Survival Rates, Longevity, and Population Fluctuations in the White-footed Mouse, *Peromyscus leucopus*, in Southeastern Michigan

BY

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University of Massachusetts

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CONTENTS

ILLUSTRATIONS

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INTRODUCTION

KNOWLEDGE of survival rates and longevity of organisms is often of importance to the ecologist. A considerable amount of data, for both vertebrates and invertebrates, has accumulated from various studies. Some of them deal with wild or natural populations, others with animals kept in the laboratory. Pearl and Miner (1935) and Deevey (1947) summarized and analyzed much of this work. Farner (1949) listed some of the more recent studies which deal with birds. Much related literature may be found in a review by Comfort (1954). In the present study an attempt has been made to determine the survival and mortality rates which operated for several seasons on a population of the white-footed mouse, *Peromyscus leucopus*, in a small area in southeastern Michigan.

The field work was carried out on the Edwin S. George Reserve of the University of Michigan, a locality about 22 miles northwest of Ann Arbor. The principal area, an oak-hickory woodlot, was divided into two approximately equal plots (Fig. 1). After some survey trapping in July and August, 1949, plot A was completely covered by grid trapping, beginning in September, 1949, and continuing through April, 1951. Plot B was trapped in a similar manner from July, 1950, until April, 1951. In addition, nine other wooded areas were trapped for short periods.

This study was made possible by the grant of an Edwin S. George Reserve Fellowship, for which I was most grateful. To Dr. W. H. Burt, who was my adviser, I should like to express my sincere appreciation for his guidance and encouragement throughout. I am also grateful to the other members of my doctoral committee, the late Dr. J. Speed Rogers and Drs. S. A. Graham, Stanley A. Cain, and F. F. Hooper, for their suggestions in the preparation of this paper. Dr. Rogers McVaugh generously gave his time to identify many plants and to check my determinations. Dr. C. C. Craig kindly furnished much aid and advice in the statistical treatment of the data. Dr. Irving J. Cantrall, Curator of the Reserve, was most helpful. Mr. Lawrence Camburn, Custodian, obtained various materials for me needed in the field work, and Mrs. Camburn graciously supplied my board during the first year of the field study. I wish to express my appreciation

to both Mr. and Mrs. Camburn and to Dr. and Mrs. Cantrall for the kind
hospitality extended to me while living at the Reserve. I am indebted to
Mr. William Brudon and Mr. Clifford J. Morrow, Jr. for the preparation
of the line drawings.

DESCRIPTION OF AREA

The woods in which most of the work was done occupy a morainic up-
land with well-drained sandy soil. The central portion is relatively flat,
but toward the edges, except on the south and southwest, the ground slopes
considerably. Abandoned fields border the area on the north, south, and
part of the west sides. Marshes occur along the rest of the western and
most of the eastern boundary, and there is a swamp around the south-
eastern corner. The general aspect is one of fairly open and rather dry
oak-hickory woods with much variation in amount of herb and shrub cover.
Cantrall (1943:41) termed this and similar woodlots on the Reserve
"xeromesic associations."

The dominants are white oak (*Quercus alba*), black oak (*Q. velutina*),
shagbark hickory (*Carya ovata*), and small-fruited hickory (*C. ovalis*). A
small semipermanent pond is bordered by a few American elm (*Ulmus
americana*) and red ash (*Fraxinus pennsylvanica*) trees. Throughout the
area are occasional American elm and black cherry (*Prunus serotina*).
Wherever the woods border the wet lowlands, red maple (*Acer rubrum*) is
frequent. The understory of trees, in addition to saplings of the dominant
oaks and hickories, contains American elm, black cherry, and sassafras
(*Sassafras albidum*). Reproduction of the dominants is good. The sub-
dominant shrubbery is composed chiefly of witch hazel (*Hamamelis vir-
giniana*) and black huckleberry (*Gaylussacia baccata*), but these are not
evenly distributed over the area. Less abundant shrubs are hazelnut
(*Corylus americana*), gray dogwood (*Cornus racemosa*) seedlings, Canada
blueberry (*Vaccinium myrtilloides*), hawthorn (*Crataegus* sp.), shadbush
(*Amelanchier arborea*), *Rubus* sp., prickly ash (*Xanthoxylum americanum*),
snowberry (*Symphoricarpos* sp.), and frost grape (*Vitis vulpina*). In ad-
dition to the widely distributed sedge, *Carex pensylvanica* (probably also
C. communis), the herbaceous cover is chiefly grass (*Poa compressa*), hog
peanut (*Amphicarpa bracteata*), tick clover (*Desmodium* spp.), and bed-
straw (*Galium* spp.). Several colonies of may apple (*Podophyllum pel-
tatum*) are evident in spring and early summer. Other herbs, either be-
cause of infrequent occurrence or the small number of individuals, add
little to the total cover. Tall stubs of dead trees are rather common, as
are short stumps and fallen trees in various stages of decay. The litter
and unincorporated humus layer of the soil (A_{00} and A_0 horizons) together
average about 5 cm. in thickness. Further description of the vegetation,
with a quantitative summary, is given in the original thesis which is de-
posited in the University of Michigan Library.
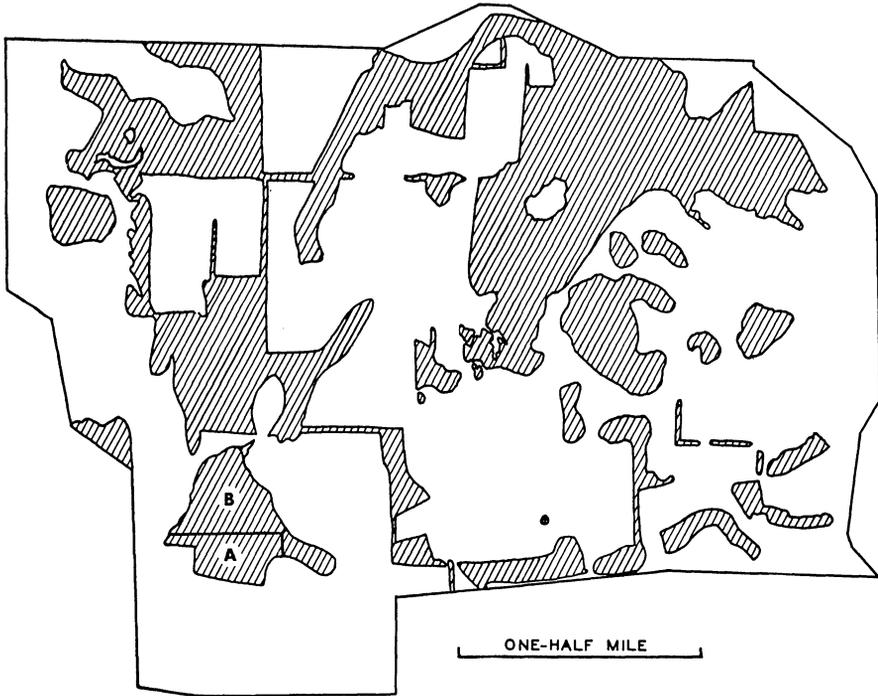
FIG. 1. Outline of Edwin S. George Reserve. Shaded areas are oak-hickory woodlots. Study plots are marked A and B.

METHODS AND MATERIALS

Traps. Two kinds were used. One was a multiple-catch trap, which was described by Burt (1940). It was made of one-half inch wood, which offers more protection from both heat and cold than a metal or fiber material, and at the same time is small and simple to build and operate. The other was a single-catch trap, similar in operating principle to one described by Blair (1941) but constructed of one-half-inch wood instead of the one-quarter-inch pressed wood such as he used. Occasionally, mice gnaw their way out of these wooden traps, but they are easily repaired, and the added insulation is well worth this extra work. Of the two types the Burt multiple-catch trap was, in my experience, preferable for catching *Peromyscus leucopus*. The mechanism of the single-catch trap is more easily damaged, or jammed, by the captive animal, by bait or nesting material, or by moisture which blows into the entrance and freezes. The traps were placed under pieces of roofing paper which were shaped into the form of a half-cylinder. These covers were of great value in keeping the traps and contents dry and also served as further insulation against heat and cold. The paper was sufficiently heavy to retain its shape and no supporting framework was required. This cover is a simplified version of a device

TABLE I

Comparison of Actual Catch (Left Column) with Possible Catch (Right Column) of Marked *Peromyscus leucopus* for Each Trapping Period during the Study

Only those individuals known to be present both before and after each period are included in the figures for the period. First and last captures indicated by X.

In each cell the left number is the Actual Catch and the right number is the Possible Catch. Column headings give the trapping-period dates (year shown above the date).

1949 Sep.19-23	1949 Oct.4-8	1949 Oct.17-21	1949 Oct.31/Nov.5	1949 Nov.14-18	1950 Jan.10-14	1950 Apr.23-27	1950 May7-11	1950 May23-27	1950 June6-8	1950 June16-21	1950 June27/July1	1950 July11-23	1950 Aug.22/Sep.2	1950 Sep.18-22	1950 Sep.26/Oct.5	1950 Oct.10-19	1950 Oct.24/Nov.2	1950 Dec.4-14	1951 Jan.11-20	1951 Feb.13-23	1951 Apr.12-21	Total
X	0 1	0 1	0 1	1 1	1 1	0 1	1 1	1 1	1 1	0 1	0 1	0 1	0 1	1 1	1 1	0 1	X					7 16
X	1 1	1 1	1 1	1 1	1 1	0 1	1 1	1 1	0 1	X												7 9
X	1 1	1 1	1 1	1 1	1 1	0 1	X															5 6
X	0 2	1 2	0 2	1 2	1 2	X																3 10
X	2 2	2 2	2 2	1 2	X																	7 8
X	1 2	2 2	2 2	X																		5 6
X	1 1	0 1	X																			1 2
	X	0 1	1 1	X																		1 2
	X	1 1	X																			1 1
		X	1 2	2 2	1 2	2 2	0 2	X														6 10
		X	1 1	1 1	0 1	X																2 3
		X	1 3	2 3	X																	3 6
		X	0 2	X																		0 2
			X	1 1	1 1	1 2	1 1	X														4 5
			X	5 5	X																	5 5
						X	0 1	1 2	1 1	0 1	0 1	0 1	0 1	1 1	0 1	1 1	X					4 12
						X	1 1	1 1	1 1	1 1	X											4 4
						X	1 1	1 1	X													2 2
							X	1 1	1 1	X												2 2
							X	1 1	1 1	X												2 2
							X	0 1	0 1	0 1	0 1	0 1	1 1	0 1	X							1 7
							X	0 1	0 1	0 1	1 1	0 1	X									1 5
								X	1 1	1 1	0 1	X										2 3
								X	1 1	1 1	X											2 2
								X	0 1	0 1	0 1	0 1	0 1	0 1	0 1	X						0 7
								X	1 2	1 2	X											2 4
								X	0 1	X												0 1
									X	0 1	0 1	0 1	0 1	1 1	0 1	0 1	0 1	X				1 8
									X	1 2	1 1	1 1	1 1	X								4 5

	Actual Catch	Possible Catch	Efficiency (Per Cent)
	193	327	59
	8	10	80
	11	17	65
	12	21	57
	18	33	55
	20	32	63
	19	28	68
	1	3	33
	10	24	42
	2	6	33
	4	11	36
	6	12	50
	10	18	56
	5	13	38
	10	14	71
	8	12	67
	10	14	71
	17	19	89
	10	18	56
	7	12	58
	5	10	50

used by Dr. F. C. Evans of the Institute of Human Biology, University of
Michigan, and I am indebted to him for the idea.

Trap arrangement. Traps were placed in a grid pattern spaced at 18-
meter (about 20-yard) intervals. Since the traps were not left in place at
all times, their positions were permanently marked with wooden or metal
stakes. The single-catch trap was used only in alternate rows and then
only at alternate positions. Thus, any rectangle of four traps included one
single-catch and three multiple-catch traps.

Trapping periods. During breeding seasons each plot was trapped for
five, occasionally six, days every two weeks. This arrangement was de-
signed to catch as many young mice as possible and still keep disturbance
to the population at a practicable minimum. In nonbreeding seasons the
five-day period was retained, but there was only one such period every
four to six weeks, and during the winter of 1949-50 there was one interval
of about 15 weeks when most of the area was not trapped. When both plots
A and B were in use, one was trapped for five days, then the traps were
shifted and the other was trapped for a similar period, so that ten days
were required to cover the whole area.

At the beginning of a trapping period, traps were set in the afternoon.
On succeeding days they were visited each morning to record and release
the captive animals. Traps in which *Peromyscus leucopus* were caught
were left unset for the following night and then reset. This procedure pre-
vented the retaking of a mouse at the same trap on successive nights.
Such repeat catches in the same trap would give an erroneous idea of the
area covered by the individual.

Bait. A mixture of corn, wheat, oats, sunflower seed, and rolled oats
was used for bait and food. Rarely, clover seed was added.

Marking. Captured animals were serially numbered in a manner simi-
lar to that described by Burt (1940). A combination of ear notching and toe
clipping was used to mark *Peromyscus*. Other animals caught were also
marked. But, since few were taken, ear notching was sufficient for flying
squirrels (*Glaucomys*) and chipmunks (*Tamias*) and toe clipping for shrews
(*Blarina, Sorex*) and the bog lemming (*Synaptomys*).

TRAPPING EFFICIENCY

Efficiency of trapping is difficult to determine accurately. Hacker and
Pearson (1946:339) used the ratio

$$\frac{\text{actual catch of marked mice}}{\text{possible catch of marked mice}}$$

to determine their chance of catching a mouse that was known to be on the
area. From Table I, a table similar to one devised by Hacker and Pearson,
the trapping efficiency can be calculated for any given trapping period.
The catches were grouped in the following manner. All mice caught for the
first time in one trapping period and again for the last time in a subsequent
period were placed in one group. Each horizontal line of the table repre-
sents one such group and shows for each trapping period the possible catch

and the actual catch. The first and last captures are indicated by X's since they cannot be used in the calculation. By adding the lines vertically the ratio is obtained for each period. This calculation, of course, gives only the chance of recapturing, in a given period, a marked mouse known to be present both before and after the period in question. The chance of capturing a new mouse is much harder to determine, since we do not know how many unmarked mice are on the area at any given time. Since immigrants must cover more area than residents, they probably stand more chance of being caught. The same holds true for juveniles, at least as soon as they begin to move away from the nest area. On this assumption, then, the actual trapping efficiency for all mice on the area should be higher than that calculated for the marked mice.

The considerable variation from period to period evident (Table I) may result from a difference in degree of activity, which in turn may be correlated with changes in the physical environment. The relatively low average of about 59 per cent may mean that the distance between the traps was sufficiently great so that not all mice contacted a trap even once in a five-day period. Or, it may mean, perhaps, that not every mouse entered a trap when it came upon it. Indeed, tracks in the snow indicate that some mice passed very close to a trap without entering. Another possibility is that some individuals do not live continuously in one place, but have two or more residences, perhaps some distance apart. This last would account for the inability to catch all the marked mice in every five-day period. I have records of two mice that moved away from an early residence for a time but later returned. Both were males which were marked when they were juveniles. Some time after being marked, each mouse was recaptured several times on another part of the area and, eventually, each was retaken in the vicinity where it had first been captured. In another instance a male and a female, both marked originally on the study plot, were recaptured in an adjoining woodlot. They were not away long, however, for both were taken on the study plot in the periods just before and just after this excursion. If this kind of behavior, a tendency to make trips away from the usual area of activity, accounts for the results in the table, it would indicate an error in the premise on which the calculation is based rather than inefficiency of the trapping method.

If the data of Table I are rearranged so that the comparison is between groups of mice which have been recorded on the area over different lengths of time, some light may be shed on this question. Table II shows the percentage of possible catch for mice grouped according to the number of weeks between first and last catches. From this table it appears that mice which have been recorded on the area for as long as 40 weeks are likely to be caught just as often as those that have been present for only a few weeks. The variation in the last two columns is probably a result of the smallness of the sample. If many individuals spend periods of several weeks away from the area, then the percentage of catches should be lower for the mice with the longer records. Since the above data do not give any definite evidence for this, such behavior must not have been widespread. More study, however, is needed to clarify this. If it should be found that some individuals do make relatively long excursions, even though they are

TABLE II

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

| | No. of Weeks between First and Last Captures | | | | | |
	0–8	9–16	17–24	25–32	33–40	57–64
No. of Mice in Group . . .	37	39	28	13	2	1
Actual Catch	31	51	55	37	12	7
Possible Catch	49	86	100	61	15	16
Efficiency (Per Cent)	63	59	55	61	80	44

of short duration, it would partly explain the ability of some mice to return to their home area from distances of several hundred yards or even a mile or more, as was observed by Murie and Murie (1931; 1932), Burt (1940), and others.

During the summer of 1950 raccoons repeatedly disturbed the traps. At times as many as 100 traps (more than 60 per cent of the total in use) were upset in a single evening. The number of captures usually dropped on such nights, but generally remained near the average for the period as a whole. This was because the returns happened to be high, before the peak of disturbance, which usually occurred the last two days of the trapping period.

ACCIDENTAL DEATH OF MICE

Disturbance of the traps by other animals occasionally resulted in the accidental trapping of mice. Between periods of trapping the traps were usually left in the field, but were turned upside down so that a mouse could not, supposedly, become trapped. Other animals, particularly the raccoons, sometimes righted the self-setting, multiple-catch traps. Whenever this did occur, any mouse that was caught died. As soon as this difficulty was discovered, it was remedied by leaving the back door of the trap open, but in the meantime several mice were lost.

Predators killed a few mice as evidenced by blood and bits of fur that were left in the traps. In one instance the remains of two mice, which apparently had been trapped, were lying just outside the trap. Since only the hind quarters remained, the individuals could not be identified by number. Once a young female weasel (*Mustela frenata*) was captured with a mouse, which she had evidently killed but not yet eaten. Four other mice were killed by animals caught in the trap with them, two by short-tailed shrews (*Blarina*) and two by chipmunks (*Tamias*). One mouse was killed by another caught in the same trap with it. The greatest accidental loss, however, was the death of mice from the effect of capture. That such deaths frequently resulted from exposure, rather than shock or "fighting the

trap," may be evidenced by the occurrence of most of such deaths in the
fall. Perhaps, before the mice have become acclimated to cooler weather,
they are more susceptible to chilling. Sometimes the bait would be com-
pletely eaten, but at others there seemed to be sufficient food. The known
accidental deaths are itemized in Table III.

TABLE III

Deaths of *Peromyscus leucopus* Resulting from Trapping

Cause	Number
Trap Accidentally Set by Other Animals	6
Intraspecific Fighting in Multiple- catch Traps	1
Predation	7
Unknown (perhaps shock, exposure, or other factors)	
First Captures	16
Recaptures	37
Total	67

ESTIMATION OF AGE

As the ages of individual mice must be known in order to determine
differential survival rates with respect to age and since the ages of adults
cannot be successfully determined in the field, only mice caught as juve-
niles or subadults can be used to observe these rates. Age of young mice
was estimated as follows. The length of time young mice remain in the
nest was assumed to average 23 days. Svihla (1932:19) found that in *Pero-*
myscus leucopus noveboracensis the mean period of gestation was 23 days
for nonlactating females. The minimum length of gestation for lactating
females was also 23 days. Since females commonly have litters in im-
mediate succession, the weaning age of juveniles must be adapted to the
minimum time, which is 23 days. If a second litter is not forthcoming, the
young may not be weaned at this age, but they may, perhaps, venture out of
the nest.

To determine the length of the juvenal period (defined here as the in-
terval between the time a mouse leaves the nest and the beginning of the
postjuvenal molt), an average was obtained for 33 mice in this age group.
Since trapping periods were frequent, it was possible to reckon that a
juvenal mouse, when caught for the first time, had left the nest midway
between this capture date and the last day of the previous period. If this
mouse was caught after the molt had started, the time of beginning of molt
was considered to be the mid-point between the last capture as a juvenile
and the first capture as a subadult. An average for the 33 mice gave the
length of time between leaving the nest and the beginning of molt as 14 ± 1

day. The length of time a mouse spends in the postjuvenal molt (here referred to as the subadult period) was ascertained in a similar manner. This calculation, based on 18 individuals, gave a mean of 17 ± 2 days. There was no significant variation between the sexes for either of these periods.

By the use of these figures every immature mouse captured could be placed in an age group. Mice in gray pelage (juveniles) were estimated to average 30 days of age. This estimate is based on the assumption that mice caught when in gray pelage were, on the average, at the mid-point of the juvenile age interval of 14 days. Thus, 23 days in the nest plus seven days as a juvenile out of the nest gives 30 days as the average age of all mice caught in the juvenal pelage. Those caught for the first time in the postjuvenal molt were, under the same assumptions, estimated to average 46 days of age, 23 days in the nest plus 14 days as juveniles outside the nest, plus nine days to the mid-point of the postjuvenal molt. These estimates give somewhat lower ages than those given by Nicholson (1941), for the same species and for the same stages of development. Although in my estimates there may be an error of several days, it could not be greatly significant for this study, since the calculations to be made on survival rates are based on weekly intervals. The errors are not cumulative and would likely shift an individual no more than one such interval.

CAPTURES

The captures of *Peromyscus leucopus* are itemized in Table IV. For each trapping period are listed the total number of captures (including recaptures), the total number of unmarked individuals, the number of unmarked immature mice, and the number of unmarked adults. On all areas trapped 559 individual white-footed mice were caught a total of 1823 times. On plots A and B only, 437 mice were caught 1601 times. If all individuals are considered, the sex ratio was 315 males to 244 females. The apparent excess of males may result from a larger area of activity of males. Burt (1940:26), found that the maximum as well as the average home range of males was greater than that of females. Townsend (1936:38, 82, 83) believed that the greater wandering tendency of males influenced the trap-revealed sex ratio. A comparison of only the immature individuals, which should reduce the effect of this differential movement, gives for the present study a ratio of 140 males to 130 females.

Several other species were caught on the plots during the study. Five masked shrews (*Sorex cinereus*), 118 short-tailed shrews (*Blarina brevicauda*), 10 flying squirrels (*Glaucomys volans*), 47 chipmunks (*Tamias striatus*), one bog lemming (*Synaptomys cooperi*), and one weasel (*Mustela frenata*) were taken from the traps.

POPULATIONS

Although the study area is isolated from other woodlots except for narrow lanes of shrubs or trees, some mice caught in the woods occupied

TABLE IV

Captures of *Peromyscus leucopus*

Date	Plot	Number of Unmarked Individuals Captured					Total Number of Captures (Including Recaptures)
		Adult		Immature		Total	
		♂	♀	♂	♀	♂ + ♀	
1949							
9/19-9/23	A	4	3	2	15	24	41
10/4-10/8	A	1	0	4	4	9	19
10/17-10/21	A	2	0	5	6	13	31
10/31-11/5	A	1	2	11	4	18	46
11/14-11/18	A	3	2	12	13	30	88
1950							
1/10-1/14	A	10	6	1	1	18	68
4/23-4/27	A	2	2	3	3	10	47
5/7-5/11	A	0	1	8	1	10	45
5/23-5/27	A	0	0	7	9	16	42
6/6-6/8	A	4	0	3	5	12	36
6/16-6/21	A	5	3	6	5	19	67
6/27-7/1	A	3	0	2	2	7	25
7/11-7/23	A, B	18	23	8	9	58	160
8/22-9/2	A, B	16	4	0	2	22	153
9/18-9/22	A	9	4	1	2	16	39
9/26-10/5	A, B	9	5	9	9	32	100
10/10-10/19	A, B	8	3	16	18	45	116
10/24-11/2	A, B	5	2	11	6	24	94
11/6-11/10	B	1	3	9	5	18	108
12/4-12/14	A, B	7	9	0	1	17	108
1951							
1/11-1/20	A, B	5	1	0	0	6	45
2/13-2/23	A, B	4	1	0	0	5	58
4/12-4/21	A, B	7	1	0	0	8	65
Total	Plots A and B	124	75	118	120	437	1601
Total	Other Areas	51	39	22	10	122	222
Total	All Areas	175	114	140	130	559	1823

the surrounding area also. Therefore, in calculating density of population, it is necessary to consider that the area comprises the woods plus a surrounding strip. The width of this strip is usually reckoned as half the diameter of the average home range. Stickel (1946) pointed out that the addition of a strip so wide could lead to inaccuracies, since the area of the home ranges of the mice theoretically living along it would not be equally distributed on either side of the original boundary. Rather than one-half, she suggested that the fractional part of the mean diameter of home range to be added should be só selected that the area added outside the original boundary is equal to that of a similar strip just inside it. The width of

this inner strip would be the remaining fractional part of the mean diameter of the home range. In the present study the irregularities of the area would make such calculation difficult and, furthermore, in view of the lack of knowledge about the actual shape of home ranges, such an exact calculation as her method requires would probably not be a significant refinement. Therefore, the width of this outer strip was estimated and then checked by planimeter measurements. The proper correction turned out to be approximately one-third of the mean diameter of home range. This diameter for the sexes combined was determined by Burt (1940) to be 250 feet. Separate calculations for each sex are not warranted by the data here. The effective census areas calculated as above are given in Table V.

TABLE V

Size (in Acres) of Census Areas

	Plot A	Plot B	Combined Plots
Original Area	10.0	12.2	22.2
Added Strip	9.5	11.9	12.0
Effective Area	19.5	24.1	34.2

The sum of the adjusted areas for plot A and plot B does not equal the adjusted area for the combined plots, since the added strips overlap where the two plots are contiguous.

The population is calculated on the basis of the number of individuals present during each trapping period. The number of different individuals caught during one period plus any additional caught in periods both before and after were added to obtain the population figure for each period. The results are given in Table VI. For purposes of comparison, figures based on the original area as well as those based on the adjusted area are included. The densities for the combined plots are in some instances greater than for either plot separately. This is true because in those particular cases the number of individuals shared by the two plots is less than would be expected. Thus, the effective census area for the combined plots is decreased more by the elimination of the overlapping sections than the total number of mice is reduced by elimination of duplicate individuals. This discrepancy apparently results from the small size of the plots and should therefore be reduced if a larger census plot were used. The true value of the density figure should be nearer to that obtained for the combined plots, for which a larger sample is available.

The densities calculated by using the added strip range from 0.5 to 2.9 individuals per acre (1.2 to 7.2 per hectare). Figure 2 illustrates the trend from month to month during the study. Most reports in the literature indicate a higher density for this species. Burt (1940) found 3.08 to 10.87 per acre in upland woods on the Reserve. Working in isolated woodlots he did not use an extra strip in calculating the census area. Stickel (1946), using such a strip, estimated the adult population in bottomland

TABLE VI

Total Numbers and Number Per Acre of *Peromyscus leucopus* Estimated
to be on the Study Area at Each Trapping Period

Date	Adult		Immature		Total	Number per Acre					
						Based on Adjusted Area			Based on Original Area		
	♂♂	♀♀	♂♂	♀♀		Plot A	Plot B	Comb. Plots	Plot A	Plot B	Comb. Plots
1949											
9/19-9/23	4	3	2	15	24	1.2	..	..	2.4	..	..
10/4-10/8	4	3	4	10	21	1.1	..	..	2.1	..	..
10/17-10/21	5	7	6	9	27	1.4	..	..	2.7	..	..
10/31-11/5	7	10	13	9	39	2.0	..	..	3.9	..	..
11/14-11/18	11	18	13	15	57	2.9	..	..	5.7	..	..
1950											
1/10-1/14	20	24	1	1	46	2.4	..	..	4.6	..	..
4/23-4/27	11	13	3	3	30	1.5	..	..	3.0	..	..
5/7-5/11	8	9	8	4	29	1.5	..	..	2.9	..	..
5/23-5/27	6	7	12	11	36	1.8	..	..	3.6	..	..
6/6-6/8	9	4	11	15	39	2.0	..	..	3.9	..	..
6/16-6/21	16	10	10	8	44	2.3	..	..	4.4	..	..
6/27-7/1	12	5	2	5	24	1.2	..	..	2.4	..	..
7/11-7/23	26	27	8	10	71	1.1	2.2	2.1	2.1	4.3	3.2
8/22-9/2	36	21	1	3	61	1.6	1.5	1.8	3.1	3.0	2.7
9/26-10/5	32	20	9	10	71	1.9	1.5	2.1	3.8	2.9	3.2
10/10-10/19	30	17	18	22	87	1.6	2.4	2.5	3.1	4.8	3.9
10/24-11/2	30	18	19	17	84	2.0	1.9	2.5	3.9	3.8	3.8
12/4-12/14	30	37	1	1	69	1.3	2.0	2.0	2.5	3.9	3.1
1951											
1/11-1/20	14	19	0	0	33	.9	.7	1.0	1.8	1.3	1.5
2/13-2/23	11	15	0	0	26	.5	.9	.8	.9	1.7	1.2

forest in Maryland in September to be 6 to 7 per acre. Hanson (1946), also
with an adjusted area, reported for woodlands 1.8 to 8.8 mice per acre.
All three workers used quadrats larger than the average home range of the
mice. Earlier estimates of over 200 per acre (Williams, 1936) resulted
from the use of quadrats smaller than the home range. A density figure
based on a census area smaller than the home range of an individual
mouse would obviously be erroneous, even if only one mouse were caught
in such an area. Because more than one individual will usually be taken at
any given trap, the census area should always be as large as the home
range and preferably several times larger, that is, if absolute rather than
relative density is wanted.

There are at least two factors, and probably more, that could account
for the relatively low density found in this study. The population level
may vary from one region to another in response to some unknown en-
vironmental differences. Trapping results in other woodlots on the Re-
serve indicated that such variation was of significant proportions. The
number of mice also fluctuates from year to year. The density recorded
for plot A (Table VI) was approximately six times as high in late 1949 as
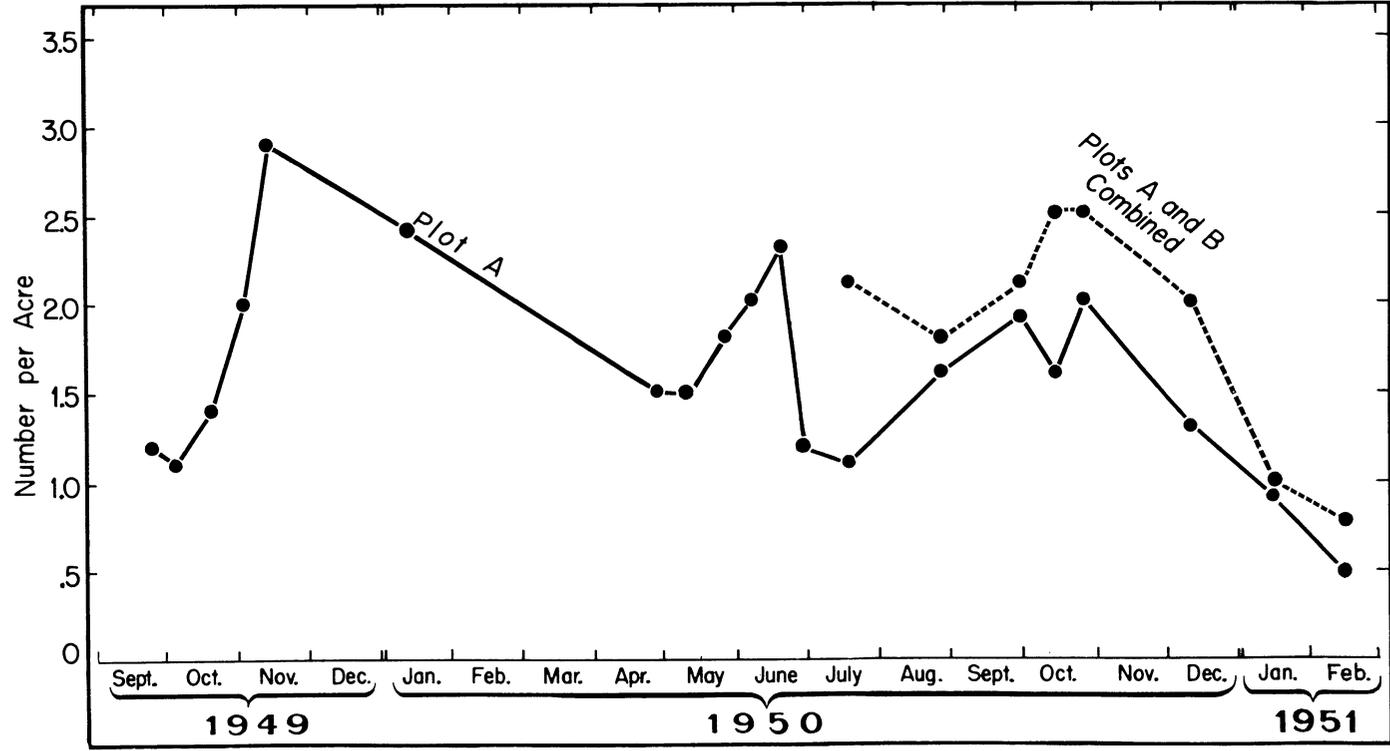
FIG. 2. Number (per acre) of *Peromyscus leucopus* on the study area from September, 1949, to February, 1951.

in February, 1951. The population level in each case may have been nearer a minimum than a maximum. Continuous study of the *Peromyscus leucopus* population on the Reserve for several years would be necessary in order to determine the nature of the long-term population fluctuations and the positions of these density levels on such a curve. In New Jersey Jackson (1952) reported that the density level of *P. leucopus* on an area that he studied dropped appreciably between 1950 and 1951. This similarity in timing of population decrease in New Jersey and Michigan could very well be coincidence, but it is possible that some common factor was involved. Bole (1939) found the population of *P. leucopus* in Ohio varied greatly from year to year; average populations in upland forests ranged from 5.2 per acre to 29 per acre. The densities in Bole's study, which were based on quadrats smaller than home ranges of individual mice, are perhaps above the true value, but they do indicate the fluctuating tendency of the population.

SURVIVAL RATES AND LONGEVITY

Rate of disappearance of mice from the study area. The rate of mortality or survival cannot be interpreted directly from the count of marked mice which disappear between one trapping period and the next, because it is likely that some absent individuals have not died but simply moved off the area. Thus, the rate of disappearance of marked mice is made up of two other rates, a mortality rate and an emigration rate. The disappearance rate would be less than the sum of these rates by an amount equal to the product of the two. This product is quite small and in most cases probably not too important.

The mortality rate would be equal to the disappearance rate if there were no emigration. Thus, although the mortality rate may be less than disappearance rate, it cannot be more. The first problem then is to determine the rate of disappearance and to discover whether it varies with age. This may be done by studying the series of mice which were caught when young enough to be satisfactorily aged.

If the rate of disappearance is age constant, then the number of individuals remaining on the area should decrease at a constant rate from one age level to the next. The mathematical formula for this would be a curve of the type,

$$Y = ab^X , \tag{1}$$

where X is the age level, Y is the number of individuals still on the area that have attained age X, and a and b are constants. To determine how well the data fit such a curve it is transformed into a straight-line equation by restating it in the logarithmic form,

$$\log Y = \log a + X \log b , \tag{2}$$

and the data are fitted to this line by the method of least squares (Rider, 1939:27-34). The sum of the squared deviations of the observed values from a line so calculated is at a minimum. Hence, by this criterion, we obtain the best-fitting line.

The value of log a in the equation depends on the number of individuals in the series and does not enter into the discussion of rates. The value of log b, however, is important, since it indicates the slope of the logarithmic curve and, hence, is a function of the rate of disappearance of the marked mice.

The data were divided into six sets, one for each sex at each of three seasons of birth (fall of 1949, spring and summer of 1950, and fall of 1950), to be fitted to the above curve. These six series are shown in Table VII.

TABLE VII

Number of *Peromyscus leucopus*, Marked as Juveniles or Subadults, that Remained on the Area in Succeeding Weeks

Column X, gives the age in weeks;
Column Y, the number of mice that have reached age X and are still on the area; and column Z, the logarithm of number in Y.

	Males						Females					
	Fall-born 1949		Spring- and Summer-born 1950		Fall-born 1950		Fall-born 1949		Spring- and Summer-born 1950		Fall-born 1950	
X	Y	Z	Y	Z	Y	Z	Y	Z	Y	Z	Y	Z
5	24	1.3802	36	1.5563	37	1.5682	37	1.5682	34	1.5315	31	1.4914
7	17	1.2304	26	1.4150	36	1.5563	27	1.4314	22	1.3424	28	1.4472
9	6	.7782	13	1.1139	24	1.3802	14	1.1461	15	1.1761	22	1.3424
11	5	.6990	6	.7782	13	1.1139	14	1.1461	8	.9031	18	1.2553
13	3	.4771	6	.7782	12	1.0792	14	1.1461	7	.8451	16	1.2041
15	3	.4771	4	.6021	8	.9031	13	1.1139	5	.6990	15	1.1761
17	3	.4771	4	.6021	7	.8451	12	1.0792	4	.6021	15	1.1761
19	3	.4771	3	.4771	5	.6990	12	1.0792	4	.6021	12	1.0792
21	1	.0000	2	.3010	5	.6990	11	1.0414	4	.6021	10	1.0000
23	1	.0000	2	.3010	4	.6021	8	.9031	3	.4771	9	.9542
25	0	....	2	.3010	4	.6021	8	.9031	2	.3010	9	.9542
27	...	....	1	.0000	3	.4771	7	.8451	2	.3010	7	.8451
29	...	....	1	.0000	2	.3010	5	.6990	1	.0000	4	.6021
31	...	....	1	.0000	2	.3010	5	.6990	0	....	3	.4771
33	...	....	0	....	0	....	4	.6021	...	....	2	.3010
35	...	....	...	....	...	....	4	.6021	...	....	1	.0000
37	...	....	...	....	...	....	3	.4771	...	....	0	....
39	...	....	...	....	...	....	2	.3010	...	....	...	....
41	...	....	...	....	...	....	1	.0000	...	....	...	....
43	...	....	...	....	...	....	1	.0000	...	....	...	....
45	...	....	...	....	...	....	0	....	...	....	...	....

Individuals accidentally killed in the traps are excluded. Column X gives the age in weeks from five weeks on. Five weeks was the youngest age group that contained a representative sample. The number of marked individuals known to be on the area is given in column Y. Column Z lists the logarithms of the numbers in column Y.

The values of log a and log b were calculated and substituted in (2) to give,

Males born in fall of 1949	log $Y = 1.5841 - .07032\,X$ (3)
Females born in fall of 1949	log $Y = 1.6624 - .03430\,X$ (4)
Males born in spring and summer of 1950	log $Y = 1.6276 - .05778\,X$ (5)
Females born in spring and summer of 1950	log $Y = 1.6445 - .05428\,X$ (6)
Males born in fall of 1950	log $Y = 1.7590 - .04960\,X$ (7)
Females born in fall of 1950	log $Y = 1.7954 - .04194\,X$ (8)

The coefficient of correlation, r, a measure of the amount of error in the values of log Y predicted from the above regressions, is quite high, indicating that the equations fit the data well and that the disappearance rates are relatively age constant. The values of r are given below.

Regression Equation	Correlation Coefficient
(3)	– .9448
(4)	– .9615
(5)	– .9642
(6)	– .9711
(7)	– .9808
(8)	– .9497

The regressions (3) through (8) have been plotted along with the observed values of Y in Figure 3. The deviations of the observed values from each of the lines are the errors of prediction, a measure of which is given by the respective correlation coefficients. However, this measure gives no indication whether the deviations are random or whether the deviations occur at certain positions in each series. If they are random, the above equations give the best practical fit. If the deviations are not random, then other curves could be fitted to the six series to reduce the error still further and perhaps to define more precisely the biological processes being observed. A glance at the figures will show that there is a tendency in some cases for the deviations to be regular. These fluctuations may be related to age, season, or some other factor, but the determination of their reality and importance will have to await the accumulation of more data. In this study the error appears to be sufficiently small, so that the general trend may be used as a base for further investigation.

In further references to age-constant rates for the mice studied, it shall be implied that individuals younger than five weeks are excluded and that minor deviations from the rates do exist and may later be shown to have a biological significance. It may be that five weeks is still too young and that rates do not tend to become age constant until later.

The conclusion that the disappearance rate is not greatly affected by age is in agreement with the findings of other workers. In a study of the Tulare kangaroo rat (*Dipodomys heermanni*) on an eighty-acre area, Fitch
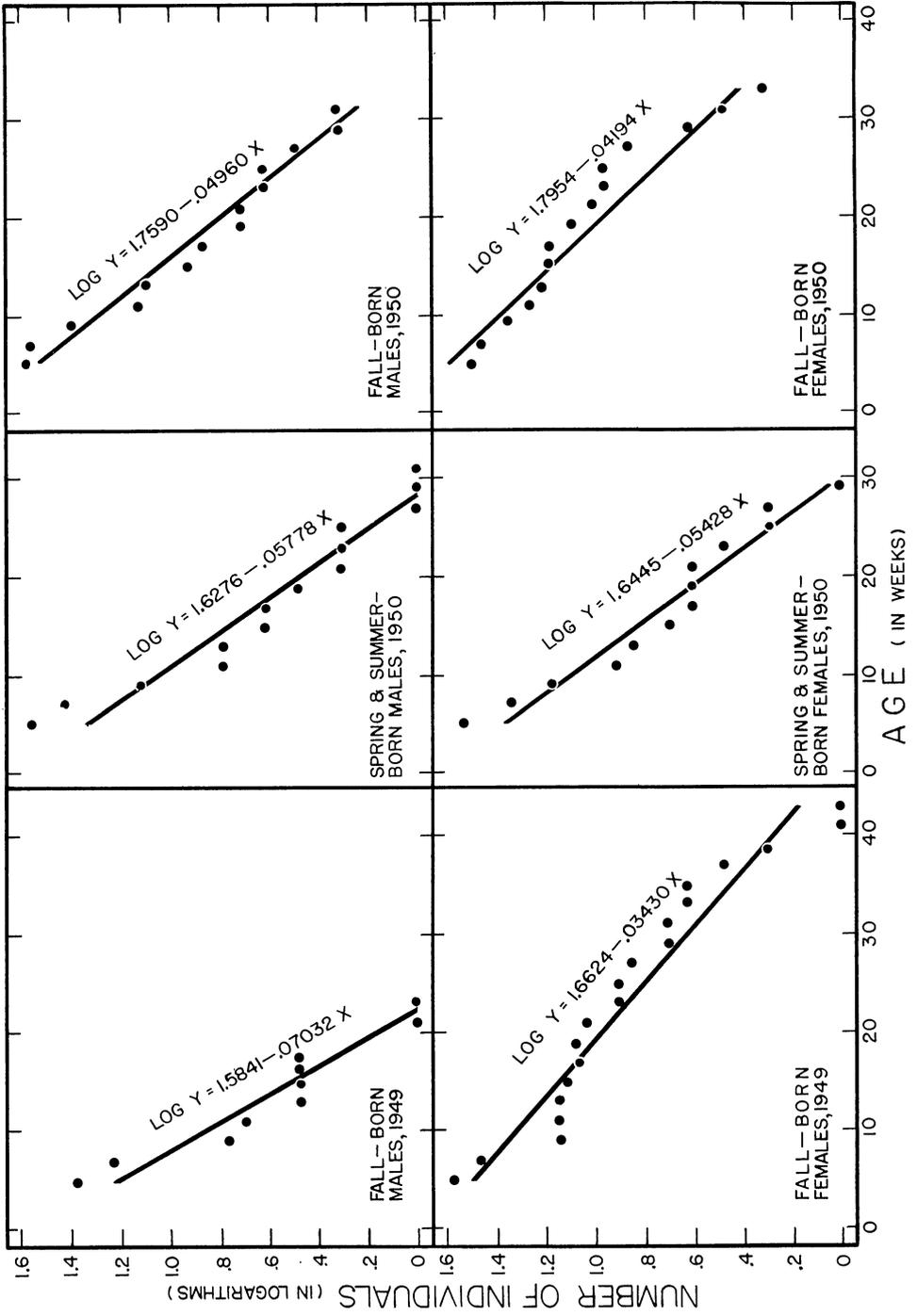
FIG. 3. Number of *Peromyscus leucopus* marked as juveniles or subadults that remained on the census plots at ages shown.

(1948:28) found that young rats had essentially the same survival expectancy as adults, and that females did not differ significantly from males in this respect. Green and Evans (1940) reported mortality rates for snowshoe hares (*Lepus americanus*) as more or less age constant, although if I correctly understand their methods, this mortality could include emigration from the area and, hence, would actually be a disappearance rate. Blair (1948) found that the disappearance of both *P. maniculatus* and *P. leucopus* from a census area was similar for four seasons of the year. Since the age composition is different in different seasons, the rates are likely to have been independent of age. Hacker and Pearson (1946) found the survival rate for *Apodemus sylvaticus* in England to be quite constant during the winter months.

Tests were next made to determine the significance of the differences in disappearance rates among the six sets of data. A significant difference in the values of log b for any two sets was considered to represent significant differences in disappearance rates. The test used is one given by Rider (1939:94-95). Differences were highly significant between males and females born in the fall of 1949, but not between sexes born at other seasons. However, the actual calculated rates are consistently higher for males than for females. Even though these differences are statistically significant only in the 1949 instance, they may be true differences resulting from the greater range of movement of the males. The tests also show that season of birth may affect disappearance rate. In males there was a significant difference between those born in the fall of 1949 and those born in the fall of 1950. In females, on the other hand, there was a significant difference between the fall-born and spring- and summer-born individuals. Because of these differences the data could not be combined further in any consistent manner. Therefore, the sexes are treated separately for each season (as in equations 3 to 8), even though in some instances real differences have not been demonstrated.

Winter Mortality. An estimate of mortality rate may be arrived at by measuring the change in population size during nonbreeding seasons. Although some individuals are lost by emigration, others come in to take their place. If this interchange is assumed to be approximately balanced, the net loss throughout the winter represents the mortality. The rates, based on one-week intervals, have been determined from the decrease in total population from the latter part of November until April for 1949-50; and during December, January, and February for 1950-51. The method is the same as that used in calculating the disappearance rate. The data were fitted to equation (2) and the value of log b determined. Since we are now interested in actual rates (rather than regression slopes) the antilog (b), which gives the weekly survival rate, is obtained. By subtracting b from one, we arrive at the mortality rate. The results of this procedure are given in Table VIII. The difference between sexes is not significant by the test used above (Rider, 1939:94-95); hence, the values for the combined data are used for further calculations. By the same test the difference between the two seasons appears to be real, with the probability of deviation from the same rate between 0.02 and 0.01. The seasonal rates are, therefore, considered separately.

TABLE VIII

Average Weekly Rate of Decrease of Population (Mortality Rate)
of *Peromyscus leucopus* on the Study Area During the Winter Seasons

Season	Males	Females	Sexes Combined
1949-50	.0328	.0425	.0377
1950-51	.0835	.0776	.0806

In order to compare this mortality with disappearance, rates for the
latter were also computed from log *b* for regressions (3), (4), (7), and (8).
The results are given in Table IX, along with the mortality rates from
Table VIII. In the winter of 1949-50, mortality rates were low compared
with disappearance rates; many marked individuals must have moved out
and been replaced by unmarked mice from other areas. This was es-
pecially pronounced among the males. The next winter season, 1950-51,

TABLE IX

Comparison of Weekly Disappearance Rates and Weekly Mortality Rates
of Fall-born *Peromyscus leucopus* on the Study Plots During the Winter Seasons

	Males		Females	
	1949-50	1950-51	1949-50	1950-51
Disappearance Rate	.1495	.1079	.0759	.0921
Mortality Rate	.0377	.0806	.0377	.0806

when the mortality rate was considerably higher in both sexes, the disap-
pearance rate was somewhat lower in males and only slightly higher in
females. Since most of the loss of marked individuals could be accounted
for by mortality, movement out of the area must have been reduced. An
interesting point here is that the lower mortality occurred during the
winter of 1949-50 when population density was relatively higher. When the
density was less, 1950-51, the mortality rate was higher.

These results indicate that during the nonbreeding season, in the par-
ticular area studied, mortality and emigration tended to vary inversely
with respect to time. From the nature of the data it would seem that these
varying rates were not related to age distribution but to some other factor
(or factors), perhaps environmental rather than inherent in the population
and not age specific in its effects. If age-constant disappearance rates
were maintained under mortality rates which were age specific, the mor-
tality would necessarily vary inversely with emigration with respect to
age. The evidence does not point to this possibility, and the alternative,
that age-constant rates for both mortality and emigration produce age con-
stant disappearance rates, is a simpler explanation. This alternative re-
quires only that (with respect to age) mortality and emigration occur at
random. If environmental factors produce a change in rates, this change
would occur alike at all ages; new rates would be observed for both

mortality and emigration, but they would still not necessarily be age specific. Two different concepts are involved here and they should be restated for clarity (in both, reference is to individuals over five weeks of age). (1) Mortality and emigration may vary inversely over a period of time but without respect to age. (2) Mortality and emigration at any given time probably are constant with respect to age. The data which have been presented indicate that the first concept is valid for the area studied. The second concept gives the simplest explanation of the age-constant disappearance shown by the data. Age-constant mortality is not unknown in other warm-blooded vertebrates. Many species of birds exhibit age-constant rates (Farner, 1945; Lack, 1943a, b, c; Nice, 1937). In certain instances laboratory populations of mice have shown age-constant mortality (Greenwood, 1928); and this point will be discussed further, below.

The inverse relationship between mortality and migration is not in agreement with the theory of Kalabuchow (1935). His paper has only a short English summary, but much of his discussion is given by Elton (1942). Kalabuchow believed predation important in regulating population levels and that high populations, by causing increased movement in search of food, resulted in greater vulnerability to predators and, hence, higher mortality, and that low populations had the opposite effect. But, in the present study, low mortality seems to accompany high-movement rates, and high mortality low-movement rates. This is more like Errington's (1946) concept of compensatory actions in regulation of population size. Whenever density is high because of low mortality (as a result of unknown factors), there is a tendency to move out into other areas. If mortality is high, the population decreases rapidly and the need for dispersion is consequently lessened.

The question resolves itself into one of cause and effect, with the present data indicating that the amount of movement is a result and the mortality rate a cause. Mortality indirectly affects dispersal by its influence on population density. These data give no evidence that dispersal movements affect mortality, at least in any obvious manner. This conclusion is based on conditions during a short period of less than two years in one restricted area, and thus furnishes only a small bit of evidence in the overall picture. Certainly, more investigation is needed. Since rate of disappearance from a given area is not necessarily a reliable estimate of the mortality rate in that area (unless loss by migration can be accurately measured), additional techniques are desirable. Perhaps the more precise but somewhat more involved methods recently developed, particularly in England (Leslie and others, 1953; Moran, 1952), will lead to a better solution of this problem.

Longevity. Using the inferred winter mortality rates (.0377/week, 1949-50; .0806/week, 1950-51) and considering them age constant, we can set up a table of survival to show the mean longevity and life expectancy which would occur under the winter conditions that existed during the study. The mortality at other seasons is unknown, but it probably lies well below the disappearance rates (.1246/week, males; .1175/week, females) recorded for spring-born and summer-born mice. Table X records the number out of a group of 1000 five weeks of age that would

TABLE X

Theoretical Number of Survivors to Ages Shown,
Out of a Group of 1000 *Peromyscus leucopus*, Aged Five Weeks

Group I is based on the age-constant mortality rate (.0377/week)
for the winter of 1949-50;
Group II, on the rate (.0806/week) for the winter of 1950-51.
X, is the age in weeks; l_x, is the number of survivors at age X.

X	Group I	Group II
	$\bar{l}_x$	l_x
5	1000	1000
13	735	511
21	541	261
29	397	133
37	292	68
45	215	35
53	158	18
61	116	9
69	85	5
77	63	2
85	46	1
93	34	1
101	25	0(<.5)
109	18	. . .
117	13	. . .
125	10	. . .
133	7	. . .
141	5	. . .
149	4	. . .
157	3	. . .
165	2	. . .
173	2	. . .
181	1	. . .
189	1	. . .
197	1	. . .
205	0(<0.5)	. . .
Average Length of Life beyond Five Weeks of Individuals that Reached Five Weeks	26.5 weeks	12.4 weeks
Average Longevity of Individuals that Reached Five Weeks	31.5 weeks	17.4 weeks

survive to various ages under each mortality rate. Since the data do not
show any significant difference in winter mortality between males and
females, the table is based on the mortality of the population with sexes
combined. However, the rates probably do vary to some extent between
the sexes, especially during the breeding season.

With the high rate of mortality in the winter of 1950-51 only one mouse
in a thousand would be expected to reach an age of 93 weeks; with the
lower rate of the previous winter 34 mice could be expected to reach 93

weeks, and at least one would probably reach 197 weeks. Such old individuals are not generally caught, probably because the mortality rates seldom, if ever, remain continuously at low levels; and even if they did, these old mice would constitute only a very small proportion of the population. Out of 1382 marked, Burt (1940) found a few mice living to one year of age and only one approaching two years. Some of these, of course, would not have been a year old when his study ended, but the small proportion of old individuals is still significant. In this study, I have record of only one individual, a male, that was more than a year old. Pearson (1953:206) noted a comparable situation in *Peromyscus* populations in Florida. He stated, "Records of longevity...suggested that at least 28 per cent of the resident population of *gossypinus* lived at least 100 days after reaching adulthood, with one individual living nearly two years under natural conditions. Sixty per cent of the resident *nuttalli* population lived longer than three months after reaching adulthood and one individual survived nearly two and a half years."

The mean length of life, beyond five weeks, of individuals that have attained that age, would be 26.5 weeks under the low mortality rate and 12.4 under the higher rate. The mean length of life from birth for such individuals would be 31.5 and 17.4 weeks, respectively. It is not possible at this time to calculate the average longevity for an entire group of mice which are born, because mortality rates for the early weeks are unknown. Presumably, rates for very young individuals are higher than those given above, and if these were included the average life span would be reduced accordingly.

Blair (1948) estimated the average life span of *P. leucopus* to be a little less than five months, and he believed that survival was about the same at all seasons. Since he based his figures on disappearance from the study plots, actual length of life was probably longer. Five months would be within the range indicated by my data (Table X). McCabe and Blanchard (1950) give roughly comparable data for *P. maniculatus gambeli*, *P. truei gilberti*, and *P. c. californicus*. Their estimates of the average life span of these three forms are 152 days, 190 days, and 275 days, respectively. Their figures are based on individuals which have reached a trappable age and not on total number born.

Lankester (1870) long ago distinguished, particularly with respect to lower animals, between potential longevity and mean duration of life, which he called specific longevity. Mitchell (1911) suggested that comparison of these measures of longevity would give a rough indication of the severity of the natural conditions of living, and he applied the idea to captive animals in zoological parks. In the present study a comparison of these measures was made to emphasize the difference between relatively fast-breeding species, like *Peromyscus leucopus*, with high population densities and slower breeding, low-density species.

Some idea of potential longevity may be obtained from captive animals. Flower (1931) and Mitchell (1911) have listed the ages of many of the longest lived zoo animals, and Bourlière (1951) has added some recent information. Reports by Sumner (1922; 1932) and Dice (1933) show that the potential life span of mice of the genus *Peromyscus* may be as high as six

to eight years. My study, like preceding ones (Blair, 1948; Burt, 1940; Hamilton, 1942), indicates that the great majority of the individuals never reach such potential ages. Thus, most of these small herbivorous mammals live only through their prime and probably do not experience physiological old age. In the case of birds this point has been made by Farner (1945:69) in relation to age-constant mortality rates. He stated, ". . . it is possible, if mortality rates in Robins are affected by experience over a period of years or by physiological old age, that the vast majority die before they reach the age at which these factors become effective." If this statement is true for the American robin, which has an average natural longevity (for birds that reach their first November 1st) of about 10 to 20 per cent of the potential longevity, it may be even more applicable to *P. leucopus* which, according to the present study, has an average natural longevity of only 5 to 10 per cent of potential longevity. This low ratio of mean to potential longevity may account for the relatively constant rate of mortality (after the juvenile period) found for this mouse. Perhaps the same situation occurs in other small, relatively fast-breeding mammals. Fitch (1948) reported that 35.2 per cent of the kangaroo rats taken during a four-year live-trapping program had records that extended over not more than one month, 34.2 per cent had records of one to six months on the study area, and only 4.7 per cent had records extending for more than a year. The longest record was 33 months for an individual marked as a partly grown juvenile. Fitch believed mortality accounted for more of the disappearance from the study area than did migration. As already noted (p.23), these rates found by Fitch were not age specific, and the average longevity would seem to be a small per cent of potential. The mean longevity of a wild population of *Rattus norvegicus* (Davis, 1948) was much less than the potential, but in this study there was some evidence that mortality increased with age.

Some of the larger, slower breeding, less numerous herbivores appear to have age-specific mortality rates such as are experienced by man; that is, there is a decrease in rate through middle life and an increase again in later life. Figures for the Dall sheep (*Ovis d. dalli*), given by Murie (1944) and further analyzed by Deevey (1947), show the latter type of mortality. In this case, which is possibly representative of the larger herbivores, physical condition or some other factor gives the individuals in early adult life a better chance of survival than older ones have. Perhaps the older animals are experiencing physiological old age; if so, these sheep may have an average longevity approaching 50 per cent of potential, a figure roughly comparable to that for man. Flower's figures (1931) for zoo animals show that many Carnivora and some ungulate families have a mean to potential longevity ratio of about 50 per cent. However, it might be expected that the mean length of life for zoo animals would be somewhat higher than for wild populations.

Age-specific rates of mortality show up in laboratory populations of small herbivorous mammals. These mammals probably reach physiological old age because they are in a protected environment. Such curves have been shown by Leslie and Ranson (1940) for *Microtus agrestis*, by Wiesner and Sheard (1935) for albino rats (*Rattus norvegicus*, from Wistar

stock) and by Greenwood (1928) for "mice." But Greenwood (1928:277-78), discussing the survival of mice subjected to the risk of fatal infection, stated that once mortality rates had reached an early maximum they remained constant with respect to age. Here disease substitutes for some of the natural mortality factors and may approximate more closely the conditions in a wild population.

Bidder (*fide* Pear and Miner, 1935) believed that age-constant mortality rates are characteristic of aquatic organisms and that indeterminate growth accounted for the absence of senescence. However, if mortality rates are high enough, as they appear to be in many small animals, such conditions do not have to be postulated for age-constant mortality. Many of the species which have high reproductive potentials might be found to have age-constant mortality rates (for the life span over which they have any practical chance of surviving), if they could be studied under natural conditions, in which practically all factors can operate and in which the probability of reaching senility is negligible in comparison to the probability of dying during the period of physiological optimum. In the laboratory, with many of the mortality factors removed and the mean length of life greatly increased, these same species would be expected to experience a mortality rate which varied with age.

SUMMARY

This study to determine survival rates and longevity in *Peromyscus leucopus* was carried out on the Edwin S. George Reserve of the University of Michigan. Data were obtained by live trapping, marking, and releasing individual mice from July, 1949, to April, 1951. The study plot was an oak-hickory woodlot 22.2 acres (9.0 hectares) in size. Traps were placed in a grid pattern at 18-meter intervals.

Average trapping efficiency for a five-day trapping period, based on the assumption that individuals did not leave the plot between captures, was 59 per cent. Individuals with long records (25-64 weeks) on the area proved about as likely to be recaptured at any given trapping period as individuals with only short records (0-24 weeks). This result furnished evidence against the possibility that a sizable proportion of the mice spent periods of several weeks on areas other than the study plot. It did not rule out, however, the possibility that some of the individuals may make relatively long excursions for short periods of time and thus become familiar with much of the region outside their home range. These brief excursions were noted only once during the study, but they might, if common, account for the ability of some mice to return to their home area from relatively long distances.

During the study 67 mice were accidentally killed as a result of the trapping procedure. Fifty-three of these deaths were caused by the traps directly; interference by other animals accounted for the others.

Age estimates of immature mice were based on pelage. Mice in gray pelage when first captured (juveniles) were estimated to average 30 days of age; mice which were undergoing the postjuvenal molt when first captured (subadults) were estimated to average 46 days.

In the course of the study 559 individual *Peromyscus leucopus* were captured a total of 1823 times. Density of population was calculated (1) by using an adjusted area to account for individuals living partly inside and partly outside the trapped area and (2) by using only the original study plot as the effective census area. Based on the adjusted area the density varied from 0.5 to 2.9 individuals per acre (1.2 to 7.2 per hectare). The highest density occurred in the fall of 1949, the lowest in February, 1951.

The rates of disappearance of marked individuals of known age were determined for each sex for each of three seasons of birth (fall of 1949, spring and summer of 1950, and fall of 1950). The data for each of the six groups were fitted to the curve log Y = log a + X log b, with a relatively high correlation ($>$ -0.94) being obtained in each instance. The disappearance rates were thus believed to be essentially constant with respect to age for mice over five weeks. The rates tended to vary, however, between sexes and in some instances from season to season.

On the assumption that migration into and out of the area was approximately balanced, mortality rates were calculated from decrease of the population during the winter seasons. In the winter of 1949-50, mortality was low as compared to disappearance, and emigration must have accounted for a large share of the loss of marked individuals. In the winter of 1950-51, most of the disappearance could be accounted for by mortality; hence, emigration must have been reduced. The low mortality rate of the winter season of 1949-50 occurred when population density was relatively high. The higher rate of mortality during the winter of 1950-51 was accompanied by lower population density.

Calculated mortality rates for the two winter seasons were 0.0377 per week in 1949-50 and 0.0806 per week in 1950-51. A survival table was constructed for each rate. Under the lower rate, the mean duration of life for mice which reached five weeks of age would be 31.5 weeks, with one individual out of 1000 (aged five weeks) expected to reach 197 weeks. Under the higher rate, the mean duration of life for mice which reached five weeks would be 17.4 weeks, with only one individual out of 1000 (aged five weeks) expected to reach 93 weeks.

The ratio of mean to potential duration of life was used to compare small, relatively fast-breeding species with high population densities with slower breeding, low-density species. A low ratio (5 to 10 per cent) and age-constant mortality rates (after very early life) seem to be characteristic of fast-breeding species under natural conditions, whereas a high ratio (50 per cent or higher) and age-specific mortality rates are characteristic of some of the slower breeding, low-density species. It appears likely that many small mammals which, in the laboratory, show age-specific mortality experience age-constant mortality rates during the life span which they normally cover in the wild.

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