

THE ROLE OF REPRODUCTION AND MORTALITY IN
POPULATION FLUCTUATIONS OF PEROMYSCUS MANICULATUS
AND MICROTUS OCHROGASTER ON NATIVE PRAIRIES

by

ROBERT G. ROLAN

B. S., Kansas State University, 1959

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Zoology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1961

LD
2668
T4
1961
R65
C 2
Document

TABLE OF CONTENTS

INTRODUCTION	1
MATERIALS AND METHODS	5
RESULTS	8
Preliminary Studies	8
Population Fluctuations	23
Population Structure	30
Reproduction	32
DISCUSSION	49
SUMMARY	63
ACKNOWLEDGMENT	65
LITERATURE CITED	66
APPENDIX OF TABLES OF SIGNIFICANT CHI-SQUARES	72

INTRODUCTION

Fluctuations in the numerical populations of small mammals have been the subject of intensive study during the past 30 years. Such changes in population density typically begin with a moderate growth rate, accelerate to an abnormally high rate and end with a "crash" after peak density has been reached. The fluctuations of some species of animals have been observed to be cyclic in character, with peaks and troughs occurring at regular intervals. Interest in these changes in density has been spurred by economic considerations. First, large populations of mice may cause extensive damage to crops due to their feeding habits. Second, such large populations may contribute to the increase of predators which may turn to livestock when the mice become less plentiful. Third, mice and/or their parasites may carry infectious diseases transmittable to man or livestock.

It was recognized from the outset that these fluctuations are expressions of two major factors, natality and mortality; and subsequent studies have been primarily concerned with phenomena modifying the intensity of each. The earlier investigators studied the causes of population fluctuation so well summarized by Hamilton (1937).

Increased population is fostered by three reproductive factors:

1. An acceleration of the breeding rate;
2. an increased number of young per litter, and
3. the lengthening of the reproductive season, which allows for greater numbers of litters per year.

Causes responsible for a decline in numbers of mice may be abiotic, such as climatic influences, or biotic, such as disease and predation.

Jenkins (1948) listed factors inflicting death on Microtus, in what he considered to be declining order of importance, as predation, climate, shortage of food and disease. In giving predation the primary role he was supported

by Blair (1948) who based his conclusions on observations of both Microtus and Peromyscus.

Following Selye's (1946) original report on the general adaptation syndrome (GAS) and the diseases of adaptation, many workers began to study if and how stress might affect population dynamics. Christian (1956) studying the house mouse, and Louch (1956), the meadow vole, found decreased reproduction and increased mortality in their laboratory populations following the stress of overcrowding. Frank (1957) attributed the decimation of wild populations of Microtus arvalis to the exhaustion phase of the general adaptation syndrome.

Chitty (1952), studying Microtus agrestis, however, could not find that weather, disease, overcrowding, food deficiencies, predation, migration, change in age structure, season of birth, nor infestation with parasites were controlling factors in the mortality that he observed. They might better be termed contributing factors. He suggested that: "(1) strife during the breeding season resulted in (2) the early death of the young and physiological derangement among the adults. (3) The later progeny of these adults survived, but (4) were abnormal from birth and thus more susceptible to various mortality factors. (5) These constitutional defects, in a more severe form, were transmitted to the next generation." Experimental results in support of Chitty's theory were found by Clarke (1955) with Microtus agrestis, and by Christian and LeMunyan (1958) with Mus musculus. Christian and LeMunyan attributed the weakened physiological state of the progeny of crowded mice to insufficient quality or quantity of lactation. This weakened condition was persistent for two generations following removal of the stress. Such poor lactation, it should be noted, may be related to Louch's finding

of aberrant maternal behavior in Microtus pennsylvanicus under the same stress, overcrowding. Several recent field studies have yielded results more in accordance with Chitty's theory than with the general adaptation syndrome theory. The studies of Jameson (1953) on Peromyscus in California, and of Godfrey (1955) on Microtus are not inconsistent with the former. In another study, Hoffman (1958) noted that overwintering adult California and Montane voles from the peak population of a previous fall do not suffer the greatest mortality, as they might be expected to under the GAS theory, but it is rather their juvenile descendants that are the least viable. Chitty (1960) concluded that it is highly improbable that the action of physical factors is independent of population density. The effects of such "density independent" events as weather and climate become more severe as the number of animals increase and the physiological quality falls. "This hypothesis", he says, "overcomes two difficulties often met with in population studies: that there is no consistent evidence of (a) the mortality factors that are themselves influenced by population density in the manner required by one system of thought, or (b) the climatic catastrophes required by other systems."

Numerous factors have been advanced as ones modifying reproductive success in small mammals. Asdell and Sperling (1941) studied the relation between size of the reproducing female and reproductive success; Baker and Ranson (1932) and Whitaker (1940) studied the effect of photoperiod on reproduction in Microtus and Peromyscus. Eskridge (1956) determined the effect of cold on male Peromyscus. Beer et al. (1957) and Helmreich (1960) were interested in the regulation of reproductive rate by prenatal mortality. Others have been concerned with techniques for measuring fecundity and

reproductive success. Jameson (1947, 1950) found morphological criteria of fecundity in the testes of Microtus and Peromyscus. Deno (1937) discovered that placental scars indicate parousness in female mice. Davis and Emlen (1948) and Conaway (1955) investigated the possible use of placental scars for estimating litter size. Lauckhart (1957) and Hoffman (1958) have suggested that the quality of the available food is one of the biotic factors especially conducive to high reproduction. Most interesting, however, in the light of recent emphasis on the general adaptation syndrome and intraspecific competition, are the relationships found between population density and reproduction. Hamilton (1937, 1940, 1941) maintained that, in the meadow vole, high levels of density were favorable to a high rate of reproduction; further increasing the rate of pregnancy, litter size, and length of the breeding season. Christian (1956) and Louch (1956), however, both demonstrated experimentally that reproductive success declined as the population increased. Hoffman (1958) showed this to be true of wild populations of Microtus californicus and Microtus montanus, as have Martin (1956) and Fitch (1957) with Microtus ochrogaster. The majority of reports have upheld this conclusion, but conflicting reports have also been published. Jameson (1953) could find no consistent correlation between population density and reproduction, and Davis (1956) found reproductive rates to vary from time to time, but the wild population of Peromyscus observed remained essentially unchanged in numbers during the study period. It is the intent of this study to determine some of the factors affecting reproduction in Peromyscus maniculatus and Microtus ochrogaster in Kansas, and how these changes are reflected in the population.

The term "cycle" has become so closely identified with population work that it is often used incorrectly as a synonym for fluctuation. Cole, Rowan, Errington, and others (1954) have discussed the cyclic nature of certain population fluctuations from several viewpoints. Cole proposed that such cycles could be merely random variations, and gave certain empirical evidence to support his claim. The consensus, however, holds the view that cycles indeed occur in some species, but there is no agreement on the controlling mechanism. In this paper the use of the term "cycle" will be restricted to regularly recurring peaks and troughs of population density, except in certain quoted material.

MATERIALS AND METHODS

Data for this study was collected by the Kansas Small Mammal Census. The K.S.M.C. was organized by Dr. H. T. Gier of Kansas State University in 1949, independently of, but in general agreement with the principles used in the North American Small Mammal Census. Mammals were taken by the trap-line method, with two standard, snap mouse traps and one museum special placed in a cluster, but located in positions most likely to attract specimens, with 30 clusters spaced 40 to 50 feet apart. All traps were baited with a peanut butter-rolled oats mixture to which DDT was occasionally added when insects were likely to remove the bait. Cooperators throughout the state (Table 1) selected typical native grass prairie locations for the trap-lines. The lines were run twice a year, spring and fall; the spring trapping occurring during March and April, and the fall trapping during November and December, commencing after the first freeze. Each run was maintained for three consecutive nights, and the traps checked, emptied, and rebaited each morning. Specimens were frozen and sent to Dr. Gier for

Table 1. Trapping localities, cooperators, and dates of operation.

County	Cooperator	Institution	Dates
Anderson	Bill R. Brecheisen	-	1959-60
Atchison	Eugene W. Dehner	St. Benedict's College	1953
Cloud	Harry C. Duncan	Concordia High School	1951-52
Cowley	William K. Bunyan	Kansas State University	1958-59
Crawford	Claude Leist	Kansas State College, Pittsburg	1951-52
	Ted Sperry		1953-55
	Horace Hays		1956-60
	H. T. Gier	Kansas State University	1956-57
Decatur	Dolf Jennings	Oberlin High School	1954-56
	Paul Frederick	Kansas State University	1958
Ellis	Edwin P. Martin	Ft. Hays Kansas State College	1952-1960
Finney	Mickey Penny	Garden City High School	1951-56
	Roscoe C. Waldorf	Garden City Jr. College	1958-60
Johnson	Virgil E. Boatwright	Shawnee Mission North H.S.	1953-56
	Dwight L. Spencer	" " " "	1957-59
Linn	Marvin D. Schwilling	Kansas Forestry, Fish and Game Commission	1956-58
Lyon	Ted Andrews and Delta Kappa Chapter, Beta Beta Beta	Kansas State Teachers College	1951-60
McPherson	Eugene Krehbiel	Kansas State University	1958
	Robert G. Bellah	Bethany College	1959-60
Osage	Dolf Jennings	Quenemo High School	1951-52

Table 1. (concl.)

County	Cooperator	Institution	Dates
Republic	Donald Gier	Soil Conservation Service	1958-59
Riley	H. T. Gier	Kansas State University	1951-60
Saline	Ronald R. Clothier	Kansas Wesleyan University	1953-54
	William V. Houston	Salina Jr. High School	1955-60
Sedgwick	Harold D. Swanson	Friends University	1951-53
Shawnee	Donald W. Janes	Washburn University	1958-60
Smith	Virgil E. Boatwright	Smith Center High School	1952-53
Sumner	James K. Maupin	Wellington High School	1953-55

further analysis after weights and measurements were recorded. Data taken include weight, total length, tail length, hind foot length, and ear length. Female animals were examined for pregnancy and number of embryos, and for presence and number of placental scars. A limited number of male animals were examined for position, size, and condition of testes by macroscopical observation. In all, 48,898 trap-nights were set during the ten-year period from 1951 to 1961, resulting in a catch of 1,761 Peromyscus maniculatus bairdii and P. maniculatus nebrascensis, the prairie deer mice, and 467 Microtus ochrogaster ochrogaster, the prairie vole. In addition, these species: Peromyscus leucopus, Microtus pinetorum, Sigmodon hispidus, Reithrodontomys megalotis, Reithrodontomys montanus, Perognathus hispidus, Onychomys leucogaster, Dipidomys ordii, Synaptomys cooperi, Spermophilus tridecimlineatus, Blarina brevicauda, and Cryptotis parva were trapped in lesser numbers.

The census data from all localities were pooled in order to increase the reliability of statistical procedures, and each locality was regarded as a random sample of the type of habitat specified. Statistical methods as outlined in Snedecor (1956) were used throughout this paper. Specimens were identified from descriptions in Hall (1955), and representative study skins were prepared and stored in the Museum of Zoology, Kansas State University. All vernacular names used in this paper are those recommended by the American Society of Mammalogists Committee on Nomenclature (Hall, 1957).

To count placental scars the uterus of each mouse was removed in toto and placed on an index card. When held up to a light the scars were plainly visible along the mesometrial border of the uterus. In multiparous females two criteria were used to distinguish between sets of scars. Since the embryos tend to implant evenly spaced within a uterine horn, spacing of the scars was used to differentiate between sets. The intensity of pigmentation was used to determine the most recent set. Deno (1937) noted that this pigment, hemosiderin, gradually fades with age. A small colony of white mice was maintained in order to compare estimates of litter size made from placental scars with observed litters.

RESULTS

Preliminary Studies

One of the major problems to be solved before an analysis of the reproductive data could be made was what constituted a sexually mature animal. For the most part, data were incomplete or unavailable on pelage patterns and tooth wear condition. A preliminary study was undertaken to determine which measurements to use as a substitute for known ages in the

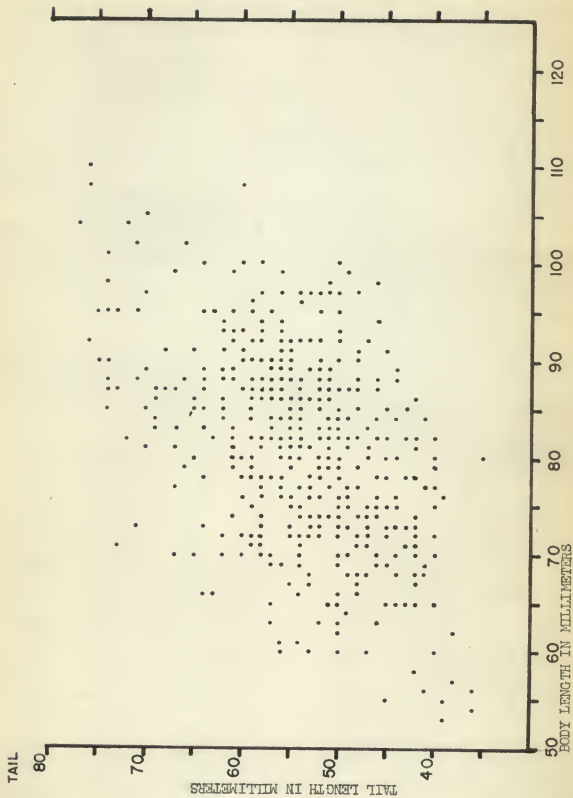
prairie deer mouse and prairie vole. Plates I and II show the extreme variability of tail length compared to body length in both species. It was concluded, therefore, that total length would include this additional variability if used. Next, weight and body length were compared in a similar manner as shown in Plates III and IV. Fitch's (1957) method of determining pregnancy by weight change suggested that pregnant females might introduce a certain amount of extra variability when age was estimated by weight. The weights of pregnant females are given as small circles in Plates III and IV. A great number of these animals tend toward the upper extremes of each body length coordinate. Fitch noted that other factors may also influence weight, one of the most important being the availability of moisture. Hence, body length was the dimension used for this study, reducing variability as much as possible.

Female deer mice and voles were recorded accumulatively on graphs according to body length if they showed some indication of sexual maturity. The criteria used were the presence of corpora lutea, placental scars; and pregnancy. Such arrangement of these data resulted in the normal distributions shown in Plate V. One of the characteristics of the normal distribution is the fact that approximately 95 per cent of the population showing the measured characteristic are expected to fall between two standard deviations on either side of the mean. The means and standard deviations were calculated for both species. The mean body length of sexually mature deer mice was 88.5 millimeters, and that of the voles 116.5 millimeters. The standard deviations were 7 and 9.5 respectively. Two standard deviations below the mean of the female deer mice was 75 millimeters. The lower limit for the voles was 97 millimeters. These values were taken to be unbiased

EXPLANATION OF PLATE I

The points on this scatter diagram represent the intersections of body length and tail length coordinates of a random sample of Peromyscus maniculatus.

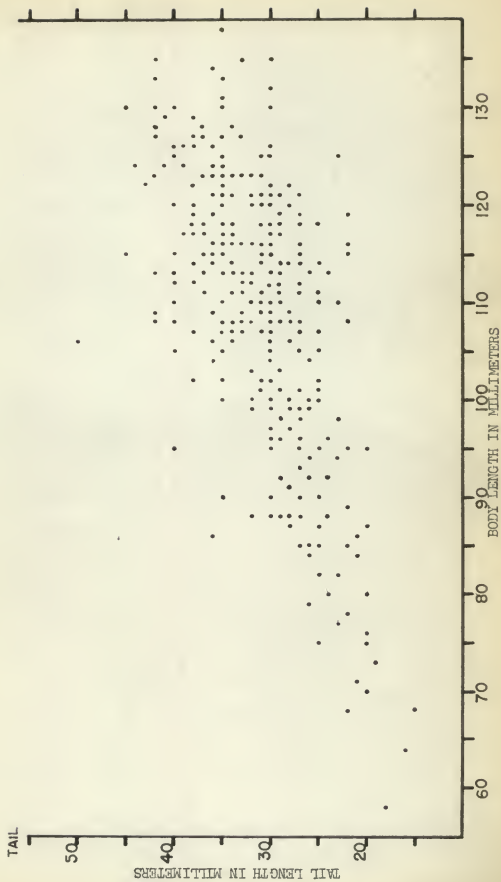
PLATE I



EXPLANATION OF PLATE II

The points on this scatter diagram represent the intersections of body length and tail length coordinates of a random sample of Microtus ochrogaster.

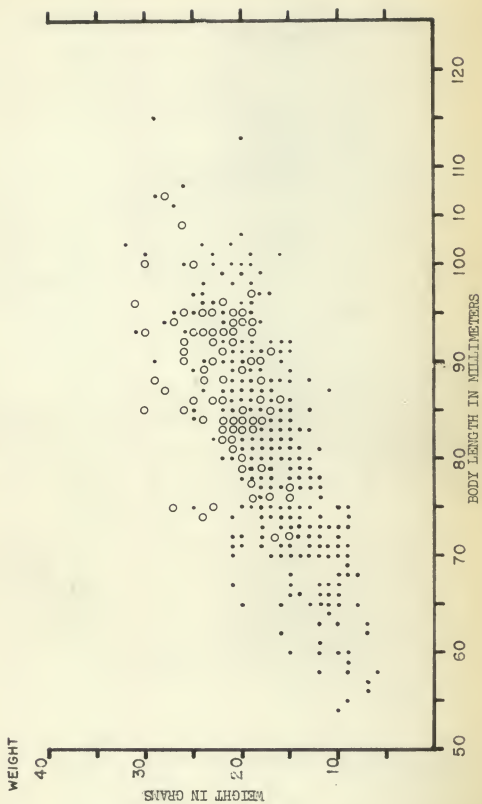
PLATE II



EXPLANATION OF PLATE III

The points and circles on this scatter diagram represent the intersections of weight and body length coordinates of a random sample of Peromyscus maniculatus. The circles represent pregnant females. The points represent all other mice.

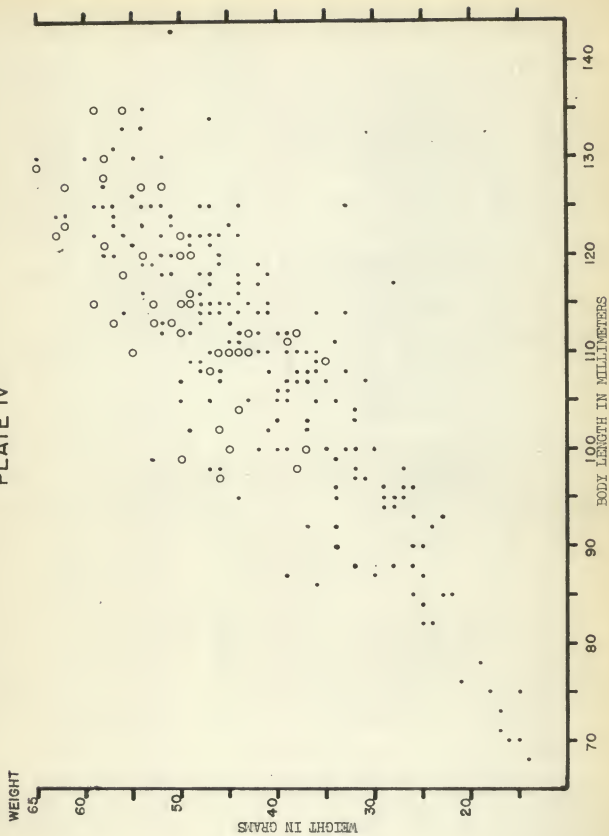
PLATE III



EXPLANATION OF PLATE IV

The points and circles on this scatter diagram represent the intersections of weight and body length coordinates of a random sample of Microtus ochrogaster. The circles represent pregnant females. The points represent all other mice.

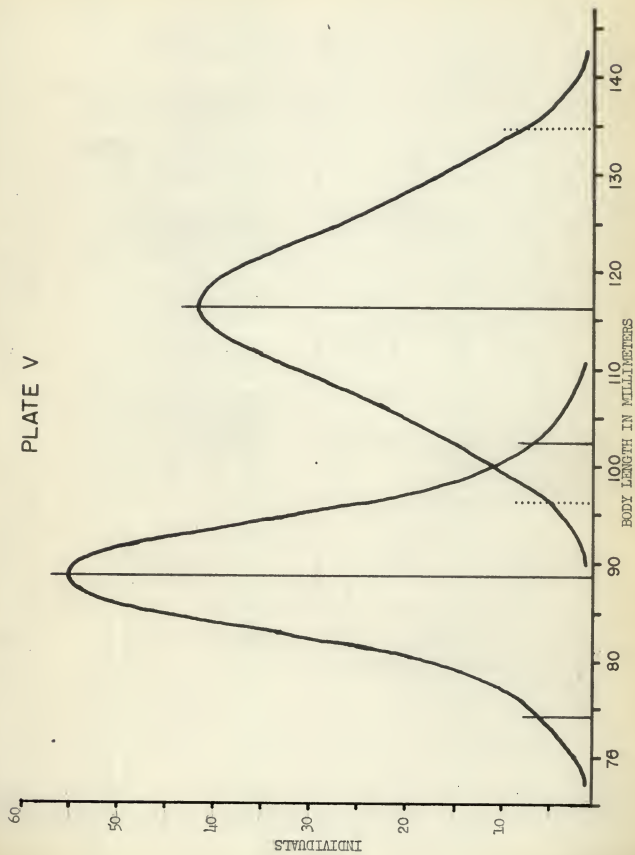
PLATE IV



EXPLANATION OF PLATE V

Distribution of body lengths of parous *P. maniculatus* and *M. ochrogaster* females in millimeters. The tallest curve is that of *P. maniculatus*. The long vertical lines through the middle of each curve represent the mean of these body lengths in each species. The short, solid, vertical lines represent two standard deviations on either side of the *Peromyscus* mean. These points are represented by dotted lines for *Microtus*.

PLATE V



estimates of the mean body length of females of the two species of rodents at attainment of sexual maturity, with a 95 per cent level of confidence.

Sexual maturity in the males was determined on the basis developed by Jameson (1950) of testis length and epididymal condition. He gives the minimum length of the sexually active deer mouse testis as 8 mm. Jameson's previous report (1947) gives this minimum length of functional testis in the prairie vole as 7 mm. Only a small number of males were examined for testis condition, and all of these with testis measuring the minimum length or over fell well within the range of mature female body length, hence no size difference between the sexes could be discovered. The work of Martin (1956) and Fitch (1957) suggests that male voles grow at a slightly more rapid rate and mature at a slightly greater weight and length. This difference is probably not significant for the purposes of this study.

One of the difficulties inherent in all trapping studies is that nestling mice cannot be caught, at least not consistently. An attempt was made to estimate how soon young mice become ambulatory and susceptible to trapping after their birth. Two litters of deer mice were raised in the laboratory and weighed daily. The daily mean weights for these two litters are presented in Table 2. The second litter was obtained some days after birth and the age was estimated from the date the eyes opened, this being 11 days post partum. The daily rate of gain varied a great deal between the two litters, but both weaned at approximately the same weight, 10 and 10.6 grams, and at the same age, 19 days. It was concluded that young deer mice of three weeks of age or slightly younger are susceptible to trapping. Reference to Plate III will show that deer mice of 10 gram body weight are frequently caught.

Table 2. Average weights of two litters of *P. maniculatus* for the first 21 days of life.

Age (days)	Average weight in grams	
	Litter 1	Litter 2
At birth	1.62	
1	2.06	
2	2.74	
3	3.00	
4	3.60	3.29
5	4.16	3.87
6	4.46	4.43
7	4.64	4.95
8	4.98	5.28
9	5.50	5.91
10	5.94	6.23
11	6.30 eyes open	6.62 eyes open
12	6.64	7.04
13	6.82	7.43
14	7.10	7.80
15	7.42	7.96
16	8.19	8.40
17	8.95	8.90
18	9.13	9.68
19	10.64 weaned	10.00 weaned
20	12.13	10.65
21	14.50	11.44

After entering the population, young deer mice remain sexually immature for 10 to 40 days. Clark (1958) gives the age at maturity of deer mice females as 49 days, and that of the males as 59 days. This agrees well with Jameson's (1953) finding of 60 days for males, but not for the females which he gives as 35 days. Further complicating this matter, Blair (1940) gave this age as 63 days. On the basis of the methods used to determine sexual maturity it was decided to use Jameson's estimate of 35 days for the females. It is probable, therefore, that female deer mice are available as juveniles for only about half the time that their male litter mates are.

Fitch (1957) gave the mean weight of newborn voles as 2.9 grams. Young voles began to appear in our trapping samples at 15 grams, and according to Fitch this weight is reached around 20 days of age. Probable age at sexual maturity of female prairie voles was estimated by Fitch as being 40 days. There seems to be great variability associated with age at sexual maturity in voles. Fitch estimated the age at mating of some pregnant prairie voles as one month. Hamilton (1941) estimated the minimum age of mating of Microtus pennsylvanicus females as 25 days, and Greenwalt (1956) made an estimate of 14 days for M. californicus. The total length of prairie vole females was given as about 130 millimeters which corresponds roughly with the body length range between Age Classes I and II as presented in Table 3.

For the purpose of detecting reproductive differences between animals of varying ages the mice were arbitrarily placed in six groups by body length. These groups were based on the standard deviations calculated for the distributions represented by Plates III and IV. Age Classes II, III, IV, and V represent ranges of one standard deviation each. Age Classes I and VI are the extremes beyond two standard deviations from either side of the mean. These classes and their corresponding ranges, in millimeters, for each species are presented in Table 3.

Table 3. Age classes of Peromyscus maniculatus and Microtus ochrogaster.

Class	I	II	III	IV	V	VI
<u>Peromyscus</u>	74 or less	75-81	82-88	89-95	96-102	103 and up
<u>Microtus</u>	96 or less	97-106	107-116	117-126	127-136	137 and up

Population Fluctuations

The number of trap nights run in each month of the Kansas Small Mammal Census were not consistent from month to month, therefore the absolute number of animals caught could not be taken as a direct indication of the population density. Moreover, Stickel (1946, 1948) raised some objections to trap line censusing for estimating actual numerical densities. Fitch (1954) pointed out that trapping results may vary from month to month depending on the food supply of the animal in question. These trapping results are, therefore, presented in the form of a relative index determined by dividing the number of animals caught by the number of trap nights set. All statistical comparisons of population density are based on the mean index of the same month.

These fluctuations in population density between successive trapping dates are presented in Plate VI for Peromyscus and Plate VII for Microtus. A general similarity of the fluctuations in these species is obvious. Both started in 1951 with peak populations, both declined in April, both recovered to again peak in November. Vole numbers declined in December, but the deer mice remained at a peak. By March of 1952 the deer mice had declined, but voles had reached a low, but significant peak. The voles were unable to remain at high densities and by April had dropped quite low, a decline from which they were not to recover for four years. Deer mice had, however, reached their maximum density of the decade in that April before declining to the moderate densities maintained throughout 1953, 1954, and 1955. Deer mouse numbers fluctuated sharply through 1956 and the spring of 1957, reaching very low densities in March and November of 1956, and in March and April of 1957. By November of 1957, deer mouse density began to increase again.

EXPLANATION OF PLATE VI

Fluctuations in numerical populations of Peromyscus maniculatus in the trapping months of each year; March, April, November, and December are represented on a relative index. This density index was found by dividing the number of mice caught by the number of trap-nights set for each month.

EXPLANATION OF PLATE VII

Fluctuations in numerical populations of Microtus ochrogastrus in the trapping months of each year; March, April, November, and December are represented on a relative index. This density index was found by dividing the number of mice caught by the number of trap-nights set for each month.

Voles seem to have begun to recover from the depression of their numbers in 1956, and by April 1957 they peaked. They subsequently declined for the rest of the year and ensuing winter. In 1958 both deer mice and voles reached simultaneous peak densities in April. Microtus were able to maintain their numbers through the summer, but Peromyscus went into an immediate decline. Voles remained at moderate densities throughout 1959, but deer mice were rather scarce in March and November of that year. Both species were at quite low densities in April 1960, but recovered somewhat by November:

Table 4. Population indices of Peromyscus maniculatus and Microtus ochrogaster caught 1951-1960.

Year	<u>P. maniculatus</u>		<u>M. ochrogaster</u>		Trap-nights
	Index	Numbers	Index	Numbers	
March					
1951	.0711	33	.0150	17	450
1952	.0320	46	.0185	43	1437
1953	.0305	53	.0006	1	1737
1954	.0353	20	-	-	567
1955	.0346	31	.0078	7	897
1956	.0108	9	.0144	11	837
1957	.0119	10	.0036	3	837
1958	.0428	37	.0023	2	864
1959	.0120	17	.0142	20	1413
1960	-	-	-	-	-
April					
1951	.0333	36	.0056	6	1080
1952	.0848	84	.0020	2	990
1953	.0254	49	.0031	6	1926
1954	.0240	33	-	-	1377
1955	.0330	65	.0010	2	1971
1956	.0372	55	.0047	8	1477
1957	.0107	7	.0441	29	657
1958	.0804	170	.0201	40	1989
1959	.0302	77	.0086	22	2544
1960	.0055	13	.0038	9	2373

Table 4. (concl.)

Year	<u>P. maniculatus</u>		<u>M. ochrogaster</u>		Trap-nights
	Index	Numbers	Index	Numbers	
November					
1951	.0656	50	.0709	53	747
1952	.0415	71	.0023	4	1710
1953	.0485	134	.0011	3	2761
1954	.0256	29	.0009	1	1134
1955	.0219	88	.0047	18	4015
1956	.0140	16	.0044	5	1143
1957	.0506	71	.0085	12	1404
1958	.0286	66	.0217	50	2304
1959	.0144	29	.0124	25	2019
1960	.0366	69	.0095	18	1890
December					
1951	.0747	60	.0049	4	810
1952	.0207	18	.0000	0	870
1953	.0481	13	.0000	0	270
1954	.0296	8	.0037	1	270
1955	.0514	37	.0014	1	720
1956	.0444	36	.0111	9	810
1957	.0406	23	.0018	1	567
1958	.0348	108	.0110	34	3099
1959	-	-	-	-	-
1960	-	-	-	-	-

Table 5. Peromyscus maniculatus. Population index, ten year monthly and seasonal averages.

	Population index	Animals caught	Trap-nights
March	.0283	256	9039
April	.0366	589	16084
Spring	.0336	845	25423
November	.0321	554	17238
December	.0403	303	7416
Fall	.0347	857	24654

Table 6. Microtus ochrogaster. Population index, ten year monthly and seasonal averages.

	Population index	Animals caught	Trap-nights
March	.0125	104	9039
April	.0076	124	16384
Spring	.0090	228	25423
November	.0099	171	17238
December	.0067	50	7416
Fall	.0090	221	24654

Population Structure

Sex Ratio. There were no significant variations of the total sex ratio of either species from the expected 1:1 ratio. Peromyscus consistently averaged more males than females, and the March totals are significantly in favor of the males at the .05 level. Microtus, on the other hand, exhibited a significant ratio in favor of the females in April. These mean sex ratios are shown in Tables 7 and 8. The possible meaning of these findings will be discussed later.

Age Structure. The ten year mean percentage of the six age classes were calculated for each month. These data are presented in Tables 9 and 10. Monthly age structures are shown by Plates VIII and IX. It should be noted that these very seldom formed the pyramidal structure theoretically expected. The general picture presented by the ten year mean age distributions, for both species, is that of a relatively old population in March becoming increasingly younger, as a group, through the breeding season; then aging again in December. The ten year mean percentages of juvenile deer mice in April and November are high and about equal, but by far the greatest proportion of juvenile voles are present in November. This would indicate a

Table 7. Peromyscus maniculatus. Sex ratios. Ten year monthly and seasonal averages.

	Sex ratio	Males	Females
March	61	130	84
April	56	262	206
Spring	58	392	290
November	53	235	205
December	58	151	109
Fall	55	386	314

Table 8. Microtus ochrogaster. Sex ratios. Ten year monthly and seasonal averages.

	Sex ratio	Males	Females
March	56	52	41
April	36	39	68
Spring	46	91	109
November	53	76	67
December	36	15	27
Fall	49	91	94

Table 9. Peromyscus maniculatus. Age structure. Ten year monthly average distribution in per cent.

	I	II	III	IV	V	VI
March	12	18	30	30	8	2
April	20	23	38	17	2	1
November	17	22	35	21	5	less than 1
December	7	30	29	23	10	i

Table 10. Microtus ochrogaster. Age structure. Ten year monthly average distribution in per cent.

	I	II	III	IV	V	VI
March	7	22	31	19	18	3
April	9	23	38	18	11	1
November	27	7	36	28	2	0
December	8	28	18	41	5	0

somewhat later peak of breeding for Microtus.

No correlation could be established for either deer mice or voles between the make up of the age structure and the density of the population. For example, in March of 1951 deer mouse population was high and so was the percentage of juveniles or Class I mice. In November of the same year the population density was great, but the percentage of juveniles was significantly low.

Frequently there is great similarity between the age structures of the deer mice and voles. For instance, the above cited example applies also to voles. April 1955, November 1958, and April 1959 compare for low percentages of juveniles. November 1958 and March and April of 1959 are notable for their comparison of large percentages of old adult animals. This would imply that similar forces are working on the two species and they are responding in the same way; however, there are equally notable divergences such as December 1956 when juvenile voles were plentiful, but juvenile deer mice were not.

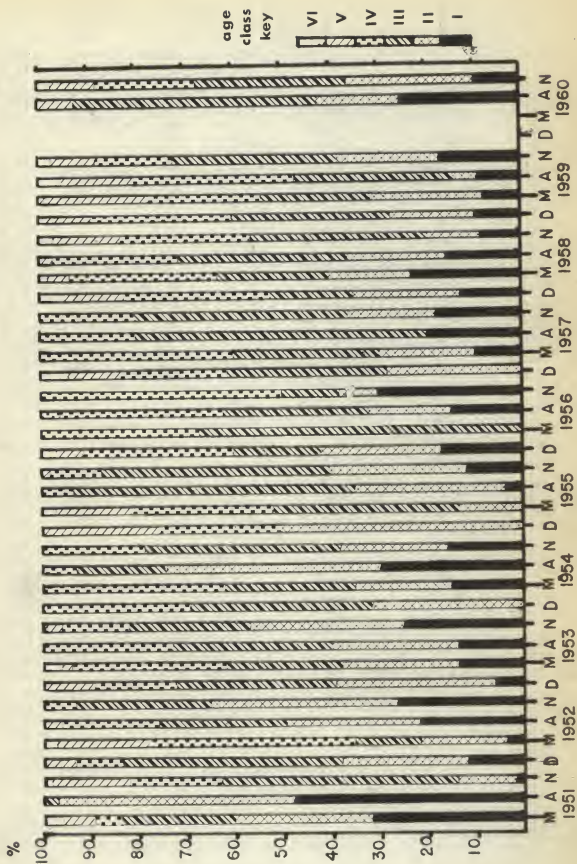
Reproduction

Two aspects of the reproductive history of these rodents could be determined by dissection, the percentage of the population pregnant or

EXPLANATION OF PLATE VIII

The per cent age composition of the sample of Peromyscus maniculatus trapped in each month of the ten year period, 1951-1960, are represented.

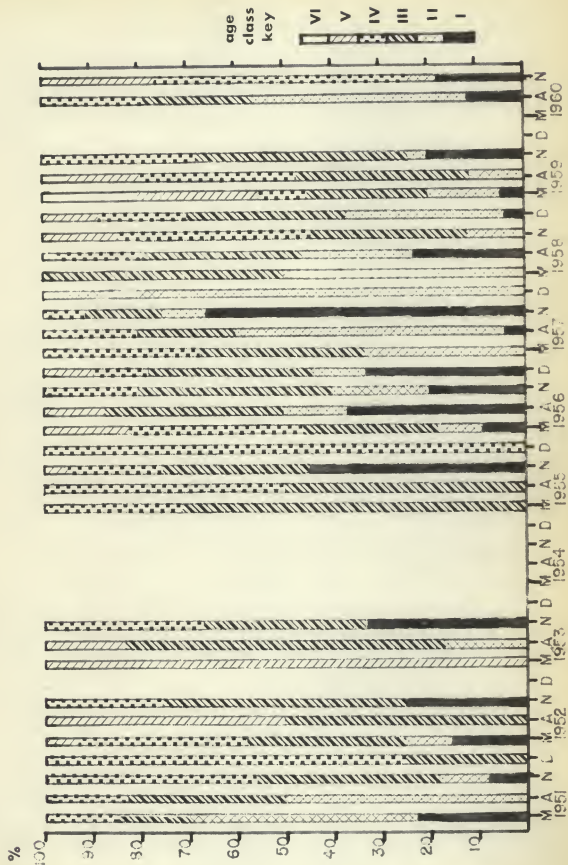
PLATE VIII



EXPLANATION OF PLATE IX

The per cent age composition of the samples of Microtus ochrogaster trapped in each month of the ten year period, 1951-1960, are represented.

PLATE IX



recently pregnant and the litter size. Two others, prenatal mortality and litter succession could not be so determined for this study.

The monthly percentages of deer mice and voles pregnant or having placental scars are given in Plates X and XI. These were statistically compared with their ten year monthly means that are to be found in Tables 11 and 12. The greatest percentages of pregnancy were found in the spring months in both deer mice and voles. The percentages of females with scars increased steadily, on the average through the year in both species. No correlation could be established between the intensity of reproduction and the litter size. Similarly, no correlation could be found between reproduction and resulting population changes. For example, deer mouse reproduction was slightly below average in March 1951. The April population declined and was extremely low in juvenile content. In March 1952 reproduction was even lower, but the population increased to peak density with a moderate proportion of juveniles.

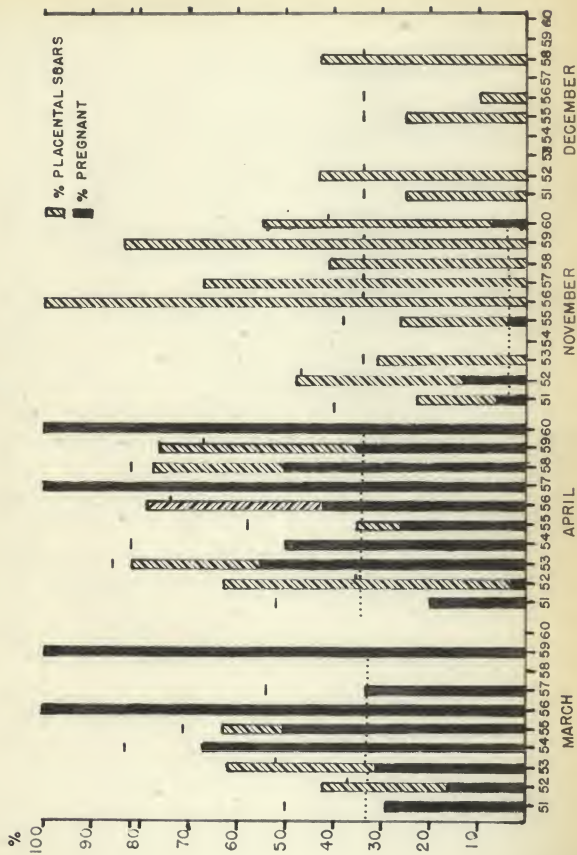
Litter size was determined by two different methods, embryo counts and placental scar counts. Neither of these are counts of the actual numbers of young born, and prenatal mortality may alter the accuracy of these estimates somewhat. Like other population parameters, prenatal mortality undoubtedly varies in intensity with external factors. This has been demonstrated experimentally in the deer mouse by Helmreich (1960). Hamilton (1937) maintained that:

Embryo counts of necessity do not give an exact criteria of the young produced. Resorption of embryos frequently occurs, especially in the period approaching the peak of a cycle, or at its culmination. Young are occasionally stillborn in captivity, and this undoubtedly occurs also in the wild state. Yet sufficient embryo counts made over a period of years do indicate whether the number of young per litter is increasing or decreasing.

EXPLANATION OF PLATE X

Per cent female *Peromyscus maniculatus* of each monthly sample examined for reproductive condition that were pregnant or had placental scars are shown in this bar graph. Per cent placental scars is added to the per cent pregnant line so the top of each bar represents the total per cent parous females. Ten year means are represented by the dotted horizontal lines. The placental scar ten year mean, represented by dashes, is measured from the per cent pregnant ten year mean line, not from the zero line.

PLATE X



EXPLANATION OF PLATE XI

Per cent female Microtus ochrogaster of each monthly sample examined for reproductive condition that were pregnant or had placental scars are shown in this bar graph. Per cent placental scars is added to the per cent pregnant line so the top of each bar represents the total per cent parous females. Ten year means are represented by the dotted horizontal lines. The placental scar ten year mean, represented by dashes, is measured from the per cent pregnant ten year mean line, not from the zero line.

PLATE XI

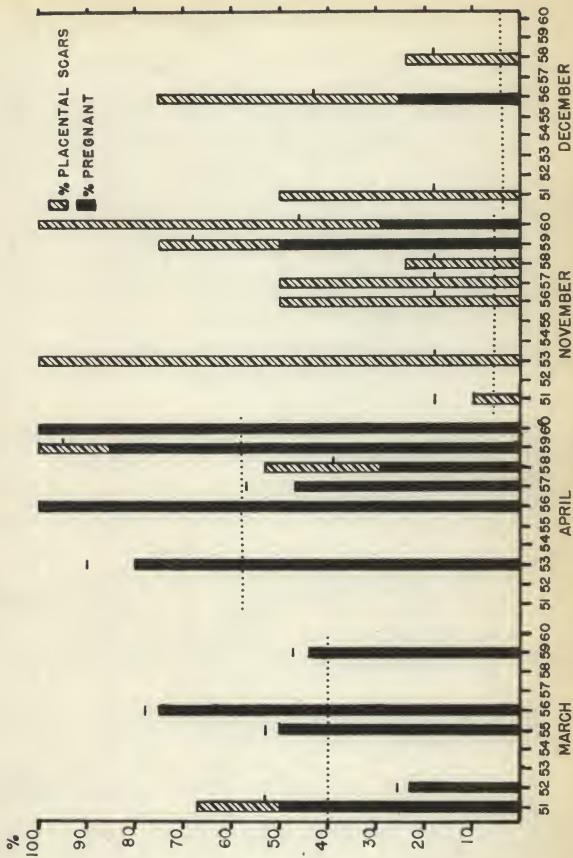


Table 11. Peromyscus maniculatus. Ten year monthly averages of per cent pregnant and per cent with placental scars.

	% pregnant	Number pregnant	% with scars	Number with scars	Sample size
March	33	22	21	14	66
April	34	56	32	53	164
November	4	5	34	39	116
December	0	0	34	20	59

Table 12. Microtus ochrogaster. Ten year monthly averages of per cent pregnant and per cent with placental scars.

	% pregnant	Number pregnant	% with scars	Number with scars	Sample size
March	40	14	3	1	35
April	58	34	10	6	59
November	5	4	16	12	77
December	4	1	30	8	27

As previously stated, no consistent relation was observed between decrease in reproduction, as indicated by decrease in litter size, and population decline. Embryo counts are, however, subject to the same random error throughout, and are hence good relative estimates of actual litter size at any given time.

Some objections have also been raised against the use of placental scars in estimating litter size, notably by Davis and Emlen (1948), who observed that placental scars accumulate and remain in the uterus with each succeeding litter. They apparently made no effort to differentiate between sets of scars. For the purposes of the present study only the most recent scars were counted, determined by the intensity of pigmentation and the spacing within the uterine horn. This is not difficult to do with a little experience.

Plate XII shows the method of counting placental scars. The litter size estimates made by this method compared very closely with those made by the embryo count method, as is shown in Tables 13 and 14. The composite mean embryo count for P. maniculatus was 4.29 and the mean placental scar count was 4.38. The mode was 4 with extremes of 1 to 7. Deer mouse litter size has variously been estimated at 3.05 (Svihla, 1932), 5.38 (Coventry, 1937), 4.60 (Jameson, 1953), and 4.51 (Beer et al., 1957). M. ochrogaster embryo counts gave a mean litter size estimate of 4.19, and scar counts one of 4.17. The modal number was again 4 with extremes of 1 to 9. The upper extremes for both species are based only on embryo counts. Whether or not these many young can be weaned undoubtedly depends on mammary function. Jameson (1947) estimated prairie vole litter size at 3.4, Martin (1956) at 3.18, and Fitch (1957) at 3.37. These counts were made from live-trapping data and are, therefore, probably somewhat lower due to mortality acting in the time span between the two methods.

Tables 13 and 14 also illustrate the principle first shown by Asdell and Sperling (1941) and subsequently confirmed by other workers, that mean litter size tends to increase with the age of the mother. However, there seems also to be a slight decrease in mean litter size in the oldest mice. There is no mention of this apparent decrease in the literature. Also in agreement with the findings of Asdell and Sperling, the percentage of female deer mice and voles that are pregnant or have placental scars generally increases with age. These data are shown in Table 15.

An experiment was undertaken to check the validity of placental scar counts. Ten female white laboratory mice with litters of known size were examined at various lengths of time after the birth of their young, up to 45 days, for placental scars. The results are shown in Table 16. Some of

EXPLANATION OF PLATE XII

Fig. 1. Ventral view of the reproductive tract of a female Peromyscus maniculatus, in situ. Intestines, stomach, liver, and some other abdominal organs have been removed. Approximately 4X.

R-Kid	-	right kidney
OV	-	ovary
C	-	colon
UT	-	left uterine horn
VAG	-	vagina
UB	-	urinary bladder

Fig. 2. The same reproductive tract removed from the mouse to show placental scars. This mouse was approximately three weeks post-partum, having had an observed litter of five young. Five placental scars are present. Approximately 4X.

OV	-	ovary
UT	-	uterine horn
PS	-	placental scar
VAG	-	vagina
MM	-	mesometrium

PLATE XII



Fig 1

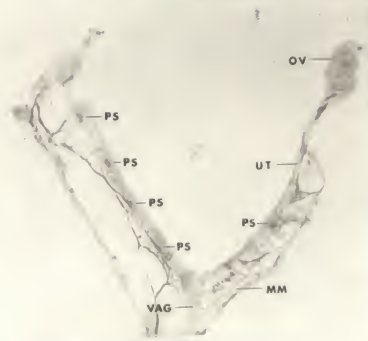


Fig 2

Table 13. Peromyscus maniculatus. Ten year average litter sizes.

Age class	Average litter size	Number of litters	Number of embryos
<u>Embryo counts</u>			
I	3.0	2	6
II	4.3	7	30
III	4.3	22	94
IV	4.4	33	144
V	5.3	4	21
VI	1.0	1	1
<u>Scar counts</u>			
			Number of scars
I	2.5	2	5
II	4.4	12	53
III	4.5	36	163
IV	4.5	49	220
V	4.1	4	21
VI	3.3	3	10
<u>Combined embryo and scar counts</u>			
			Number of embryos and scars
I	2.8	4	11
II	4.4	19	83
III	4.4	58	257
IV	4.4	82	364
V	4.3	19	82
VI	2.8	4	11

Table 14. Microtus ochrogaster. Ten year average litter sizes.

Age class	Average litter size	Number of litters	Number of embryos
<u>Embryo counts</u>			
I	0	0	0
II	3.8	8	30
III	3.9	15	58
IV	4.9	10	49
V	3.9	7	27
VI	4.0	1	4
<u>Scar counts</u>			
			Number of scars
I	0	0	0
II	3.0	1	3
III	4.1	7	29
IV	4.7	12	56
V	3.0	4	12
VI	0	0	0
<u>Combined embryo and scar counts</u>			
			Number of embryos and scars
I	0	0	0
II	3.7	9	33
III	4.0	22	87
IV	4.8	22	105
V	3.5	11	39
VI	4.0	1	4

Table 15. Per cent animals pregnant or having placental scars in each age class.

	Age Class					
	I	II	III	IV	V	VI
<u>Peromyscus</u>	8	23	41	75	64	80
<u>Microtus</u>	0	21	42	53	70	50

Table 16. Comparison of placental scar counts to litter counts in Mus musculus.

	Mouse No.										Total
	1	2	3	4	5	6	7	8	9	10	
Scars	11	2	9	11	6	2	12	7	11	5	76
Litter	11	1	11	10	8	1	12	8	11	4	77

these females contained scars of previous pregnancies, but these were distinguished by pigmentation and spacing, and were not used in estimating the size of the litter. Several explanations may be offered for the discrepancies that appear between the two counts. Where litter size is less than the scar count, as is the case in Mouse 2, 4, 6, and 10, the discrepancy may be due to the mother eating one or more of her young before the litter was counted, or it may be due to intrauterine loss after implantation. Conaway (1955) has shown that placental scars are not formed in rats prior to the seventh day of pregnancy, but after the ninth day scars of embryos dying before term are indistinguishable from those of survivors. More difficult to explain are deviations in the other direction. Liu (1954) has occasionally found fusion of two placentae in deer mice and such placentae would, of course, leave but one scar. It seems unlikely, however, that this occurs frequently enough to explain the occurrence of more young than scars in mice 3, 5, and 8. There remains, of course, the possibility of error in counting. Whatever the cause of these deviations may be, they apparently cancel one another out in a series of counts. That is, they are random errors. This, and the empirical proof provided by the similarity in embryo and scar counts in the wild populations, should establish the validity of placental scar counts.

No significant seasonal differences in mean litter size could be found in either the prairie deer mouse or prairie vole. Data presented by Jameson

(1947) and Fitch (1957) suggested that such might be the case. However, the major seasonal variations shown in those papers were in months other than those sampled by the Kansas Small Mammal Census. Deviations from expected litter size are shown in Plate XIII for each month. These data were found by subtracting from the actual mean litter size a hypothetical mean litter size of a sample of the same age composition with individual litter sizes based on the means shown in Tables 13 and 14.

Mean precipitation for each month, 1950-60 was taken from the U. S. Department of Commerce Climatological Data for Kansas. These data are shown as quarterly distribution, and accumulatively, for each year of the study in Plate XIV. They indicate a five-year drought extending from 1952 through 1956. Comparison of the annual precipitation to the population fluctuations of deer mice and voles shows a general positive correlation.

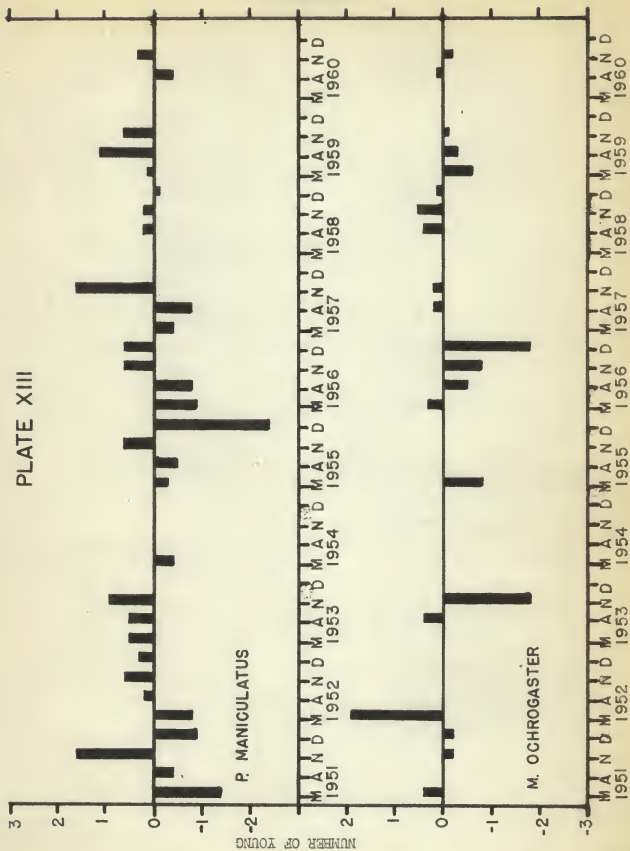
DISCUSSION

The most striking correlation between population density and environment is seen in the parallel of population fluctuations and amount of precipitation. This correlation has been noted in Microtus ochrogaster by Martin (1956), and in Microtus and Peromyscus by Bradshaw (1956). The effect of rainfall is apparently through the plant growth that it initiates, for Martin found that changes in vole density follow the curve for the rate of growth of grasses. The emphasis here should be on the rapid growth of plants, for the preferred food of voles is the tender, growing stems. Martin, therefore, stated that mixed vegetation constitutes a more desirable habitat for voles, due to the variety of growing seasons represented, than do more homogenous vegetation. In this connection, it should be noted that

EXPLANATION OF PLATE XIII

The positive or negative deviations of actual mean litter size from the mean litter size expected for samples of the particular age composition in each month are represented. Expected mean litter sizes were calculated from the ten year average mean litter sizes for each age group. All estimates are based on combined embryo and placental scar counts. In no case is the deviation from expected mean litter size zero.

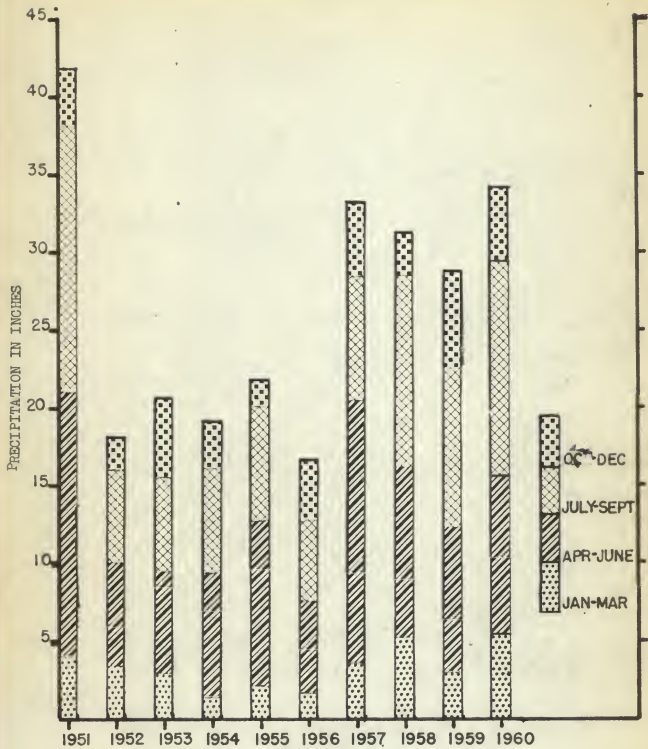
PLATE XIII



EXPLANATION OF PLATE XIV

Mean quarterly distribution of precipitation in Kansas recorded
accumulatively by years.

PLATE XIV



Johnson (1926) maintained that the entire biotic association, rather than any single agent, determines the distribution of Microtus ochrogaster. Interestingly, Hoffman (1958) observed that the height of the reproductive season for California and Montane voles corresponded with the peak growing seasons of grasses in their respective environments. He thought there might be some relation between grass protein content and reproduction.

Peromyscus maniculatus differs from the vole in food habits in the relative amounts of leafy vegetation and seeds eaten, deer mice preferring the fruiting parts (Jameson, 1952; Williams, 1959). Following unfavorable conditions, the availability of preferred food occurs some months later for deer mice than for voles, the time it takes for the seed crop to mature. One would expect, therefore, that any response of deer mice to precipitation would be delayed. This expectation was met following the drought of the fifties. Microtus responded almost immediately to the increased precipitation in 1957 while the response of deer mice did not reach full expression until a year later.

Another difference observed throughout the ten year period is the difference in relative density between deer mice and voles. Voles remained at consistently lower densities than deer mice, and during certain parts of the drought approached or reached local extinction. Apparently the high prairie habitat is not as favorable to voles as it is to deer mice. Dice (1922), Black (1937), Goodpastor and Hoffmeister (1952), and Martin (1956) all note that the prairie vole needs a relatively moist environment, although not as humid as that required by the meadow vole, M. pennsylvanicus. The vole needs fairly dense vegetation in which to construct runways that will provide effective protection against raptorial birds and other large predators. Another moisture need of voles is mentioned by Jameson (1947). Voles must,

apparently, dig their underground tunnels and chambers when the soil is moist. Numbers of voles may well be limited, in part, during dry periods by shortage of burrows and their inability to construct more in dry soil. Prairie voles are much more plentiful in riparian situations (Jameson, 1947; Martin, 1956; Fitch, 1957), and remain available in such places during drought as long as water is also available. These areas undoubtedly serve as reservoirs for the repopulation of prairie grassland during prolonged dry weather. Such repopulation is accomplished by successive generations of juvenile voles (Martin, 1956) until the available habitat is filled.

Precipitation may not be of an entirely beneficial nature. Martin (1956) suggested that the heavy rainfall in the spring of 1951 destroyed the infant voles. This would not account for the sudden drop in population density observed in both Microtus and Peromyscus in that spring, for such young animals do not contribute to the trapping data. Analysis of the percentage of juveniles in April, 1951, indicates that young voles might very well have been killed by the excessive rainfall, but deer mice certainly were not greatly affected. This observed population drop can be attributed only to mortality among the adults.

Snow-cover during the winter may also have an effect on the population. Both Microtus (Martin, 1956) and Peromyscus (Dunmire, 1960) store food for the winter. Snow-cover, therefore, would not be particularly harmful, at least when it does not remain too long. Dunmire (1960) measured the temperature of deer mouse nests beneath snow-cover, and found that the temperature seldom fell below freezing, even when the air temperature dropped to well below 0° Fahrenheit. The experimental work of Howard (1951),

Seelander (1951, 1952), Eskridge and Udall (1955), and Eskridge (1956) indicated that deer mice are quite capable of withstanding prolonged periods of freezing temperatures so long as food and nesting material were available. Huddling together of two or more mice also reduced loss of body heat. Inferentially, voles are equally capable of withstanding low temperatures; theoretically even more capable, due to their greater size and smaller extremities. Eventually, however, food reserves are bound to be depleted if snow-cover remains long enough. Tunneling through the snow may provide a little more food, but certainly with hardship for the mice. The reduction of deer mouse and vole populations over the winter of 1959-60 may have been due to prolonged snow-cover with resulting cold starvation of the mice.

The apparent sex ratios observed in deer mice and voles present another interesting contrast. Consistently more male than female deer mice were trapped in each sample month during the decade. In March this difference is statistically significant. One must conclude that there actually were more males present than females, or some non-random factor influenced the trapping. There is no evidence to indicate that there was differential survival of the sexes during the winter; thus the first possibility must be discarded. Male deer mice may have larger home ranges than females. Blair (1943) found this to be so in *P. maniculatus gracilis*, as did Williams (1955) with *P. maniculatus rufinus*. Clayton (1952) was unable to detect any such difference, but since his study was done during the middle of winter a different situation may exist then than that of the breeding season. Quite possibly then, larger home ranges exist during the sample months, accounting for the apparent difference in sex ratios.

The especially large difference found in March might be explained as increased activity of males within their home ranges, or invasion of the home ranges of other mice in the search for mates at the beginning of the breeding season. Voles, on the other hand, did not exhibit an apparent sex ratio in favor of the males in March. This does not necessarily mean that male voles are not highly active during the breeding season. The peculiar habit of building runway systems, and the sharing of them by neighboring animals would tend to randomize the trapping results. A large group of voles may use a single runway system, and an individual vole will use several adjacent systems (Martin, 1956; Fitch, 1957). The especially low proportion of male voles in April may be explained by Frank's (1957) "condensation potential". He observed high mortality of male Microtus arvalis and resultant communities of females and shrinkage of home ranges at peak population densities. Such mortality was due, directly and indirectly, to aggressive behavior of the females, usually resulting in the males being driven away. These males were then more susceptible to predation. Frank thought this phenomenon delayed for a time the inevitable decline of the population, and termed it "Verdichtungspotential". The two April peaks observed in the Kansas Small Mammal Census, 1957 and 1958, were quite low in males, thus influencing the ten year average. Add to this the normal high antagonism of nursing female voles toward males observed by Fitch (1957) and another cause of low sex ratio during the breeding season can be perceived. Apparently, then, different forces are influencing the observed sex ratios of deer mice and voles; the former being due to the larger home ranges of the males, and the latter to antagonistic behavior on the part of the females.

The annual reproduction of a species must be analyzed for three main parts, as noted by Hamilton (1937); breeding rate, litter size, and length of breeding season. The latter was more accurately termed "litter succession" by Frank (1957). In the early years of rodent population study it was thought that multiplication of the three terms would give a good estimate of natality. Several authors have actually presented formulae for this purpose. It is now known that it is not quite as simple as this for it is quite difficult to define the three terms. Two factors enter to complicate the picture; the age and the physiological state of the population as a whole. It is now well known that the age of a mouse bears a direct relation to the frequency with which it becomes pregnant, and the size of its litter, both of these increasing with age (Asdell and Sperling, 1941; Beer, et al., 1957; Jameson, 1947; Fitch, 1957). The Kansas Small Mammal Census data indicate that there may be a slight decline in the reproductive potential of mice in the oldest group. Obviously, a shift in the age composition of a population may introduce a large error into any calculations; such shifts are constantly occurring and are pronounced from season to season.

The physiological state of the mice may also introduce error. Christian (1956), Christian and LeMunyan (1958) with house mouse, Louch (1956) with meadow voles, and Helmreich (1960) with the prairie deer mouse have shown experimentally that stress, in these cases overcrowding, reduces the natality by increasing intrauterine mortality. When complete loss of litters occurs, the effective breeding rate is reduced, and when part of a litter is lost, of course, litter size is reduced.

Litter succession also presents several problems. First of these is the length of the breeding season. This may be partly under the control of photoperiod, which is relatively constant from year to year in a given

locality (Baker and Ranson, 1932a,b; Whitaker, 1940), but certain other factors must influence breeding season too. There is clear evidence that the breeding season of Peromyscus may be prolonged in certain years (Brown, 1945; Beidleman, 1954). Beidleman found such late breeding to be correlated with above normal temperatures. Voles may even breed throughout the entire winter in some years, although at a greatly reduced rate (Martin, 1956). In both deer mice and voles, the factors which suppress breeding appear to act mainly on the females. Jameson (1947) found this to be so for Microtus. as did Howard (1950) for Peromyscus. The cauda epididymi of mature males remained swollen and filled with motile sperm throughout the winter even though the testes may have been in the abdominal position. Eskridge (1956) has shown experimentally that freezing temperatures are not sufficient to inhibit the fecundity of male deer mice provided they have adequate food and nesting material.

Secondly, mice do not reproduce at a maximum or constant rate throughout the breeding season. Female mice may become immediately pregnant after the birth of a litter due to a short post-partum estrus (Jameson, 1953; Fitch, 1957). The gestation period of such a pregnant, lactating mouse is several days longer than usual, apparently due to a delay in implantation while the embryos are temporarily arrested at the blastula state and float free in the lumen of the uterus (Kirkham, 1916). Following implantation development proceeds at a normal rate. No measurement of the frequency of post-parous breeding has ever been made for any species. Hamilton (1937) believed that post-parous breeding was more frequent during high populations. Moreover, one must also allow for the summer oestival drop-off of breeding which occurs in deer mice (Blair, 1940; Jameson, 1953) and prairie voles

(Fitch, 1957). Thus the breeding season usually has two peak parts, vernal and autumnal, with lesser gradations of breeding intensity in between. Obviously, no constant can be found here for use in estimating annual natality. Estimates of natality can be made for specified times, and trends may be indicated when the population is sampled at frequent intervals, but these can be expressed only relatively, not in absolute numbers of young produced. It is clear from the Kansas Small Mammal Census data that natality is not necessarily reflected in corresponding changes in population density of either deer mice or voles.

Various conditions have been advocated as mortality factors causing decline in rodent populations, these generally being infectious disease, predation, food supply, weather, and pathological hormone imbalances. Previously, the hypothesis most consistent with the facts available was that overcrowded rodent populations were decimated by epidemics, due to the increased probability of infection. Investigation by Chitty (1954) showed that murine tuberculosis was not necessarily associated with population decline in voles, and may be epidemic in thriving populations. Bradshaw (1956) could find no evidence of tularemia or paratyphoids in Kansas rodents during a population low by serological techniques.

Predation also has been credited with a controlling part in population processes. Situations occur where the density curves of a predator and its primary prey fluctuate in sequence with one another. The key question, of course, is does the predator destroy its food supply or is the decline of the prey due to some other reason. The observations of Chitty (1955), Godfrey (1955), and Lockie (1955) indicate that recurrent declines in vole numbers occur whether the pressure of predation is heavy or light.

The nature of rodent plagues such as that occurring in Oregon in 1957, has suggested the possibility that mice may consume their whole food supply and be faced with subsequent starvation. Summerhayes (1941) could find no evidence that Microtus agrestis destroyed its food supply to the extent that it would seriously limit their numbers. This does not mean that voles cannot do serious agricultural damage. The other possibility is that the food supply is ruined by poor weather, and thus the mice decline. Evidence presented by the Kansas Small Mammal Census seems to implicate this latter possibility. It is suggested that the latter would be the usual pattern inasmuch as extremely high populations are relatively rare. Certainly there has been no plague of deer mice or voles in Kansas during the past ten years. It is likely that voles would be much more seriously limited by such failure of vegetation than deer mice, since the former are less adaptable to a wide range of environmental conditions (Jameson, 1955). The extreme low numbers of voles during the drought of the fifties, while the deer mice remained at moderate numbers, suggests that this is true.

It is well documented that hormonal imbalances occur in many species of rodents under adverse environmental conditions. The main difficulty in the GAS theory is that mortality due to hypoglycemic shock has not been satisfactorily demonstrated in the field, or in caged populations of mice and voles for that matter. Christian (1950), Louch (1956), and Helmreich (1960) have demonstrated that a reduction in natality results from the stress of overcrowding. Louch, however, could not produce a numerical decline of adults in his experimental population of voles, although intraspecific competition and symptoms of adrenal hyperactivity were high. Young voles in this

experiment were frequently killed or neglected by their mothers, suggesting that prolactin output may have been affected. Such a view would certainly agree with Christian and LaMunyan's (1958) hypothesis on the effect of milk quality or quantity on the progeny. Both of these views concur with that of Chitty (1960). Also of interest, Lindeborg (1950) has observed that pregnant female deer mice require better than twice as much water as others. Here is a factor that quite obviously might have a retarding effect on lactation during droughts such as the one observed in Kansas in the fifties. The idea that responses of rodent populations to mortality factors is modified by prenatal or neo-natal influences fits the data better than any other hypothesis. The varying responses of Kansas deer mice and voles cannot be explained by the GAS theory alone. The decline in vole numbers during the 1957 breeding season, and the decline of deer mice during the 1958 breeding season are not due to adverse climate, nor GAS, as severe mortality would be expected at the onset of winter or some other "catastrophic" event. Reproduction at these times was sufficient, and adult mortality did not seem to be especially severe; "senile" mice constituted a fair proportion of the population. The decrease in numbers must have been due to the failure of younger mice to survive in sufficient numbers to replace normal loss. The possibility that intraspecific strife between the parents of these young served as a teratogenic agent may have some credence.

Thus the factors that modify death rate are also the ones modifying birth rate, by either decreasing ovulation or increasing intrauterine mortality. The fact that the same mortality factor does not always have the same effect, or any effect on the population density at all, is due to

the physiological state of the individual mice. No matter how many possible deaths a mouse escapes, one must eventually be the last. The previous experiences of that individual certainly play a major role in determining its susceptibility to the next crisis. Therefore, Errington's (1946, 1956) principle of population intercompensations is not strictly applicable. The death of one animal does not necessarily contribute materially to the survival of the remaining in physiologically deranged populations, for the effect of that animal lives on for a time.

The Kansas Small Mammal Census does not indicate that either Peromyscus or Microtus undergo cyclic population changes in this state. The accumulation of data over several more decades will be needed to clear this point.

SUMMARY

A statistical analysis of population characteristics and reproduction of Peromyscus maniculatus, the prairie deer mouse, and Microtus ochrogaster, the prairie vole, from random samples of the high prairie habitat in Kansas from 1951 to 1960 was made. Certain methods used were critically examined. In the absence of known age, some available measurement had to be used to estimate age. Total length and weight were found to be highly variable, hence body length was the measurement used. Six age classes were established on the basis of body length, with the first denoting immature animals. The use of placental scars in estimating litter size was investigated by comparing observed litters with scar counts in laboratory mice, and empirically by comparing embryo counts and scar counts of deer mice and voles. Such counts were found to be unbiased estimates of litter size.

Population structure, sex ratio, and age composition constantly changed. Deer mice males were found to average above the 1:1 expected ratio in March. This apparent high sex ratio was explained as being due to increased activity of the males at the start of the breeding season. Conversely, Microtus males averaged quite low in April. Since several April populations were very dense in numbers, this sex ratio was explained on the basis of the condensation potential of voles. Age structure, too, was fluid. On the average, populations of both species were rather old in March, became progressively younger during the breeding season, and aged again by December.

No consistent correlation could be found between reproductive rate and population changes. Similarly, no consistent relation between the age composition, or population changes, and the reproductive rate was discovered. Deer mouse and vole fluctuations from 1951 to 1958 paralleled the annual precipitation. It was concluded that mortality due to the drought was the major factor limiting population growth, possibly obscuring other factors operative during years of more normal precipitation. The inconsistencies of the various statistics at different times suggests that susceptibility to mortality factors varies from time to time, dependent on the physiological state of the animals.

ACKNOWLEDGMENT

The writer wishes to express appreciation to his major professor, Dr. H. T. Gier, for access to the Kansas Small Mammal Census data, and for thought-provoking guidance and criticism of this study. Thanks are also due to all of the cooperators in the Census and their assistants. He wishes to thank his father-in-law, Dr. Maynard S. Johnson, and his father, Lt. Col. G. T. Rolan, for the financial aid that has permitted the completion of this paper. Finally, appreciation is due his wife, Caroline, for invaluable hours of help in arranging the data, and numerous other secretarial chores.

LITERATURE CITED

Asdell, S. A., and G. Sperling.

The influence of age and rate of reproduction upon the ability of the female rat to reproduce and raise young. Cornell Univ. Agric. Exp. Stat. Memo 238:3-28. 1941.

Baker, J. R., and R. M. Ranson.

Factors affecting the breeding of the field mouse (*Microtus*). Part I. Light. Proc. Royal Soc. London, B., 110:335-344.

Factors affecting the breeding of the field mouse (*Microtus*). Part III. Locality. Proc. Royal Soc. London, B., 113:486-495. 1932.

Beer, J. R., C. F. MacLeod, and L. D. Frenzel.

Prenatal survival and loss in some Cricetid rodents. Jour. Mamm. 38(3):392-402. 1957.

Black, T. D.

Mammals of Kansas. Kansas State Board of Agric., 13th Biennial Rep., 1935-36:116-217. 1937.

Blair, W. F., Jr.

A study of prairie deer mice populations in southern Michigan. Amer. Midl. Nat. 24:273-305. 1940.

Populations of the deer mouse and associated small mammals in the mesquite association of southern New Mexico. Contrib. Lab. Vert. Biol., Univ. Mich. 21:1-40. 1943.

Population density, life span, and mortality rates of small mammals in the bluegrass meadow and bluegrass field associations of southern Michigan. Amer. Midl. Nat. 40:394-419. 1948.

Bradshaw, Gordon Van Rensselaer.

Kansas small mammal census: A five year study with attempts to determine factors in population fluctuations. Unpublished Master's Thesis, Kansas State University, Manhattan, Kansas. 1956.

Christian, J. J.

Adrenal and reproductive responses to population size in mice from freely growing populations. Ecology. 37:258-273. 1956.

Christian, J. J., and C. D. LeMunyan.

Adverse effects of crowding on lactation and reproduction of mice and two generations of their progeny. Endocrinology. 63:517-529. 1958.

Chitty, Denis.

Mortality among voles (Microtus agrestis) at Lake Vyrnwy, Montgomeryshire in 1936-39. Phil. Trans. Royal Soc. London, B., 236:505-552. 1952.

Tuberculosis among wild voles: with a discussion of other pathological conditions among certain mammals and birds. Ecology. 35:227-238. 1954.

Adverse effects of population density upon the viability of later generations. In "the Numbers on Man and Animals". Edited by J. B. Cragg and N. W. Pirie. Oliver and Boyd, Ltd., Edinburgh. p. 57-67. 1955.

Population processes in the vole and their relevance to general theory. Canad. Jour. Zool. 38(1):99-113. 1960.

Clark, F. H.

Age of sexual maturity in mice of the genus Peromyscus. Jour. Mamm. 19:230-234. 1938.

Clarke, J. R.

Influence of numbers on reproduction and survival in two experimental vole populations. Proc. Royal Soc. London, B., 144:68-85. 1955.

Clayton, Kenneth.

Some phases of the winter ecology of some small mammals in a blue stem bluegrass meadow of Lyon County, Kansas. Unpublished Master's Thesis, Kansas State Teachers College, Emporia, Kansas. 1952.

Cole, LaMont C.

Some features of random population cycles. Jour. Wildl. Mgmt. 18(1):2-24. 1954.

Conaway, C. H.

Embryo resorption and placental scar formation in the rat. Jour. Mamm. 36:516-532. 1955.

Coventry, A. P.

Notes on the breeding of some Cricetidae in Ontario. Jour. Mamm. 18:489-496. 1937.

Davis, D. E.

A comparison of natality in white-footed mice for four years. Jour. Mamm. 37(4):513-516. 1956.

Davis, D. E., and J. T. Emlen.

The placental scar as a measure of fertility in rats. Jour. Wildl. Mgmt. 12:162-167. 1948.

- Deno, R. A.
Uterine macrophages in the mouse and their relation to involution.
Amer. Jour. Anat. 60:433-471. 1937.
- Dice, L. R.
Some factors affecting the distribution of the prairie vole, forest
deer mouse, and prairie deer mouse. Ecology. 2:232-238. 1922.
- Dunmire, William W.
An altitudinal survey of reproduction in Peromyscus maniculatus.
Ecology. 41(1):174-182. 1960.
- Errington, P. L.
Predation and vertebrate populations. Quart. Rev. Biol. 21:144-177.
1946.
-
- On the hazards of overemphasizing numerical fluctuations in studies
of "cyclic" phenomena in muskrat populations. Jour. Wildl. Mgmt.
18(1):66-90. 1954.
-
- Factors limiting higher vertebrate populations. Science. 124:304-307.
1956.
- Eskridge, P. S.
Relationships between environmental stress as represented by freezing
temperatures and lack of nesting material and reproductive activity
and viability in Peromyscus maniculatus. Unpublished Ph.D. dissertation,
Univ. Pittsburgh, Pittsburgh, Pennsylvania. 1956.
- Eskridge, P. S., and R. H. Udall.
The effect of cold starvation upon carbohydrate reserves in Peromyscus
maniculatus. Jour. Mamm. 36:139-140. 1955.
- Fitch, H. S.
Seasonal acceptance of bait by small mammals. Jour. Mamm. 35:39-47.
1954.
-
- Aspects of reproduction and development in the prairie vole, Microtus
ochrogaster. Univ. Kansas Museum Nat. Hist. Pub. 10(4):129-161. 1957.
- Frank, Fritz.
The causality of Microtine cycles in Germany. Jour. Wildl. Mgmt.
21(2):115-121. 1957.
- Godfrey, G. K.
Observations on the decline in numbers of two Microtus populations.
Jour. Mamm. 36:209-214. 1955.

- Goodpastor, W. W., and D. F. Hoffmeister.
Notes on the mammals of eastern Tennessee. Jour. Mamm. 33:362-371.
1952.
- Greenwald, G. S.
Reproductive cycle of the field mouse, Microtus californicus. Jour.
Mamm. 37(2):213-222. 1956.
- Hall, Raymond E.
Handbook of Mammals of Kansas. Univ. Kansas Mus. Nat. Hist., Misc.
Pub. 7. 1955.
-
- Vernacular names of North American mammals north of Mexico. Univ.
Kansas Mus. Nat. Hist., Misc. Pub. 14. 1957.
- Hamilton, W. J., Jr.
The biology of Microtine cycles. Jour. Agric. Res. 54:779-790. 1937.
-
- Life and habits of field mice. Sci. Monthly. 1:425-434. 1940.
-
- Reproduction of the field mouse Microtus pennsylvanicus (Ord.)
Cornell Univ. Agric. Exp. Stat. Memo 237:3-22. 1941.
- Helmreich, R. L.
Regulation of reproductive rate by intrauterine mortality in the deer
mouse. Science 132:417-418. 1960.
- Hoffman, Robert S.
The role of reproduction and mortality in population fluctuations of
voles (Microtus). Ecol. Monogr. 28(1):79-109. 1958.
- Howard, W. E.
Winter fecundity of caged male white-footed mice in Michigan. Jour.
Mamm. 31(3):319-321. 1950.
-
- Relation between low temperature and available food to survival of
small rodents. Jour. Mamm. 32:300-313. 1951.
- Jameson, E. W., Jr.
Natural history of the prairie vole. Univ. Kansas Museum Nat. Hist.
Pub. 1:125-151. 1947.
-
- Determining fecundity in male small mammals. Jour. Mamm. 31(4):
433-436. 1950.

Food of deer mice, Peromyscus maniculatus and Peromyscus boylei in the northern Sierra Nevada, California. Jour. Mamm. 33:50-60. 1952.

Some factors affecting the fluctuation of Microtus and Peromyscus. Jour. Mamm. 36:206-209. 1955.

Jenkins, H. O.

A population study of meadow mice (Microtus) in three Sierra Nevada meadows. Proc. Calif. Acad. Sci. 26:43-67. 1948.

Johnson, Maynard S.

Activity and distribution of certain wild mice in relation to biotic communities. Jour. Mamm. 7:245-277. 1926.

Kirkham, W. E.

The prolonged gestation period in suckling mice. Anat. Record. 11:31-40. 1916.

Lauckhart, J. Burton.

Animals cycles and food. Jour. Wildl. Mgmt. 21(2):230-234, 1957.

Lindeborg, Robert G.

An adaptation of breeding Peromyscus maniculatus bairdii females to available water, and observations on changes in body weight. J. Mamm. 31(1):74-78. 1950.

Liu, T. T.

Monozygotic twinning in Peromyscus maniculatus. Jour. Mamm. 35:449-450. 1954.

Lockie, J. D.

The breeding habits and food of short-eared owls after a vole plague. Bird Study 2:53-69. 1955.

Louch, C. D.

Adrenocortical activity in relation to the density and dynamics of three confined populations of Microtus pennsylvanicus. Ecology 37:701-713. 1956.

Martin, E. P.

A population study of the prairie vole (Microtus ochrogaster) in northeastern Kansas. Univ. Kans. Mus. Nat. Hist. Pub. 8(6):361-415. 1956.

Rowan, William.

Reflections on the biology of animal cycles. Jour. Wildl. Mgmt. 18(1):52-60. 1954.

Sealander, J. A.

Survival of Peromyscus in relation to environmental temperatures and acclimation at high and low temperatures. Amer. Midl. Nat. 46:257-311. 1951.

Food consumption in Peromyscus in relation to air temperature and previous thermal experience. Jour. Mamm. 33:206-218. 1952.

Selye, Hans.

The general adaptation syndrome and the diseases of adaptation. Jour. Clin. Endocrinology. 6:117-231. 1946.

Snedecor, George W.

Statistical methods applied to experiments in agriculture and biology. Iowa State College Press, Ames, Iowa. 1956. p. 523.

Stickel, L. F.

Experimental analysis of methods for measuring small mammal populations. Jour. Wildl. Mgmt. 10:150-159. 1946.

The trap line as a measure of small mammal populations. Jour. Wildl. Mgmt. 12:153-161. 1948.

Summerhayes, V. S.

The effect of voles (Microtus agrestis) on vegetation. Jour. Ecology 29:14-48. 1941.

Svihla, Arthur.

A comparative life history study of the mice of the genus Peromyscus. Univ. Mich. Mus. Zool., Misc. Pub. 24. 1932.

Whitaker, W. L.

Illumination and reproduction in mice. Jour. Exp. Zool. 83:33-60. 1940.

Williams, Olwen.

Home range of Peromyscus maniculatus rufinus in a Ponderosa pine community. Jour. Mamm. 36:42-45. 1955.

Food habits of the deer mouse. Jour. Mamm. 40:415. 1959.

APPENDIX
OF TABLES OF SIGNIFICANT CHI-SQUARES

Table 17. Peromyscus maniculatus. Population index. Significant chi-squares. $\alpha_{.05}$

Year	Spring	Fall	Special Monthly Tests		
1951			March 5.49	November 5.49	December 8.59
1952			April 12.37		
1953					
1954					
1955					
1956					
1957					
1958	5.49		April 8.59		
1959					
1960					

Table 18. Microtus ochrogaster. Population index. Significant chi-squares. $\alpha_{.05}$

Year	Spring	Fall	Special Monthly Tests		
1951			March 16.16	November 49.49	
1952	4.04	16.16	March 9.09		
1953					
1954					
1955					
1956					
1957	4.04		April 20.45		
1958			April 4.04	November 4.04	
1959					
1960					

Table 19. Peromyscus maniculatus. Sex ratio. Significant
chi-squares. $\alpha_{.05}$

Year	March	April	November	December
1951	6.76		4.84	29.16
1952				4.84
1953	14.44		14.44	
1954	25.00	4.00	11.44	17.64
1955				
1956		4.84	6.76	
1957	4.00	6.76		
1958	5.76			
1959	5.76	6.76		
1960		11.44		

Table 20. Microtus ochrogaster. Sex ratio. Significant
chi-squares. $\alpha_{.05}$

Year	March	April	November	December
1951				11.44
1952			11.56	
1953		43.56		
1954				
1955	11.44		7.84	
1956		4.00		11.44
1957	11.44	25.00	25.00	
1958				7.84
1959		5.76	4.00	
1960				

Table 21. Peromyscus maniculatus. Age structure. Significant monthly chi-squares. $\alpha_{.05}$

	Age Class					
	I	II	III	IV	V	VI
<u>March</u>						
1951	37.88	8.20		29.70		
1952	6.06		57.47	6.90	19.56	
1953		4.34		4.89		
1954					8.69	
1955	13.64		3.86		8.69	
1956	13.64	21.95	65.19		8.69	
1957				4.76	8.69	
1958	9.47					
1959					30.58	
1960						
<u>April</u>						
1951	52.56	76.34	52.00	20.48		
1952			5.13			
1953				7.09		
1954	6.25	24.90	16.98	7.09		
1955	25.00		16.98	7.09		
1956	25.00			20.48		
1957		29.87	20.55			
1958				5.75		
1959	9.00	25.28		18.14	225.00	16.16
1960			6.11	20.48	12.76	
<u>November</u>						
1951	17.42	5.69	8.62		100.00	
1952	5.74	16.42		11.81		
1953	4.53	6.88	5.32			
1954						
1955			5.32	6.03		
1956	11.98	8.19	27.49	50.67		
1957						
1958	5.74	6.88			73.47	
1959					25.00	
1960						
<u>December</u>						
1951	3.84		17.53	9.54		
1952						
1953	7.53		3.84		11.11	
1954	7.53	19.04	40.85		25.00	
1955	15.37		7.00			
1956	7.53					
1957	3.84		7.00			
1958		9.04				
1959						
1960						

Table 22. Microtus ochrogaster. Age structure. Significant monthly chi-squares. ^a.05

	Age Class					
	I	II	III	IV	V	VI
<u>March</u>						
1951	39.32	36.42	11.97		21.95	
1952		9.85		16.63	8.20	
1953	7.45	28.21	44.93	23.46	445.56	
1954						
1955	7.53	28.21	74.80	6.49	21.95	
1956		28.21		18.78		
1957	7.53	7.05		12.74	21.95	
1958	7.53	45.69	16.88		21.95	
1959				5.26		99.31
1960						
<u>April</u>						
1951	9.89	26.43			12.36	
1952	9.89	29.87		21.95	155.36	
1953	9.89		33.28	21.95		
1954						
1955	9.89		6.11	8.20	12.36	
1956	175.26	5.65		21.95		
1957		5.65	13.76		12.36	
1958	23.78				6.54	
1959	9.89	19.17		13.28		16.16
1960			10.87		12.36	
<u>November</u>						
1951	18.32			12.70		
1952		7.53	6.25			
1953		7.53				
1954						
1955	15.66	7.53			4.59	
1956		25.96				
1957	58.65		27.36	13.39		
1958	36.99	3.84		7.14	100.00	
1959						
1960						
<u>December</u>						
1951		38.89			5.26	
1952						
1953						
1954						
1955		38.89	21.95	908.02	5.26	
1956	84.51	17.90	17.34	37.20	7.58	
1957		257.14	21.95	69.49	5.26	
1958			6.78	21.87	10.32	
1959						
1960						

THE ROLE OF REPRODUCTION AND MORTALITY IN
POPULATION FLUCTUATIONS OF PEROMYSCUS MANICULATUS
AND MICROTUS OCHROGASTER ON NATIVE PRAIRIES

by

ROBERT G. ROLAN

B. S., Kansas State University, 1959

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Zoology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1961

The purpose of this study was to determine some of the factors affecting reproduction in Peromyscus maniculatus and Microtus ochrogaster in Kansas, and how these changes are reflected in the population. The small mammals were snap-trapped at various locations throughout the state in areas representing the high prairie habitat. From 1951 to the present this trapping program has been known as the Kansas Small Mammal Census, and has been coordinated by Dr. H. T. Gier of Kansas State University. The mice caught were measured, weighed, and analyzed for reproductive condition; pregnancy or presence of placental scars. To facilitate statistical analysis the census data were pooled without regard for locality, each of these being viewed as a random sample of the high prairie habitat of Kansas.

Certain preliminary studies were made in order to examine critically some assumptions requisite to analysis of the data. In the absence of known ages of the mice, age had to be estimated by some measurement available. Total length and weight were found to be highly variable measurements. Thus, body length was the measurement used. The body lengths of parous females were found to be normally distributed. Six age classes were established on the basis of the probabilities of normal distribution, each class consisting of one standard deviation from the mean. Age Class I consisted of juvenile and sub-adult females, and the remaining five classes were all adults of varying ages. An attempt was made to establish a similar distribution of sexually mature males. Such data were quite limited and no difference could be found when compared to the distribution of parous female body lengths. Males were, therefore, assigned to the age classes previously established, by body length.

Neonatal mice were not subject to snap-trapping. Observations on the growth of two litters of deer mice indicate that young mice are attracted to traps shortly after weaning. Numerous mice estimated to be recently weaned appear in the census data.

Fluctuations in numerical populations were examined. Both deer mice and voles attained peaks of population density in 1951 and early 1952, but soon declined. Peromyscus maintained moderate numbers to 1958, but Microtus practically disappeared from the high prairie. Voles attained peak densities again in 1957, a full year ahead of the deer mice. Both species stayed at moderate levels until the winter of 1959-60. In the spring of 1960 mice were quite scarce. From 1951 to 1958 the population levels were positively correlated with annual precipitation. The influence of precipitation is thought to be through its effect on plant growth. The earlier peak of Microtus following the drought of the fifties is attributed to differences in feeding habits. Voles tend to eat vegetation while deer mice prefer seeds.

Sex ratios of deer mice averaged significantly high in males during March. It was concluded that this sex ratio was only apparent, being due to increased activity and range of male deer mice at the beginning of the breeding season, thus exposing them to a greater probability of being trapped. In Microtus, male voles averaged quite low in April. It was reasoned that the same factors are not operative in vole populations, in this regard, as in deer mice, due to the use of runway systems by numerous voles. The low ratio of male voles in April was considered real, and attributed to the phenomenon of condensation potential since two April populations were extremely dense.

Age structure of the populations changed constantly. The general pattern was for the population to be proportionally high in older individuals in March, become progressively younger during the breeding season, and to age again in December. No correlation could be established, however, between age composition of a population and its numerical density. Comparison between age structure of a population and its density through succeeding months was used to estimate survival or mortality in each age class.

In general, the greatest percentage of the population found to be pregnant occurred in the spring. As the breeding season progressed, fewer females were pregnant at any given time, but the number with placental scars increased. Litter size was estimated for deer mice and voles by two methods; embryo and placental scar counts. Placental scar counts were validated with a control colony of laboratory mice, and by the empirical evidence of the great similarity of mean embryo and mean scar counts in Peromyscus and Microtus. Mean litter size was found to increase with age of the females except in the oldest group (Age Class VI) which averaged a somewhat smaller litter size. Frequency of breeding was found to increase with age.

No consistent relation could be shown between high population density, age composition, climate, and mortality. Frequently, the heaviest mortality after adverse conditions occurred among the juvenile mice, but just as often it was among the adults. The discrepancy of the mortality patterns forces one to conclude that the mice responded differently at various times due to their own peculiar physiology. Thus a given mortality factor might be fatal to physiologically deranged population, but not to healthy ones. Any adverse

condition may either reduce natality or contribute to the death of an animal; probably both. The major role in the dynamics of deer mice and vole population is, therefore, assigned to mortality. It has not been possible to demonstrate high natality overcoming the effects of adverse conditions in these species.

If there are cyclic fluctuations independent of climatic conditions of Peromyscus and Microtus in Kansas, this study has not been of sufficient duration to show them.

The division of the population into statistical age classes has been essential to this study. Splitting of sexually mature females into five groups, by body length, has permitted the demonstration of increased reproduction with increased age. A decreased reproductive potential was found in the oldest females, a point not noted in the literature. Most important, however, has been the demonstration of differential survival of the age classes at various times. Conclusions cannot be properly drawn about the dynamics of wild mice from reproductive and density data alone; some measure of the relative survival of the young and adults must be considered. During some declines of Kansas deer mice and voles the major mortality has occurred among the adults, as one would expect from the general adaptation syndrome theory. Other declines, however, have been due to heavy mortality of the juvenile mice with only normal attrition of the adults. This latter type closely fits Chitty's theory of population mortality.