

REPRODUCTIVE SUCCESS AND SURVIVAL  
OF THE YOUNG IN PEROMYSCUS

by

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## ABSTRACT

The object of this study was to compare the role of changes in reproduction and mortality in regulating population density in the deer mouse, Peromyscus maniculatus, and if possible to discover some of the factors affecting the reproductive rate. Observations were made on natural and experimentally reduced populations on the University Endowment Lands in 1964 and 1965.

In both years numbers remained relatively steady during the summer, increased in the fall, when immature animals replaced the adults, and gradually declined over the winter. Animals were about equally abundant at comparable times in both years, fall densities being about 4.72 mice per acre.

The stationary state of these populations was associated with a poor reproductive performance on the part of the females, whose breeding success varied between areas, and was greater in 1964 than in 1965. No change in litter size or in prenatal loss was observed during the period of study.

The males, in contrast, were sexually active from March to September on all areas in both years.

The greatest loss of mice occurred between birth and age at first capture, after which juveniles survived at the same rate as the adults. Survival was poorer during the breeding season than during the winter, and survival of males was poorer than that of females.

Populations whose numbers had been experimentally reduced and whose age structure had been altered were not significantly different from the natural populations in mean monthly body weights, reproductive performance, or survival. Mean monthly body weights and reproductive performance were lower, and survival of the young from birth to age at first capture was higher in 1965 than in 1964. The proportion of subadults which became fecund was greatest on this area in 1964.

The stationary state of these populations was maintained by changes in survival rather than by changes in reproductive rate. The reproductive performance of the females was fairly constant whereas the loss of young from birth to age at first capture varied. Loss of the young is attributed to their death or emigration in response to aggressive interactions within the population.

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## I. INTRODUCTION

The numbers of small mammal populations are frequently determined by changes in both birth rates and death rates. There is some controversy in the literature over the relative importance of these changes in regulating population numbers. Regulation is sometimes thought to be achieved by variations in one parameter while the other remains constant.

One concept is that reproductive rate is relatively constant and, therefore, any adjustment to population density is achieved essentially through variations in death rate (Lack, 1954). In birds, for example, Southern (1959) suggests that their birth rate "is not flexible enough to raise or lower the population level for adjustment to normally observed deviations." Adjustments through changes in death rate rather than birth rate are typical of fluctuating populations such as snowshoe hares (Green and Evans, 1940a, 1940b, 1940c), lemmings (Krebs, 1964), and voles (Chitty, 1952), though as reported by Chitty (1952) and Chitty and Chitty (1962), declines may be accompanied by reduced reproductive rates.

The contrasting point of view maintains that the reproductive rate is sufficiently reduced to account for a stationary or declining state of a population. Indeed, according to Christian (1957), such changes are mainly responsible for the regulation of numbers. Wynne-Edwards (1962, p.20) contends that animal populations can limit their numbers by decreasing

their reproductive rates as population density increases.

The purpose of the present study was to make an accurate description of reproductive rates and factors affecting them, and to compare the role of changes in reproduction and mortality in determining population numbers in the deer mouse, Peromyscus maniculatus austerus (Baird). Field work was carried out from 20 February - 16 December, 1964 and 26 February - 25 October, 1965 on the University Endowment Lands, University of British Columbia.

## II. STUDY AREAS

The University Endowment Lands are in the Puget Sound Lowlands biotic area (Cowan and Guiguet, 1965). The forest is dominated by Douglas fir (Pseudotsuga taxifolia), western red cedar (Thuja plicata), and western hemlock (Tsuga heterophylla) with mixtures of red alder (Alnus rubra), vine maple (Acer circinatum) and broadleaf maple (Acer macrophyllum). Regrowth sections are dominated by red alder. The dominant plants of the undergrowth are salmon berry (Rubus spectabilis), red elder (Sambucus callicarpa), red huckleberry (Vaccinium parvifolium), salal (Gaultheria shallon), sword fern (Polystichum munitum), and bracken (Pteridium aquilinum). The forest floor is covered with fallen logs in various stages of decay and a thick, spongy layer of leaf litter.

Mice were trapped on several areas in the Endowment Lands (Fig.1) during the two summers of field work. The areas used for mark-recapture studies were as follows:

Acadia (A): A semi-isolated area of approximately 8.8 acres, bounded by roadways on three sides and by a stand of young red alder on the fourth, in which very few deer mice were trapped. This area was used for experimental populations in 1964 and 1965. (37 trap positions)

Golf Course (G): A semi-isolated area of approximately 2.3 acres on the University Golf Course used for a natural population in 1964. (7 trap positions)

Chancellor (C.), Lookout (L), Marine Drive (M), and Wreck Beach (W): Areas in the general forest of approximately 0.7 acre, 2.1 acres, 1.2 acres, and 0.8 acre, respectively, used for natural populations

in 1965. The sizes given for these areas do not include an extra strip to allow for ranges extending outside the area trapped. (5, 8, 10 and 5 trap positions, respectively).

The areas used for collecting material for autopsy were as follows:

	<u>1964</u>	<u>1965</u>
Spring	A, B, H	A, I, K, M
Summer	H, M	C', D, E, F, H, I, N, O
Fall	A, F, G, J	A, I, L, M
Winter	H, M	----

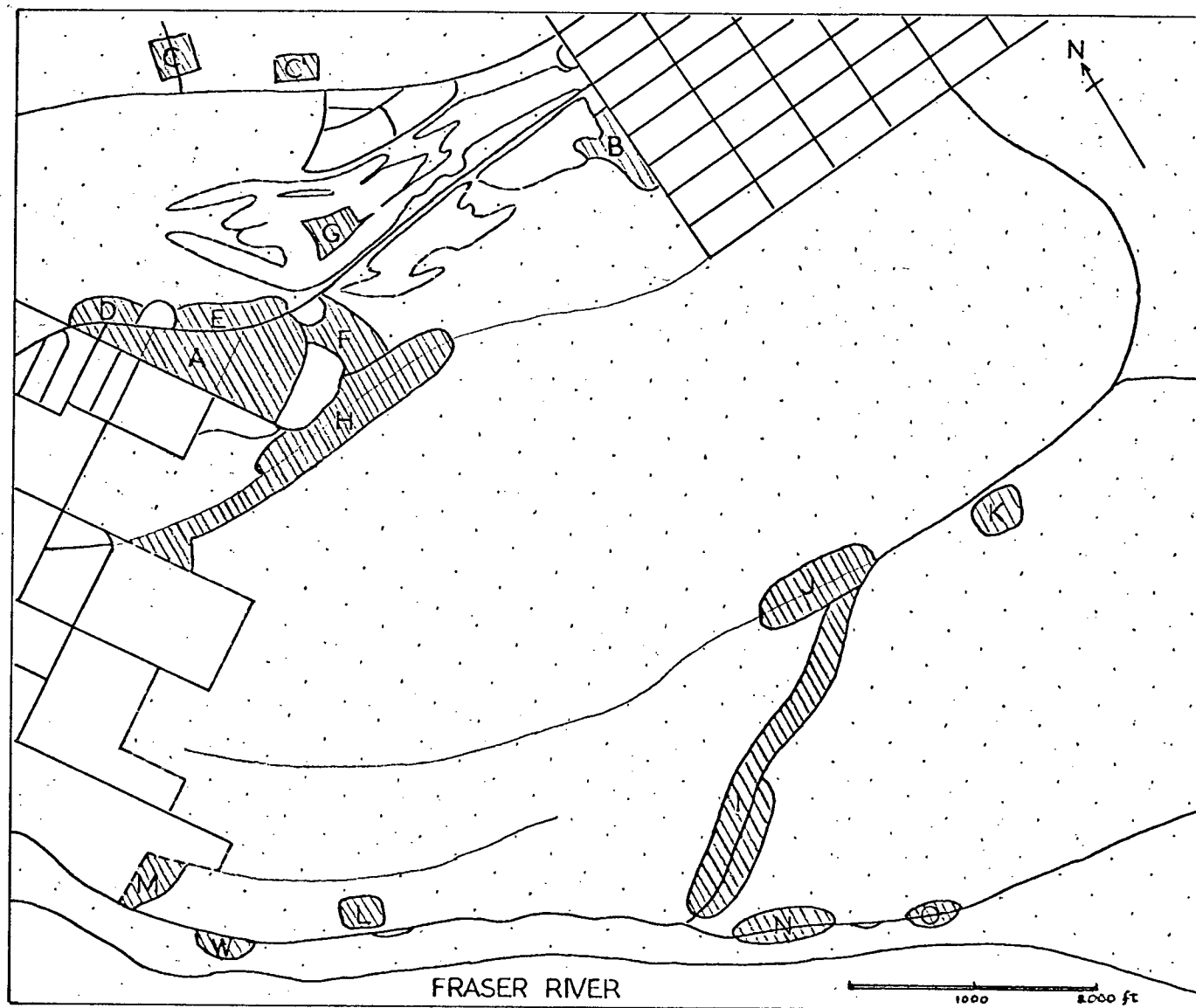


Fig.1. Map of part of University Endowment Lands showing trapping areas and roads.  
Dots indicate forested areas.

### III. METHODS

Changes in population structure, reproduction, and survival were studied by autopsy of dead specimens and by mark-recapture studies. All deer mice were trapped with Longworth live traps.

#### A. DEAD SAMPLES

Data on maturity, organ weight, reproductive rate, and prenatal mortality were obtained from dead samples. Autopsies were performed on the deer mice collected from the field areas listed above, corpses were saved, and the following data were recorded:

All specimens: Date, location, sex, body weight, pelage, degree of tooth wear, and in 1964, spleen weight and adrenal weight. All mice were weighed to 0.5 gm; all organs to 0.1 mg.

Males: Testes size and weight, seminal vesicle size or weight, and in 1965, visibility of tubules and presence of sperms in the cauda epididymis.

Females: State of lactation, size of nipples, size of mammary glands, perforation of the vaginal orifice, number of corpora lutea, number and approximate age of embryos, number of scars, and weight of entire uterine tract.

Because preliminary analysis of changes in weight of the spleen and adrenal glands indicates that no new information was being added to that already available in the literature, this thesis will be concerned only with changes in population structure, reproductive rate, and survival rate of the study populations.

## B. MARK-RECAPTURE STUDIES

Data on population growth and survival were obtained from mark-recapture studies. Each study area was trapped once each week, but for one night only so that lactating females were kept away from their litters as little as possible. The deer mice were brought into the laboratory, marked with numbered monel metal ear tags (fingerling fish tags), examined, and returned to the field the same morning. The following data were recorded:

All specimens: Date, location, tag number, sex, body weight, and pelage. All mice were weighed to 0.5 gm.

Males: Testes size.

Females: State of lactation, size of nipples, perforation of the vaginal orifice, and pregnancy.

### 1. Acadia (experimental populations).

Many mice were removed from this area in November 1963 in an extensive trapping-out program (Chitty, unpub. data). In February 1964 the remaining population of 21 males and 29 females was reduced to five males and seven females in an attempt to create a population of low density that might lead to an increased production and survival of young. Breeding began in mid-March, but because recruitment of the juveniles was poor, the adults were removed at the end of May. Four young males and seven young females were left on the area, and, in addition, one young male and two young females born in the laboratory were introduced.



In February 1965 the overwintered population of 30 males and 45 females was again reduced, leaving six pairs of resident animals on the area. Because several of the deer mice had disappeared, four females from the laboratory were released a month later, and five more males and six females were introduced at the end of June.

## 2. Natural populations.

Several populations were trapped to obtain information about population changes and reproductive changes under natural conditions and to serve as controls for the experimental populations.

### C. LABORATORY COLONY

A breeding colony, started in the spring of 1964, provided animals for field and laboratory experiments. The estrous cycle was studied from vaginal smears, which were made by pipetting warm isotonic saline solution into the vagina, withdrawing the liquid and spreading it on a microscope slide to dry. The smear was stained with methylene blue. No regular estrous cycle was observed.

Timed matings were set up in order to determine the age of embryos found in the field samples. Males and females were kept in separate cages during the day and put together at night. Vaginal smears were made the following morning. The presence of sperms indicated that mating had occurred. The females were autopsied between the seventh and eighteenth day of gestation

and the following data were recorded: number of corpora lutea, number of embryos, and the weight of the entire uterine tract.

## IV. RESULTS

## A. POPULATION STRUCTURE AND CHANGES

1. Density.

Population density changes continuously, more noticeably in the fall than during the breeding season. In order to calculate density, one must know the number of resident animals on a study plot of known area. The areas of the study plots in the general forest were corrected for ranges extending outside the area trapped by addition of a strip, arbitrarily 100 feet wide, to each side of the plot. Twice this distance gives a value of similar magnitude to the 199 and 258 feet given by Stickel (1960) as the average distances between successive captures for Peromyscus leucopus populations at high and low densities and the 172 feet given by Brant (1962) for P. maniculatus. The 200 feet assumed for these populations may be too small as mice occasionally moved 400 feet or more between successive trapings. The longest distance recorded was approximately 950 feet. Densities on all areas were of similar order of magnitude ( $< 10$ ) (Table I).

By making comparisons within an area, one can determine the direction of change in numbers, or density, in a population. On the Golf Course in 1964, for example, the number of deer mice remained relatively steady during the summer breeding season, began to increase in September, and continued to rise through the end of October. With two exceptions, this pattern of increasing

TABLE I. Monthly changes in numbers and density of marked populations.

Area	Acadia 1964-5 8.8a		Acadia 1965 8.8a		Golf Course 1964 2.3a		Chancel- lor 1965 3.4a*		Look- out 1965 5.7a*		Marine Drive 1965 4.8a*		Wreck Beach 1965 3.8a*	
Month	<u>N</u>	<u>D</u>	<u>N</u>	<u>D</u>	<u>N</u>	<u>D</u>	<u>N</u>	<u>D</u>	<u>N</u>	<u>D</u>	<u>N</u>	<u>D</u>	<u>N</u>	<u>D</u>
Mar.	12	1.36	12	1.36	7	3.04	19	5.59	7	1.23	-	-	19.	5.00
Apr.	15	1.71	12	1.36	7	3.04	28	8.23	11	1.93	-	-	22	5.79
May	20	2.28	13	1.48	7	3.04	24	7.06	13	2.28	15	3.12	19	5.00
June	17	1.93	14	1.59	6	2.61	26	7.65	12	2.11	12	2.50	15	3.95
July	20	2.28	13	1.48	5	2.18	25	7.35	10	1.75	16	3.33	19	5.00
Aug.	32	3.62	15	1.71	7	3.04	30	8.82	13	2.28	21	4.38	24	6.32
Sept.	44	5.00	21	2.39	9	3.91	26	7.65	10	1.75	19	3.96	19	5.00
Oct.	50	5.68	28+	3.18	17+	7.39	14	4.12	17+	2.98	30+	6.25	13	3.42
Nov.	56	6.36	-	-	-	-	-	-	-	-	-	-	-	-
Dec.	51	5.80	-	-	-	-	-	-	-	-	-	-	-	-
Feb.	45+	5.11	-	-	-	-	-	-	-	-	-	-	-	-

N - no.of deer mice captured

D - density

\* - adjusted acreages of study areas in the general forest,  
actual acreages are given in text, p.3

+ - data from first trap-out period only

numbers in the fall was observed on the other areas, the amount of increase from the beginning to the end of the breeding season being two to three fold. On the Chancellor and Wreck Beach areas, however, numbers dropped in the fall.

## 2. Age structure.

Age structure influences both reproduction and mortality and, therefore, the direction of change in numbers of a population. The age groups used in this study were based on body weight and pelage. The arbitrary weight groups roughly correspond to age groups or phases in the life cycle. These groups are as follows:

TABLE II. Weight group, pelage, and maturity of deer mice.

<u>Weight group</u>	<u>Pelage</u>	<u>Proportion mature*</u>	
6.0 - 10.5 gm.	juvenal	0.000	(56)
11.0 - 13.5 gm.	juvenal, subadult	0.068	(236)
14.0 - 16.5 gm.	adult	0.268	(205)
17.0 - 19.5 gm.	adult	0.716	(116)
20.0 - 22.5 gm.	adult	0.857	(35)
23.0 +	adult	1.000	(5)

\* Data from autopsy specimens, number examined in parentheses.

Juveniles and adults were easily separated by the appearance of the pelage, but subadults were less easily distinguished from adults. The gray juvenal pelage is replaced by the dark brown subadult pelage at about two months of age; the subadult pelage is replaced over a period of several months by the lighter brown adult pelage. McCabe and Blanchard (1950) reported a similar molt sequence.

Separation of mice of different age groups was checked independently by the degree of tooth wear. The criteria for the following groups, based on the amount of wear of the enamel and cusps of the upper molars, were adapted from Sheppe (1958). The ages of deer mice indicated in the groups were obtained from animals of known age, used in mark-recapture studies (Table III).

- I. M 3 (third upper molar) not fully erupted; mice approximately 2-6 weeks of age and in juvenal pelage;
- II. M 3 fully erupted but showing little or no wear; mice approximately 2-3+ months of age and in subadult pelage;
- III. M 3 basined but cusps still apparent, M 1 and M 2 showing appreciable wear but cusps still prominent; mice approximately 4-8 months of age and in adult pelage;
- IV. All molars basined, cusps of M 3 worn away, cusps of M 1 and M 2 greatly worn but re-entrant angles still apparent; mice 10-14 months of age;
- V. Cusps and re-entrant angles of M 1 and M 2 almost entirely worn away, roots usually protruding well beyond the alveolus; mice more than 15 months of age.

Shorten (1954), studying squirrels from different areas, also found that the amount of tooth wear progressed with age, and that the rate of tooth wear may have been affected by varying food conditions. Variations in food conditions may have affected the rate of tooth wear in mice from different parts of the Endowment Lands.

The age structure and body weight distributions of the marked populations are given in Tables IV and V. The weight

TABLE III. Aging of deer mice in groups based on degree of tooth wear.  
Deer mice from mark-recapture studies.

<u>Group</u>	<u>N</u>	<u>Mean body weight (gm.)</u>	<u>S.E.</u>	<u>Estimated Age</u>
I	11*	7.64	$\pm 0.32$	2-6 wks.
II	27	12.50	$\pm 0.33$	2-3 mos.
III	12	15.96	$\pm 0.59$	4-8 mos.
IV	18	17.78	$\pm 0.63$	10-14 mos.
V	1	20.50	-	15+ mos.

N - No. of deer mice examined

\* - Deer mice in Group I from dead samples

used for each animal is its average weight during each month's trapping. Year classes are separated by the dashed line.

Analysis of variance shows that the mean monthly body weights of the natural populations tended to decrease slightly from 1964 to 1965, but that the differences are not significant ( $.10 > P > .05$ ). With the exception of the Wreck Beach area, on which the mice were heavier, the differences between areas are not significant ( $P > .05$ ). Examination of criteria other than body weight indicates that all the natural populations were very similar; therefore, data on age structure were pooled.

The approximate age structure of the natural populations, shown in Table IV, is seen to change from the beginning to the end of the breeding season. The mice gradually gained weight from the 11.0-13.5 gm. and 14.0-16.5 gm. weight groups in March to the 17.0-19.5 gm. weight group in July. In August animals in the 11.0-13.5 gm. and 17.0-19.5 gm. weight groups formed a bimodal distribution. In October animals in the 11.0-13.5 gm. and 14.0-16.5 gm. weight groups made up most of the population.

By March the overwintered deer mice had begun to come into breeding condition and a few had begun to produce young. Even though the females were fecund, few pregnancies were recorded before May. Few young appeared before July, and most not until September. By September the older animals had begun to lose weight and to go out of breeding condition, many had died, and few overwintered.



Similar weight changes were observed in the experimental populations on Acadia in the two years. In 1964 the adults began to breed at the end of March, and juveniles began to appear at the end of April. The adults were removed at the end of May, leaving the juveniles on the area. The juveniles matured in June and their young began to appear in July. A few of these young matured later in the summer, but most did not. The adults went out of breeding condition in September. Toward fall unmarked adults appeared which may have been young that had grown up on the area or may have been immigrants. The fall and winter population was composed of a few adults born in the spring ( $> 17.0$  gm.) and younger animals born in the summer and fall ( $< 17.0$  gm.).

In 1965 the adults on Acadia did not come into breeding condition until April. Young began to appear in May but few were caught before August. The adults began to go out of breeding condition in September and by October few remained. Immature mice in the 11.0-13.5 gm. and 14.0-16.5 gm. weight groups made up the fall population.

The mean monthly body weights of the experimental populations decreased from 1964 to 1965, as tested by analysis of variance ( $.05 > P > .01$ ), but were not significantly different from those of the natural populations.

### 3. Sex ratio.

The distribution of sexes by body weight for the marked

populations is shown in Tables IV and V. The distribution of sexes in the natural populations was nearly equal in March, June, and July. In the other months the number of males was greater than the number of females, perhaps reflecting greater movement of the males. There were more adult males than females, especially in the 17.0-19.5 gm. weight group. The sex ratio for the other weight groups was nearly equal.

The distribution of sexes in the experimental population on Acadia in 1964 was nearly equal for each month until August, when the number of females became greater than the number of males, especially in the 11.0-13.5 gm. and 17.0-19.5 gm. weight groups. During the breeding season there were more females than males in the 20.0-22.5 gm. and 23.0+ gm. weight groups. In 1965 the sex ratio for months and for weight groups was nearly equal. The data for both years contrast with those of the natural populations, in which there were more adult males than adult females.

#### 4. Maturity.

##### a. Males.

The mean monthly testes weights, given in Table VI, were much lower in 1965 than in 1964 ( $.01 > P$ ,  $t = 3.692$ , 7 d.f.). In both years, however, the mean testes weight increased from March until August and then rapidly decreased until late fall. This seasonal change in mean testes weight reflects changes in both age structure and fecundity.

A male is fecund when there is an abundance of motile sperms

TABLE IV. Age structure and body weight distribution of deer mice in natural populations, data for 1964-5 combined.  
Dashed line separates year classes.

Body weight (gm.)	Mar.		Apr.		May		June		July		Aug.		Sept.		Oct.		Total		Grand Total ♂+♀
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
6.0-	-	-	-	1	1	1	-	1	-	-	4	2	2	1	1	6	8	12	20
11.0-	3	7	4	12	2	10	1	2	5	2	12	5	13	9	30	28	70	75	145
14.0-	4	5	22	10	24	16	10	25	3	5	6	7	12	11	27	18	108	97	205
17.0-	7	1	9	1	22	2	20	6	25	23	23	20	19	15	13	5	138	73	211
20.0-	-	-	-	-	3	1	1	2	3	3	4	7	1	2	1	2	13	17	30
23.0+	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	2	2
Total	14	13	35	24	52	30	32	36	36	35	49	41	47	38	72	59	337	276	613

TABLE V. Age structure and body weight distributions of deer mice in experimental populations, 1964-5.  
Dashed line separates year classes.  
Dotted line separates second and third generations.

1964

Body weight (gm.)	Mar.		Apr.		May		June		July		Aug.		Sept.		Oct.		Nov.		Dec.		Total		Grand Total
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀			
6.0-	-	-	1	-	-	-	1	-	1	1	-	-	-	1	-	1	1	1	2	5	6	11	
11.0-	-	-	-	-	1	4	1	-	3	-	2	2	5	2	3	4	4	9	4	10	23	31	54
14.0-	-	5	-	-	1	2	5	4	-	-	1	1	9	7	7	7	15	9	12	15	50	50	100
17.0-	5	1	5	4	3	2	1	3	3	5	4	1	4	6	5	8	2	8	2	3	34	41	75
20.0-	-	-	-	1	2	4	-	2	-	1	-	4	1	7	-	5	1	1	-	-	4	25	29
23.0+	-	1	-	2	-	1	-	-	-	1	-	3	-	2	-	1	-	-	-	-	-	11	11
Total	5	7	6	7	7	13	8	9	7	8	7	11	19	25	15	26	23	28	19	30	116	164	280

1965

Body weight (gm.)	Mar.		Apr.		May		June		July		Aug.		Sept.		Oct.		Total		Grand Total
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
6.0-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	2	2	3	2	5
11.0-	-	2	-	2	-	1	-	-	1	1	1	1	8	6	13	13	23	26	49
14.0-	2	1	-	-	1	6	2	5	2	1	4	1	2	2	6	4	19	20	39
17.0-	4	2	3	-	3	-	1	1	3	3	1	2	1	5	1	6	17	19	36
20.0-	-	-	3	-	2	1	4	1	1	1	2	2	-	1	-	1	12	7	19
23.0+	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	1
Total	6	5	6	2	6	9	7	7	7	6	9	6	11	14	22	26	74	75	149

TABLE VI. Mean monthly testes weights, 1964-5.

Month	<u>1964</u>			<u>1965</u>		
	<u>No.males examined</u>	<u>Mean testes weight (mg.)</u>	<u>+ S.E. -</u>	<u>No.males examined</u>	<u>Mean testes weight (mg.)</u>	<u>+ S.E. -</u>
Mar.	16	231.31	25.72	12	126.52	21.57
Apr.	9	244.88	24.11	13	89.53	24.94
May	15	301.95	55.39	27	129.48	13.83
June	3	302.47	7.71	28	129.72	11.22
July	18	323.55	40.29	15	347.36	45.07
Aug.	36	145.92	30.63	19	46.21	12.22
Sept.	24	116.52	33.19	6	24.60	3.73
Oct.	32	19.63	6.90	67	17.69	2.41
Nov.	11	7.96	1.41	-	-	-
Dec.	7	11.93	1.74	-	-	-

and a certain amount of semen produced. Fecundity was determined in 1965 from the presence of motile sperms in the cauda epididymis (Perry, 1945) and from the enlargement of the tubules in the cauda epididymis (Jameson, 1950) and from the development of the seminal vesicles. The distribution of males with and without motile sperms is as follows:-

TABLE VII. Distribution of sperms in cauda epididymis by testes weight.

Testes Weight (mg.)	<u>Presence of Sperms</u>	
	<u>No. without sperms</u>	<u>No. with sperms</u>
0 - 100	102	16
100 - 200	5	32
200 - 300	0	14
300 - 400	0	11
400 +	0	7

Sperms were present in animals with small testes, but many of these males, especially those with testes weighing less than 100 mg., had only a few sperms; therefore, only males whose testes weighed more than 100 mg. were considered to be fecund.

Table VIII shows that growth of the seminal vesicles initially lagged behind that of the testes but continued after the testes had stopped increasing in weight. Preliminary analysis of the data indicates that this lag in the growth of the seminal vesicles may be seasonal.

The testes of live animals cannot be weighed; therefore, the relative size of the testes, determined by slipping them between the thumb and forefinger, was recorded as regressed or

small (S), small-medium (S/M), medium (M), medium-large (M/L), or large (L) to correspond with testes weighing 0-100 mg., 100-200 mg., 200-300 mg., 300-400 mg., or 400+ mg., respectively. In order to test the accuracy of these subjective measurements, testes of dead specimens were given a relative size and then dissected out and weighed.

Analysis of the data shows that the correlation between relative size and actual weight is highly significant in both years. The data for the two years is combined in Table IX. Since males with testes weighing more than 100 mg. were considered to be fecund and the correlation between testes size and testes weight is highly significant, then males with testes scored as small-medium or larger should also be fecund. These criteria of fecundity were used to estimate the proportion of fecund animals in the populations studied.

The proportion of fecund males in the autopsy samples and the marked populations is shown in Tables X and XI. In 1964 the adult males in the dead samples were fecund from March through October, though they began to go out of breeding condition in August. In 1965 the males were fecund from March through August, the maximum being in July, followed by a sudden drop in August. This rapid change in breeding condition may have been hastened by an outbreak of botfly larvae (Cuterebra sp.) which parasitized the deer mice. The proportion of fecund males was lower in 1965 than in 1964 ( $.01 > P$ ,  $X^2 = 41.609$  with 1 d.f.).

TABLE VIII. Distribution of weight of seminal vesicles in relation to weight of testes, data for 1964-5 combined.

Testes weight (mg.)	Weight of seminal vesicles (mg.)							
	<u>0.0-</u>	<u>50.0-</u>	<u>100.0-</u>	<u>150.0-</u>	<u>200.0-</u>	<u>250.0+</u>	<u>300.0-</u>	<u>350.0+</u>
0.0-	175	-	-	-	-	-	-	-
50.0-	35	-	-	-	-	-	-	-
100.0-	30	1	-	-	-	-	-	-
150.0-	17	3	-	-	-	-	-	-
200.0	12	5	-	-	-	-	-	-
250.0-	2	8	4	2	1	-	-	-
300.0-	2	6	6	1	-	-	-	-
350.0-	-	1	2	6	4	1	1	-
400.0-	-	-	4	3	3	3	1	-
450.0+	-	-	5	3	-	2	1	3



TABLE IX. Distribution of testes size in relation to testes weight, data for 1964-5 combined.

Testes weight (mg.)	Relative testes size				
	<u>S</u>	<u>S/M</u>	<u>M</u>	<u>M/L</u>	<u>L</u>
0.0-	137	-	-	-	-
50.0-	32	-	-	-	-
100.0-	7	22	-	-	-
150.0-	-	18	6	-	-
200.0-	-	4	13	2	-
250.0-	-	-	7	5	-
300.0-	-	-	-	13	-
350.0-	-	-	-	7	4
400.0-	-	-	-	-	10
450.0+	-	-	-	-	14

The seasonal changes in the proportion of fecund males was also observed in the marked populations. In both the natural and experimental populations the males were fecund from March through September, but the proportion of fecund males was lower in the natural populations ( $.05 > P > .01$ ,  $\chi^2 = 5.811$  with 1 d.f.). More juveniles became fecund in the experimental population in 1964 (4/18) than in either 1965 (0/16) or the natural populations (1/41).

b. Females.

The sexual maturity of females in autopsy specimens may be determined by the presence of corpora lutea in the ovaries (Leslie, Venables, and Venables, 1952; Jameson, 1953). In both 1964 and 1965 there were females with corpora lutea throughout the year (Table X), and in 1964, four of six females in November and one of two females in December had corpora lutea. The proportion of females with corpora lutea increased during the summer and then decreased in the fall, as the females went out of breeding condition.

Although corpora lutea indicate ovarian activity, the rest of the uterine tract may be inactive (Jameson, 1953). In many of the females with corpora lutea, the vaginal orifice was imperforate and the females could not have mated. Perforation of the vaginal orifice, particularly in live animals, may be used as an indication of sexual activity (Clark, 1938). In young females the vagina opens at the first estrum; hence, perforation

of the vaginal orifice may be used to assess the sexual maturity of young animals brought in from the field. As an indication of reproductive condition, however, perforation of the vaginal orifice is not always reliable. The vagina becomes open only during the breeding season, but it may be closed for a short time during pregnancy. A female that had a perforate vagina, that was visibly pregnant, or that was lactating was considered to be fecund.

The proportion of fecund females in the dead samples and marked populations is given in Tables X and XI. The seasonal aspects of the breeding season are more apparent than they were in the males.

Preliminary analysis of the autopsy data indicated that females with corpora lutea were not necessarily fecund. In 1964 females were fecund from March through September, the height of the breeding season being from June through August; in 1965 the females were fecund from May through September, the peak being in July. The proportion of fecund females was lower in 1965 than in 1964 ( $.01 > P$ ,  $X^2 = 10.964$  with 1 d.f.).

The period of fecundity in the marked populations was similar to those reported for the dead samples. Females in the natural populations and on Acadia in 1964 were fecund from March through September and, on Acadia in 1965 from May through September. More juveniles became fecund on Acadia in 1964 (3/23) than in either 1965 (0/12) or the natural populations (0/23).

TABLE X. Comparison of reproductive data for dead samples, 1964-5.

Month	Males		No. adults	Females		No. pregnant
	No. adults	No. fecund		No.with corpora lutea	No. fecund	
<u>1964</u>						
Mar.	16	16	13	4	4	0
Apr.	9	9	7	3	3	0
May	15	15	10	10	6	1
June	3	3	4	4	4	2
July	14	14	11	11	11	6
Aug.	22	13	21	21	20	5
Sept.	8	7	7	6	6	3
Oct.	12	8	8	7	0	0
Total	99	85	81	66	54	17
<u>1965</u>						
Mar.	12	7	4	3	0	0
Apr.	13	5	13	4	0	0
May	26	17	25	7	2	0
June	28	17	28	10	10	2
July	14	14	13	13	13	8
Aug.	14	4	18	15	8	1
Sept.	5	0	11	11	1	0
Oct.	31	0	21	15	0	0
Total	143	64	133	78	34	11

TABLE XI. Comparison of reproductive data for marked populations, 1964-5.

<u>Month</u>	<u>Males</u>		<u>Females</u>			<u>No. juveniles (both sexes)</u>
	<u>No. Adults</u>	<u>No. fecund</u>	<u>No. adults</u>	<u>No. fecund</u>	<u>No. pregnant</u>	
Natural populations, data for 1964-5 combined.						
Mar.	14	9	13	2	1	0
Apr.	35	23	23	4	0	1
May	51	43	29	12	2	3
June	31	29	33	30	7	1
July	31	30	33	32	15	10
Aug.	33	21	34	22	10	26
Sept.	32	6	28	4	0	8
Oct.	41	0	25	0	0	12
Total	268	161	218	106	35	61
Experimental population, 1964.						
Mar.	5	5	7	5	1	0
Apr.	5	5	7	7	3	1
May	6	5	9	7	5	6
June	6	6	9	7	7	6
July	3	3	7	9	6	6
Aug.	5	5	9	9	6	6
Sept.	14	9	22	13	4	10
Oct.	12	0	21	0	0	6
Total	56	38	91	57	32	41
Experimental population, 1965.						
Mar.	6	6	5	0	0	0
Apr.	6	6	2	0	0	0
May	6	6	8	8	1	1
June	7	7	7	6	4	1
July	6	5	5	5	3	3
Aug.	7	7	5	4	3	4
Sept.	3	2	7	1	0	12
Oct.	7	0	9	0	0	7
Total	48	39	48	24	11	28

## B. REPRODUCTION

Mature females breed from March to October, bearing litters of 2-9 young (Asdell, 1964). The females are polyestrous and have a postpartum estrus. These characteristics, plus a short gestation period of 22-27 days and the rapid maturation of young of both sexes in 7-8 weeks (Clark, 1938), endow the mice with a high potential rate of increase.

### 1. Length of the breeding season.

The number of pregnant females caught in 1964 and 1965 is given in Tables X and XI. In 1964 the first pregnant female was caught on Acadia in March, and the last, also caught on Acadia, in September. The first pregnant female in the natural population was not caught until May. Mice in juvenal pelage were last caught in early November.

In 1965 the first pregnant female was caught on Chancellor in March, and the last on Acadia in late August. Breeding did not begin on Acadia until May, and on Lookout until July. Mice in juvenal pelage were last caught in late October.

### 2. Proportion of pregnant females.

Females in all stages of pregnancy or with recent parturition sites were used to calculate the proportion of pregnant females in the dead samples. More females were pregnant in 1964 (0.240) than in 1965 (0.115) ( $.01 > P$ ,  $X^2 = 7.154$  with 1 d.f.) The greatest proportion of pregnant females was in July.

The proportion of pregnant females in the marked populations was estimated from females which were more than 12-14 days pregnant or which were obviously lactating. Females less than 12-14 days pregnant were missed because the embryos are not large enough to cause a marked increase in body weight or distension of the abdomen. Vaginal smears were impractical, as a series of smears is needed to determine a female's reproductive condition.

The proportion of pregnant females varied in the natural populations from 0.094 on Lookout to 0.265 on Marine Drive, and in the experimental populations on Acadia from 0.352 in 1964 to 0.216 in 1965. The proportion of pregnant females in the experimental populations was not statistically greater than those in the natural populations, as tested by analysis of variance ( $P > .05$ ), but tended to be greater in 1964 ( $.10 > P > .05$ ,  $\chi^2 = 2.807$  with 1 d.f.).

### 3. Number of litters per season.

Throughout the breeding season breeding appeared to be random rather than synchronized. In 1965, however, many of the females became pregnant during the first two weeks of July. This was the only period of synchronized breeding observed.

With the exception of Acadia, 1964, the number of litters per season for females that were present in the marked populations for the duration of the breeding season is tabulated below. In 1964 the overwintered females on Acadia were removed

at the end of May and the juveniles left on the area began breeding in June. Had the overwintered females not been removed, they would probably have borne two to three more litters during the summer.

TABLE XII. Mean number of litters per season.

Population	No. of females	No. of litters	Mean no. of litters per female - S.E.	
Natural				
Mar.-Sept., 1964	2	3	1.50	$\pm .50$
Mar.-Sept., 1965	20	28	1.40	$\pm .11$
Experimental				
Mar.-May, 1964	7	9	1.29	$\pm .18$
June-Sept., 1964	5	14	2.80	$\pm .37$
Mar.-Sept., 1965	7	14	2.00	$\pm .31$

The average number of litters per season appeared to be greater in 1964 from June to September and in 1965 on Acadia than in the natural populations in the respective years, but the differences are not statistically significant, as tested by Student's t-test.

#### 4. Factors affecting litter size.

Litter size may vary with maternal age and weight, parity, and season of birth (Snell, 1941; Beer et al, 1957; Newson, 1964; Caldwell and Gentry, 1965). Litter size was recorded for the deer mice in the laboratory colony and for the autopsy specimens.

Inspection of the laboratory data showed no consistent relation between litter size and maternal age or between litter size and parity. Preliminary analysis of the field data, however, indicates that there may be some relationship between the



number of visible embryos per litter and maternal weight and between the number of embryos per litter and season of birth. The data for the two years were combined.

The tendency for litter size to increase in heavier (or older) females is shown in Table XIII. The number of litters was greater in the heavier females.

The seasonal changes in litter size are shown in Table XIV. The number of embryos per litter increased from May to a peak in August and then decreased. The number of litters was greatest in July.

#### 5. Ovulation rate and litter size.

Information on ovulation rate, litter size, and prenatal mortality was obtained from field and laboratory animals. The reproductive tracts were preserved in a mixture of acetic acid, ethanol, and formalin, cleared through benzene into benzyl benzoate and viewed with oblique light (Orsini, 1962a, 1962b, 1963). The number of corpora lutea, implantation sites, embryos, recent parturition sites, and uterine scars was counted. Only those data pertaining to pregnant uteri were used because I was unable to separate different sets of corpora lutea or different sets of scars in several cases.

The approximate stage of development of pregnant uteri in the field material was estimated by comparing their development with known stages from timed pregnancies set up in the laboratory. The state of development used to separate implantation

sites and embryos was placentation, or, approximately, day nine. Further information on pregnant uteri is given in Appendices A, B and C.

Table XV shows the average number of corpora lutea, implantation sites, embryos, and live young born per litter in 1964 and 1965. None of the differences between means in each category in the two years is statistically significant, as tested by the Student's t-test. The difference between the number of young per litter and the number of corpora lutea per litter is not significant ( $P > .05$ ). The mean litter size, calculated from the pooled data and used in further computations, was 4.82 young per litter.

The number of corpora lutea formed was assumed to be equal to the number of ova shed even though some evidence of polyovuly was found. Two pregnant uteri in which the number of corpora lutea was one less than the number of embryos were found in the field material. In a third instance, a female from the colony had no corpora lutea in the right ovary and five in the left, and of nine embryos, the four in the horn having no corpora lutea were dead and the five in the left horn were alive. It seems unlikely to me that four embryos in one pregnancy should have arisen from multiple ovulations. The incidence of multiple ovulation in Peromyscus maniculatus reported by Beer et al (1957) is very low, but can be greater in some individuals (Hartman, 1926). If polyovuly did not occur, then the corpora lutea may

have atrophied. The literature, however, indicates that the corpora lutea are present for the duration of pregnancy in this and other species (Beer et al, 1957; Snell, 1941; Long and Evans, 1922; Harper, 1964; Newson, 1964).

The average number of corpora lutea was  $5.18 \pm 0.16$ .

The average number of implantation sites per litter was  $5.00 \pm 0.20$  and the average number of embryos per litter was  $4.95 \pm 0.23$ . The range in number of embryos per litter was three to seven and the mode five.

The average number of young per litter born in captivity was  $4.60 \pm 0.14$ . The range was one to eight and the mode five.

#### C. MORTALITY AND SURVIVAL RATES

Death may occur at any stage of development from the time of ovulation on. Both prenatal and postnatal mortality affect the size, structure, and reproductive capacity of a population.

##### 1. Prenatal mortality.

Prenatal mortality includes losses before and after implantation (Davis and Golley, 1963; Newson, 1964). Loss of unfertilized and nonviable ova is expected prior to implantation (Harper, 1964) and loss of embryos, possibly through lack of sufficient blood to the placenta, is expected during mid-pregnancy (Reynolds, 1955). Owing to the small number of pregnant uteri in various stages of development, the only divisions used were implantation and placentation. Placentation was used to separate implantations from embryos. The method used to esti-

TABLE XIII. Litter size in relation to maternal weight,  
data for 1964-5 combined.

<u>No. visible embryos per litter</u>	<u>Maternal weight (gm.)</u>			<u>Total No. litters</u>
	<u>14.0-</u>	<u>17.0-</u>	<u>20.0-</u>	
3	2	-	1	3
4	1	4	-	5
5	2	2	6	10
6	-	5	4	9
7	-	-	1	1
Total	5	11	12	28
Avg.no.embryos per litter	4.00	5.09	5.33	5.00

TABLE XIV. Monthly distribution of litter size,  
data for 1964-5 combined.

<u>No.visible embryos per litter</u>	<u>May</u>	<u>June</u>	Month <u>July</u>	<u>Aug.</u>	<u>Sept.</u>	<u>Total No. litters</u>
3	1	1	-	-	1	3
4	-	1	3	1	-	5
5	-	2	6	1	1	10
6	-	-	5	3	1	9
7	-	-	-	1	-	1
Total	1	4	14	6	3	28
Avg.no.embryos per litter	(3.00)	4.25	5.14	5.80	4.67	5.00

TABLE XV. Number of ova and embryos in wild females and number of young born in the laboratory.

Stage of development	<u>1964</u>			<u>1965</u>			<u>Years combined</u>		
	N	$\bar{X}$	$\pm$ S.E	N	$\bar{X}$	$\pm$ S.E.	N	$\bar{X}$	$\pm$ S.E.
Corpora lutea (ova)	21	5.29	$\pm 0.21$	12	5.00	$\pm 0.25$	33	5.18	$\pm 0.16$
Implantation sites	21	5.14	$\pm 0.29$	12	4.75	$\pm 0.28$	33	5.00	$\pm 0.20$
Embryos	13	5.23	$\pm 0.28$	7	4.43	$\pm 0.37$	20	4.95	$\pm 0.23$
Live young at birth <sup>1</sup>	10	4.50	$\pm 0.40$	79	4.61	$\pm 0.15$	89	4.60	$\pm 0.14$

N - No. of litters.

<sup>1</sup> - litters born in colony

mate the approximate stage of development of pregnant uteri was given on page 33.

a. Loss of ova prior to implantation.

Loss of ova prior to implantation was estimated from the difference between the number of corpora lutea and the number of implantation sites. No attempt was made to recover free ova or blastocysts from the uteri; hence, only uteri in which some of the ova survived to implantation were used. The proportion of litters showing loss was about 0.30, and the proportion of ova lost prior to implantation was about 0.10 (Table XVI A). There was no indication that losses were disproportionately greater where the number of ova shed was greater. Total loss of ova prior to implantation was not estimated.

b. Loss of embryos after implantation.

Loss of embryos after implantation was estimated from the difference between the number of implantation sites and the number of live embryos. Although the amount of loss may vary with the stage of pregnancy (Perry, 1955, Harper, 1964), the small number of pregnant uteri made further subdivision impractical. The proportion of litters showing loss was 0.20-0.25, and the proportion of embryos lost after implantation was about 0.05 (Table XVI B). Total litter loss was not estimated.

In Table XVI C preimplantation loss is shown as loss of ova and postimplantation loss, as loss of embryos. Total loss of ova from ovulation in litters 10-23 days old was about 0.08,

with losses distributed nearly equally before and after implantation. The differences in loss of ova between the two years are not significant ( $P > .05$ ).

## 2. Postnatal mortality.

### a. Loss of young from birth to first capture.

The proportion of young lost at birth in the field is unknown, but if the estimate of the number of young born per litter in the laboratory is representative of the field situation, then the drop from 4.95 embryos per pregnancy to 4.60 young per litter at birth is a loss of 7.1 per cent. Complete loss of litters is probably quite low, as 87.1 per cent (61/70) of the pregnant females were lactating when subsequently caught. The proportion of pregnant females which suckled litters was not significantly greater in the experimental population (34/38) than in the natural populations (27/32).

Nothing is known about the loss of young from birth to about 4-6 weeks of age, when they would have been captured for the first time. In further discussion this will be referred to as age at first capture. Loss of nestlings may be due to inherent weakness, disease, desertion by the mother, predation, and other accidents such as flooding.

The estimate of loss must cover this entire period from birth to age at first capture, and enables one to compare the potential number of young born on an area with the number of juveniles caught. Loss of young, however, may be greater than



such an estimate would indicate.

There are various possible estimates of litter size and, therefore, of numbers born. Litter size may be estimated from the number of embryos per litter or the number born per litter or from the combined data on litter size. The potential number born is then calculated by multiplying the number of young per litter by the number of pregnancies (litters).

It is probable, however, that not all pregnancies were recorded. Several females which had had litters during the breeding season, but which had not been caught when pregnant, were caught and autopsied in the fall. Females, which showed signs of having lactated when caught for the first time, may or may not have had their litters on the same area.

Juveniles, in dispersing, may have migrated onto or away from the study areas. A few juveniles appeared on some of the study areas in 1965 before any pregnancies had been recorded for those areas. Some of the unmarked immature animals, caught in the fall, may have been present earlier in the breeding season, but not caught, or they may have been immigrants onto the study areas. This influx of young in the fall was especially noticeable on Lookout and Acadia in 1965.

The loss, or survival, of young for each month may be estimated by comparing the number of pregnancies with the number of juveniles caught in the following months (Table XI). The survival of young was poor during the breeding season but tended

TABLE XVI. Prenatal mortality, 1964-5.

## A. Preimplantation mortality in litters 4-9 days old.

Year	No. ova lost				Total	Litters		No. corpora lutea	Ova	
	0	1	2	3		No. with loss	Proportion with loss		No. sites	Proportion ova lost
1964	7	2	0	1	10	3	.300	50	45	.100
1965	5	1	1	0	7	2	.286	36	33	.083
Total	12	3	1	1	17	5	.294	86	78	.093

## B. Postimplantation mortality in litters 10-23 days old.

Year	No. embryos resorbing			Total	Litters		No. sites	Embryos	
	0	1	2		No. with loss	Proportion with loss		No. embryos	Proportion embryos lost
1964	6	2	0	8	2	.250	42	40	.048
1965	4	1	0	5	1	.200	25	24	.040
Total	10	3	0	13	3	.231	67	64	.045

## C. Total proportion of ova lost in litters 10-23 days old.

Year	No. litters	No. corpora lutea	No. sites	No. embryos	Proportion ova lost	Proportion embryos lost	Combined loss of ova and embryos
1964	13	73	70	68	.041	.029	.068
1965	7	34	33	31	.029	.061	.088
Total	20	107	103	99	.037	.038	.075

to improve toward fall.

The overall survival of young from birth to age at first capture was estimated by comparing the number of young that could have been produced by pregnant females on each area with the number of juveniles actually caught. Numbers born were estimated from the number of pregnancies observed and from the number of young per litter (4.82), calculated from the combined data.

TABLE XVII. Proportion of young surviving to 4-6 weeks of age.

<u>Population</u>	<u>N</u>	<u>B</u>	<u>C</u>	<u>P</u>
Natural				
Golf Course, 1964	4	19.28	7	0.363
Chancellor, 1965	11	53.02	16	0.302
Lookout, 1965	3	14.46	7	0.484
Marine Dr., 1965	9	43.38	19	0.438
Wreck Beach, 1965	8	38.56	12	0.312
Experimental				
Acadia, 1964	32	154.24	41	0.266
Acadia, 1965	11	53.02	28	0.528

N - no. of pregnancies

B - estimated no. of young born

C - no. of juveniles captured

P - estimated proportion of young surviving to 4-6 weeks of age.

The differences between areas are not significant, as tested by analysis of variance ( $P > .05$ ); therefore, the data for all areas were combined to give 78 pregnancies and 130 juveniles. Of the 376 young expected from these pregnancies, the proportion of young caught was 0.346. Thus, even on a conservative basis, only about one third of the young born were marked.

Although the differences between the experimental and

natural populations in the proportion of young surviving to 4-6 weeks of age are not statistically significant, the differences in survival on Acadia in 1964 and in 1965 are highly significant ( $.01 > P$ ,  $X^2 = 12.100$  with 1 d.f.).

b. Minimum survival rates of juveniles and adults.

Deer mice that were no longer caught on an area may have died, emigrated, or have been missed for some other reason. Individuals lived an unknown time after their last capture and, therefore, one knows nothing about the mortality rate. One can calculate the minimum survival rate, the proportion of animals released at time  $t$ , caught at time  $t + 1$ .

Juvenile and adult survival for each four-week trapping period were compared before calculating the minimum survival rates for the study populations. Preliminary analysis of the data shown below indicates that the rates of disappearance for the juveniles are fairly uniform throughout the breeding season.

TABLE XVIII. Minimum survival rates of juveniles and adults.

<u>Month</u>	<u>Juveniles</u>				<u>Adults</u>			
	<u>Males</u>		<u>Females</u>		<u>Males</u>		<u>Females</u>	
	<u>R</u>	<u>MSR</u>	<u>R</u>	<u>MSR</u>	<u>R</u>	<u>MSR</u>	<u>R</u>	<u>MSR</u>
Apr.	3	0.667	3	1.000	55	0.745	41	0.976
May	7	0.714	9	0.778	50	0.780	45	0.844
June	9	0.667	7	0.714	41	0.756	43	0.744
July	16	0.688	10	0.700	37	0.757	41	0.732
Aug.	25	0.680	17	0.706	50	0.580	54	0.685
Sept.	13	0.769	16	0.812	19	0.684	20	0.850
Oct.	8	0.875	12	0.667	6	1.000	15	0.800

R - No. of mice released  
MSR - Minimum survival rates

Analysis of variance shows no significant differences between either age or sex, but does show differences between trapping periods ( $.05 > P > .01$ ); therefore, the data for age and sex were pooled. In other words, once a juvenile had been marked, its chances of survival were as good as an adult's.

The minimum survival rates for each four-week trapping period are given in Tables XIX and XX. Because the numbers are so small, minimum survival rates vary rather widely. Analysis of variance reveals no significant differences in survival between areas, even though survival began to decrease on Chancellor in July 1965 and on Wreck Beach in August 1965. The reason for the decline in numbers and in survival on these two areas is not known.

The survival rates for males were significantly lower than those for females, averaging 0.758 and 0.816, respectively ( $.05 > P > .01$ ). These rates were calculated by dividing the total number of males recaptured by the total number of males released, and similarly for the females.

Clear seasonal changes in survival were observed ( $.01 > P$ ). Survival was lowest during the breeding season from June through August (0.711) and highest during the winter (0.832). Survival was a little poorer in 1965 than in 1964 ( $.05 > P > .01$ ). The seasonal and yearly rates were calculated as for the males. The overall survival per month was 0.790.

### 3. Disease, parasitism, and predation.

With the exception of two females caught on the Wreck Beach area, none of the deer mice from the field appeared diseased. The two mice had damp, clumped fur even though the cotton in the nest boxes was dry. One female remained on the area for three months, the other four months.

The deer mice were parasitized by ticks, lice, and fleas, and during July and August, by larvae of the botfly, Cuterebra sp. Of 40 mice parasitized with botfly larvae, all but nine badly parasitized ones were recaptured in apparently good health. Sadleir (1965) also reported parasitism by botfly larvae.

The traps were disturbed sporadically by raccoons (Procyon lotor) but only once was there evidence of a kill. Douglas squirrels (Tamiasciurus douglasi) may also have disturbed the traps. Four short-tailed weasels (Mustela erminea) were caught and removed from the areas during the two years. Owls and house cats were also heard or seen.

TABLE XIX. Minimum survival rates for the natural populations, 1964-5.

<u>Period</u>	Males			Females		
	<u>R</u>	<u>C</u>	<u>MSR</u>	<u>R</u>	<u>C</u>	<u>MSR</u>
26 Feb., 1964	4	4	1.000	3	3	1.000
26 Mar., 1964	3	3	1.000	3	3	1.000
23 Apr., 1964	4	3	0.750	2	2	1.000
21 May, 1964	3	2	0.667	3	2	0.667
18 June, 1964	3	3	1.000	2	2	1.000
16 July, 1964	3	2	0.667	2	2	1.000
13 Aug., 1964	7	5	0.714	3	1	0.333
10 Sept., 1964	4	-	-	1	-	-
26 Feb., 1965	11	9	0.818	11	11	1.000
26 Mar., 1965	25	21	0.840	21	19	0.905
23 Apr., 1965	43	30	0.698	26	25	0.962
21 May, 1965	36	27	0.750	31	25	0.806
18 June, 1965	32	23	0.719	30	24	0.800
16 July, 1965	33	25	0.758	34	24	0.706
13 Aug., 1965	45	25	0.556	42	26	0.619
10 Sept., 1965	27	-	-	28	-	-

R - no. of deer mice released at time t.  
 C - no. of deer mice recaptured at time t + 1.  
 MSR - minimum survival rate.

TABLE XX. Minimum survival rates for experimental populations, 1964-5.

<u>Period</u>	Males			Females		
	<u>R</u>	<u>C</u>	<u>MSR</u>	<u>R</u>	<u>C</u>	<u>MSR</u>
26 Feb., 1964	4	4	1.000	7	7	1.000
26 Mar., 1964	5	5	1.000	7	7	1.000
23 Apr., 1964	6	5	0.833	9	9	1.000
21 May, 1964	6	5	0.833	9	9	1.000
18 June, 1964	5	4	0.800	6	4	0.667
16 July, 1964	8	7	0.875	10	7	0.700
13 Aug., 1964	13	10	0.769	18	15	0.833
10 Sept., 1964	18	16	0.889	20	20	1.000
8 Oct., 1964	14	13	0.929	27	20	0.741
5 Nov., 1964	23	20	0.870	33	26	0.788
3 Dec., 1964	19	11 <sup>1</sup>	0.833 <sup>2</sup>	32	24 <sup>1</sup>	0.909 <sup>2</sup>
26 Feb., 1965	6	5	0.833	4	2	0.500
26 Mar., 1965	6	4	0.667	7	4	0.571
23 Apr., 1965	5	5	1.000	7	7	1.000
21 May, 1965	7	6	0.857	8	7	0.875
18 June, 1965	9	7	0.778	10	6	0.600
16 July, 1965	9	5	0.556	5	4	0.800
13 Aug., 1965	9	6	0.667	8	7	0.875
10 Sept., 1965	12	-	-	13	-	-

R - no. of deer mice released at time t.

C - no. of deer mice recaptured at time t + 1.

MSR - minimum survival rate.

1 - no. of deer mice recaptured 26 Feb., 1965.

2 - average MSR for three trapping periods.



## V. DISCUSSION

In this section the data will be integrated with the results of other workers. Following this will be a discussion of the relevance of these observations on deer mice to existing theories on the regulation of numbers.

### A. POPULATION CHANGES

Each year since 1962, when Sadleir (1965) began trapping deer mouse populations on the University Endowment Lands, numbers have remained relatively steady during the summer, increased suddenly to a peak in the fall, and then gradually declined over the winter. With one exception, no marked decrease in numbers prior to the onset of the breeding season has been observed. Sadleir (1965) observed a drop in numbers in one of his study populations in June 1963, the population began breeding in July. There has been little fluctuation in numbers from year to year.

The changes in population structure have been that most adults of the summer breeding population die by fall and are replaced by sexually immature animals which overwinter and mature in the following spring to form a new breeding population. Few juveniles appear during the summer breeding season. Thus, there is an annual turnover of individuals in the population.

Similar changes in population numbers and structure have been reported by many workers (Howard, 1949; Snyder, 1956; Hoffmann, 1958; Newson 1964; Krebs, 1964).

## B. REPRODUCTION

The length of the breeding season has been quite variable. Breeding had begun when Sadleir began his studies in May 1962 and extended to September. In 1963 the breeding season extended from June to September, in 1964 from March to September, and in 1965 from May to August. No estival pause has been observed. Breeding seasons of similar duration have been reported by Sheppe (1958) for this subspecies (P. m. austerus), by Beer et al (1957) for P. m. bairdii and P. m. gracilis, and by McCabe and Blanchard (1950) for P. m. gambelii. Winter breeding has been reported for P. m. gambelii in California (Jameson, 1953).

Few females, however, started breeding in the natural populations until May in 1964 and in all populations until May in 1965, even though, as also noted by Sadleir (1965), the females were perforate earlier in the spring. A possible reason for this delay in breeding is that the first estrous cycles may have been sterile, as has been observed in Clethrionomys (Brambell and Rowlands, 1936), Peromyscus leucopus (Bendell, 1959), and in P. maniculatus (Jameson, 1953).

The proportion of adult or overwintered females that became pregnant was low, 0.163 in 1963, 0.161 in the natural populations in 1964 and 1965, and 0.352 and 0.216 in the experimental populations in 1964 and 1965, respectively. The frequency of pregnancy in females alive throughout the breeding season in the natural populations in 1964 and 1965 was 1.5

litters per breeding female, and in the experimental populations, 1.3 before June 1964 and 2.8 after, and 2.0 in 1965. The incidence of postpartum mating in the marked populations was very low, ( $6/27 = 0.222$ ), most females only becoming pregnant again two to three weeks after parturition. This gap between pregnancies suggests a period of lactation anestrus. McCabe and Blanchard (1950) reported an average of four litters per breeding female per season.

The number of embryos per litter observed in the field was 4.95 and the number of young per litter in the laboratory was 4.60. Sheppe (1958) reported 5.6 embryos per litter for several subspecies of P. maniculatus in British Columbia. The number per litter reported for other subspecies is 4.28 young for P. m. bairdii in Michigan (Howard, 1949), 5.06 embryos for P. m. gambelii near Berkeley (McCabe and Blanchard, 1950) and 4.60 embryos in the Sierra Nevada in northern California (Jameson, 1953), and 5.38 embryos for P. m. gracilis in Ontario (Coventry, 1937).

The average litter size in P. m. austerus was affected by maternal weight, or age. Larger females carried larger numbers of embryos. This phenomenon was also observed by Beer et al (1957) for P. m. bairdii and P. m. gracilis. A larger number of young per litter has been reported at higher altitudes, but a longer breeding season and more litters at lower elevations (Asdell, 1964).

## C. MORTALITY

The decrease in litter size during pregnancy was from 5.18 ova shed (corpora lutea) to 5.00 implantation sites to 4.95 embryos. The proportion of ova lost was approximately 0.10. This decrease is comparable to that observed by Beer et al (1957) for P. m. bairdii, 5.77 ova to 5.25 sites to 5.08 embryos, and a proportion of 0.12 ova lost; and for P. m. gracilis, 5.86 ova to 5.45 sites to 5.32 embryos, and a proportion of 0.10 ova lost.

Complete loss of litters is probably quite low, as shown by the proportion of pregnant females which, when subsequently caught, were lactating ( $61/70 = .871$ ). Neither loss at birth nor nestling mortality was observed. Howard (1949) reported that several litters born in the spring were dead at birth or died shortly after. He observed a decrease in litter size of nestlings in P. m. bairdii from 4.28 young per litter at 0-2 days, to 4.17 at 3-7 days to 3.39 at 8-21 days and 3.28 from 21 days to dispersal. He also observed that the largest loss of young occurred at about three weeks after birth, or just after weaning.

The proportion of young lost from birth to age at first capture was 0.65 in P. m. austerus compared with 0.82 in P. m. gambelii (McCabe and Blanchard, 1950). I found that the survival of the young was poor during the breeding season and improved toward fall, but that once the juveniles had been marked,

they survived as well as the adults. Sadleir (1965), however, observed that juveniles entering the summer breeding population survived worse than those entering the fall population. My observations on natural populations were made over a shorter period of time and could not be used to make this comparison. Bendell (1959) found similar survival rates for juveniles and adults in P. leucopus populations, and that no matter what time of year the young entered the population, they survived as well as the adults.

The survival of adults was good during the winter (0.832) but dropped during the summer breeding season (0.711). The observed average survival per month of 0.80 was also reported by Sadleir (1965) for this subspecies, and by Bendell (1959) for P. leucopus.

#### D. EXTRINSIC FACTORS

Disease may be an important mortality factor in nature, but Chitty (1954) has shown that the presence of an epizootic is not necessarily correlated with high mortality in natural populations. Except for two mice caught on the Wreck Beach area, none of the animals from the field appeared diseased. Hence, there was no evidence of an endemic epizootic disease killing animals in larger numbers in the spring than in the fall.

Predators have been assumed to be responsible for keeping numbers in P. maniculatus populations in check (Howard, 1949), and even, to cause population declines (Brant, 1962). Although predators were present on the University Endowment Lands, there is no indication that they took more mice at the beginning of the season than at the end.

Variations in weather could explain part of the differences in length of the breeding season, and, perhaps, the amount of reproduction between the two years. The mild weather in 1964 was probably conducive to reproduction and the cold spring and hot, dry summer in 1965 were probably inimical, but in both years the amount of breeding was below the potential capacity. In each year breeding began at different times in the marked populations. Thus, weather by itself did not inhibit breeding.

Weather may also have affected survival in the two years although differences in the survival rates between populations were not statistically significant. More sensitive analysis did point up differences between years, survival being poorer in 1965 than in 1964. There is no direct evidence, however, that these differences were due to adverse weather conditions.

The food supply was assumed to be sufficient, and no extra food was put in the field. Food, however, could be scarce in the spring and become more plentiful during the summer and enough food could be stored in the fall to carry the population through the winter. Food was probably not scarce on Acadia in the spring

of 1965 since the number of deer mice was experimentally reduced from 75 to 12; hence, neither the onset of breeding in the spring nor production of litters later in the summer could be directly controlled by the food supply. The mice caught in the spring, many of which were unmarked, may have been living on the area but not previously caught or may have immigrated onto the area to fill the vacuum created by trapping it out.

Population numbers were very stable from year to year, especially on the Golf Course, while the food supply probably varied; therefore, food supply by itself was not regulating the populations. Bendell (1959), working on P. leucopus, and Krebs and DeLong (1965), working on Microtus, have reported that populations do not increase indefinitely when given an unlimited supply of food, and the problems of population regulation still remain.

Trapping may have caused an increase in loss of litters being suckled. Lactating females which were caught in the traps were kept away from their litters overnight, leaving the young without food or protection for a maximum of about 12 hours. Total loss of litters, however, was fairly low, as only 9 out of 70 pregnant females showed no signs of having lactated when subsequently caught. The observed seasonal change in survival of young is not due to trapping, as females were subjected to the same trapping procedure in the fall as in the spring.

## E. SEASONAL INCREASE IN NUMBERS

The seasonal increase in numbers observed in the marked populations was only 1.04. This figure was calculated by comparing the number of adults present in April (77) with the number still alive in October (10) plus the number of juveniles surviving to October (70). Some of the unmarked animals caught in the fall may have grown up on the area but were not included in this calculation, as they may equally well have been immigrants. The total observed three fold increase in numbers was probably due to immigration into the populations.

The potential seasonal increase in numbers can be estimated from the following assumptions about reproduction and survival.

## Reproduction:

Number of young per litter is 5.00.

Sex ratio at birth is unity.

Adults bear one litter per month between May and September.

Juveniles mature at 8 weeks of age.

## Survival:

Adult survival rate per 4 weeks is 0.80.

Juvenile survival rate from birth to 4 weeks is 0.35.

By applying these assumptions to a cohort of 10 females and 10 males alive in April (week 0), one finds that 61.86 animals would be present in October (week 28) (Table XXI). This represents a three fold potential increase in numbers in contrast to virtually no increase due to reproduction in the marked populations. Loss of mice over the winter at the rate of 0.17 per month would reduce numbers to the previous spring's level. A population of



100 mice in the spring, for example, would grow to 300 mice by fall and dwindle to 98 mice by the next spring.

The model allows for exact replacement of the population, but other patterns of population change are also possible. Under certain conditions such as a clement winter, survival would probably be better and the spring population could increase. On the other hand adverse weather conditions would reduce population numbers.

#### F. REVELANCE OF PRESENT DATA TO EXISTING THEORIES

Andrewartha and Birch (1954) have suggested that the number of animals in a natural population is limited by extrinsic environmental factors, particularly by shortage of time due to adverse weather conditions when the rate of increase  $r$  is positive. In a previous section on extrinsic factors it was decided that variations in weather were not of primary importance in population regulation since there were no significant changes in breeding success between the two years and since population numbers were very stable from year to year. Although mortality is the main factor, changes in it are not due to climatic conditions alone but, perhaps, to social interactions within the populations.

Wynne-Edwards (1962, 1964) has advanced the idea that animal populations can adjust their reproductive rates to avoid over-exploitation of the renewable resources of the environment. He says that a population receives information about its numbers

TABLE XXI. Potential seasonal increase in numbers.

Survival of parental cohort of 10 females and 10 males and their offspring.								
Time (weeks)	0	4	8	12	16	20	24	28
Generation								
Parental								
Males	10.00	8.00	6.40	5.12	4.10	3.28	2.62	2.10
Females	10.00	8.00	6.40	5.12	4.10	3.28	2.62	2.10
First F <sub>1</sub>	-	40.00	14.00	11.20	8.96	7.18	5.74	4.59
First F <sub>2</sub>	-	-	-	-	22.40	7.84	6.28	5.02
Second F <sub>2</sub>	-	-	-	-	-	17.94	6.28	5.02
Third F <sub>2</sub>	-	-	-	-	-	-	14.35	5.02
Second F <sub>1</sub>	-	-	32.00	11.20	8.96	7.18	5.74	4.59
First F <sub>2</sub>	-	-	-	-	-	17.94	6.28	5.02
Second F <sub>2</sub>	-	-	-	-	-	-	14.35	5.02
Third F <sub>2</sub>	-	-	-	25.60	8.96	7.18	5.74	4.59
First F <sub>2</sub>	-	-	-	-	-	-	14.35	5.02
Fourth F <sub>1</sub>	-	-	-	-	20.25	7.18	5.74	4.59
Fifth F <sub>1</sub>	-	-	-	-	-	16.40	5.74	4.59
Sixth F <sub>1</sub>	-	-	-	-	-	-	13.10	4.59
Total							61.86	

## Assumptions:

## Reproduction:

Number of young per litter is 5.00.

Sex ratio at birth is unity.

Adults bear one litter per month between weeks 4 and 28.

Juveniles mature at 8 weeks of age.

## Mortality:

Adult survival rate per 4 weeks is 0.80.

Juvenile survival rate from birth to 4 weeks is 0.35.

through social interactions and territorial behavior and that these interactions between members of the population can prevent some of them from breeding and so, in effect, reduce the birth rate. According to these ideas, the high aggressive level observed at the beginning of the breeding season by Sadleir (1965) and Healey (1966) would be interpreted as an adaptation which favors survival of the population by limiting the number of breeding animals in an area, and the shortened breeding seasons observed in some populations and the low proportion of pregnancies as further adaptations for preventing over-population. That is, he believes that populations that don't control their reproductive rates will destroy themselves and be replaced by populations that do control their reproductive rates.

Various authorities, however, have objected to this view on the grounds that it is contrary to the present view on natural selection of the individual (Braestrup, 1963; Lack, 1964; Perrins, 1964; Smith, 1964). Smith (1964) discusses behavior which "leads an individual not to breed in circumstances in which other members of the species are breeding successfully" and points out that "if the difference between breeders and non-breeders is genetically determined, then it is the breeders whose genotype is perpetuated." He also points out that "it is unlikely that species are often divided into a large number of small and completely isolated groups," which would allow altruistic behavior to evolve and be perpetuated, especially if mating is random.

Christian (1957) has suggested that a behavioral-physiological mechanism, operating through the pituitary-adrenocortical axis, affects reproduction and mortality (also see Christian and Davis, 1965; Christian, Lloyd, and Davis, 1965). He says that "there is decreased fertility and fecundity, increased intrauterine and infant mortality with increased population density and that the increased infant mortality is at least partly due to partial failure of lactation." According to this view, the low reproductive rate would be interpreted as a necessary consequence of relatively high numbers or high social pressure, and the hypertrophy of the adrenal glands in the summer, found in this study and in those reported by Chitty, 1961; Chitty and Clarke, 1963; Christian, 1962; and Krebs, 1964 as evidence for endocrine feed-back mechanisms, acting to reduce reproduction and increase prenatal mortality. Negus et al (1961) discussed evidence which implies that density and social contact are not "necessarily important factors influencing adrenal weight changes in natural populations."

In this study no significant differences in prenatal mortality were found. The proportion of pregnant females which were lactating when subsequently caught was not significantly greater in the experimental populations (34/38) than in the natural populations (27/32). The actual density on the study areas was quite low if one considers the number of mice the areas could have supported, as indicated by the number of mice removed from

Acadia in February 1965. The amount of reproduction on Acadia tended to be greater in 1964 than in 1965 and may have been inversely related to the number of mice on the area immediately prior to the breeding season. These observations could equally well be explained by variations in the weather in the two years or, perhaps, by changes in behavior.

Crowcroft and Rowe (1958, 1963) have reported that fecundity and reproduction decreased in house mice caged together in large numbers, and that breeding was resumed when the density was reduced by allowing the populations to disperse into larger areas. New dominance-subordination relationships were formed in the additional area. Petrusiewicz (1957, 1963) induced population growth by changing a population to a different kind of cage, by adding or removing mice. He suggested that his results were caused by altered social relations in the population.

Increased reproduction in field populations has also been attributed to disruption of social structure. Lloyd (1963) found that when the number of rabbits in a population was reduced immediately prior to the onset of spring breeding, the population increased more than if no rabbits had been removed. Sheppe (1965) obtained midsummer breeding in populations of P. leucopus, which normally have an estival pause, by introducing mice in very large numbers onto islands in Ontario.

Social contacts have been shown to increase prenatal mortality. The presence or odor of strange males for several hours

within a few days after insemination may cause resorption of litters in Mus musculus (Parkes and Bruce, 1961) and in P. m. bairdii (Bronson and Eleftheriou, 1963). Strange males, however, seldom remained in an area for any length of time, as 27 per cent (45/165) of the males in the marked populations were caught only once. The only prolonged exposure to strange odors would be in the traps four nights per month. Thus the resorption of litters due to pregnancy block would not be expected to be important in reducing the birth rate. The effects of odors need not be deleterious. Odors and scent markings leave information about animals and their activities, as in the hamster (Eibl-Eibesfeldt, 1953) and the dog (Lorenz, 1954).

Chitty (1960) has proposed that "under appropriate circumstances, indefinite increase in population density is prevented through a deterioration in the quality of the population [and] that the effects of independent events such as weather, become more severe as numbers rise and quality falls." He has related changes in survival, reproductive success, and body weight to phases in the population cycle in voles (Chitty, 1952; Chitty and Chitty, 1962). Krebs (1964), working on lemmings, reported a shortened breeding season, failure of juveniles to mature, and increased body weights of adults when numbers were greatest. He suggested that the changes in numbers could be related to changes in aggressive behavior. Sadleir (1965) observed that deer mice were more aggressive during the breeding season than in the fall,

and that the level of aggressiveness in field populations was greater at times of decreased survival. Healey (1966) found that juvenile survival was inversely related to the level of aggressiveness of the adults. McCabe and Blanchard (1950, p. 97) suggested that "the key to survival [of juveniles] lay in successful establishment elsewhere, not in intolerance or competition near the nests, "but once a juvenile had left its nest it would be driven away from any refuge already occupied.

According to these ideas, the poor reproductive performance observed in this study would be interpreted as a change in the quality of the populations, perhaps reflecting the level of aggressiveness, and as a symptom of living in an unfavorable environment. The greater productivity and maturation of the young observed in 1964 could be associated with higher mean monthly body weights.

Lack (1954) has suggested that changes in survival rather than changes in birth rate regulate population numbers. The reasons given for this point of view are that, in birds, birth rate is not flexible enough to affect population numbers and that fewer young are fledged from clutches of larger than average size. The number of embryos per litter, however, was quite variable (3-7) but no evidence was observed for more embryos dying in larger litters than in smaller ones, or, in the laboratory, for fewer young to be weaned in larger litters. No significant differences between years were found in the average num-

ber of embryos per litter.

That changes in population numbers are adequately accounted for by changes in survival is shown by the differences in reproductive rate and survival of the young in the two years on the experimental area. Numbers at the end of each season were approximately the same. In 1964 reproductive performance was comparatively good but survival of the young was poor; in 1965, the reverse was observed. Differences in reproductive performance were not statistically significant; differences in survival were statistically significant.

Deer mouse populations are self-regulatory, changes in death rate rather than changes in reproductive rate being more important in maintaining the stationary state of these populations. There is some evidence that agonistic behavior is the mechanism tending to space the animals out and eliminating the excess animals from the populations. The suggestion was made that changes in reproductive performance may be associated with changes in the aggressive level of the population.



## VI. SUMMARY

1. The role of changes in reproductive rate and death rate in determining population numbers in the deer mouse, Peromyscus maniculatus, was compared by studying natural and experimental populations on the University Endowment Lands in 1964 and 1965.
2. Weekly live trapping of the populations showed that numbers remained relatively steady over the summer, increased in the fall, and gradually declined over the winter. In two populations numbers did not increase in the fall of 1965. By fall immature animals which overwintered to form the next year's breeding population had replaced most of the adults from the summer breeding population, resulting in an annual overturn of the populations.
3. Males were fecund from March to September in both years. Females bore litters from March to September in 1964 and from March to August in 1965. Few litters were born before May in either year. Seasonal variations in breeding condition were not so marked in the males as they were in the females.
4. Litter size was similar in both years and seemed to be independent of parity, but to be greater in heavier females and to change seasonally.
5. The proportion of ova lost was 0.10 and was relatively constant during the period of study. The rate of loss of young

from birth to age at first capture averaged 0.65 and was greatest during the breeding season, decreasing toward fall. The survival rates of the juveniles and the adults were not statistically different. Survival was significantly lower during the breeding season (0.711) than during the winter (0.832), and significantly lower in the males (0.758) than in the females (0.816). The overall survival rate of the adults was 0.790 per month.

6. Reduction of overwintered populations prior to the breeding season in attempts to induce the populations to have higher reproductive rates were not entirely successful. Although there were no significant differences between the natural and experimental populations in mean monthly body weights, reproductive performance, or survival, there were differences between the experimental populations in 1964 and 1965. Body weights and reproductive performance were lower, and survival of the young from birth to age at first capture was higher in 1965 than in 1964. The proportion of subadults that became fecund was greatest in this area in 1964.

7. The effects of extrinsic environmental factors on population numbers were examined. The effects of disease, parasites, and predators did not seem to be severe enough to account for the regulation of numbers. Clement weather was associated with the longer breeding season observed in 1964 but variations in weather did not seem to affect mortality. The food supply was assumed to

be adequate although it was not studied; evidence from other studies indicates that an unlimited food supply does not prevent population numbers from declining.

8. Changes in death-rate rather than in birth-rate were more important in regulating population numbers. Wynne-Edwards's concept of group selection and self-limitation of numbers by conveniently decreasing the reproductive rate was rejected on theoretical grounds. Christian's idea that changes in reproductive rate are mainly responsible for regulation was not supported. That changes in population numbers are adequately accounted for by changes in mortality was supported by the data. The suggestion was made that changes in reproductive performance may be associated with changes in the aggressiveness of the population.

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APPENDIX A. Pregnant uteri from dead samples, 1964.

Date female caught	Maternal weight (gm.)	No. corpora lutea		No. embryos		Uterine weight (mg.)	Avg. wt. per embryo (mg.)	Approximate day of pregnancy
		R	L	R	L			
9 May, 1964	14.0	2	2	1*	3	708.4	236.1	13
17 June, 1964	19.0	4	2	4	1	-	-	Recent parturition
29 June, 1964	15.0	2	2	2	2	4893.5	1223.4	21
2 July, 1964	19.0	1	4	1	4	1657.5	331.5	14
2 July, 1964	21.5	3	4	2	4	-	-	Recent parturition
18 July, 1964	20.0	3	3	3	3	180.9	30.2	5
18 July, 1964	21.5	4	1	4	1	1250.5	250.1	13
18 July, 1964	22.0	2	2	2	3	6956.9	1391.4	22
19 July, 1964	22.0	3	2	3	2	187.8	37.6	7
19 July, 1964	20.5	1	3	1	3	98.4	24.6	14
23 July, 1964	17.0	3	1	3	1	83.4	20.8	4
2 Aug., 1964	20.0	3	3	3	3	-	-	Recent parturition
3 Aug., 1964	17.0	4	2	4	1	107.1	21.4	4
3 Aug., 1964	21.0	1	5	1	5	-	-	Recent parturition
8 Aug., 1964	18.0	3	3	3	3	5897.8	983.0	19
14 Aug., 1964	19.0	3	2	0	2	66.4	33.2	4
16 Aug., 1964	21.0	3	3	3	4	11652.4	1665.3	24
16 Aug., 1964	20.5	2	4	2+	4	9528.8	1905.8	25
11 Sept., 1964	17.0	2	4	2	4	143.4	23.9	5
11 Sept., 1964	15.0	2	2	2	1	105.0	35.0	7
12 Sept., 1964	15.5	4	2	1	4	-	-	Recent parturition

R - right, L - left.  
 \* - all embryos dead.  
 + - includes one dead embryo.

APENDIX B. Pregnant uteri from dead samples, 1965.

Date female caught	Maternal weight (gm.)	No. corpora lutea		No. embryos		Uterine weight (mg.)	Avg. wt. per embryo	Approximate day of pregnancy
		R.	L	R.	L			
25 June, 1965	15.5	1	4	1	4	1156.5	231.3	13
25 June, 1965	22.5	1	3	1*	3	-	-	Recent parturition
11 July, 1965	17.0	1	4	1	4	7296.0	1459.2	23
15 July, 1965	18.0	1	5	1	5	287.0	47.8	8
19 July, 1965	17.5	2	2	2	2	3586.6	896.6	18
20 July, 1965	19.0	4	2	5+	0	2495.8	624.0	16
20 July, 1965	19.0	3	1	3	1	118.9	29.7	6
21 July, 1965	17.0	2	4	2	4	147.0	24.5	6
26 July, 1965	21.0	0	5	0	5	116.0	23.2	5
27 July, 1965	12.0	3	2	3	2	40.2	13.4	4
30 July, 1965	17.5	6	0	6	0	597.1	99.5	11
4 Aug., 1965	18.0	2	2	2	2	-	-	Recent parturition

R - right, L - left.

\* - all embryos dead.

+ - includes one dead embryo.

APPENDIX C. Pregnant uteri of known age from colony.

Date female autopsied	Maternal weight (gm.)	No. corpora lutea		No. embryos		Uterine weight (mg.)	Avg. wt. per embryo (mg.)	Known day of pregnancy
		R	L	R	L			
5 Aug., 1965	21.0	0	5	4*	5	2661.6	532.3	15
18 Aug., 1965	22.0	4	2	4	2	772.7	128.8	12
19 Aug., 1965	19.5	3	4	1	3+	636.8	212.3	13
25 Aug., 1965	16.5	4	2	4	2+	457.0	91.4	11
26 Aug., 1965	19.0	5	2	5	2	5049.8	721.4	17
29 Aug., 1965	21.0	2	5	1	4	231.0	46.2	8
21 Feb., 1966	18.0	2	3	2	3	364.6	72.9	10
9 Mar., 1966	19.0	2	3	2	3	214.1	42.8	7
21 Mar., 1966	19.0	1	4	1	4	255.5	51.1	9
14 Apr., 1966	19.0	3	2	3	2	4801.3	960.3	18

R - right, L - left.

\* - all embryos dead.

+ - includes one dead embryo.