate, density per acre, total *Microtus* captured, ratio of increase, and the number dead in traps for each trap period, is given in Table 4. The population trends and confidence limits at the five percent significance level are shown in Figure 4. Comparisons of the populations are based upon the population estimate, not upon the total mice captured, because there were always some mice that were not captured during a particular trap period.

Table 3. Trap period designation, June, 1963 through January, 1964.

Designation	ENCLOSURES 4	5	6	7
June	————	June 25-29	————	June 25-29
July	July 9-12	July 15-18	July 9-12	July 15-18
August	Aug. 6-9	Aug. 13-17	Aug. 6-9	Aug. 13-17
September-I	Aug. 27-29	Sept. 4-6	Aug. 27-29	Sept. 4-6
September-II	Sept. 17-21	Sept. 23-27	Sept. 17-21	Sept. 23-27
October	Oct. 9-12	Oct. 15-19	Oct. 9-12	Oct. 15-19
November	Oct. 29-Nov. 2	Nov. 5-7	Oct. 29-Nov. 2	Nov. 5-7
December	Dec. 3-7	Dec. 3-7	Nov. 20-23	Dec. 3-7
January	Feb. 4-8	Feb. 4-8	Jan. 14-17	Feb. 4-8

Table 4. Population estimate, density per acre, total mice captured, ratio of increase, and the number dead in traps for the enclosures from June, 1963 to January, 1964.

Trap Period Designation	Total Captured	Population Estimate	Density Per Acre	Ratio of Increase	Dead in Trap
E 4					
July	9	9±0	36	1.8	0
August	27	30±8	120	6.0	0
September-I	36	39±7	156	7.8	0
September-II	40	44±9	176	8.8	1
October	57	62±10	248	12.4	2
November	71	81±17	324	16.2	4
December	205	269±43	1,076	53.8	1
January	59	69±18	276	13.8	3
E 5					
June	13	13±4	52	1.6	0
July	14	15±3	60	1.9	0
August	25	27±6	108	3.4	0
September-I	25	26±5	104	3.3	0
September -II	47	51±9	204	6.4	0
October	68	81±18	324	10.1	0
November	94	122±29	488	15.3	3
December	255	345±54	1,380	43.1	1
January	34	47±22	186	5.9	0
E 6					
July	7	7±0	28	1.4	0
August	29	37±17	148	7.4	2
September-I	41	45±9	180	9,0	0
September-II	80	91±18	364	18.2	3
October	117	124±17	496	24.8	10
November	165	195±27	780	39.0	2
December	210	295±53	1,180	59.0	0
January	83	115±35	460	23.0	0
E 7					
June	5	5±0	20	.6	0
July	19	19±0	76	2.4	0
August	38	39±7	156	4.9	3
September-I	42	50±14	200	6.3	0
September-II	63	71±15	284	8.9	2
October	76	98±51	392	12.3	2
November	134	185±41	740	23.1	5
December	248	409±84	1,636	51.1	0
January	46	82±52	328	10.3	0

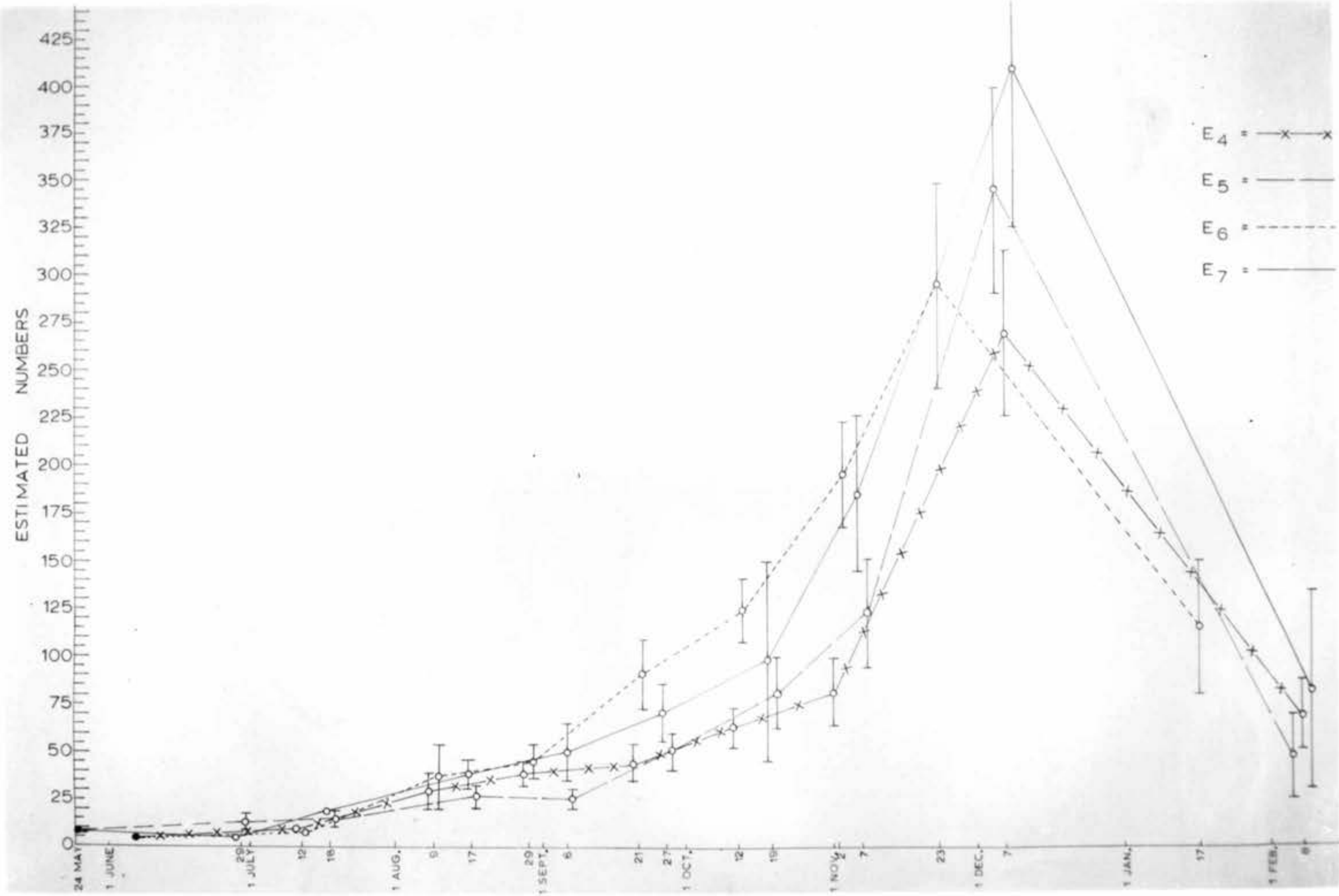

Figure 4. Estimations of numbers of mice and confidence intervals for E 4, E 5, E 6, and E 7 from June, 1963, to January, 1964.

The estimated densities of the four enclosures increased gradually from a July estimate of 36, 60, 28, and 76 *Microtus* per acre for E 4, E 5, E 6, and E 7, respectively, until November when the estimate was 324, 488, 780, and 740. Between the November and December trapping period each enclosure sharply increased and reached peak densities of 1,076, 1,380, 1,180, and 1,636 mice per acre for E 4, E 5, E 6, and E 7, respectively. Following the peak density of December, each enclosure declined sharply to a January density of 276, 186, 460, and 328 mice per acre for E 4, E 5, E 6, and E 7, respectively.

Based upon the population estimates, a ratio of increase from initial densities can be calculated. By determination of a ratio of increase, it can be seen that peak densities were 53.8 and 59.0 times greater than the initial populations in E 4 and E 6, respectively. E 5 and E 7 had a ratio of increase to peak density of 43.1 and 51.1 times, respectively.

During this study E 4 possessed a significantly higher density than E 5 only in the September-I trapping period. E 4 was significantly lower than E 6 during the trapping periods of September-II, October, and November. In the trap periods of September-II, November, and December, E 4 had significantly lower densities than did E 7. With the exception of the December trapping period E 5 had significantly lower population densities than E 6 from September-I until the end of the study. September-I was the only trapping period when E 5 was significantly lower than E 7. The population estimates of E 6 and E 7 were never significantly different during this study.

An index to total recruitment for each enclosure can be obtained by knowing the total number of new mice captured during the study. Total mice captured in E 4, E 5, E 6, and E 7 were 282, 346, 383, and 355, respectively. These numbers include the untagged mice captured in the dispersal ramps in E 5 and E 6. By assigning the largest number the value of 1.00, the enclosures can be arranged as follows: E 6: 1.00, E 7: .93, E 5: .90, and E 4: .74. E 6 supported the highest number of mice, E 7 and E 5 intermediate numbers and E 4 the lowest number.

In summary, peak densities were essentially the same, except that E 4 was significantly lower than E 7. The ratio of increase was greatest in E 4 and E 6 throughout most of the study, E 4 and E 5 had consistently lower population estimates than did E 6 or E 7. The largest estimated populations were in E 5 and E 7 in December, E 6 supported the largest number of mice and E 4 the smallest, with E 5 and E 6 supporting intermediate numbers.

Sex and Age Composition

Sex ratios for each enclosure are given in Table 5. Males were more numerous in E 4 until October and in E 7

Table 5. Number of males and females and the sex ratio for E 4, E 5, E 6 and E 7 from June, 1963 to January, 1964.

Trap Period Designation	No. Males	No. Females	Sex Ratio
E 4			
July	6	3	200:100
August	18	9	200:100
September-I	18	18	100:100
September-II	22	18	122:100
October	26	31	84:100
November	27	44	61:100
December	104	101	103:100
January	29	30	97:100
E 5			
June	6	7	86:100
July	6	8	75:100
August	8	17	47:100
September-I	8	17	47:100
September-II	12	35	34:100
October	21	47	45:100
November	27	67	40:100
December	119	136	88:100
January	15	19	79:100
E 6			
July	2	5	40:100
August	12	17	71:100
September-I	16	25	64:100
September-II	36	44	81:100
October	50	67	75:100
November	77	88	88:100
December	115	95	121:100
January	52	31	168:100
E 7			
June	3	2	150:100
July	13	6	217:100
August	25	13	192:100
September-I	18	24	75:100
September-II	28	35	80:100
October	28	48	58:100
November	53	81	65:100
December	119	129	92:100
January	21	25	84:100

until September-I. Thereafter, with the exception of E 4 in December, females were dominant in E 4 and E 7. Females were predominant in E 5 throughout the study. In E 6, there were more females than males in every trap period except the December and January periods.

Table 6 gives the percent of juveniles, sub-adults, and the mean percent of young for each enclosure during each trapping period. Young animals are those classified as juveniles or sub-adults.

In July, E 4, E 5, and E 6 respectively, had 22, 7, and 14 percent young mice. E 7 had 68 percent young mice during July. The above percentages may be misleading because of the small size during July (19 or less total mice captured for each enclosure).

E 4, E 5, and E 6 respectively, had 37, 48, and 46 percent young animals during August. E 7 had only 24 percent young for the same period.

During the September-I trap period, E 4 and E 6 had considerably smaller percentages of young animals than E 5 and E 7. The percentages were: 9, 28, 7, and 38, for E 4, E 5, and E 7, respectively.

In the September-II trap period, E 5 and E 6 respectively had 28 and 33 percent young mice. During the same trap period, E 4 had 23 percent young, and E 7 had only 6 percent young animals.

The October trapping period showed only slight

Table 6. Percentage of juveniles and sub-adults, number of mice captured and the mean percent of young for the enclosures from June, 1963, to January, 1964.

Trap period Designation	Juveniles	Sub-adults	Total Mice Captured
E 4			
July	22	-	9
August	22	15	27
September-I	6	3	36
September-II	8	15	40
October	12	18	57
November	1	7	71
December	9	26	205
January	-	-	59
MEAN % YOUNG	23		
E 5			
June	23	54	13
July	-	7	14
August	48	-	25
September-I	12	16	25
September-II	13	15	47
October	7	26	68
November	14	16	94
December	10	39	255
January	-	-	34
MEAN % YOUNG	38		
E 6			
July	14	-	7
August	18	28	29
September-I	7	-	41
September-II	24	9	80
October	20	10	117
November	6	25	165
December	2	32	210
January	-	-	83
MEAN % YOUNG	30		
E 7			
June	-	-	5
July	26	42	19
August	8	16	37
September-I	-	38	42
September-II	-	6	63
October	5	21	76
November	6	31	134
December	10	23	248
January	-	-	46
MEAN % YOUNG	27		

differences in enclosure percentages. The percentages varied from a low of 26 percent young for E 7 to a high of 33 percent young mice for E 5.

In November, E 5, E 6, and E 7 respectively, contained 30, 31, and 37 percent young, and E 4 had only eight percent.

In December E 4, E 6, and E 7 respectively, had almost the same percentages of young, that is 35, 34, and 33. E 5 had a high of 49 percent young during this trap period. All of the enclosures had juveniles present during the December trapping period. During this trap period E 6 had the lowest percentage (2) of juveniles, while the other enclosures had nine or 10 percent juveniles.

There were no young animals captured during the January trapping period in any enclosure.

During this study the mean percent of young animals produced in E 4, E 5, E 6, and E 7 respectively, was 23, 38, 30, and 27.

In summary, males were dominant in E 4 and E 7 through most of the study. Females were predominant in E 5 throughout the study, and in E 6 until the December trap period. The percentages of young during July ranged from seven to 68 percent. In August, E 5 and E 6 had the largest percentages of young mice; E 7, the smallest. In September-I, E 5 and E 7 had the largest; E 4 and E 6, smallest. In the September-II period, E 4, E 5, and E 6 had almost equal percentages of young, while E 7 had the lowest. In October, all enclosures had between 26 and 33 percent young mice with E 6 having 20 percent juveniles and E 7 only five percent. During November, E 4 had the lowest percentage of young mice and E 7 the highest. In December, E 5 had the highest and E 4, E 6, and E 7 the lowest and almost equal percentages of young mice. January captures did not include any young mice. E 5 produced the largest mean percent of young and E 4 the smallest. Young animals exceeded or were close to 50 percent of the population in E 5 in August and December, in E 6 in August and in E 7 in July. In E 4, the percentage of young never exceeded 37 percent (August). E 5 generally had higher or close to the same percentages of young as the other enclosures, except during July.

Reproduction

Reproductive data showing the percentages of females perforate, pregnant, and with large or lactating mammary glands is given in Table 7. Also given in this table, is the average percent for the entire study of the above categories. Because breeding condition of males is difficult to determine in live animals, the male reproductive data is not presented. Due to the small number (less than 10) females captured in each enclosure before August, the following results are given only for trap periods from August

Table 7. The percentage of females perforate, pregnant, and mammary glands large or lactating for E 4, E 5, E 6, and E 7 from July, 1963, to January, 1964.

Trap Period Designation	Females Perforate	Females Pregnant	Mammary Glands Large or Lactating
E 4			
July	67	33	33
August	88	38	13
September-I	65	30	-
September-II	87	42	8
October	65	27	15
November	73	28	14
December	15	-	1
January	13	-	-
AVERAGE%	59	25	11
E 5			
July	65	25	-
August	47	33	-
September-I	64	20	11
September-II	54	20	10
October	53	26	13
November	22	2	10
December	13	-	0.9
January	11	-	-
AVERAGE %	41	16	6
E 6			
July	80	-	20
August	71	27	18
September-I	80	32	-
September-II	70	30	11
October	49	17	24
November	27	6	11
December	7	-	7
January	3	-	-
AVERAGE %	48	14	11
E 7			
July	33	50	25
August	62	18	-
September-I	92	8	-
September-II	60	20	11
October	40	13	22
November	25	7	18
December	6	-	2
January	12	-	-
AVERAGE %	41	15	10

through January.

Females Perforate

E 4 had over 65 percent of the females perforate during each trap period until December when the percentage dropped to only 15. With the exception of August (47 percent) E 5 had over 50 percent of its females perforate each trap period until November when the percentage declined to 22 percent. E 5 had 13 percent perforate females in December. During each trapping period until October, E 6 had 70 percent or over of its females perforate. In October, November and December, E 6 had 49, 27, and seven percent perforate females.

The largest percent (92) of perforate females for E 7 occurred during the September-I trapping period; the lowest percent (six) in December. All of the enclosures had perforate females in January. The percentages of perforate females in January are: 13, 11, 3, and 12, for E 4, E 5, E 6, and E 7, respectively. The average percent of females perforate from July through January are: 59, 41, 48, and 41 for E 4, E 5, E 6, and E 7, respectively.

Females Pregnant

E 4 had higher percentages of pregnant females in each trap period than any other enclosure with the exception of the September-I trap period when E 6 had 32 percent pregnant and E 4 had 30 percent. E 4 reached its highest percentage in September-II (42). The highest percentage of pregnant females in E 5 was in August with 33 percent. E 6 and E 7 had their highest percentages during September, E 6 in the September-I trap period and E 7 in the September-II trap period. The percentages of females pregnant in E 7 were consistently lower than in the other enclosures. The percentage of pregnant females was 28, 2, 6, and 7, for E 4, E 5, E 6, and E 7, respectively, in November. The November trapping period was the last time pregnant females were found in any enclosure. The average percent of females pregnant from July to January was 25, 16, 14, and 15, for E 4, E 5, E 6, and E 7 respectively.

Mammary Glands Large or Lactating

The peak percentages of females with mammary glands large or lactating occurred in October for all enclosures. The percentages for E 4, E 5, E 6, and E 7, are as follows: 15, 11, 24, and 22, respectively. The smallest percentages were in December with 1, 0.9, 7, and 2 percent for E 4, E 5, E 6, and E 7, respectively. The average percent of females with mammary glands large or lactating for the entire study was 11, 6, 11, and 10 for E 4, E 5, E 6, and E 7.

In summary, reproduction stopped sometime after the November trap period and before the December trap period. This is evidenced by the small percentage of pregnant females captured in November and by the fact that no pregnancies occurred in December. Also, in that month there was only a very small percentage of females with large or lactating mammary glands. The percentage of pregnant females was highest in E 5 in August, E 6 in September-I, and in E 4 and E 7 in September-II trap period. Some females were perforate in each enclosure during every trapping period. E 4 and E 6 had slightly higher over-all reproductive rates than did E 5 and E 7. E 4 had the highest average percent of females perforate, pregnant, and with large or lactating mammary glands. E 6 had the next highest percentages, and E 5 and E 7 had the lowest percentages.

Body Weights

The mean body weights for all animals captured within each enclosure during each trapping period after July were calculated and the results are shown in Table 8. In August there was no significant difference between enclosures. E 7 had the largest mean weight and E 5 the smallest. During September-I E 4 and E 6 had significantly higher weights than did E 5 or E 7. In September-II trap period mean body weights in E 4 were significantly higher than in E 5 or E 6; E 7 had weights significantly higher than did E 6. The mean body weights in October were significantly higher in E 4 than in E 6. During November E 4 had significantly higher body weights than any of the other enclosures. Mean body weights in December were significantly higher in E 4 than in E 5. E 6 had weights significantly higher than in E 4, E 5, and E 7. The weights in E 7 were significantly higher than in E 5. During January the mean body weights were similar, with no significant difference between the four enclosures.

In summary, the body weights in E 4, although not necessarily statistically significant, were higher than in E 5 throughout the study. E 6 had weights higher than E 4 only in September-I and December. E 7 had higher body weights than E 5 throughout the study except during September-I and November trap periods. The body weights in E 6 were slightly higher than those in E 7 during this study.

Table 8. The mean body weights for all animals captured in the enclosures during each trap period from August, 1963 to January, 1964.

Trap Period Designation	MEAN WEIGHTS IN GRAMS			
	E 4	E 5	E 6	E 7
August	43.7	38.4	41.7	45.5
September-I	50.6	44.4	51.5	44.2
September-II	52.6	46.2	44.5	49.1
October	50.0	45.0	44.6	47.2
November	49.5	43.8	43.2	41.0
December	39.5	35.8	42.4	39.5
January	43.1	42.6	42.8	44.0

Survival

Survival rates for the different age classes of each cohort are presented in Tables 9 through 12. Survival of the combined age classes is shown in Figures 5 through 8.

Initial Population:

The percentage of survival through December was highest in E 4 with 40 percent. E 5 and E 6 respectively, had intermediate percentages of 13 and 20, and E 7 had the poorest survival with no animals living until December. The only enclosure having mice surviving until January (34-week interval) was E 4 with a 20 percent survival (one mouse).

June Cohorts: (E 5 and E 7)

The survival of the June cohort until December in E 5 was 30 percent, and until January, 20 percent. In E 7, one animal made up the total June cohort and it survived only through August trap period. In E 5, 67 percent of the juveniles survived through December and January. The sub-adults had only 14 percent survival through December, with none surviving until January.

July Cohorts:

E 5 had only one animal in the July cohort. This mouse survived through the November trap period. Survival

Table 9. Survival of adults, sub-adults, and juveniles in E 4 from June, 1963, to January, 1964.

MONTH AGE	NO.	%	JULY NO.	JULY %	AUGUST NO.	AUGUST %	SEPTEMBER-I NO.	SEPTEMBER-I %	SEPTEMBER-II NO.	SEPTEMBER-II %	OCTOBER NO.	OCTOBER %	NOVEMBER NO.	NOVEMBER %	DECEMBER NO.	DECEMBER %	JANUARY NO.	JANUARY %
JUNE																		
ADULT	4	100	3	75	3	75	2	50	1	25	1	25	1	25	1	25	–	–
SUB-ADULT	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
JUVENILE	1	100	1	100	1	100	1	100	1	100	1	100	1	100	1	100	1	100
TOTAL	5	100	4	80	4	80	3	60	2	40	2	40	2	40	2	40	1	20
JULY																		
ADULT	3	100			3	100	2	67	2	67	2	67	1	33	1	33	1	33
SUB-ADULT	0	0			–	–	–	–	–	–	–	–	–	–	–	–	–	–
JUVENILE	2	100			1	50	1	50	1	50	1	50	1	50	1	50	–	–
TOTAL	5	100			4	80	3	60	3	60	3	60	2	40	2	40	1	20
AUGUST																		
ADULT	12	100					8	67	8	67	6	50	4	33	2	17	1	8
SUB-ADULT	4	100					4	100	3	75	3	75	3	75	2	50	–	–
JUVENILE	6	100					6	100	5	83	5	83	4	67	3	50	–	–
TOTAL	22	100					18	82	16	73	14	64	11	50	7	32	1	5
SEPTEMBER-I																		
ADULT	10	100							8	80	8	80	8	80	6	60	2	20
SUB-ADULT	1	100							1	100	1	100	1	100	1	100	–	–
JUVENILE	2	100							2	100	2	100	2	100	1	50	1	50
TOTAL	13	100							11	85	11	85	11	85	8	62	3	23
SEPTEMBER-II																		
ADULT	5	100									4	80	3	60	1	20	–	–
SUB-ADULT	5	100									4	80	4	80	3	60	–	–
JUVENILE	3	100									2	67	2	67	–	–	–	–
TOTAL	13	100									10	77	9	69	4	31	–	–
OCTOBER																		
ADULT	5	100											5	100	4	80	2	40
SUB-ADULT	9	100											8	89	7	78	–	–
JUVENILE	7	100											3	43	2	30	2	30
TOTAL	21	100											16	76	13	62	4	19
NOVEMBER																		
ADULT	19	100													14	74	4	21
SUB-ADULT	5	100													2	40	1	20
JUVENILE	1	100													1	100	–	–
TOTAL	25	100													17	68	5	20
DECEMBER																		
ADULT	84	100															12	14
SUB-ADULT	52	100															9	17
JUVENILE	19	100															–	–
TOTAL	155	100															21	14

Table 10. Survival of adults, sub-adults, and juveniles in E 5 from May, 1963, to January, 1964.

MONTH AGE	NO.	%	JUNE NO.	JUNE %	JULY NO.	JULY %	AUGUST NO.	AUGUST %	SEPTEMBER-I NO.	SEPTEMBER-I %	SEPTEMBER-II NO.	SEPTEMBER-II %	OCTOBER NO.	OCTOBER %	NOVEMBER NO.	NOVEMBER %	DECEMBER NO.	DECEMBER %	JANUARY NO.	JANUARY %
MAY																				
ADULT	8	100	5	63	4	50	3	38	2	25	-	-	-	-	-	-	-	-	-	-
SUB-ADULT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
JUVENILE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TOTAL	8	100	5	63	4	50	3	38	2	25	-	-	-	-	-	-	-	-	-	-
JUNE																				
ADULT	1	100			1	100	1	100	-	-	-	-	-	-	-	-	-	-	-	-
SUB-ADULT	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
JUVENILE	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TOTAL	1	100			1	100	1	100	-	-	-	-	-	-	-	-	-	-	-	-
JULY																				
ADULT	2	100					2	100	1	50	1	50	1	50	-	-	-	-	-	-
SUB-ADULT	8	100					7	88	4	50	4	50	3	38	3	38	3	38	-	-
JUVENILE	5	100					3	60	3	60	3	60	3	60	2	40	2	40	1	10
TOTAL	15	100					12	80	8	53	8	53	7	47	5	33	5	33	1	7
AUGUST																				
ADULT	13	100							9	69	9	69	5	38	5	38	4	31	-	-
SUB-ADULT	7	100							4	57	4	57	4	57	4	57	4	57	2	29
JUVENILE	3	100							2	67	2	67	2	67	2	67	2	67	-	-
TOTAL	23	100							15	65	15	65	11	48	11	48	10	43	2	9
SEPTEMBER-I																				
ADULT	5	100									5	100	5	100	5	100	3	60	-	-
SUB-ADULT	15	100									13	87	13	87	11	73	9	60	1	7
JUVENILE	-	-									-	-	-	-	-	-	-	-	-	-
TOTAL	20	100									18	90	18	90	16	80	12	60	1	5
SEPTEMBER-II																				
ADULT	20	100											18	90	14	70	12	60	3	15
SUB-ADULT	4	100											2	50	2	50	2	50	-	-
JUVENILE	-	-											-	-	-	-	-	-	-	-
TOTAL	24	100											20	83	16	67	14	58	3	13
OCTOBER																				
ADULT	10	100													10	100	5	50	3	30
SUB-ADULT	16	100													14	88	11	69	1	6
JUVENILE	4	100													3	75	3	75	-	-
TOTAL	30	100													27	90	19	63	4	13
NOVEMBER																				
ADULT	20	100															13	65	3	15
SUB-ADULT	39	100															22	56	5	13
JUVENILE	9	100															3	33	-	-
TOTAL	68	100															38	56	8	12
DECEMBER																				
ADULT	75	100																	6	8
SUB-ADULT	50	100																	4	8
JUVENILE	26	100																	1	4
TOTAL	151	100																	11	7

Table II. Survival of adults, sub-adults, and juveniles in E 6 from June, 1963, to January, 1964.

MONTH AGE	NO.	%	JULY NO.	JULY %	AUGUST NO.	AUGUST %	SEPTEMBER-I NO.	SEPTEMBER-I %	SEPTEMBER-II NO.	SEPTEMBER-II %	OCTOBER NO.	OCTOBER %	NOVEMBER NO.	NOVEMBER %	DECEMBER NO.	DECEMBER %	JANUARY NO.	JANUARY %
JUNE																		
ADULT	4	100	4	100	3	75	2	50	1	25	1	25	1	25	1	25	-	-
SUB-ADULT	1	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
JUVENILE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TOTAL	5	100	4	80	3	60	2	40	1	20	1	20	1	20	1	20	-	-
JULY																		
ADULT	2	100			2	100	1	50	1	50	1	50	1	50	-	-	-	-
SUB-ADULT	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-
JUVENILE	1	100			1	100	1	100	1	100	1	100	1	100	1	100	1	100
TOTAL	3	100			3	100	2	67	2	67	2	67	2	67	1	33	1	.33
AUGUST																		
ADULT	10	100					9	90	9	90	7	70	5	50	4	40	-	-
SUB-ADULT	8	100					8	100	6	75	6	75	4	50	3	38	-	-
JUVENILE	5	100					3	60	3	60	3	60	2	40	-	-	-	-
TOTAL	23	100					20	87	18	78	16	70	11	48	7	30	-	-
SEPTEMBER-I																		
ADULT	14	100							14	100	13	93	12	86	10	71	2	14
SUB-ADULT	-	-							-	-	-	-	-	-	-	-	-	-
JUVENILE	3	100							2	67	2	67	2	67	1	33	-	-
TOTAL	17	100							16	94	15	88	14	82	11	65	2	12
SEPTEMBER-II																		
ADULT	19	100									19	100	17	89	14	74	1	5
SUB-ADULT	7	100									7	100	6	86	3	43	1	14
JUVENILE	19	100									17	89	13	68	10	53	4	21
TOTAL	45	100									43	96	36	80	27	60	6	13
OCTOBER																		
ADULT	19	100											17	89	15	79	8	42
SUB-ADULT	12	100											11	92	11	92	5	42
JUVENILE	22	100											17	77	11	50	3	14
TOTAL	53	100											45	85	37	70	16	30
NOVEMBER																		
ADULT	34	100													23	68	11	32
SUB-ADULT	33	100													20	61	4	12
JUVENILE	10	100													4	40	1	10
TOTAL	77	100													47	61	16	21
DECEMBER																		
ADULT	37	100															10	27
SUB-ADULT	52	100															8	15
JUVENILE	4	100															-	-
TOTAL	93	100															18	19

Table 12. Survival of adults, sub-adults, and juveniles in E 7 from May, 1963, to January, 1964.

MONTH AGE	NO.	%	JUNE NO.	JUNE %	JULY NO.	JULY %	AUGUST NO.	AUGUST %	SEPTEMBER-I NO.	SEPTEMBER-I %	SEPTEMBER-II NO.	SEPTEMBER-II %	OCTOBER NO.	OCTOBER %	NOVEMBER NO.	NOVEMBER %	DECEMBER NO.	DECEMBER %	JANUARY NO.	JANUARY %
MAY																				
ADULT	8	100	3	38	3	38	3	38	3	38	3	38	3	38	3	38	1	13	-	-
SUB-ADULT	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
JUVENILE	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TOTAL	8	100	3	38	3	38	3	38	3	38	3	38	3	38	3	38	1	13	-	-
JUNE																				
ADULT	0	0			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SUB-ADULT	7	100			7	100	5	71	4	57	4	57	2	29	2	29	1	14	-	-
JUVENILE	3	100			3	100	3	100	3	100	3	100	3	100	3	100	2	67	2	67
TOTAL	10	100			10	100	8	80	7	70	7	70	5	50	5	50	3	30	2	20
JULY																				
ADULT	1	100					1	100	1	100	1	100	1	100	1	100	-	-	-	-
SUB-ADULT	0	0					-	-	-	-	-	-	-	-	-	-	-	-	-	-
JUVENILE	0	0					-	-	-	-	-	-	-	-	-	-	-	-	-	-
TOTAL	1	100					1	100	1	100	1	100	1	100	1	100	-	-	-	-
AUGUST																				
ADULT	1	100							1	100	1	100	1	100	1	100	1	100	-	-
SUB-ADULT	0	0							-	-	-	-	-	-	-	-	-	-	-	-
JUVENILE	12	100							9	75	9	75	9	75	6	50	3	25	-	-
TOTAL	13	100							10	77	10	77	10	77	7	54	4	31	-	-
SEPTEMBER-I																				
ADULT	3	100									3	100	3	100	3	100	2	67	1	33
SUB-ADULT	3	100									3	100	3	100	2	67	2	67	-	-
JUVENILE	3	100									3	100	1	33	1	33	1	33	-	-
TOTAL	9	100									9	100	7	78	6	67	5	56	1	11
SEPTEMBER-II																				
ADULT	12	100											10	83	9	75	9	75	2	17
SUB-ADULT	5	100											5	100	5	100	5	100	1	20
JUVENILE	6	100											4	67	3	50	2	33	-	-
TOTAL	23	100											19	83	17	74	16	70	3	13
OCTOBER																				
ADULT	10	100													8	80	6	60	1	10
SUB-ADULT	15	100													14	93	13	87	2	13
JUVENILE	5	100													5	100	4	80	-	-
TOTAL	30	100													27	90	23	77	3	10
NOVEMBER																				
ADULT	20	100															13	65	2	10
SUB-ADULT	12	100															10	83	1	8
JUVENILE	13	100															4	31	-	-
TOTAL	45	100															27	60	3	7
DECEMBER																				
ADULT	62	100																	5	8
SUB-ADULT	89	100																	4	4
JUVENILE	25	100																	1	4
TOTAL	176	100																	10	6

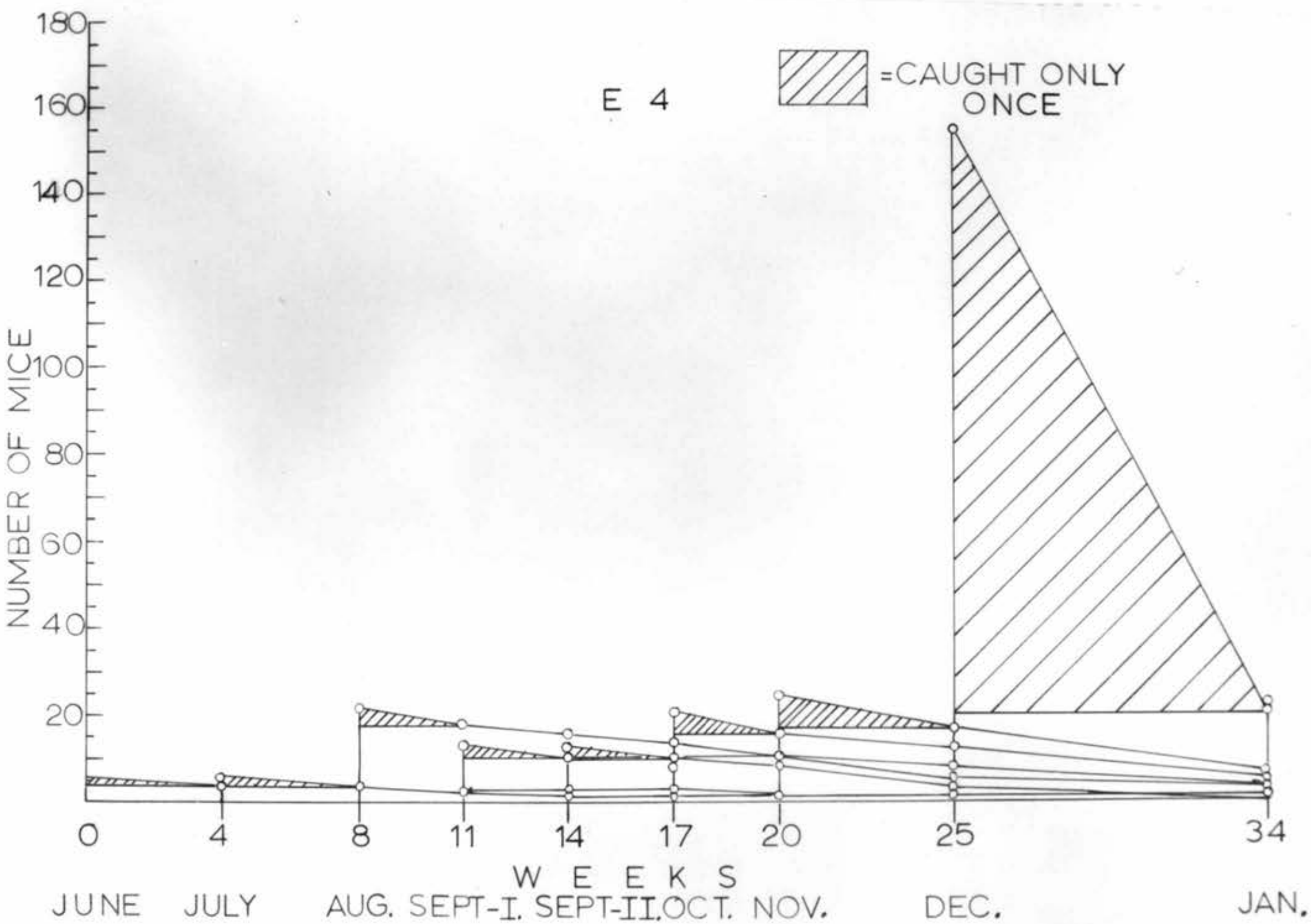

Figure 5. Combined survival of males and females (all age classes) in E 4 from June, 1963, to January, 1964.

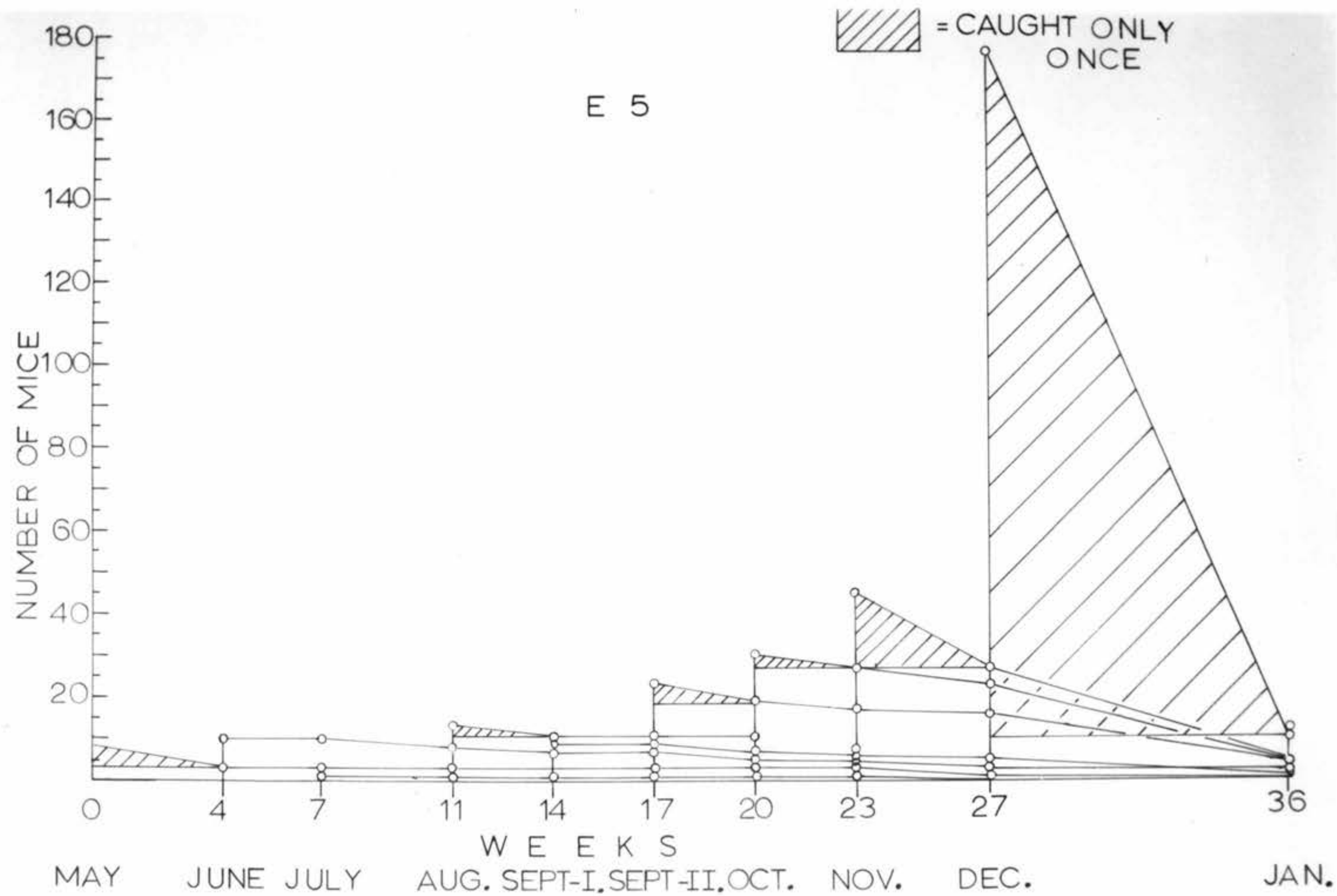

Figure 6. Combined survival of males and females (all age classes) in E 5 from May, 1963, to January, 1964.

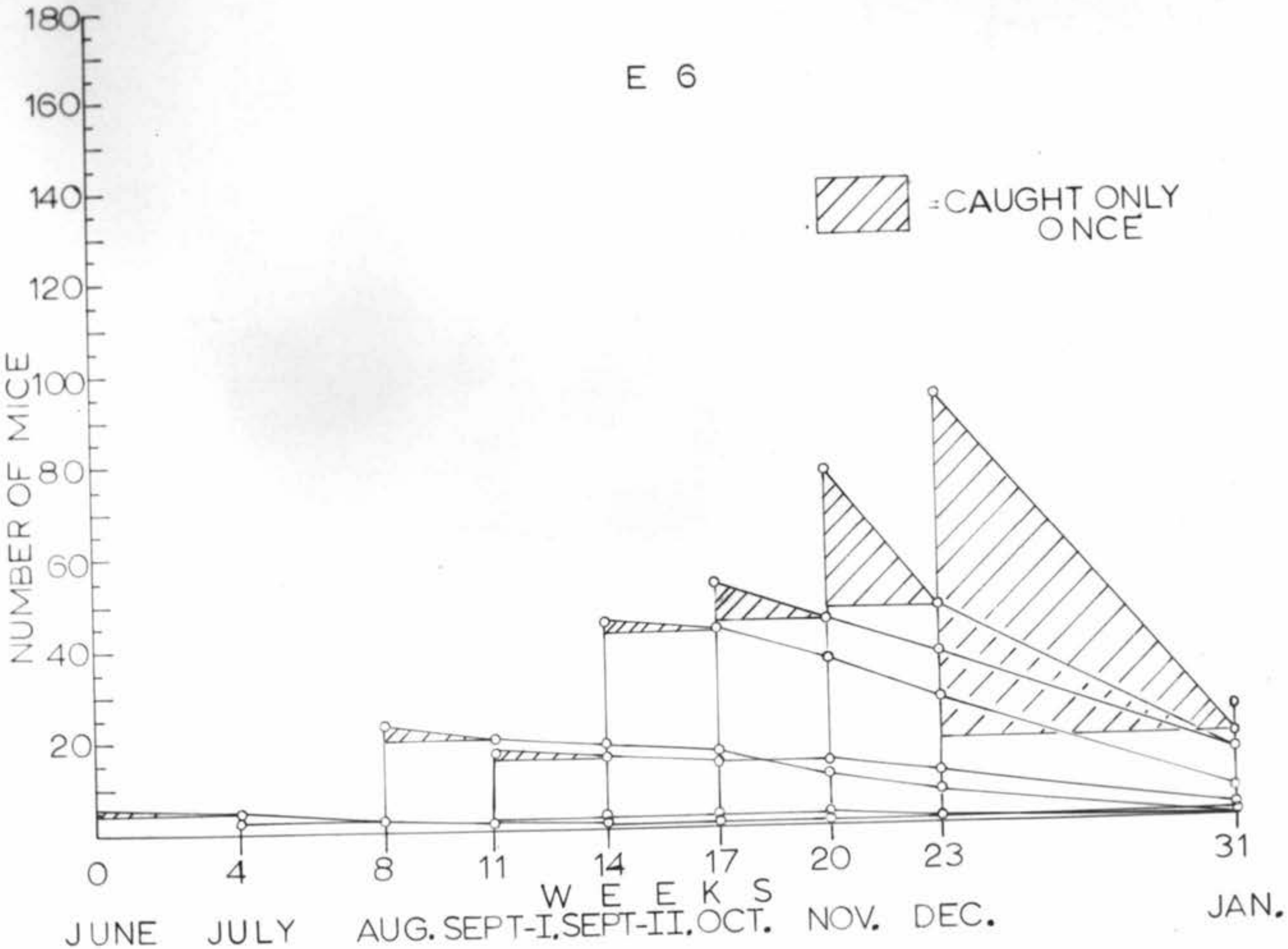

Figure 7. Combined survival of males and females (all age classes) in E 6 from June, 1963, to January, 1964.

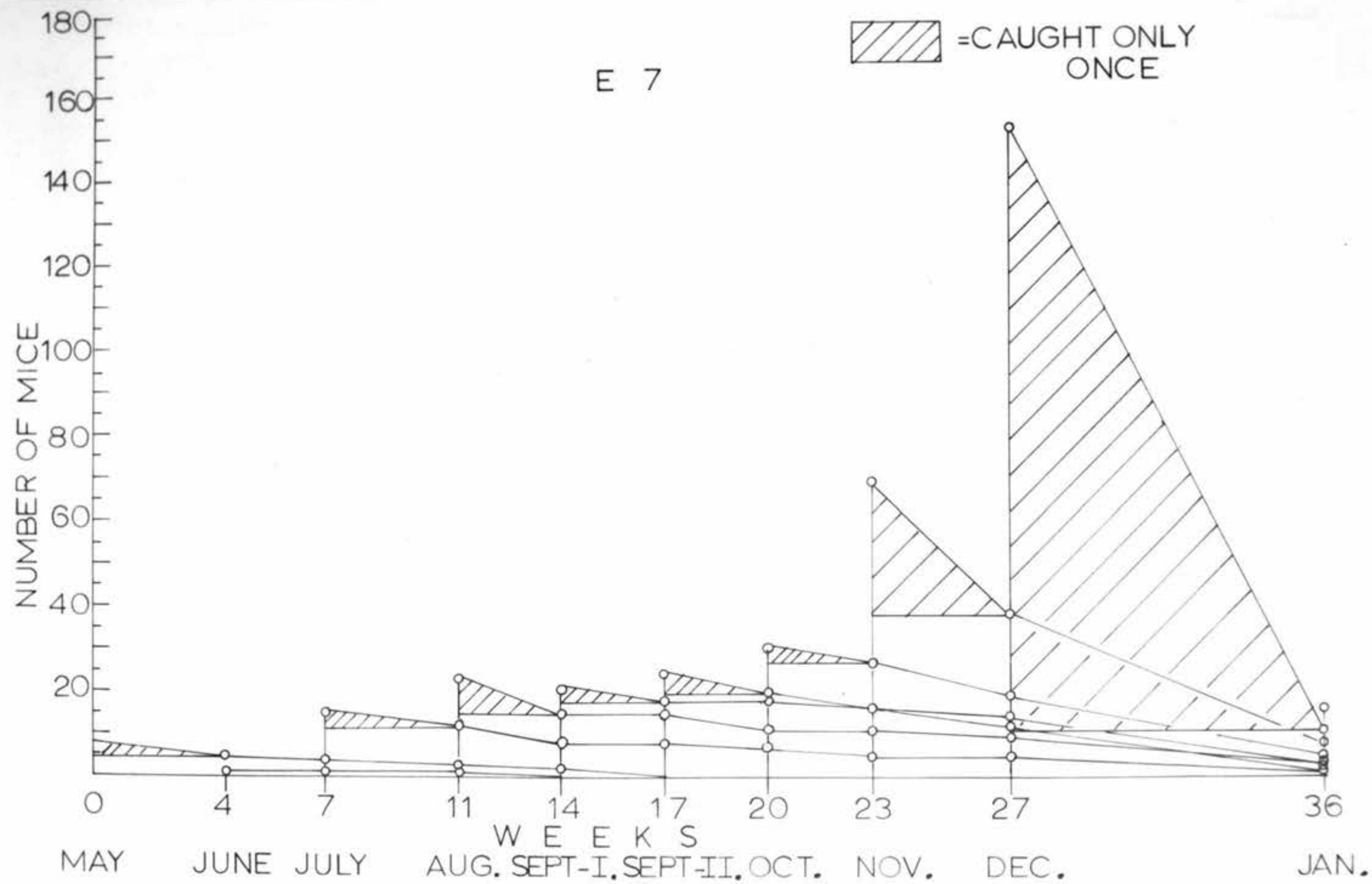

Figure 8. Combined survival of males and females (all age classes) in E 7 from May, 1963, to January, 1964.

Through November for E 4, E 6, and E 7 respectively, was 40, 67, and 33 percent. E 4 and E 6 had 20 and 33 percent survival through January, while E 7 had only seven percent. In all enclosures, juveniles had consistently better survival than the other age classes.

<u>August Cohorts:</u>

Survival was good for all enclosures until October. In October the survival was 64, 77, 48, and 48 percent for E 4, E 5, E 6, and E 7, respectively. Survival through January was best in E 4 and E 7 with five and nine percent, respectively. E 5 and E 6 had no August cohorts surviving until January. Juveniles survived better in E 4 and E 5 while sub-adults had the better survival in E 6 and E 7.

<u>September-I Cohorts:</u>

Survival was good for all enclosures through the December trapping period (13 week interval). Percentages of survival through December for E 4, E 5, E 6, and E 7 respectively, are: 62, 56, 65, and 60. Survival until the January trapping period was highest in E 4, E 5, and E 6 respectively, with 23, 11, and 12 percent, and lowest in E 7 with five percent. Best survival was in the adult and sub-adult classes for all enclosures.

September-II Cohorts:

The survival through the December trapping period was good in all enclosures except E 4 (31 percent). E 5, E 6, and E 7 respectively, had 70, 60, and 58 percent survival through December. Survival through January was 13 percent for E 5, E 6, and E 7, with E 4 having no September-II cohorts surviving. The best overall survival was in the adult and sub-adult age classes.

October Cohorts:

Survival through December was good in all age classes and in all enclosures. The percentages of survival through December for E 4, E 5, E 6, and E 7 respectively, are 62, 77, 70, and 63. The percentages of October cohorts surviving until January was: 19, 10, 30, and 13 for E 4, E 5, E 6, and E 7, respectively. In all enclosures, the October adult mice survived best.

November Cohorts:

The November cohorts had fair survival until December. Percentage wise, E 4 (68), E 5 (60), and E 6 (61) had slightly better survival than did E 7 (56). Survival until January was best in E 4 and E 6 respectively, with 20 and 21 percent. E 5 and E 7 had seven and 12 percent of their November mice living in January. Adults and sub-adults had the highest survival rates.

December Cohorts

Survival of the December mice until January was best in E 4 and E 6, with E 5 and E 7 having the lowest survival rates. The percentages of survival for E 4, E 5, E 6, and E 7 respectively, are: 14, 6, 19, and 11. Juveniles had the poorest survival with less than four percent surviving in any enclosure.

The survival of all cohorts from December through January was poor and may have been affected by the presence of tularemia, Pasteurella tularensis. On December 18, 1963, 20 Microtus were found dead at different locations throughout the E. A. Geary Ranch, including the immediate vicinity of the enclosures. One mouse was found dead within E 4. The mice were sent for examination to Frank M. Prince, Chief of the Public Health Service Field Station, located in San Francisco, California. Mr. Prince reported that all specimens were positive for tularemia. Since tularemia is commonly carried by water, and since water was present throughout the enclosures, it was reasonable to conclude that tularemia was present in all the enclosures during December.

Male and Female Survival:

Table 13 shows the survival of males and females that were produced in the enclosures through the August cohort, and the percentage surviving until December and January. The survival of the sexes in the remaining cohorts was analyzed with essentially the same results.

The males had poorer survival than females in all of the enclosures throughout the study. If all tagged males captured in the dispersal ramps (from the cohorts through August) had remained in the population and survived until December, the percentage surviving would have been: 23, 18, 31, and 20 for E 4, E 5, E 6, and E 7, respectively. The actual male survival until December for E 5 and E 6 respectively, was zero and seven percent. Survival of both sexes into January was very poor due to the probable presence of tularemia in the enclosures.

Table 13. Comparison of male and female survival to December, 1963 and January, 1964 based on the total mice produced in the enclosures through the August, 1963, cohort.

Enclosure	Sex	Total caught through August Cohort	Survival To December No.	Survival To December %	Survival to January No.	Survival to January %
4						
	Males	22	5	23	-	-
	Females	10	5	50	3	30
5						
	Males	14	-	-	-	-
	Females	18	8	44	2	11
6	Males	14	1	7	-	-
	Females	17	8	47	1	6
7						
	Males	30	6	20	1	3
	Females	16	9	56	2	13

General Survival:

The mean survival rate (index) is calculated for each enclosure by using the method described by Clarke (9, p.77). Calculation is made by dividing the total number of *Microtus* recaptured for a given trap period by the total number of mice produced in all previous trap periods. Subtracted from this figure was trap mortality and the number of tagged mice caught in the dispersal ramps (E 5 and E 6). The survival index for the enclosures were compared statistically by using a 2 X 2 contingency table as described by Cochran and Cox (10, p.103-105).

Each enclosure had a survival index calculated through the December trapping period and the January trapping period. The survival rates of the enclosures were compared at both the five percent and the one percent level of significance, with one degree of freedom. The mean survival rates through December for E 4, E 5, E 6, and E 7 are: .546, .622, .724, and .554, and through January are: .143, .073, .215, and .091. E 6 was found to have better survival than E 4 and E 7 at the five percent level through December. The mean survival rate for E 6 was significantly better at the one percent level than either E 5 or E 7 through January. There was no significant difference between E 4 and E 6 in January.

In summary, there was very good survival in all enclosures through December but poor survival through January. This is graphically illustrated in Figures 5 through 8, which show the gradual increase in mortality rate until December when the largest mortality occurred. Therefore, the poorer survival from December to January was no doubt caused, in part, by the presence of tularemia in the enclosed populations.

In E 4 and E 6, survival was consistently better than in E 5 or E 7. This was true in every cohort except the August and September-II cohorts. The order of best survival for the August cohort to January was E 7, E 4, E 6, and E 5 respectively, with nine, five, zero and zero percent. E 4 had the poorest survival through January of the September-II cohorts, while E 5, E 6, and E 7 had the same percentage of mice surviving.

Juvenile mice had generally better survival in all enclosures through the August trapping period. Adults and sub-adults had higher survival from August through the December trapping periods. After December, all age classes were affected similarly with the exception of December juveniles, which suffered the greatest loss.

Female survival was better than male survival in all enclosures at all times. Because of dispersal movement, E 5 and E 6 had poorer male survival than did E 4 or E 7.

The mean survival rate through December showed that E 6 had statistically better survival than did E 4 or E 7.

The total mean survival rates indicate that E 6 had significantly better survival through January than did E 5 or E 7.

Movement

Figures 9 through 12 show the average distance (av. D.) between successive captures of males and females for each enclosure.

The av. D for females in E 4 fluctuated from a high of 22.8 feet in July to 11 feet in December. The males had a high of 41 feet in July and a low of eight feet in December. Females had a larger av. D during the November and December trapping periods, than did males.

Females in E 5 had a high av. D. of 29.6 feet in June and a January low of 5.8 feet. In July the males' av. D. was 46.6 feet and in December only 6.9 feet. During November and December the females' av. D. was greater than the males.

E 6 females decreased steadily from a July high of 30.6 feet (av. D.) to a December low of 7.5 feet (av. D.). The males' high was 29.6 feet in August and the low was 6.7 feet av. D. in November. The av. D. of females was greater than the av. D. of males during the November trapping period and equal in December.

The av. D. for females was highest for E 7 in July with 24.2 feet and lowest in November with 8.4 feet. Males

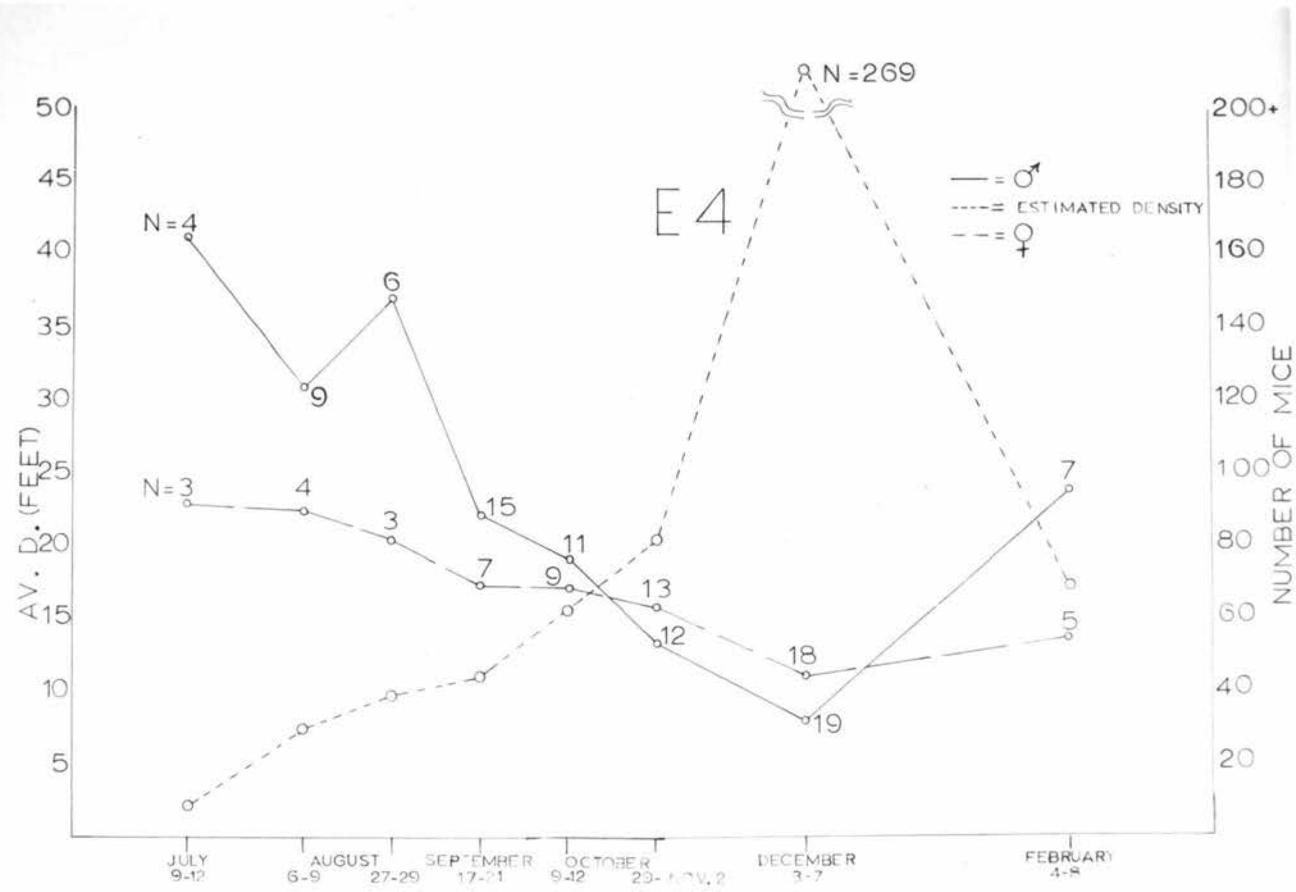

Figure 9. Average distance between successive captures of mice in E 4 caught three to five times during a trapping period and the estimated density during each trapping period from July, 1963, to February, 1964.

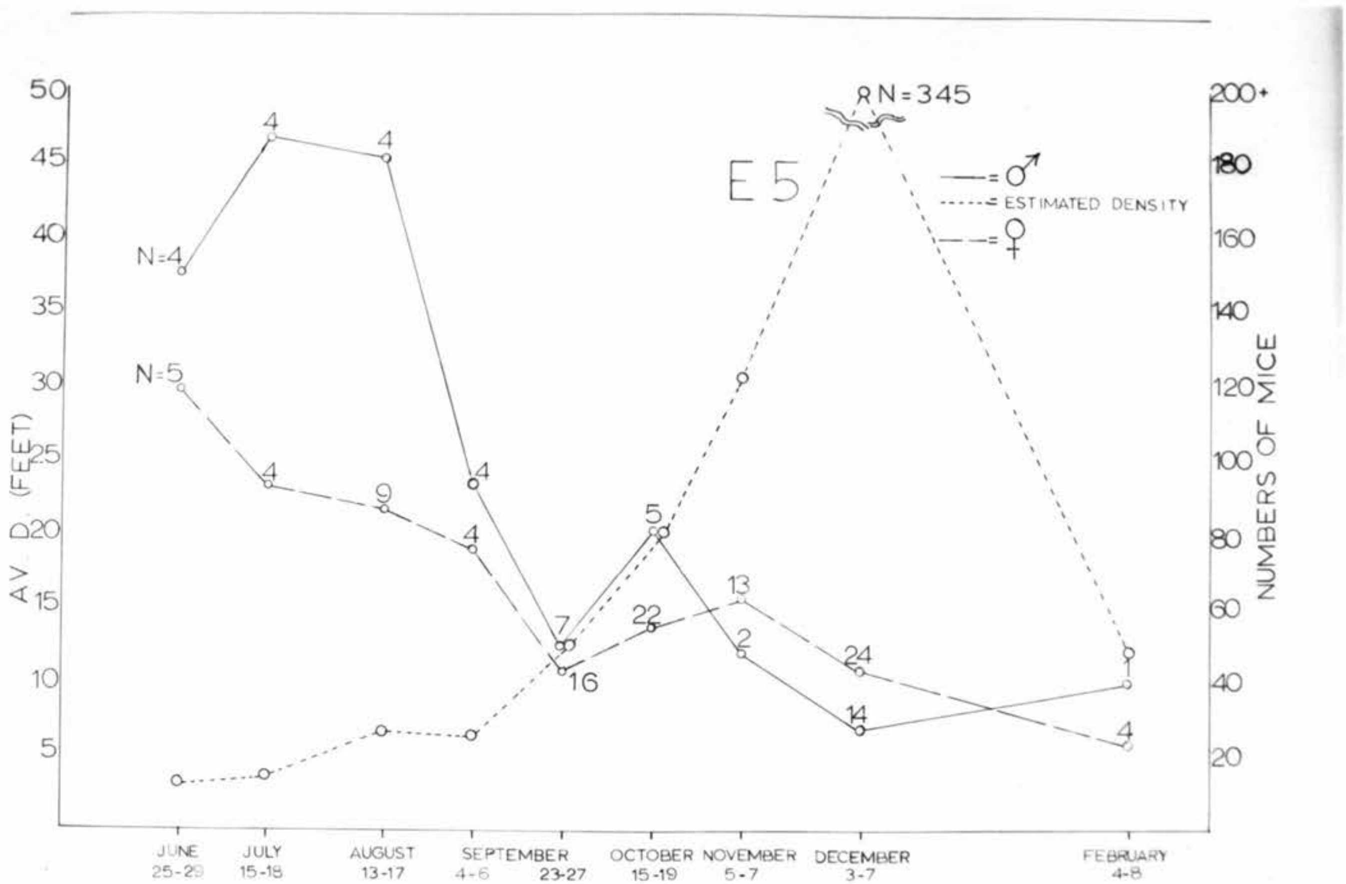

Figure 10. Average distance between successive captures of mice in E 5 caught three to five times during a trapping period and the estimated density during each trapping period from June, 1963, to February, 1964.

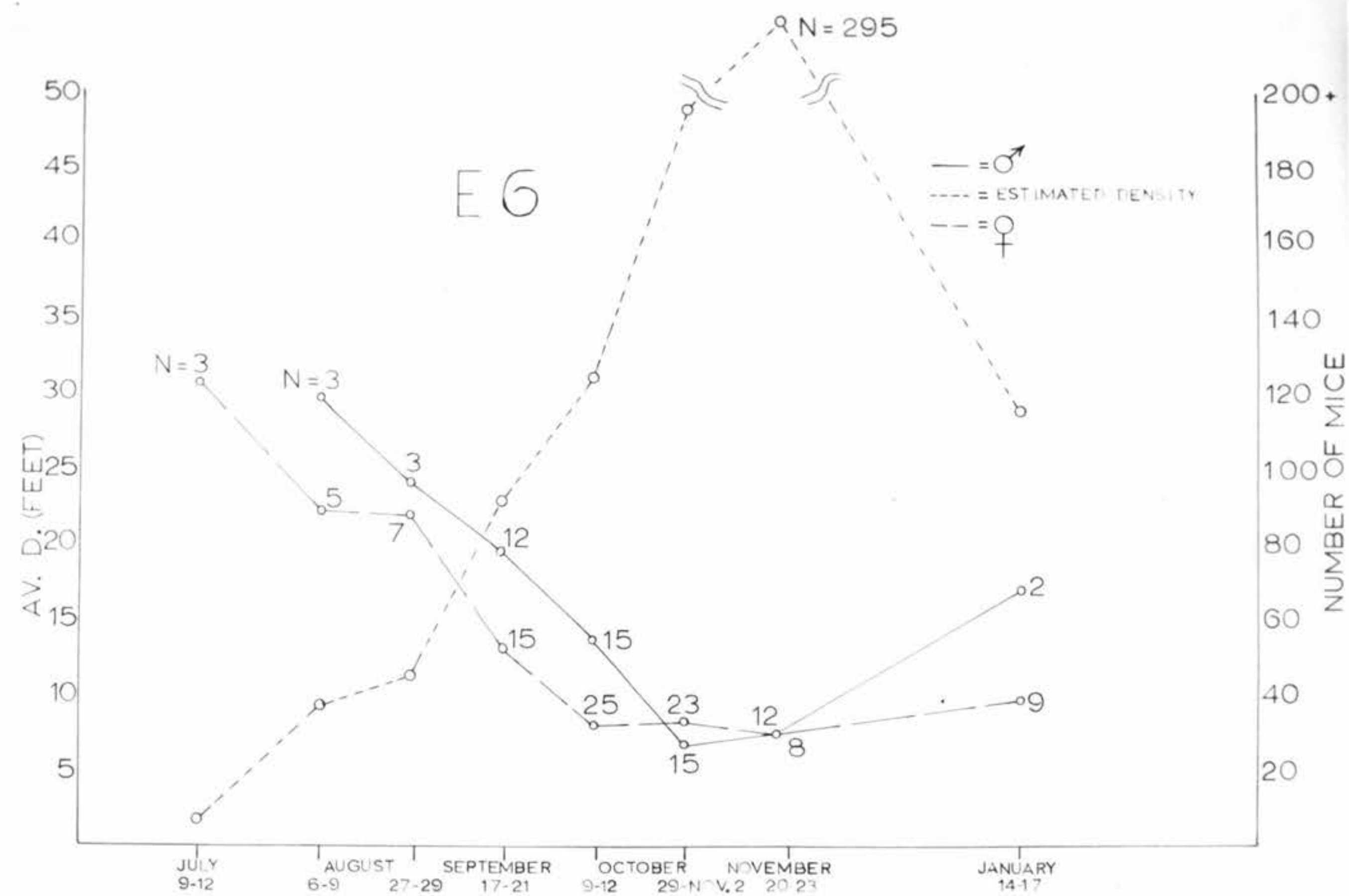

Figure 11. Average distance between successive captures of mice in E 6 caught three to five times during a trapping period and the estimated density during each trapping period from July, 1963, to January, 1964.

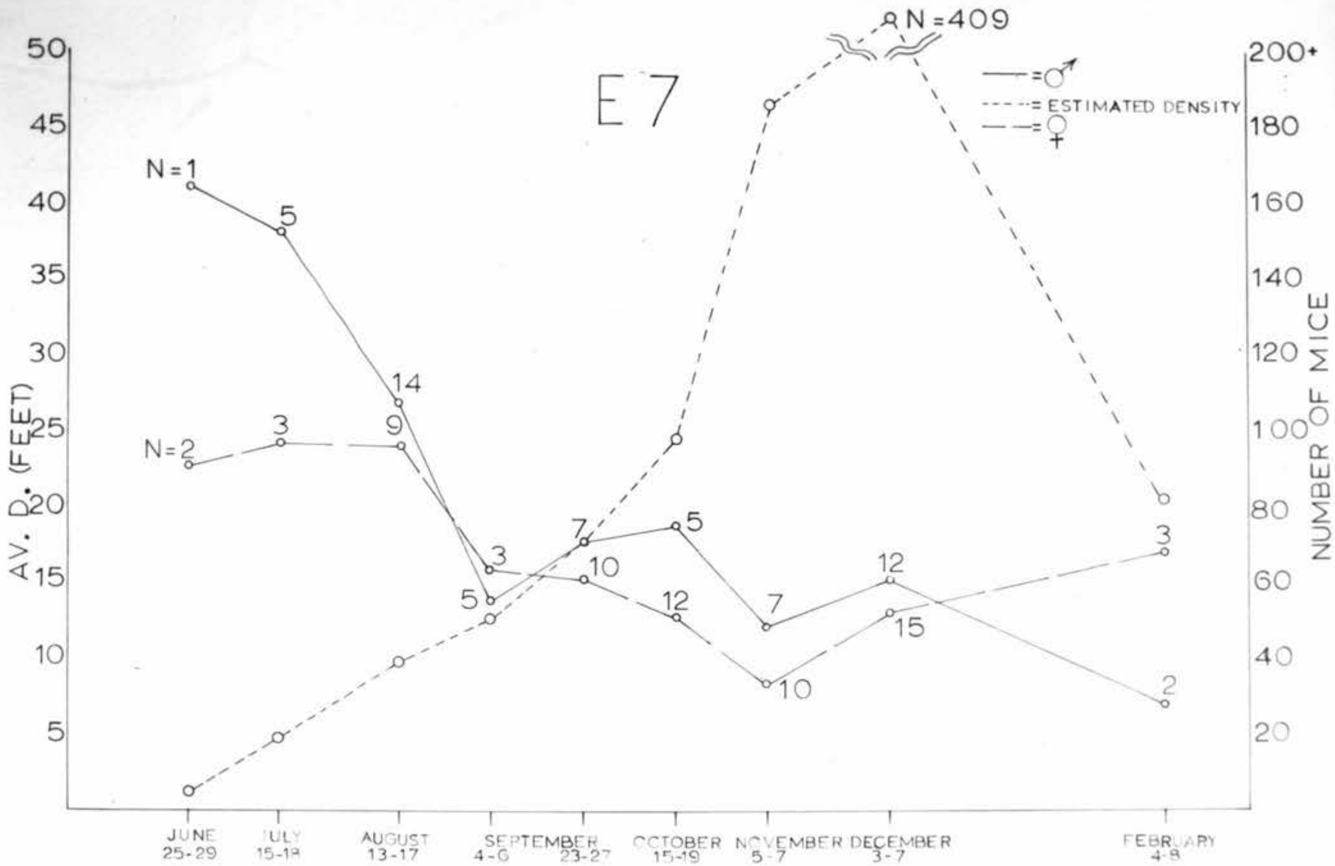

Figure 12. Average distance between successive captures of mice in E 7 caught three to five times during a trapping period and the estimated density during each trapping period from June, 1963, to February, 1964.

were high in June with 41 feet and low in the January trap period with an av. D. of 7.0 feet. Females had a larger av. D. during the September-I and the January trap periods.

In summary, the av. D. was greater for males than females in all enclosures at all times with the following exceptions: E 4, November and December; E 5, November and December; E 6, November (equal in December); E 7, September-I and January. In general, the changes in av. D. were inverse to population density for all enclosures. The only major exceptions were in E 5 and E 7. E 5 reached its low in the January trap period and E 7 obtained its low av. D. in November and not when peak densities occurred in December.

Dispersal Ramps

Table 14 shows the months the dispersal ramps were open, the total *Microtus* caught, captures per ramp day, enclosure density, and sex and age composition of the animals caught in Ramp 5 and Ramp 6.

In July, the number of mice captured in Ramp 5 and Ramp 6 respectively, were three and four. The percentage of males captured in Ramp 5 was 67 and in Ramp 6 all the captures were males. The one female caught in Ramp 5 was a sub-adult.

During August four mice were caught in Ramp 5 and nine in Ramp 6. Ramp 5 had 75 percent females, which were

Table 14. Numbers, captures per ramp day, and the sex and age composition of the mice caught in the dispersal ramps and the enclosure density from July, 1963, through November, 1963.

Month	Total Caught	Captures per Ramp Day	No. Tagged	Enclosing Density/Acre	Males No.	Males %	Females No.	Females %	Males % Ad.	Males % SA	Males % Juv.	Females % Ad.	Females % SA	Females % Juv.
RAMP 5														
July	3	.21	1	60	2	67	1	33	100	-	-	-	100	-
August	4	.19	2	108	1	25	3	75	100	-	-	-	33	67
Sept.	6	.33	0	204	5	83	1	17	80	20	-	-	100	-
October	10*	.67	4	324	6	60	4	40	100	-	-	-	100	-
Nov.	3	1.00	2	488	1	33	2	67	-	100	-	100	-	-
TOTAL	26	.37	9	--	15	58	11	42	87	13	-	18	64	18
RAMP 6														
July	4	.29	1	28	4	100	0	-	100	-	-	-	-	-
August	9	.43	2	180	7	78	2	22	71	29	-	-	50	50
Sept.	20	1.11	1	364	14	70	6	30	50	50	-	-	83	17
October	13**	.87	7	780	5	39	8	61	80	20	-	-	100	-
Nov.	25***	8.33	17	1180	12	48	13	52	75	25	-	54	46	-
TOTAL	71	1.00	28	-	42	59	29	41	69	31	-	28	65	7

* One male was released into the enclosure to observe survival.

** Three adult males and one sub-adult female were returned to the enclosure to observe survival.

*** Two adult males were caught that were released into the enclosure from the ramp in October.

juveniles and sub-adults; while Ramp 6 had only 22 percent females, all juveniles and sub-adults.

A total of six animals were captured in Ramp 5 in September and Ramp 6 had a total of 20 captures. Males made up 83 and 70 percent of the captures for Ramp 5 and Ramp 6, respectively. The females captured in both ramps were either juveniles or sub-adults.

In October, 10 animals were caught in Ramp 5 and 13 in Ramp 6. Females accounted for 40 percent of the captured mice in Ramp 5 and 61 percent in Ramp 6. All females were sub-adults.

In November, three animals were captured in Ramp 5 and 25 in Ramp 6. Females were predominant in both ramps during this period. Ramp 5 captured 67 percent females and Ramp 6 captured 52 percent females. This month was the first time either ramp captured adult females. All of the females in Ramp 5 were adults and 54 percent of the females in Ramp 6 were adults. The capture of female adults for the first time in November might be attributed to the fact that breeding in the enclosures was practically ended by the first week of November (See Reproduction, Table 7).

Five mice were caught in the dispersal ramps on October 23, 1963. One mouse was caught in Ramp 5 and four in Ramp 6. The five mice included four male adults and one female sub-adult. The female was caught in Ramp 6. The mice were released into the enclosures from which they had dispersed. This was done for the purpose of observing their movement and survival. On November 6, two of the males that were released in E 6 were caught again in Ramp 6. The sub-adult female that was released in E 6 was live trapped during the November and December trap periods. This female was not recaptured in January. The fourth mouse that was released in E 6 and the one released in E 5 were never recaptured in either enclosure by live trapping or by capture in the dispersal ramps.

The movement patterns of mice before they are captured in a dispersal ramp are obscured by lack of data. In the first place, only 34 and 40 percent of the mice captured in Ramp 5 and Ramp 6, respectively, were tagged: that is, they were live trapped before entering a ramp. Secondly, since most of the tagged mice had trapping records showing only one or two captures before entering a dispersal ramp, analysis of movement was extremely difficult.

The data for dispersal mice that did have extensive recapture records, suggests that dispersal movement is often quite sudden. A few males and females were recaptured numerous times before being caught in a dispersal ramp. By calculating the av. D. (See Movement) it was found that each mouse had a quite small av. D. before his entrance into a dispersal ramp. This move was quite often the greatest distance the mouse moved at any one time, as observed by recapture data. Some males were found to have a far greater av. D. than mice not dispersing. This suggests a continuous search by some individuals for a way out of the enclosure.

During September, 16 males and six females that were caught in the dispersal ramps, were autopsied. It was found that 15 males and two females were in breeding condition. The females were perforate; but all were classified as being nulliparous; that is, they had never been pregnant.

Eighteen mice which were caught in the ramps were autopsied in October. Seven were males, all in breeding condition; 11 were females, with six perforate. The females were all nulliparous with the exception of one, which had embryos in the early implantation stage of pregnancy.

Twenty-eight mice, 14 males and 14 females, collected in the ramps during November were autopsied. Four males and three females were in breeding condition. All females were nulliparous with the exception of five, which had numerous placental scars, an indication of many births.

The captures per ramp day were largest when density was highest. E 5 had a 1.00 capture per ramp day in November when density was 488 per acre and 0.21 captures per day in July when density was 60 mice per acre. E 6 had 8.33 captures per ramp day in November when density was 1,180 mice per acre and only 0.29 captures per ramp day in July, when density was 28 mice per acre in the enclosure.

In summary, both ramps captured approximately the same total percentage of males, 58 and 59 for Ramp 5 and Ramp 6, respectively. Adults made up the largest percentage of males caught and sub-adults were the most numerous class of females. Female adults were not captured in either ramp until November. Movement patterns for mice caught in the ramps suggest two kinds of dispersal movement: 1) quite sudden, and 2) continuous movement. Ninety-six percent of the males autopsied through October were in breeding condition and only 29 percent were in breeding condition during November. The females autopsied in September and October were 94 percent nulliparous, with only one animal showing signs of having been bred. In November, 36 percent of the autopsied females were found to have had litters. Twenty-one percent of the females were perforate during November. Ramp 5 had 1.00 captures per ramp day when enclosure density was 488 mice per acre and Ramp 6 had 8.33 captures per ramp day when enclosure density was 1,180 *Microtus* per acre.

Disease

Streptococcus infection, as evidenced by enlarged limbs or internal abscesses, was present in all enclosures during each trap period after the September-I trap period. The incidence was very low, and it is believed to have had only slight effect upon the four populations.

Tularemia was found to be definitely present in E 4 during December. It could have been present in the other enclosures at the same time. The possible effects of this disease upon the populations have been already established (See Survival).

DISCUSSION AND CONCLUSIONS

Although the four enclosures, two with dispersal ramps, had two different initial populations (five mice and eight mice) derived from 1962 high and low densities, peak densities were reached in all enclosures during the December trapping period. The peak densities were essentially the same except that E 4 was significantly lower than E 7. By comparing the data in Table 15, it can be seen why E 4 had a lower peak density than E 7. E 4 had the largest number of pregnant females during the study. The number of females in E 4 with mammary glands large or lactating was lower than the number in E 6 and E 7, and about the same as in E 5. E 4 also had the smallest number of young animals captured during the study. The above data indicate that E 4 had a far greater prenatal mortality than did the other enclosures. E 7 had the lowest prenatal mortality. This mortality in E 4 would account for the lower densities obtained in that enclosure. This mortality could have been caused by intraspecific strife affecting the physiology and behaviour of the females as pointed out by Chitty (7, p.538-539). According to Krebs (24, p.674) intraspecific strife is measured by wounds on the skin. This strife is further indicated by the high number of animals wounded in E 4, as compared to the other enclosures.

Population estimates in December increased 3.3, 2.9

Table 15. Summary, showing the number of pregnancies, mammary glands large or lactating, young mice, total new mice captured, the mean survival rate, and the number and percent of wounding in the enclosures for the entire study.

	E 4	E 5	E 6	E 7
Number of Pregnancies	41	24	35	24
Number of Mammary Glands Large or Lactating	15	16	37	31
Number of Young Mice	125	224	229	194
Total new Mice Caught	282	346	383	355
Mean Survival to December	.546	.622	.724	.554
Mean Survival to January	.143	.073	.215	.091
Wounding				
Number	103	46	76	85
Percent of Total Captures	20	8	11	13

1.5, and 2.1 times the estimated November populations for E 4, E 5, E 6, and E 7, respectively. With the exception of E 4, this large jump in population estimates cannot be explained on the basis of November reproduction. In November, E 4 had a larger number of pregnant females than at any other time, while E 5, E 6, and E 7 had comparatively low numbers of pregnancies. This indicates that the breeding intensity was greater in E 4 during the last part of the breeding season, than in the other enclosures. This large increase in density in E 4 and E 5 may have been due in part to the increase in trapping effort in December as compared to November. During November, 65 and 78 traps were used in E 4 and E 5, respectively, while in December both enclosures contained 106 traps. The great increase in estimated densities in E 6 and E 7 was apparently the result of earlier reproduction, with the bulk of the recruitment not being captured until December.

The ratio of increase was inversely proportional to the initial population (Table 4). The lower the initial population in the spring, the higher the ratio of increase to the fall. Errington (15, p.797-924) found that muskrats (*Ondatra zibethicus*) in Iowa tended to increase proportionally more rapidly when they were few in numbers in the spring. Similar findings were reported by Chitty (7, p.541) in populations of *Microtus agrestis*. Since there was only a difference of one female in the initial populations of the enclosures (Table 2), it seems probable that something influenced the ratio of increase besides the number of mice in the initial population. The two enclosures (E 4 and E 6) containing mice derived from a high parent population, had higher ratios of increase than those populations derived from a low parent population. Therefore, it seems probable that some quality within the animals derived from a high parent population made them different from the animals derived from a low parent population. This difference could have influenced the ratio of increase.

The total recruitment was greatest in E 6 and smallest in E 4. E 6 had the second highest pregnancy rate and the largest number of females with mammary glands large or lactating. A comparison of numbers of pregnancies with the mammary glands large or lactating, determined the degree of successful pregnancies, an indication of recruitment. Based on this comparison the order of the potentially greatest recruitment should be E 6, E 7, E 5, and E 4, respectively, which is the case (Table 15). This is true regardless of the number of young animals captured, because some mice are not captured until they are sub-adults or adults.

Reproduction stopped in all enclosures in November, just before peak densities were reached. Clarke (9, p.68-85) concluded that reproduction is affected adversely by intraspecific strife. This was not the case during my study. E 4 had the largest percentage of animals wounded in November and still had the largest percentage (28) of pregnant females. This may indicate that offspring from a high parent population are better adapted for breeding under strife than offspring from a low parent population. Low density during November may also have been a contributing factor to the high pregnancy rate in E 4.

Juveniles survived best until August and thereafter the sub-adults and adults survived best. This suggests that as density increases survival of young decreases. This would follow Chitty's (7, p.505-552) suggestion that fighting among voles at high densities caused poorer survival of the immature.

Survival through December was better in E 5 and E 6 than in E 4 and E 7. It is suggested that the better survival in E 5 and E 6 can be explained on the basis of the presence of the dispersal ramps. Since the animals caught in the dispersal ramps were removed from the enclosed populations, the result was a reduction in the competition for space within the remaining populations. Chitty (7, p.540) refers to intraspecific strife as competition for space. He also states that voles seem to be less tolerant of crowding at the height of the breeding season. Since most of the dispersal movement took place during the main breeding season (Table 14), it seems reasonable to assume that because of the reduction in intraspecific strife the populations within E 5 and E 6 had better survival than did E 4 and E 7. The reduction in intraspecific strife is better visualized by referring to the number of animals wounded, as presented in Table 15. The data indicate that E 5 and E 6 had the smallest number and percent of animals wounded, while E 4 and E 7 had larger numbers and percentages of animals wounded during the study.

The survival of mice from December to January was very poor in all enclosures, but was better in E 4 and E 6 and in E 5 and E 7. Since tularemia was present within the populations during December, it may be assumed that the variation in mortality was largely the result of this disease. It is suggested that better survival in E 4 and E 6 was due to some unknown quality within the descendants from high parent populations. Chitty (8, p.99-113) made similar assumptions.

In the enclosures with dispersal ramps, females were dominant throughout the study (E 5) or until peak densities were reached in December (E 6). According to my observations, it was only after the dispersal ramps were closed for the last time that an enclosure (E 6) having a dispersal ramp had a dominance of males. This points out the importance dispersion plays in reducing the interaction among voles. This is accomplished by males, generally the more aggressive of the sexes, leaving the population in greater numbers than females. This follows the findings of Frank (16, p.116) who said that during spring and summer months, as densities increased and dispersion occurred, females predominated as a result of heavier losses among males. Frank called this "male elimination", and Wijngaarden (32, p.22) says that surplus males die during intraspecific strife with older established males. My findings showed that male loss was due mainly to dispersion in E 5 and E 6, and probably to more intense male interaction in E 4 and E 7. During peak densities, males were dominant only in E 4 and E 6; but this dominance was slight and probably not a reflection of the parent population density.

The number of young animals in the enclosures did not seem to be directly regulated by the number of pregnancies or the density of the parent population. The factor most vitally affecting the number of young was survival as correlated with dispersal movement. Because dispersion was allowed in E 5 and E 6, more young survived, at least until after they were captured in the enclosures. The reason for this better survival of the young has been partially explained in a previous section of this paper on the basis of reducing the competition for space. It is further suggested that the survival of young may be directly correlated to the number of males within a population, because more adult males disperse than adult females.

During this study, movement, as indicated by av. D., decreased as density increased. Males had a greater av. D. than females except during November and December in E 4 and E 5, November in E 6, and September-I and January in E 7. Greater movement by males than females has been pointed out by several workers, Stickle (29, p.301-307), Howard (20, p.24), and Blair (1, p.11). So, in general, the males had a larger av. D. until after the breeding season ended when movement was not apparently governed by sex. The variation in Microtus movement cannot be satisfactorily explained by either parent population density or dispersion. Stickel (28, p.433-440) points out that by variation in movement, small mammals adapt to changes in their environment. She also states that population density, habitat, changes in breeding condition, and food supply can cause variation in the range of an animal. Another influence on movement could have been trap proneness as mentioned by Chitty (7, p.526). There were some conditions besides the above-mentioned that may have affected the movement patterns during this study. The presence of tularemia could have caused changes in movement patterns. Because of wet weather, followed by freezing temperatures, and snow during December and January, adverse conditions may have varied movement. Another condition that may have caused variation in movement during the last trapping period was a change in experimental design of the trap grid. Due to deep snow, which caused difficulty in locating the trap stations, the

A, B, C, and D rows of traps (See Methods - Live Trapping) were not used.

During this study more males than females were caught in the dispersal ramps. The most numerous age classes were adult males and sub-adult females. These results differ from Howard's (20, p.26) who felt that if dispersal movement took place at all, it was just before the animals became sexually mature. Of the males captured in the ramps through October, 96 percent were in breeding condition. Brant (2, p.140) states that dispersal movements may possibly take place at almost any time during the life of a mammal. The present study substantiates this conclusion.

Since adult females were captured only in November, it is suggested that during the main breeding season, only young females disperse. Each month there were some dispersing females in breeding condition, but only a few had been bred. Males that dispersed were either sub-adults or adults, and most of them were in breeding condition.

Howard (20, p.26) states that "once an animal selects a homesite it rarely leaves, but usually remains there for the rest of its life". Burt (3, p.35) also found that dispersal is mainly by young before they have established their homes. This does not concur with the findings obtained from this study which disclosed that some males and females caught in a dispersal ramp had previously set up what appeared to be permanent "homesites".

Some females produced litters in these areas. As soon as the breeding season ended several of the animals moved long distances from their "homesites" into a dispersal ramp. This distance was generally longer than the animals previously recorded av. D.

Dispersal movements took place continuously in each enclosure. The enclosure density affected the amount of dispersal to a certain degree. Generally, the higher the density, the more dispersal movement. The enclosure with mice from a high parent population had consistently higher captures per ramp day than did the enclosure with mice from a low parent population. This occurred regardless of population density. Ramp 6 had a total capture 2.73 times greater than did Ramp 5. This indicates that the tendency to disperse may be linked with the parent population density.

Throughout the study, the mean body weights were consistently higher in E 4 than in the other enclosures. How is this explained? E 4 had a high prenatal mortality which resulted in a lower number of young animals. Since E 4 had fewer numbers of young than the other enclosures, the higher mean body weight must have been due, at least in part, to an older age structure. This indicates that the enclosures did not reach peak "cyclic" densities because Chitty (7, p.518-520) and Krebs (24, p.674) found an increase in body weights during peak years which was attributed to a change in growth rate and not age structure.

In conclusion, some differences observed in the population characteristics of the four enclosures can be attributed to parent population density and/or dispersion. E 4 and E 6 (derived from a high parent population) had a greater number of pregnancies and a higher survival rate through January than did E 5 and E 7 (derived from a low parent population). This indicates that high parent population density does not adversely affect reproductive potential or the survival of a vole after it has become established in a population. However, when an enclosure has mice from a high parent population, and where dispersion is not allowed, prenatal mortality and the amount of wounding is greater than where dispersion is allowed and/or where the mice are from a low parent population. If dispersion is allowed, recruitment is high, survival is good, and the amount of wounding is low, regardless of parent population density. It is suggested that animals from a high parent population are selected for aggressiveness. This aggressiveness probably caused a disruption in the social structure of the animals, which was observed mainly in E 4. Because of the influence of the dispersal ramp in E 6 some dynamics of that population were similar to the dynamics of E 5 and E 7. This indicates that dispersion must be very important in population processes, but the more dense a wild population becomes, the less effective is dispersion in maintaining a stable social structure. A disruption in social structure may be exemplified by prenatal mortality, poor nestling care, poor juvenile survival, and cannibalism; all of which are by-products of intraspecific strife as pointed out by Calhoun (4, p.143), Chitty (7, p.537) and Clarke (9, p.81-84). If behavioral changes in a population were more completely explained, we might have a clearer comprehension of the natural regulation of vole numbers.

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