DEMOGRAPHIC CHANGES IN FLUCTUATING POPULATIONS OF *MICROTUS CALIFORNICUS*[1]

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INTRODUCTION

Periodic fluctuations are common among the small mammals of the temperate and arctic regions. There is no agreement yet on the cause of these fluctuations. There is little detailed information on the demographic changes found in fluctuating populations, nor are there sufficient comparative data from different species to show the range of variation found in these 3-4 year cycles. Consequently we often attempt to explain these cycles without knowing the basic details of the demographic changes in birth, death, and growth rates which accompany them.

The purpose of this paper is to illustrate the demographic changes which accompany population fluctuations in the California vole, *Microtus californicus*. I hope to demonstrate that there is a specific set of demographic changes which accompanies population fluctuations in this species, in the same way that there is a specific set of symptoms which characterize a pathological disease. This work is part of a continuing program of research into the causes of periodic fluctuations in small mammals, which was begun on the lemming cycle in northern Canada (Krebs, 1964). The three objectives of this work were: first, to describe the changes which occur in populations of *Microtus californicus* during a periodic fluctuation; second, to test relevant causal hypotheses by field experiments; and third, to attempt to relate the demographic changes observed to changes in the behavior of voles in the population. Only the first and second aspects will be reported here.

Three experiments were attempted in the course of this work to find the cause of these fluctuations. The first experiment involved cropping an expanding population in an attempt to prevent the normal fluctuation from occurring. The second experiment was the introduction of voles into an area which had just suffered a decline to see if an expanding population could be produced by artificial introduction. The third experiment involved supplementing the food supply of a low population to see if this would stimulate exponential growth; this experiment has been reported elsewhere (Krebs and DeLong, 1965).

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METHODS

This study was carried out in grasslands near Berkeley, California, on the east side of San Francisco Bay. Eight different grids were trapped in three general areas. (1) Tilden Control and Tilden Experimental grids were 300 feet apart in Tilden Regional Park to the northeast of Berkeley. These grids are just south of the area trapped by Pearson (1964) in Tilden Park, and they are part of the area trapped by Hoffman (1958) and Cook (1959). Good photographs of the general area may be found in Brant (1962). (2) The Richmond Parr Field and the Richmond Ford Plant field are adjacent to each other in Richmond, California, and border the Bay, about 8 miles from the Tilden Park grids. (3) The Richmond Field Station (abbreviated RFS) grids (Nos. 3, 4, 5, 6) are nearly adjacent grids on the University of California Richmond Field Station grounds, about 2 miles southeast of the Richmond Parr Field and 6 miles from Tilden Park.

The basic field technique was intensive live trapping with Longworth live traps. The size, trap spacing, and number of traps on the eight areas are given in Table 1. Every attempt was made to use natural boundaries as borders in setting out these areas. The Tilden Park grids were each bordered on two sides by fire trails 8-12 feet wide. The Richmond Parr Field and Ford Plant were bounded by the ocean and a street and warehouse, and the Richmond Field Station areas were all bordered by dirt roads or drainage ditches. Because of these kinds of boundaries the border strips on these grids are of various sizes; where no border occurred, a strip of 25 feet was added in order to calculate the actual area trapped. Traps placed 25 feet off a grid caught very few tagged mice.

TABLE 1. Size of live trapping areas.

Area	Length (feet)	Width (feet)	Area[a] (acres)	Trap Station Spacing (feet)	Total No. of Traps
Richmond Parr Field	240	120	1.00	30x15	130
Tilden Control	300	175	1.73	25x25	200
Tilden Experimental	200	325	1.97	25x25	200
RFS 3	300	150	0.99	25x25	130
RFS 4	300	75	0.69	25x25	88
RFS 5	350	200	1.26	25x25	75
RFS 6	200	150	0.82	25x25	126
Richmond Ford Plant	300	210	1.54	30x15	210

[a]Includes border strips

The area trapped for some of these grids, particularly those at the Richmond Field Station, was subject to slight variations because of disturbances such as bulldozers straightening roads or the addition of terminal pieces to a grid to make trapping more complete. These disturbances were minimal and the areas given in Table 1 apply for most or all of the study period.

Longworth traps were used throughout the study with good success. Crimped feed oats were used for bait and the nest box was supplied with grass. All traps were protected by boards (10 x 12 inches) placed over them. Trapping could only be done overnight during the dry season (June to October) because of the intense heat. Except for a few incidents of heavy mortality during the early part of the 1963 dry season, there was almost no trap mortality. Prebaited traps were left out during the entire study on the Tilden Park grids only. The food bottles present on RFS 6 grid also served to prebait these mice. All live traps were set in runways when possible and the mouth of the trap was baited with oats. One or two (rarely three) traps were placed around each trapping station (stake). Since the object was to catch all the mice in the area and not to obtain a rigid measurement of movements, the trap was placed anywhere within a 10 foot radius of the stake. After each capture the trap was moved to another nearby runway.

Each area was trapped for 2-3 days every two weeks, except for the Ford Plant which was trapped every four weeks during 1964. The usual number of traps set on each area is given in Table 1; occasionally I doubled the number of traps on an area to see if I could increase the catch. I tried to keep the number of traps in excess of the number of mice on each area, but this was impossible for the Tilden Control and Experimental grids, and for the Parr Field and Ford Plant grids when they reached high densities. Every effort was made to catch every mouse present on the area at the time of live trapping. A maximum of 337 individuals was handled on one grid during one trapping period. At very high densities the mice simply filled every single trap as fast as I could handle them, and a complete census was impossible. At low densities other problems arose: some mice repeatedly filled the tunnels of the traps with dirt or grass cuttings and were difficult to trap; and runways became less obvious, which made trapping more difficult.

At first capture each mouse was individually tagged in its right ear with a numbered fingerling fish tag. In addition to its tag number the following data were recorded for each mouse: location on grid, weight, sex, position of testes for the males; for females, vagina perforate or not, nipples small, medium, or large, and public symphysis closed, slightly open, or open. If the mouse was recaptured during the same trapping period, only its tag number and location were recorded. Weights were obtained to the nearest gram using a specially constructed spring

balance. Animals were classified as adults ($\geq$40 g), subadults (26-39 g), or juveniles ($\leq$25 g) on the basis of weight. These data were punched on IBM cards and the entire analysis was done on the IBM 7090 computer at the Berkeley Computer Center. About 21,000 captures were recorded on nearly 7,000 mice during this study.

A limited amount of snap trapping off the live trapping grids was done to get autopsy specimens. Autopsies were also done on some mice removed from the Tilden Experimental area.

WEATHER

The dominating weather pattern of the San Francisco Bay area is Mediterranean with a winter wet season followed by a summer dry season. Almost no rain falls from June to September, and the beginning of the autumn rains is highly variable, with the first heavy rain falling between September and December. Germination of the grassland annuals begins with the first rain of ½ to 1 inch, and the growth of the vegetation ends with dry soil in May or June (Heady, 1958). During the latter part of the dry season there is almost no green material available to the mice, which subsist on seeds, roots, and dry plant matter.

Growth of the vegetation is relatively slow in the fall and winter but increases in the spring (Major, 1963; Pearson, 1964), correlated with the change in temperature.

Table 2 gives the monthly mean temperatures and precipitation for Berkeley during the study period. The first autumn rains came in early October on almost the same date in 1962 and 1963, although the initial rains of October 1962 were considerably heavier than those of 1963. The spring of 1964 was much drier than that of 1963, and there was a considerable shortage of rain from February to April 1964. This resulted in the vegetation drying out about 6 weeks earlier in spring 1964 compared with 1963. The winter of 1962-3 was warmer than that of 1963-4, but the differences are very small in such a mild climate.

TABLE 2. Climatological data for Berkeley, California. Data obtained from U. S. Department of Commerce, Weather Bureau.

Month	Mean Temperature (°F)	Departure from Normal	Total Precipitation (in.)	Departure from Normal
1962				
September	60.0	−3.4	.41	0.19
October	60.0	−1.3	7.05	5.88
November	56.5	0.3	.94	−1.25
December	51.2	0.0	3.50	−0.80
1963				
January	46.9	−2.5	4.84	0.16
February	57.4	5.5	3.10	−0.81
March	52.7	−1.3	3.51	0.32
April	53.7	−2.2	5.97	4.29
May	58.2	−0.1	.53	−0.28
June	60.4	−0.6	.08	−0.10
July	62.6	1.1	.00	−0.01
August	62.3	0.7	.06	0.02
September	65.0	1.6	.10	−0.12
October	60.6	−0.7	1.61	0.44
November	54.5	−1.7	3.38	1.19
December	47.2	−4.0	.60	−0.37
1964				
January	48.2	−1.2	4.96	0.28
February	52.5	0.6	.16	−3.75
March	51.6	−2.4	2.21	−0.98
April	54.5	−1.4	.05	−1.63
May	55.0	−3.3	.32	−0.49
June	60.4	−0.6	.76	0.58
July	61.9	0.4	.00	−0.01
August	62.5	0.9	.01	−0.03
September	63.0	−0.4	.00	−0.22
October	61.7	0.4	1.28	0.11

First autumn rain 1962: October 10-14, 7.02 inches.
Last spring rains 1963: April 25, 0.86 inches; May 7-10, 0.53 in.
First autumn rains 1963: October 9-11, 1.03 inches; October 15-16, 0.45 inches.
Last spring rains 1964: June 8-9, 0.70 inches.

VEGETATION

All the areas trapped were grasslands of the California annual type. This vegetation type has been discussed in detail by Heady (1958), Biswell (1956), and Talbot, Biswell, and Hormay (1939). The California annual type is a mixture of many species of grasses and forbs, and includes many introduced species as well as native ones. Wide variations occur from year to year in these annual grasslands, both in the relative composition and in the amount of forage produced.

The dominant plant species for the live trapping areas are given in Table 3. These data were obtained by a subjective visual assessment of each area. There was considerable variation between grids in the dominant plants. Even the closely adjacent Richmond Field Station grids had somewhat different dominants. RFS 3 and RFS 4 had denser vegetation than RFS 5 and RFS 6, and RFS 3 had the most dense grass cover of these grids. The two Tilden grids were much more similar, but even here there were some clear differences. The Control quadrat had more high cover in the form of *Conium* and *Brassica* than the Experimental. The Parr Field differed from the Ford Plant field strikingly in 1962-3, probably partly because of the high *Microtus* density on the Parr Field. *Picris* and *Cirsium* were very abundant on the Parr Field at this time, and grass density was low compared with the very dense Ford Plant grasses. In the winter of 1963-4 these two areas looked much more alike than they had the previous year.

POPULATION DENSITY

ESTIMATION OF POPULATION SIZE

The intensive live trapping program was aimed at obtaining very accurate information about changes in population density, as well as death and dilution rates, through the use of capture-recapture analysis (Leslie, Chitty, and Chitty, 1953; Jolly, 1965). A basic assumption of this estimation procedure is

TABLE 3. Dominant plant species for the live trapping areas.

Species	Area							
	Tilden Control	Tilden Experimental	RFS 3	RFS 4	RFS 5	RFS 6	Richmond Parr Field	Richmond Ford Plant
Grasses								
Avena fatua	**[a]	**	***	**	**	**	**	**
Bromus mollis	**	**	*	*	*	**	**	*
Bromus rigidus	**	**	**	*	*	*	*	***
Bromus rubens	*	*	*					
Lolium multiflorum	*	*	**	*	*			*
Festuca megalura			*				**	
Cynodon dactylon				**				
Herbs and Shrubs								
Oenothera ovata				*	*	*		
Dipsacus fullonum					*	*		
Conium maculatum	**	*						
Picris echioides	*	*		***			**	
Brassica spp.	**	*	*				*	*
Geranium spp.	*	*	*	*				
Erodium spp.			*	*	*			
Cirsium spp.	*	*					***	
Chloragalum pomeridanum	*	*						
Rumex crispus								***
Plantago lanceolata			*	*	**			
Foeniculum vulgare				**				
Raphanus sativus			***					
Ranunculus californicus						*		
Baccharis pilularis	*	*		*				
Sisyrinchium bellum	*	*				*		
Perideridia Kelloggii	*							
Grass density	**	**	***	**	*	*	*	***
High cover	**	*	**	***			**	**

[a] *** = very abundant; ** = abundant; * = moderately abundant.

that all animals in the trappable population are at equal risk of capture, and consequently that there is no differential trap response between marked and unmarked animals. Leslie *et al.* (1953) have discussed methods of testing this assumption; they found that marked and unmarked *Microtus agrestis* were not captured at random, but that within the marked population itself sampling was satisfactory.

TESTING FOR RANDOMNESS OF CAPTURE:

The assumption of randomness in sampling the *marked* vs. the *unmarked* segments of the population can only be tested in a non-breeding population in which no immigration is occurring. This is essentially a test for the absence of dilution (Leslie *et al.*, 1953). Only two areas were suitable for this type of analysis: Tilden Control between 16 September and 2 December 1963; and RFS 3 between 26 August and 22 November 1963. No young were born and reached trappable age on these grids between these dates. The RFS 3 grid is bounded on all four sides by dirt roads, and the only close source of immigrants was the RFS 4 grid to the west on which the mice were also marked. Consequently immigration can be discounted on this area as a source of dilution. The Tilden Control area was open to the east and south, and immigration could not be discounted here. Spot trapping 25-50 feet from the grid produced almost no marked mice, most of the individuals on the area did not shift their home ranges over the dry season, and it seems unlikely that much emigration or immigration was occurring on this area (see further discussion below).

The distribution of recaptures of males and females was tallied according to the week first marked for these two areas during the period of no dilution. Under the assumption that the death rate is the same in the marked and unmarked segments of the population, I calculated the expected number of marked and unmarked mice in each of the samples (Table 4) and compared these using chi-square. In every case but one the number of marked mice caught exceeded the number expected, and conversely the number of unmarked mice caught was less than that expected. Both males and females show this trapping bias, and it occurred on the prebaited area (Tilden) as well as on the area not prebaited (RFS). There is thus a systematic bias favoring the capture of marked individuals over unmarked, at least under these particular circumstances.

If the marked and unmarked segments of the population are sampled nonrandomly, total population size and dilution rates cannot be estimated validly. Nevertheless, if sampling within the marked population is random, valid inferences may still be

TABLE 4. Tests for the absence of dilution in the non-breeding season for Tilden Control and RFS 3 populations. Expected numbers in parentheses.

TILDEN CONTROL

Sample Week	Males		Females	
	Marked	Unmarked	Marked	Unmarked
46	125(109.1)	46(61.9)	110(103.0)	39(46.0)
48	132(124.4)	42(48.6)	103(95.8)	25(32.2)
50	129(123.7)	28(33.3)	103(95.9)	20(27.1)
52	87(76.2)	8(18.8)	75(72.4)	15(17.6)
54	75(68.7)	10(16.3)	65(57.4)	5(12.6)
56	42(37.4)	4(8.6)	45(40.3)	4(8.7)
chi-square	22.60		15.23	
df	5		5	
P	<.005		<.01, >.005	

RFS 3

Sample Week	Males		Females	
	Marked	Unmarked	Marked	Unmarked
43	31(25.8)	19(24.2)	19(11.4)	21(28.6)
45	43(33.8)	7(16.2)	35(25.3)	14(23.7)
47	37(33.8)	8(11.2)	36(31.3)	13(18.7)
49	33(29.3)	4(7.7)	38(30.8)	5(12.2)
51	20(16.8)	1(4.2)	35(27.2)	2(9.8)
53	17(16.8)	4(4.2)	27(25.1)	7(8.9)
55	16(16.1)	4(3.9)	25(23.5)	6(7.5)
chi-square	16.41		32.89	
df	6		6	
P	<.05, >.01		<.005	

made about death rates, which are estimated only from marked animals. Leslie *et al.* (1953) have discussed one method for testing the marked animals for randomness of capture. Unmarked animals can be ignored at each sampling, and the subpopulation of marked animals can be considered in exactly the same way as the whole population is normally considered. Animals caught only once previously are now considered as new members of this subpopulation of marked animals. Instead of compiling a table of *recaptures* according to the interval since last captured, one compiles a table of *re-recaptures* (Leslie *et al.*, 1953, Table 6). From these data we can calculate a parameter (Z) which estimates the number of animals marked for the first time and released at each trapping. Since we know this parameter from our original data, we can compare the estimates of Z with the true values. Table 5 gives the summation of these data over the entire study period for each of the grids. On only one area (RFS 4) do the observed and estimated values coincide. For the RFS 6 population the observed number is less than the estimated by 22%, but for all the other grids the observed exceeds the estimated by 7-42%. The bias appears to be greater in the males than in the females and may be greater in denser populations (e.g. Parr Field).

The conclusion is that in this particular study random sampling was not achieved either between the marked and unmarked segments of the population or within the marked segment itself. This bias seems to be produced by a segment of the marked population which is too easily caught. This segment need not contain a large number of individuals; in most cases the aberrant behavior of only one or two out of every ten individuals would be enough to produce the observed effects. The result is that neither population size nor death and dilution rates can be estimated for any of these populations by the conventional capture-recapture type of analysis. The low proportion of unmarked animals caught would tend to increase the population estimates, while the too-frequent capture of some marked individuals would tend to decrease the population estimates. Unfortunately we have no assurance that these two sources of bias cancel each other out.

ENUMERATION TECHNIQUE:

The only alternative method of population estimation is direct enumeration. This technique can be used here only because of the intensive live trapping program, which aimed at a total census. The minimum number of mice alive at time t on each area is obtained by summing two counts: (1) the actual number caught at time t; and (2) the number of previously marked individuals caught after time t, but not at that time. For example, 337 *Microtus* were caught on the Tilden Control grid from 3-7 September 1963, and 117 previously marked individuals were caught in late September or October, but were missed in the 3-7 September trapping. These 117 individuals are assumed to have been

TABLE 5. Estimated and observed total number of *Microtus* marked and released for each trapping area, November 1962 to September 1964.

Area	Estimated Number[a]	Observed Number	Percent Difference[b]
Richmond Parr			
Males	339.4	482	42.0
Females	372.2	480	29.0
Combined	686.0	962	40.2
Tilden Control			
Males	894.1	1021	14.2
Females	743.7	833	12.0
Combined	1635.9	1854	13.3
Tilden Experimental			
Males	618.3	751	21.5
Females	769.0	854	9.7
Combined	1396.6	1605	14.9
RFS 3			
Males	114.7	151	31.9
Females	138.3	149	7.2
Combined	250.0	300	20.0
RFS 4			
Combined	84.2	85	1.0
RFS 6			
Combined	366.7	287	-21.7
Richmond Ford Plant (1964)			
Combined	364.5	439	20.4

[a] The parameter Z of Leslie *et al.* (1953).
[b] Percent difference = 100 (observed — estimated) / estimated.

on the area during 3-7 September, and so the minimum number of individuals present at this time is 454.

Unfortunately I have no way of determining the accuracy of these enumerations. I feel that with the present trapping procedure I can enumerate 80-90% of the individuals in populations up to 125-150 per acre. Above this density only about 60-80% of the population could be enumerated. No areas were trapped out to verify these statements. Comparison of the observed number of mice on these areas with the capture-recapture population estimates support these beliefs, but these latter estimates contain an unknown amount of bias so that this argument cannot be relied upon. We are here running up against an ecological form of the Uncertainty Principle—we cannot know the accuracy of our enumerations without destroying the population we wish to follow.

RESULTS

Variations in population density per acre for the various study areas are shown in Fig. 1, and these data are broken down in Tables 6 and 7 for the males and females. The RFS 5 population densities are not plotted because they were so low. These variations in population size will be discussed separately for the three areas studied.

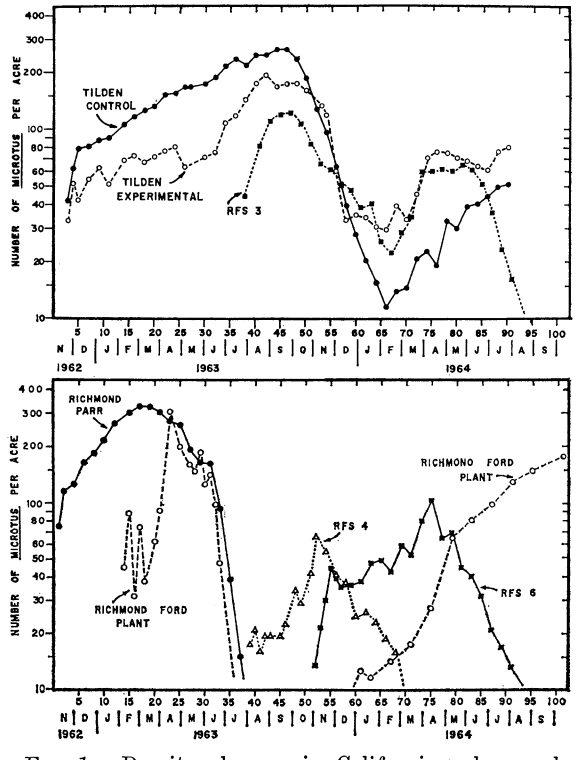

FIG. 1. Density changes in California vole populations on the live-trapping areas. All densities were obtained by direct enumeration and hence are minimum counts, except for the Ford Plant 1963 data which are capture-recapture estimates.

TILDEN PARK:

Microtus had been extremely scarce in this Tilden Park grassland during the summer of 1962; DeLong (pers. comm.) had great difficulty live trapping any mice at this time, and Pearson (pers. comm.) stopped live trapping his area after a catch of zero in March 1962. In early September when I first visited this area the vegetation was all dried out and runways were very sparse. Yet by mid-November when my live trapping began there were over 30-40 mice per acre and many juveniles were already present. The autumn rains began on 9-10 October 1962 and green vegetation appeared only about a week after this. These populations must have increased tremendously in September and October 1962, partly during the dry season when virtually no green vegetation was available for forage.

Two areas were selected for study in Tilden Park. The Tilden Control grid was followed as a natural population with no treatment. The Tilden Experimental area, which lay 300 feet to the south in a continuous grassland cut only by fire trails, was manipulated by intensive cropping of the *Microtus* population. This experiment was designed to test the prediction of Chitty (1960, p. 108) that heavy cropping of an expanding population should retain the population in the phase of increase and prevent the deterioration in survival which occurs in declining populations. All adult mice weighing 40 g or more were removed from this population from 26 November 1962 to 30 November 1963, (Table 8). I hoped to keep this experimental area reasonably free of adult mice in order that juveniles on this area could express their maximum rates of growth, survival, and reproduction. No exceptions were made to this cropping procedure; all pregnant females 40 g or over (weight including embryos) were removed. Animals less than this weight were treated normally and released.

In the Tilden Control population the count showed an initial spurt in late November, 1962, which is partly due to the initial lag in getting the majority of mice on the grid tagged. From early December 1962 to early September 1963 this population increased from 80 per acre to 260 per acre at a nearly constant rate of 3% per week. This regular increase is not found in both sexes however (Tables 6 and 7). Whereas the females seemed to increase regularly from 3 December to 12 July, the males seemed to increase from 3 December to 5 April, then stabilize or even slightly decline until 14 June, and then increase steadily to a peak at 6 September, several weeks after the females.

The Control population remained stationary through September 1963 and then began to decline in early October. This decline continued at a nearly uniform rate of 18% per week for about four months until early February 1964, reducing the population from over 250 per acre to about 11 per acre during this time. The decline appeared to start at the

TABLE 6. Minimum number of male *Microtus* alive on the different areas, November 1962 to October 1964. All densities as number per acre.

Date	Week No.	Richmond Parr	Tilden Control	Tilden Exp.	RFS 3	RFS 4	RFS 5	RFS 6	Richmond Ford
1962									
5-9 November	1	26.0							
12-23 November	2–3	41.0	17.4	14.7					
26 Nov.-7 Dec.	4–5	38.0	27.8	24.3					
10-21 December	6–7	62.0	38.8	27.9					
24 Dec.-4 Jan.	8–9	70.0	43.4	32.4					
1963									
7-18 January	10–11	88.0	42.8	25.9					
21 Jan.-1 Feb.	12–13	111.0							
4-15 February	14–15	125.0	47.5	28.4					25.6[a]
18 Feb.-1 March	16–17	140.0	52.1	29.9					26.6
4-15 March	18–19	129.0	57.3	34.0					19.8
18-29 March	20–21	130.0	62.5	34.5					80.0
1-12 April	22–23	125.0	65.4	37.0					121.5
15-26 April	24–25	111.0	64.8	38.0					118.3
29 April-10 May	26–27	76.0	70.1	23.8					31.0
13-24 May	28–29	66.0							53.0
27 May-7 June	30–31	64.0	60.8	26.9					37.2
10-21 June	32–33	34.0	67.2	26.3					36.7
24 June-5 July	34–35	16.0	82.2	42.6					
8-19 July	36–37	5.0	104.2	49.7					
22 July-2 Aug.	38–39	2.0	106.0	69.0	23.6	4.8			
5-16 August	40–41		123.9	89.2	50.5	6.5			
19-30 August	42–43		126.8	99.4	62.4	4.8			
2-13 September	44–45		138.4	83.1	63.5	4.8			
16-27 September	46–47		140.1	86.7	60.2	6.5			
30 Sept.-11 Oct.	48–49		128.5	81.1	50.5	12.9			
14-25 October	50–51		103.6	75.5	34.3	16.1		1.7	1.9
28 Oct.-8 Nov.	52–53		65.4	57.3	26.4	25.8		6.6	1.3
11-22 November	54–55		52.2	51.2	25.4	16.1		18.2	1.9
25 Nov.-6 Dec.	56–57		31.9	20.3	26.4	15.9		15.9	
9-20 December	58–59		17.4	10.7	23.3	14.5		13.4	1.9
23 Dec.-3 Jan.	60–61		12.8	11.7	22.3	8.7	1.2	15.9	6.5[b]
1964									
6-17 January	62–63		11.0	10.7	24.3	11.6	5.0	22.0	6.5
20-31 January	64–65		8.1	9.1	12.3	10.1	3.2	22.0	
3-14 February	66–67		5.2	8.6	8.1	8.7	0.8	19.5	7.1
17-28 February	68–69		7.5	13.7	9.1	7.2	2.4	26.8	
2-13 March	70–71		7.0	11.7	15.2	2.9	0.8	18.3	9.8
16-27 March	72–73		10.4	15.7	31.4	5.8	4.0	26.8	
30 Mar.-10 April	74–75		12.2	29.4	28.4	2.9	4.0	47.6	12.3
13-24 April	76–77		7.5	26.9	29.4	1.4	7.9	29.3	
27 April-8 May	78–79		13.9	24.4	25.4	2.9	7.9	34.2	26.6
11-22 May	80–81		13.3	23.8	26.4	4.3	6.3	25.6	
25 May-5 June	82–83		21.4	22.3	26.4	5.8	4.0	23.2	32.5
8-19 June	84–85		19.7	21.8	16.2	2.9	0.8	18.3	
22 June-3 July	86–87		18.5	21.8	13.2			9.8	36.4
6-17 July	88–89		20.3	32.0	10.1	2.9		8.5	
20-31 July	90–91		24.4	36.0	6.1			4.9	46.8
17-28 August	94–95								57.1
31 Aug.-11 Sept.	96–97							4.9	
14-25 September	98–99							2.4	
12-23 October	102–103								82.5

[a]Densities for Richmond Ford Plant for weeks 14-33 are capture-recapture estimates rather than minimum numbers.
[b]Beginning of Richmond Ford Plant introduction experiment.

same time in males and females and to proceed at the same rate in both sexes. The fall rains began on 10 October 1963 and the vegetation began growing within one or two weeks. Thus a major part of this decline occurred in the presence of green vegetation.

In mid-February 1964 new recruits began entering the Control population and it increased from mid-February to late August somewhat irregularly but at an average rate of 7% per week, a higher rate of population growth than had occurred the previous year. Males and females did not appear to increase at different rates or at different times. By late July this population had reached a density of about 50 per acre and was leveling off since recruitment was at an end.

The Tilden Experimental population began at the

TABLE 7. Minimum number of female *Microtus* alive on the different areas, November 1962 to October 1964. All densities as number per acre.

Date	Week No.	Richmond Parr	Tilden Control	Tilden Exp.	RFS 3	RFS 4	RFS 5	RFS 6	Richmond Ford
1962									
5-9 November	1	49.0							
12-23 November	2–3	73.0	24.9	18.2					
26 Nov.-7 Dec.	4–5	89.0	40.0	21.8					
10-21 December	6–7	101.0	42.8	26.4					
24 Dec.-4 Jan.	8–9	114.0	44.0	30.9					
1963									
7-18 January	10–11	129.0	46.9	25.3					
21 Jan.-1 Feb.	12–13	154.0							
4-15 February	14–15	176.0	59.6	40.0					20.9[a]
18 Feb.-1 Mar.	16–17	183.0	65.4	42.6					43.8
4-15 March	18–19	195.0	69.5	33.0					27.1
18-29 March	20–21	172.0	68.3	37.0					63.7
1-12 April	22–23	145.0	85.7	40.0					138.0
15-26 April	24–25	150.0	88.0	42.1					104.7
29 Apr.-10 May	26–27	116.0	96.1	39.5					127.1
13-24 May	28–29	99.0							98.3
27 May-7 June	30–31	98.0	110.6	44.6					89.3
10-21 June	32–33	59.0	120.4	49.2					31.1
24 June-5 July	34–35	23.0	132.0	65.4					
8-19 July	36–37	10.0	128.0	68.4					
22 July-2 Aug.	38–39	6.0	111.7	73.0	20.4	12.9			
5-16 August	40–41		119.9	84.2	31.2	14.5			
19-30 August	42–43		119.9	92.3	47.3	14.5			
2-13 September	44–45		124.5	84.7	55.9	14.5			
16-27 Sept.	46–47		122.7	85.7	60.1	16.1			
30 Sept.-11 Oct.	48–49		104.2	92.3	57.0	21.0			
14-25 October	50–51		82.8	83.7	49.0	25.8		3.3	0.7
28 Oct.-8 Nov.	52–53		62.5	75.5	39.5	40.3		14.9	0.7
11-22 November	54–55		43.5	67.9	35.5	38.7		26.5	1.3
25 Nov.-6 Dec.	56–57		31.3	39.6	28.4	24.6		19.5	
9-20 Dec.	58–59		22.0	22.3	24.3	23.1		23.2	1.3
23 Dec.-3 Jan.	60–61		15.1	23.8	16.2	15.9	2.5	22.0	5.9[b]
1964									
6-17 January	62–63		9.3	23.4	16.2	14.5	2.5	25.6	5.2
20-31 January	64–65		7.5	21.3	13.2	13.0	2.4	26.8	
3-14 February	66–67		6.4	20.8	14.2	10.1	0.8	23.2	7.1
17-28 February	68–69		6.4	25.8	19.3	8.7	1.6	31.7	
2-13 March	70–71		7.5	21.8	19.3	5.8	2.4	34.2	7.8
16-27 March	72–73		10.4	30.0	28.4	2.9	4.8	52.5	
30 Mar.-10 Apr.	74–75		10.4	41.6	31.4	5.8	7.9	53.7	15.0
13-24 April	76–77		11.6	49.2	32.4	4.3	11.9	35.4	
27 Apr.-8 May	78–79		19.1	50.2	34.5	8.7	7.1	35.4	38.3
11-22 May	80–81		16.8	46.2	38.5	5.8	6.3	19.5	
25 May-5 June	82–83		18.0	45.6	34.5	2.9	0.0	17.1	48.8
8-19 June	84–85		20.9	42.6	35.5	1.4	0.8	13.4	
22 June-3 July	86–87		26.1	39.1	23.3			11.0	61.7
6-17 July	88–89		29.6	44.1	13.2	1.4		8.5	
20-31 July	90–91		27.2	43.7	10.1			8.5	82.5
17-28 August	94–95								90.4
31 Aug.-11 Sept.	96–97				4.1			7.3	
14-25 September	98–99							2.4	
28 Sept.-9 Oct.	100–101				3.0				
12-23 October	102–103								93.6

[a]Densities for Richmond Ford Plant for weeks 14-33 are capture-recapture estimates rather than minimum numbers.
[b]Beginning of Richmond Ford Plant introduction experiment.

same density as the Control but was cropped intensively after the first trapping. I was unable to hold this population down by intensive cropping. A very high immigration rate, particularly of adult mice, more than offset the cropping. For example, 107 adults were removed from this two acre field between 1-5 April 1963, and two weeks later 115 adults were caught, only 20 of which were tagged residents. A total of 1758 *Microtus* were removed from this field between November 1962 and November 1963. In spite of all this removal the Experimental population continued to increase irregularly at a rate only slightly less than the Control. Unfortunately the field could not be fenced to prevent this immigration.

In early June 1963 individual growth rates began

TABLE 8. Number of *Microtus* caught and number removed from Tilden Experimental grid during the cropping experiment, November 1962 to November 1963.

Date	Week No.	Males		Females	
		No. Caught	No. Removed	No. Caught	No. Removed
1962					
19-23 Nov.	3	35	0	45	0
26-30 Nov.	4	54	25	61	28
3-7 December	5	37	14	36	18
17-21 Dec.	7	54	26	50	18
1963					
1-4 January	9	64	48	54	20
14-18 Jan.	11	49	37	43	18
4-8 February	14	52	45	73	43
18-22 Feb.	16	58	47	77	58
4-8 March	18	66	54	60	38
18-22 March	20	65	49	68	44
1-5 April	22	70	62	73	45
15-19 April	24	73	64	75	51
1-3 May	26	42	34	67	48
27-31 May	30	51	41	74	52
10-15 June	32	48	35	85	54
26-28 June	34	81	35	108	52
10-13 July	36	74	37	104	48
22-27 July	38	107	51	111	38
5-10 August	40	134	62	122	27
19-24 August	42	154	54	119	21
3-7 Sept.	44	113	25	94	13
16-21 Sept.	46	124	18	106	3
30 Sept.-5 Oct.	48	113	12	129	2
14-19 Oct.	50	118	20	115	3
4-6 Nov.	53	88	7	114	2
11-16 Nov.	54	87	52[a]	107	23[a]
25-30 Nov.	56	34	13[a]	61	24[a]
9-13 Dec.	58	12	0[b]	25	0[b]
Total Removed:			967		791

[a]All mice above 34 g removed; normally only mice above 39 g were removed.
[b]Cropping experiment terminated, no mice being removed from week 58 on.

to taper off (see below) and mice began accumulating in the 30-35 g weight group in which they pass the unfavorable dry season. This accumulation both of immigrant and resident small mice caused a great increase in the Experimental population between early June and late August. The enumeration procedure on the Experimental area was not as efficient as on the Control because of the larger area covered, and I think that both these areas reached very similar densities at their peaks in late August 1963. The capture-recapture estimates for 19-23 August are 329.3 per acre for the Control and 330.9 per acre for the Experimental (these are probably underestimates; cf. Table 5). I had clearly failed to satisfy the conditions necessary to test Chitty's prediction, since not only did I finish the 1962-3 breeding season with a very high density but also a majority of the individuals on the Experimental area where immigrants from the surrounding area which was presumably undergoing a normal fluctuation like the Control.

The Experimental population began to decline in early October like the Control. Most of the mice present at this time were below the cropping weight of 40 g; for this reason the removal rate had decreased greatly since early September. On 11 November 1963 I decided to lower the cropping weight to 35 g so that more animals could be removed. Between 11-16 November 75 mice were removed from the Experimental, and 37 more were removed between 25-30 November. The cropping experiment was then terminated to avoid driving the population to extinction. The large decline in the Experimental population between mid-November and mid-December, which superficially resembles the decline of the Control, is really quite different since it was caused in part by cropping. Between 30 September and 11 November the Experimental population declined at an average rate of 4% per week (whereas the Control declined at 18% per week), and between 11 November and 9 December at 16% per week when correction is made for the removals. The early part of this decline then was very much sharper in the Control population than in the Experimental.

After 9 December 1963 the Experimental population was followed without any more removals to see what effect, if any, the cropping had on this population. The population stopped declining in mid-December 1963 at the same time that cropping was stopped. It slowly fell to a low point of about 30 per acre in early February, reaching this low point at the same time as the Control. From late November 1963 until the end of the study females on the Experimental grid outnumbered males by about two to one.

Recruitment of new juveniles into the Experimental population began in mid-February 1964. The population increased in late February, fell back in early March, and then in a matter of four weeks in March it more than doubled in size to about 75 per acre, about three times the density of the Control at that time. The Experimental population remained at a plateau in April and began slowly declining in May and June, rising sharply in July at the end of the breeding season to a final level of 80 per acre. Both males and females showed these responses simultaneously, except for the terminal July increase which was confined almost entirely to the males.

The Control population thus showed marked divergence from the Experimental after the 1963 peak in numbers. The autumn decline was more prolonged on the Control than on the Experimental, and during the 1964 breeding season the Control showed sustained increase from February to July, whereas the more dense Experimental population increased only a short time in February and March and then remained at a plateau from April to July.

RICHMOND PARR FIELD AND FORD PLANT:

Microtus were already abundant on the Parr Field when I began live trapping in early November 1962. Unfortunately I know little about the previous history of this area. DeLong (pers. comm.) found very few runways on this field in August 1962. Part of the Parr Field had been trapped by

K. T. DeLong on 19-20 October 1962 and he noted the presence of large breeding adult *Microtus,* only 10 days after the autumn rains began. There were already large numbers of young mice in the 5-9 November sample, and again it appears that this population began to increase during the dry season.

From a density of about 100 per acre in November 1962 the Parr Field population increased rapidly to a peak of at least 325 per acre in early March 1963. The capture-recapture estimate for this peak was 464.9 per acre, and again this was probably an underestimate (Table 5). This was the highest density observed during this study. The four month increase in minimum numbers from November to March averaged 7% per week, which is the highest sustained rate of increase I have observed in a dense *Microtus californicus* population. At the time of this peak density mice could be seen readily during the daytime, about 10-15 individuals per 2 minutes of watching. The vegetation was heavily foraged and the ground was riddled with holes.

After a brief plateau in March 1963 the Parr Field population began declining and had become extinct on the live trapping area by early August. This decline was gradual and somewhat irregular from March to early June, averaging 6% per week, and then accelerated greatly during June and July to about 40% per week. This area was bulldozed in mid-August 1963 to make way for a new warehouse and so it could not be followed any longer.

The Ford Plant grid began 50 feet to the south of the Parr Field grid. The only barrier to movement between these areas was a gravel road which was overgrown with grass, and a strip of large gravel, 25 feet wide, which was overgrown with grass but presented no burrowing sites for mice. Visual inspection of this field in November and December 1962 showed a very low *Microtus* density; runways were almost impossible to find. K. T. DeLong began trapping this area in January 1963 as part of a house mouse study; he has kindly supplied me with his *Microtus* data for this area for January to July 1963. Since he made no attempt to catch all the *Microtus* on this area, I have been forced to use capture-recapture methods (Jolly, 1965) to estimate population size. These results are only crude estimates of the changes in this population, but they allow us to establish several important points.

The Ford Plant *Microtus* population was about 40-70 per acre in February and March 1963. It was very difficult to believe that these two densities could exist side by side, separated only by a strip of overgrown gravel, with one population over 300 per acre and the other about 60 per acre (cf. a similar situation in *Microtus arvalis* illustrated by van Wijngaarden, 1960, Fig. 8). The vegetation was very dense on the Ford Plant area at this time, whereas cover and forage were heavily exploited on the Parr Field. It was quite difficult to find a runway on the Ford Plant area in which a live trap could be set at this time, whereas it was difficult to find a square foot of ground on the Parr Field which did not have a runway through it.

In March and April the Ford Plant population increased greatly to approximately 200 per acre at the same time that the Parr Field reached a peak and began declining. Probably most of this increase was due to immigration from the Parr Field (see below). But during May and June the Ford Plant population seemed to decline in much the same manner as the Parr Field, and by late July it was impossible to catch any *Microtus* on the Ford Plant grid. The mice which colonized the relatively unexploited Ford Plant area seemed to do no better than the parent population on the Parr Field.

Microtus remained very sparse on the Ford Plant area during the last half of 1963. A late August trapping produced one *Microtus,* none was caught in mid September, two were caught in both mid-October and mid-November, and four in mid-December. In December 1963 I decided to use this area for an experimental manipulation. The question asked was whether an expanding population could be produced experimentally on an area by the introduction of a small number of mice taken from a naturally expanding population. This Ford Plant area was particularly suitable for this manipulation since it had just suffered a decline the previous summer and would not be expected to increase greatly for at least two years. Seven pairs of mice were released on this area on 2 January 1964. Two males and two females of these had been removed from the Tilden Experimental population in late 1962 or early 1963 and kept in the laboratory; they were thus over one year old when released. The remaining animals were laboratory-born descendants of parents brought in from the Tilden Park grids in early 1963. Unfortunately we had neither a large enough area nor sufficient manpower to do this experiment properly; we had neither a control area into which no mice were released, nor another experimental area into which mice taken from a *declining* population were introduced. Consequently this must be viewed as a pilot experiment.

The response to this introduction was rapid and striking. The Ford Plant population increased very rapidly from late January 1964 to early May at an average rate of 11% per week. From early May until October it increased at 4% per week. This population continued increasing throughout the entire dry season from July to October in complete contrast to the *Microtus* population on the same area the previous year. The capture-recapture estimate for 24-28 August is 289.5 per acre (probable underestimate).

The pattern of population change in the Parr Field and Ford Plant populations in 1962 and 1963 is in marked contrast to that of the Tilden Park areas. The population decline on these Richmond grids occurred in the spring during the main grow-

ing season of the vegetation and was complete before the dry season set in.

RICHMOND FIELD STATION:

Live trapping at the Richmond Field Station (RFS) was begun in late July 1963 when the Parr Field and Ford Plant populations disappeared. I know nothing about the past history of these populations.

The RFS 3 population was already at a high density when we began work there in July 1963. The apparent large increase in density during August on this area is mostly an artifact caused by the first weeks of live trapping a dense population. In September the population reached a plateau of at least 120 per acre, then from early October to mid-February gradually declined at an average rate of 8% per week.

Recruitment began increasing the RFS 3 population in mid-February 1964 and the pattern of change was very similar to that of the Tilden Experimental population, increasing very abruptly during late February and March and then remaining at a plateau during April, May and early June. In June this population began to decrease very rapidly at a nearly uniform rate of 19% per week, in marked contrast to the Tilden Experimental population. By September 1964 only a few individuals remained on the area.

The RFS 4 population was at a low density, 15-20 per acre, when began working this area in August 1963. In mid-September this population suddenly began increasing, and tripled in density in seven weeks during the last part of the dry season. The bulk of this increase consisted of 35 adult immigrants. Where these immigrants came from is not known; only two were marked individuals from RFS 3 even though this area seemed to be the only local source of such large numbers of mice. This population reached a peak of 60-70 per acre in late October, and just as abruptly began declining when the vegetation began to grow. This decline continued for six months from November to April at a more or less regular rate of 9% per week. The population recovered slightly in late April and early May by the influx of eight marked immigrants from RFS 6, but then continued its decline to a very low density by July.

The RFS 5 population was sparse in August 1963 when this area was first trapped. Although the area was trapped regularly from August to December scarcely any *Microtus* were caught (maximum of two in any one trapping). The population increased to about 5 per acre in January and February, then increased during March and April to a peak of 15-20 per acre in late April. It then declined during May and June at a rapid rate so that by the end of June only one *Microtus* could be caught on the area.

The population changes in the RFS 6 population have been discussed in detail elsewhere (Krebs and DeLong, 1965). This population was supplied with supplemental food in the form of oats from 21 October 1963 onward, and in addition the vegetation on the north half of the grid was fertilized on 14 January 1964 with 8N/10P fertilizer at 400 pounds per acre. The initial increase in November is largely due to immigration from the RFS 4 grid. From December to February only slight population growth occurred, but the population rose abruptly in March to a peak in early April around 100 per acre. It then declined rapidly through the rest of the spring and summer, dropping about 13% per week, to a very low density in September 1964. The pattern of population change on this area strongly resembles that found on the RFS 4 area five months earlier.

Every one of the four areas live trapped on the Richmond Field Station showed a different sequence of population changes. The only attribute they shared was in all being at a very low density at the end of the study period.

REPRODUCTION

Reproduction can only be measured indirectly in a live trapping program and this restricts one's interpretation of the results. The characteristics of the external reproductive structures are not always assessed unambiguously and there is some overlap in all the classifications. Nevertheless substantial changes in reproductive rates should show up clearly in the condition of these external indicators, and I shall concentrate here only on major reproductive changes.

LENGTH OF BREEDING SEASON

Breeding was already in full progress when work began on the Parr Field and Tilden Park grids in November 1962. Consequently we cannot pinpoint the start of breeding on these areas except to remark that breeding must have begun several weeks before the autumn rains, which began on 9 October, since young mice 4-6 weeks old were already present on these areas in November.

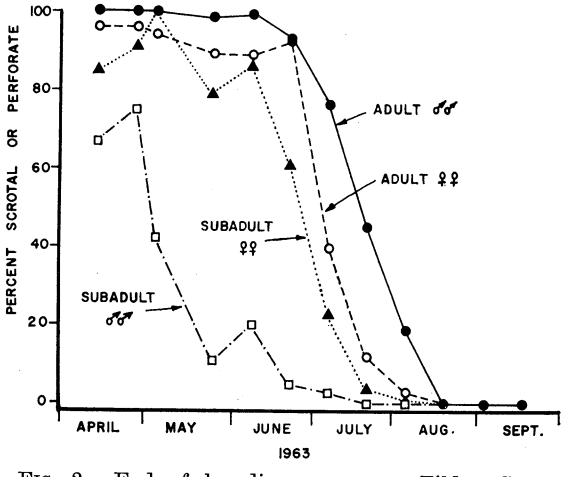

FIG. 2. End of breeding season on Tilden Control area in 1963. Subadults (26-39 g) stopped breeding earlier than adults (≧ 40 g), particularly in males.

The end of the breeding season varies with the age-group considered (Fig. 2), at least in the males. The subadult males (26-39 g group) went out of breeding condition about 6-12 weeks ahead of the adult males. This difference between subadults and adults was slight in the females.

The end of the 1962-3 breeding season was simultaneous in the males from the Parr Field, Tilden Control, and Tilden Experimental areas. The subadult males stopped breeding in May and June and the adults in July. In the females there appear to be slight differences between the Richmond Parr Field which stopped in early July, the Tilden Control which stopped in mid-July, and the Tilden Experimental which stopped in early August. These slight differences appear in both subadult and adult females.

There was considerable variation in the onset of the 1963-4 breeding season both among sex and age groups and among different areas. Males on the Tilden Control area responded to the mid-October rains by beinning to breed in early November (Fig. 3), but on the adjacent Tilden Experimental area males did not begin breeding until late December. Little difference occurred between the females on these Tilden areas; both began breeding in numbers only in late December. The Richmond Field Station grids behaved differently. On RFS 3 and RFS 6 intensive breeding began in both males and females in early November, three to four weeks after the first rains. There was a small amount of breeding throughout August and September on RFS 3. RFS 4 was unique in having continuous breeding throughout the dry season from August to October, although only a few individuals were involved.

The onset of the effective breeding season can also be measured by the date the first juveniles appear in the live traps. On RFS 3, RFS 4, and RFS 6 this occurred from 11-22 November 1963, whereas on the two Tilden grids it occurred on 17-21 February 1964. If we allow six weeks from conception to reaching trappable size, then some females on the Richmond Field Station must have conceived just at or shortly after the first October rains, while Tilden Park females did not conceive until early January, some 13 weeks after the first autumn rains. The August and September breeding activity on RFS 4 apparently did not produce any recruits to this population.

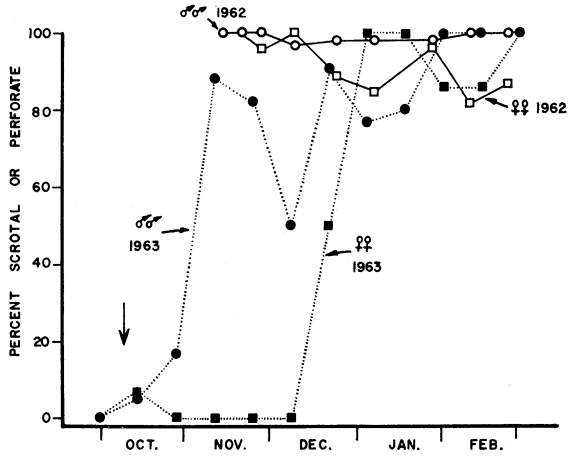

FIG. 3. Beginning of breeding season on Tilden Control in fall 1962 and 1963. Note the delayed onset of breeding particularly in females during the 1963 decline. Breeding must have begun at least six weeks before the first 1962 observations were made. Vertical arrow marks the onset of autumn rains in both years.

The end of the 1963-4 breeding season was also variable. On the two Tilden Park grids there was still a considerable amount of breeding going on at the end of the study in late July, but breeding was definitely falling off. Subadults males on these areas seemed to stop breeding in late June. Breeding definitely stopped earlier on the Richmond Field Station areas: on RFS 3 and RFS 6 breeding had stopped almost entirely by late June, at least 4-6 weeks ahead of Tilden Park. Subadult males on these Richmond areas stopped breeding in May or early June. In contrast the Richmond Ford Plant population, which was rapidly expanding, did not finish the main breeding season until late July, similar to Tilden Park.

There are thus large differences in the onset and cessation of the breeding season in the California vole. The Tilden populations which had begun breeding in the dry season in 1962 did not start breeding until late December 1963, some ten weeks after the first autumn rains. The breeding season seemed to stop slightly earlier in populations which were declining (Parr Field, 1963; RFS 3 and RFS 6, 1964) than in increasing populations (Tilden, 1963; Ford Plant, 1964).

INTENSITY OF BREEDING

The intensity of breeding on an area can be measured indirectly by various external sexual characteristics. I shall assume here that large changes in these reproductive measures are an indication of significant changes in either litter size, pregnancy rate, prenatal mortality, or age at sexual maturity. Any conclusions from these indirect measures must be made subject to a later direct test by autopsy methods.

In the California vole breeding begins each fall or winter, quickly reaches a plateau, and remains there until the following spring or summer when it falls off very rapidly. To estimate the average level or intensity of this plateau I have summed all the separate weekly observations over the entire breeding season. The same time limits were used for all grids to avoid possible seasonal effects; this means that some data must be discarded because voles on one area were still breeding while they had stopped on others (e.g. Tilden areas, July 1964). Only on one area (Parr Field, see below) could any definite trend be detected during this period. Extreme variability occurred on some areas with small samples,

TABLE 9. Intensity of breeding as measured by external characters for all populations, 1962-4. Data are summed from the entire breeding season to obtain these estimates. Sample size in parentheses. Expanding and peak populations in bold-face type.

Group	Richmond Parr		Tilden	Tilden	RFS 3	RFS 4	RFS 5	RFS 6	Richmond Ford Plant
	Increase[a]	Decrease	Control	Exp.					
Breeding Season 1962-3									
Testes Scrotal									
Adult Males	**98%** (405)	92% (309)	**98%** (960)	**98%** (624)					
Subadult Males	**59%** (119)	27% (183)	**68%** (190)	**85%** (162)					
Juvenile Males	**9%** (45)	0% (76)	**17%** (65)	**26%** (42)					
Vagina Perforate									
Adult Females	**87%** (645)	79% (487)	**92%** (1216)	**93%** (608)					
Subadult Females	**75%** (184)	58% (278)	**78%** (396)	**84%** (354)					
Juvenile Females	**51%** (71)	28% (100)	**37%** (87)	**61%** (87)					
Nipples Medium to Large Size									
Adult Females	**77%** (637)	73% (494)	**69%** (1216)	**60%** (608)					
Pubic Symphysis Open									
Adult Females	**34%** (461)	32% (494)	**35%** (1216)	**32%** (522)					
Breeding Season 1963-4									
Testes Scrotal									
Adult Males			90% (160)	96% (205)	95% (164)	84% (49)	90% (30)	92% (95)	**97%** (76)
Subadult Males			63% (38)	46% (101)	41% (63)	—	81% (16)	36% (90)	**38%** (21)
Juvenile Males			0% (14)	0% (52)	0% (18)	—	—	0% (45)	—
Vagina Perforate									
Adult Females			79% (119)	82% (385)	67% (132)	77% (31)	81% (16)	86% (132)	**92%** (106)
Subadult Females			72% (104)	72% (285)	44% (114)	69% (13)	46% (26)	54% (81)	**74%** (35)
Juvenile Females			38% (26)	51% (97)	26% (23)	—	—	59% (51)	**69%** (26)
Nipples Medium to Large Size									
Adult Females			42% (118)	49% (384)	52% (141)	32% (25)	63% (16)	74% (125)	**64%** (142)
Pubic Symphysis Open									
Adult Females			33% (118)	33% (384)	31% (141)	24% (25)	63% (16)	39% (125)	**32%** (142)

[a]Population increased from 5 November 1962 to 1 March 1963, then decreased from 11 March 1963 to 5 July 1963. These two time periods are analyzed separately

and the summation of the entire data for each breeding season for each area seemed to be a fair estimation of reproductive intensity.

Table 9 gives the various measures of breeding intensity on the eight different study areas. The Parr Field data are divided into two periods, that of population increase until March and that of decrease from March to July, since the reproductive data suggested two different plateaus corresponding to this division.

The position of the testes is an index of the reproductive condition of the males. For the adults the highest percentages of scrotal testes occur in expanding populations (97-98%), while low and declining populations fall somewhat below this (84-96%). The differences involved are rather slight. The highest percentage of subadults with scrotal testes occurred on the Tilden Experimental area in 1962-3. There is again a suggestion that low and declining populations have lower percentages of subadults scrotal, but the Ford Plant and RFS 5 data do not support this conclusion. The juvenile males show quite clear differences: The only juvenile males taken with scrotal testes were on the expanding grids in 1962-3, and the highest percentage occurred on the Tilden Experimental area. The suggestion is that males become mature at lower weights in an expanding population.

Females with a perforate vagina are usually in breeding condition. Adult females in expanding

populations have the highest percentages with perforate vagina (87-93%), compared with low or declining populations (67-86%). The same effect shows up in the subadult females, but in the juvenile females no clear trend can be seen.

The pubic bones of mice separate widely for only a few days before and after parturition (Hall and Newton, 1946), and so the recording of these open pubic symphyses should be a good indication of the frequency of birth in these populations. There was little variation in this reproductive measure either between the different years or among the different populations, except for the small sample estimates of RFS 4 and RFS 5. The suggestion from these data is that the pregnancy rate in adults is relatively constant and independent of density.

The size of the nipples is an index of lactation. The largest change in this reproductive measure occurred in the Tilden grids between 1962-3 and 1963-4. The low proportion of adults with medium to large nipples on these areas in 1963-4 suggests that either the period of lactation was shortened in this year, or that a high mortality of whole litters occurred during early lactation, or that the birth rate was not the same in these two years. Not all declining populations have low lactation rates however, for example, the Parr Field and RFS 6 populations.

The female data are thus to some extent contradictory. I can see no way to reconcile these data, and it is probably pointless to try to read too much into them. The relationship between changes in reproduction and population changes is clearly too complex to be determined from external characteristics. These data suggest some changes in breeding intensity which are probably related to the population changes, and more work is needed to find out exactly what these are.

Two different types of declines can be recognized on the basis of these reproductive data. The declines of the Tilden Control, Tilden Experimental, and RFS 3 populations which occurred in the autumn and winter of 1963-4 were *non-breeding season* declines which reversed themselves once breeding resumed. On the other hand, the declines of the Parr Field and Ford Plant populations in the spring and summer 1963, the RFS 4 decline in the winter of 1963-4, and the RFS 3 and RFS 6 declines of spring and summer 1964 were all *breeding season* declines, which began during the height of the breeding season and usually terminated in the early part of the non-breeding season.

To summarize these reproductive effects, major differences occur in the time of onset of autumn breeding. Rapidly increasing populations seem to begin breeding even before the first autumn rains, while other populations may delay as long as ten weeks after the first rains. Differences in the intensity of breeding are significant but not clarified. Changes in the weight at sexual maturity may be correlated with population differences, at least in the males. Changes in the females are somewhat contradictory and can be clarified only by an intensive autopsy program.

MORTALITY

Mortality rates can be estimated accurately only by an intensive living trapping program. There are some basic limitations to the measurement of mortality in this way. Mortality is equated to disappearance from the trapping area and thus includes emigration losses. Mortality can be estimated directly only for the trappable population, and early juvenile mortality, which may be very critical, must be estimated indirectly. A high recapture rate is necessary for obtaining accurate information on time changes in mortality rates.

There is no simple way of describing the mortality schedule of a population of mice which shows extreme flux in survival from time to time in the different sex and size groups. I have tried to solve this problem in two ways: first, by considering the changes in minimum survival rates for each area separately, with emphasis on the changes in these rates in relation to the population changes, and on variations in survival between the sexes and among weight groups; and second, by grouping the survival data for the entire breeding season or non-breeding season and then comparing the resultant survivorship curves for the different areas. This technique obscures most of the detail of time changes in survival and gives us a broad picture of variations in survival.

Survival rates were measured by direct enumeration of marked animals. These data are usually expressed as minimum survival rates per 28 days (cf. Newson and Chitty, 1962; Krebs, 1964) but I have used a 14 day base here because this was my trapping interval. The true survival rate should never be less than this rate, and its accuracy depends on the frequency of capture of marked individuals. Since the frequency of capture was high in this study, I believe that these minimum survival rates accurately express the mortality patterns in these populations.

An index of early juvenile mortality was calculated for each week by dividing the number of new animals weighing less than 36 g caught in week t by the number of females with medium or large nipples caught in week t-4. This index is an attempt to measure the number of recruits added to the trappable population per lactating female; it is high when the survival of litters before and shortly after weaning is high. Errors are introduced by the death of a female before she has completed weaning her young, by the delay in capturing a new recruit until it is 36 g in weight, and by immigration and emigration of females and young. I will assume that on the average these factors will either cancel out or form a constant source of bias on all the grids.

COMPARISONS WITHIN AREAS

The complete data on minimum survival rates in the eight populations studied are too voluminous to

TABLE 10. Minimum survival rates per 14 days and index of early juvenile survival for the Tilden Control population, 1962-4. Sample sizes in parentheses.

Date	Week	Males			Females			Index of Early Juv. Survival
		Adults	Subadults	Juveniles	Adults	Subadults	Juveniles	
19-23 Nov. 1962	3							
26-30 Nov.	4	.75(15)	.67(11)	1.00(4)	.89(18)	1.00(16)	.77(8)	—
3-7 Dec.	5	.89(17)	.69(18)	.44(3)	1.00(19)	.38(21)	.77(8)	—
17-21 Dec.	7	.83(23)	.67(27)	.75(4)	.88(25)	.86(21)	1.00(10)	0.9(20)
1-4 Jan. 1963	9	.87(30)	.77(22)	.00(1)	.97(31)	.92(24)	1.00(1)	1.7(7)
14-18 Jan.	11	.82(55)	.50(8)	1.00(3)	.89(44)	.86(14)	—	2.3(7)
4-8 Feb.	14	.73(48)	.00(5)	.33(6)	.90(40)	.96(27)	1.00(3)	0.7(31)
18-22 Feb.	16	.79(53)	.40(10)	.67(3)	.88(58)	.79(19)	.00(3)	0.5(38)
4-8 March	18	.66(62)	.50(8)	1.00(1)	.89(73)	.82(17)	1.00(5)	0.5(42)
18-22 March	20	.71(65)	.86(7)	.67(9)	.84(87)	.77(13)	.20(5)	0.5(52)
1-5 April	22	.68(68)	.38(13)	.40(5)	.89(66)	.80(25)	1.00(2)	0.5(85)
15-19 April	24	.56(73)	.40(20)	1.00(5)	.88(84)	.81(36)	.67(9)	0.4(54)
29 Apr.-3 May	26	.78(83)	.42(12)	.50(4)	.95(96)	.90(20)	.75(4)	0.3(71)
6-10 May	27	.61(77)	.07(11)	.11(6)	.87(93)	.65(31)	.00(3)	0.3(77)
27-31 May	30	.88(70)	.30(12)	.63(4)	.94(115)	.81(22)	1.00(4)	0.3(74)
10-14 June	32	.73(62)	.56(9)	.86(7)	.87(116)	.57(14)	1.00(7)	0.5(76)
24-28 June	34	.72(71)	.70(10)	.83(12)	.82(111)	.69(29)	.69(29)	0.7(93)
8-12 July	36	.72(50)	.65(40)	.70(10)	.70(111)	.74(38)	.50(8)	1.1(80)
22-26 July	38	.68(50)	.70(64)	.60(10)	.63(73)	.77(52)	.44(9)	0.7(107)
5-9 August	40	.70(77)	.70(46)	.37(8)	.74(66)	.70(51)	.60(10)	1.5(44)
19-23 August	42		.71(154)			.73(139)		
2-6 Sept.	44		.73(140)			.74(127)		
16-20 Sept.	46		.76(181)			.73(156)		
1-4 October	48		.64(170)			.62(149)		
14-18 October	50		.60(170)			.56(126)		
28-31 October	52		.53(157)			.60(122)		
11-15 Nov.	54		.64(94)			.55(89)		
25-29 Nov.	56		.54(85)			.66(68)		
9-13 Dec.	58	.55(11)	.37(35)	—	1.00(2)	.60(47)	—	—
23-27 Dec.	60	.70(10)	.67(12)	—	.50(2)	.60(30)	—	—
6-10 Jan. 1964	62	.73(11)	.67(6)	—	.00(2)	.58(19)	—	—
20-24 Jan.	64	.69(13)	.75(4)	—	.00(1)	.71(14)	—	—
3-7 February	66	.60(10)	.50(2)	—	1.00(1)	.82(11)	—	—
17-21 Feb.	68	1.00(4)	—	—	.86(7)	1.00(1)	—	3.0(1)
2-6 March	70	.78(9)	.00(1)	.00(2)	.86(7)	.50(2)	1.00(1)	3.5(2)
16-20 March	72	.57(7)	—	.75(4)	1.00(6)	.50(4)	.50(2)	1.8(8)
30 Mar.-3 Apr.	74	.33(9)	.33(3)	.60(5)	.67(3)	.80(5)	.86(7)	1.7(6)
13-17 April	76	.33(9)	.33(9)	.50(2)	1.00(7)	.75(8)	.00(2)	4.0(1)
27-30 April	78	.75(8)	.00(1)	1.00(1)	1.00(8)	.67(6)	—	3.8(4)
11-15 May	80	.64(11)	.50(8)	—	.80(15)	.45(11)	.75(4)	3.5(2)
25-29 May	82	.62(13)	.89(9)	—	.81(16)	.60(10)	—	2.1(8)
8-12 June	84	.65(23)	.43(7)	1.00(5)	.69(13)	1.00(7)	.71(7)	1.4(7)
22-26 June	86	.57(21)	.13(8)	—	.87(15)	.92(13)	—	2.4(5)
6-10 July	88	.94(16)	.33(6)	1.00(2)	.62(13)	.64(11)	1.00(4)	1.6(8)
20-24 July	90	.82(22)	.57(7)	.50(2)	.86(29)	.73(15)	.00(3)	2.3(4)
Mean Rates	3–40	.73	.60	.64	.85	.78	.72	0.6
	40–56		.65			.65		
	56–90	.67	.44	.69	.81	.71	.67	2.2

present here and are deposited in the Library of Congress.* Only the Tilden Control survival data are given to illustrate the types of survival changes which occurred (Table 10).

Three common obserations can be made on these survival data from the Tilden Control. First, during the breeding season females survived better than males almost invariably. Being a female mouse improved one's chances of surviving a given 14 days by about 10-20%. Second, adults usually survived better than subadults and juveniles during the breeding season. Mortality seemed to fall most heavily on the subadult males. Third, during the non-breeding season there was no difference in survival of the two sexes. The animals alive during the non-breeding season were all grouped as subadults since the great majority fell in this weight class. Note that the subadult males *increased* their survival rate during the non-breeding season, while the subadult females *decreased* their survival rate as they entered this unfavorable dry season.

Survival rates in the trappable population were on the whole slightly lower during the 1963-4 breeding season than they were during 1962-3, particularly in the subadult males. The major change in survival between these two years was a 3-4 fold increase in

* For supplementary tabular material order Document 8788 from the *Chief, Photo-duplication Service, Library of Congress, Washington 25, D. C., Auxiliary Publication Project.*

the index of early juvenile survival in 1963-4 over 1962-3. This change by itself accounts for the rapid rate of population increase on this area between February and July 1964 (Fig. 1). This large change in the index of early juvenile survival was not caused by the increased availability of traps to juveniles in the sparse 1964 population. Of the 1193 *Microtus* tagged on this area during the breeding season of 1962-3 17% were first caught as juveniles and 47% as subadults, whereas the comparable figures for 230 mice tagged during 1963-4 are 23% and 41% (homogeneity $\chi^2 = 5.22$, P between .10 and .05). Thus while survival of the trappable population was slightly decreased in the low year of 1963-4, early juvenile survival was much better than it had been in the dense populations of 1962-3.

The most important point to note in these survival data is the difference in mortality changes between sex and age groups. The factor causing increased mortality in 1963-4 on the Tilden Control did not operate uniformly among the age and sex groups. For example, males were surviving very poorly in early April 1962 when females were surviving well. The same type of situation occurred from late May to late June 1964, although this heavy mortality of males apparently did not affect the juvenile males. Some of these mortality changes undoubtedly can be attributed to small sample variations, but this explanation is not adequate in many cases with large samples (e.g. Table 10, adult males from mid-June to early July 1964). The cause of these mortality changes, which recur irregularly throughout these data as well as that for the other areas, is not known.

Comparisons Between Areas

Survivorship data for all *Microtus* for each area were grouped at a common origin and subdivided according to the weight group of the individuals when *first* caught. The resulting survivorship curves obscure time variations in survival when grouped over an entire breeding season, and one obtains an average survivorship curve, for example, for mice first caught as juveniles males on the Parr Field during the 1962-3 breeding season.

These cohort or generation survivorship curves (Merrell, 1947) measure a rather different aspect of mortality from the time-specific survival data I have just discussed. These cohort data attempt to summarize the mortality experience of a group of animals through time. Thus the juvenile males just mentioned are followed as they grow to subadult and adult size. The biological meaning of these average survivorship curves will obviously depend on the amount of variation in survival over the season.

The simplest way of comparing all the resulting survivorship curves is the life-table calculation for expectation of further life at time of first capture (Leslie *et al.*, 1955). The results of these calculations are given in Table 11. No data are available for Tilden Experimental population in 1962-3 because of the cropping experiment. The juvenile data in Table 11 from this area in 1962-3 are based on mice marked at the end of the breeding season.

The Parr Field data are the least satisfactory from a biological point of view because of a very marked change in the expectation of life from the beginning to the end of the 1962-3 breeding season. For example, adult males tagged in November had an expectation of 14.8 ± 1.5 weeks of life, while those tagged in May had only 2.7 ± 0.5 weeks of life expected. This change occurred in all groups, and consequently the average values in Table 11 are not a good indication of the changes which occurred in this population.

The pattern in these survivorship data is best seen by dividing the different populations into *dense* or *expanding* populations and *low* or *declining* populations. The former include Parr Field, Tilden Control and Experimental in 1962-3, and Ford Plant in

TABLE 11. Expectation of further life in weeks (± 1 SE) for cohorts of *Microtus* from all live trapping areas. Animals grouped according to their weight at first capture. Expanding and peak populations in bold-face type.

Area	Year	Males			Females		
		Adults	Subadults	Juveniles	Adults	Subadults	Juveniles
(1) *BREEDING SEASON*:							
Richmond Parr Field	1962–3	6.7±0.5	3.7±0.3	3.2±0.4	9.8±0.6	5.9±0.4	4.8±0.4
Tilden Control	1962–3	**7.8±0.4**	**6.8±0.4**	**8.6±0.9**	**12.5±0.8**	**11.3±0.6**	**12.7±1.3**
	1963–4	5.7±0.7	4.9±0.8	3.6±0.7	7.1±1.1	6.1±0.8	8.6±1.2
Tilden Experimental	1962–3	—	—	**7.5±1.1**	—	—	**10.1±1.0**
	1963–4	5.3±0.7	2.8±0.4	3.5±0.4	4.8±0.7	6.3±0.7	5.5±0.6
RFS 3	1963–4	4.0±0.8	3.6±0.6	4.0±0.9	6.6±1.2	8.1±1.0	6.7±1.3
RFS 4	1963–4	4.5±0.9	—	5.6±1.7	5.5±1.2	4.1±1.1	2.2±0.5
RFS 5	1963–4	2.9±0.5	2.1±0.3	—	1.7±0.4	2.2±0.6	2.7±0.8
RFS 6	1963–4	2.8±0.6	3.9±0.6	4.3±0.5	5.3±0.8	4.4±0.7	4.8±0.6
Richmond Ford Plant	1964	**11.6±1.5**	**9.2±1.2**	**7.7±2.1**	**12.9±1.3**	**10.3±1.3**	**12.3±1.5**
(2) *NON-BREEDING SEASON*:							
Tilden Control	1963		4.5±0.3			5.0±0.3	
Tilden Experimental	1963		7.3±0.5			8.2±0.6	
RFS 3	1963		9.2±1.0			8.1±0.8	

1964. The latter include all the others (all RFS areas and Tilden grids in 1963-4).

Expectation of life is higher in all groups in expanding populations when compared with low or declining populations. The average expectations of life range as follows:

	Dense or Expanding	*Low or Declining Populations*
Adult Males	8-12 weeks	3-6 weeks
Subadult Males	7-9 "	2-5 "
Juvenile Males	7-9 "	3-6 "
Adult Females	12-13 "	2-7 "
Subadult Females	10-11 "	2-8 "
Juvenile Females	10-13 "	2-9 "

There is no overlap in these figures and all groups show the same change. There is apparently some factor causing a general reduction in survival for all sex and age groups of a low or declining population.

Expectation of life could not be calculated for the Tilden Experimental population while cropping was going on intensively in 1962-3, but a comparison of the minimum survival data (not given here) shows that on the average Tilden Experimental mice had minimum survival rates 5-10% above those of the Tilden Control. During the non-breeding season of 1963 the Experimental mice survived significantly better than those on the Control (Table 11). Cropping of this Experimental population during 1962-3 did not have any effect on the average survival of mice on that area in 1963-4. Expectation of life was either the same on these two Tilden areas or slightly less on the Experimental grid. Thus cropping this Tilden population even in the presence of heavy immigration increased survival of juveniles and subadults, but the effect of this cropping disappeared relatively quickly in the 1963-4 breeding season after I stopped removing adults.

Providing supplemental food for the RFS 6 population did not increase the average expectation of life on this grid above that of the adjacent grids at the Richmond Field Station. Nor was survival on this area anywhere near the level found in expanding populations such as the Tilden Control in 1962-3 (Krebs and DeLong, 1965) or the contemporaneous Ford Plant population.

Since most of the areas studied showed low survival in 1963-4, one might be inclined to suggest that this was a general effect of the particular weather of that year, perhaps interacting with the growth of the vegetation (cf. Kalela, 1962). Two observations are contrary to this suggestion. First, the Ford Plant population increased greatly with very high survival during 1964. Since this area is only two miles from the Richmond Field Station, it is unlikely that the weather was different on these two areas in 1964. Second, another area in Tilden Park only one mile south of my live trapping areas was very low in density in spring 1963 but very high in spring 1964 (Krebs, pers. obs.). This out-of-phase population was unfortunately not studied.

Early juvenile survival apparently varies independently of survival in the trappable population (Table 12). Two of the areas having the highest average indices of early juvenile survival were Ford Plant in 1964 and Tilden Control in 1963-4, yet these areas had markedly different survivorship in the trappable population. Conversely, the lowest average index recorded was Tilden Control in 1962-3, when the population was expanding and survival was very good in the trappable population.

Four important points have emerged from this analysis of survival. First, all expanding populations which increased to high densities had high survival rates of the trappable population but did not necessarily have high survival rates for very young juveniles. Second, all low or declining populations had low survival rates in the trappable population but either low or high survival of very young juveniles. Third, survival was very variable from week to week, particularly in sparse populations, and these variations were not consistent among different sex and weight groups. For short periods low populations might show very high survival rates of one or more groups but these high rates were not maintained. Finally, females almost always survived better than males during the breeding season, but during the non-breeding season survival rate was equal in the two sexes.

GROWTH

There are many data on changes in mean body weights or weight distributions of small mammals in relation to periodic fluctuations (e.g. Chitty and Chitty, 1962b; Kalela, 1957), but no data have been published on both the growth rates and body weights of mice in fluctuating populations. High growth rates do not necessarily mean that the population has high mean body weights, nor conversely do low

TABLE 12. Mean index of early juvenile survival for the live trapping areas. The higher this index, the better the survival of weanlings and small juveniles. Dense or expanding populations in bold-face type.

Area	Breeding Season	Mean Index of Early Juvenile Survival	Range[a]
Richmond Parr Field	1962–3 Increase[b]	**0.7**	0.5–1.1
	Decline	0.7	0.3–1.0
Tilden Control	1962–3	**0.6**	0.3–2.3
	1963–4	2.2	1.4–3.8
Tilden Experimental	1963–4	1.4	0.5–2.4
RFS 3	1963–4	1.0	0.2–2.4
RFS 4	1963–4	0.7	0.0–1.0
RFS 5	1963–4	2.8	—
RFS 6	1963–4	1.6	0.3–4.5
Richmond Ford Plant	1963–4	**2.1**	1.0–5.6

[a]Range does not include samples based on one or two females.
[b]Population increased from 5 November 1962 to 1 March 1963, then decreased from 11 March to 5 July 1963.

growth rates mean that the population must have low mean body weights. Rapidly growing animals with a low survival rate may never reach large size because they do not live long enough.

Two aspects of growth will be considered here: first, individual growth rates in body weight; and second, body weight distributions. Body weights were the only convenient and accurate measure of growth that could be obtained from the live trapped animals. Growth rates are expressed as instantaneous relative growth rates (Brody, 1945) in percent increase per day. Only mice caught at two-week or four-week intervals were used to calculate growth rates. Only male data are presented here; the female data show the same changes as the males but have added variability because of unnoticed pregnancies.

Growth rate data for each four week period were condensed by calculating a linear regression between mean body weight and growth rate for each time period. These regressions change in slope as well as elevation seasonally. A single representative growth rate was calculated from each regression by adjusting the growth rate to a hypothetical 35 g mouse. The adjusted mean growth rate for this hypothetical *Microtus* was calculated along with its standard error as described by Snedecor (1956, p. 138). Changes in growth rates seemed to occur simultaneously in all size groups, and these adjusted mean growth rates adequately describe the pattern of growth changes for these populations.

GROWTH RATES

Table 13 gives the adjusted mean growth rates and their standard errors for the eight different trapping areas.

During the 1962-3 breeding season the Tilden Experimental population had growth rates considerably higher than those of the Tilden Control population. From November to early January the Parr Field mice had growth rates as good as or better than those of the Tilden Control animals, but from early January on until the Parr Field population became extinct, growth rates were very poor on this area. These growth rate differences parallel the survival rate differences among these three populations.

Growth rates dropped to zero in summer 1963 during the dry season, but began to rise in late October and November after the first autumn rains. Growth rates, however, remained very low during November and December on both Tilden areas and on the RFS 3 area, in contrast to the high growth rates the previous year on the Tilden and Parr Field grids. The only population with high growth rates during fall 1963 was the RFS 6 population which was supplied with supplemental food. The growth rates in this population from November to April were the highest sustained growth rates found in any population during either year of this study.

In January or February 1964 there was a sudden increase in the growth rates of the Tilden and RFS 3 populations. During March growth rates were high on these areas, and they began tapering off slowly in April, and May, as the vegetation began drying out. Tilden Control growth rates were on the average higher from February to July 1964 than from the same time in 1963. Tilden Experimental growth rates were on the contrary lower during this time period in 1964, compared with 1963, and they were also lower in 1964 than the simultaneous Tilden Control rates.

The very high growth rates of the RFS 6 population decreased in April to about the level of the other grids, and then fell below the other areas during May, June, and July with low growth rates. This complete reversal of growth rates coincided with the population decline on this area. Supplemented food and green grass were present in excess throughout this period of poor growth. The breeding season declines in population size on RFS 4 and RFS 5 also seemed to be accompanied by low growth rates, but this effect does not appear clearly in the RFS 3 decline in summer 1964.

The Ford Plant data suggest that this population had low growth rates during 1964, both low with regard to other grids at the same time and low with regard to other expanding populations. Unfortunately these data were obtained only at four-week intervals, and I suspect that they are underestimating the growth rates of these mice. The majority of mice used in these calculations were large adults, and if there is a slight curvilinear trend in the regression of growth rate on mean body weight, this would produce a low estimate of growth rate for a 35 g mouse. The large interval between initial weight and final weight when animals are caught at a four-week interval also adds a tendency to underestimation in regressions of growth rate on *mean* body weight (cf. Brody, 1945, p. 504). Consequently, I feel that the growth rates for the Ford Plant in Table 13 do not give a true picture. An accurate assessment of growth in animals like these *Microtus* which may grow from juvenile to adult size in four weeks cannot be made by trapping at monthly intervals.

Four points have emerged from this analysis. First, populations which showed breeding-season declines seemed to show lower than average growth rates during these declines (Parr Field, RFS 4, RFS 5, RFS 6). Second, cropping the Tilden Experimental population of adults caused higher than average growth rates. The same type of effect was produced by supplemental food on RFS 6, although the presence of this supplemental food was not enough to prevent growth rates from falling to below average levels when this RFS 6 population declined. Third, low growth rates were associated with a lack of recruitment on the Tilden and RFS 3 areas from November 1963 to February 1964. These low growth rates cannot be explained by lack of breeding, especially on RFS 3. Fourth, when recruitment did resume on the Tilden Control in 1964 growth rates seemed as good as, and possibly even better than,

TABLE 13. Adjusted mean growth rates (± 1 SE) for the eight populations from 1962-4. Data grouped into four week intervals. All growth rates expressed as % per day and are adjusted to a hypothetical 35 g *Microtus*.

Date	Week No	Richmond Parr	Tilden Control	Tilden Experimental	RFS 3	RFS 4	RFS 5	RFS 6	Richmond Ford Plant
1962									
5-16 November	1-2	1.24 ± .26	—	—					
19 Nov.-14 Dec.	3-6	1.37 ± .20	0.97 ± .15	2.55 ± .21					
17 Dec.-11 Jan.	7-10	2.12 ± .20	1.85 ± .17	2.58 ± .27					
1963									
14 Jan.-8 Feb.	11-14	1.43 ± .13	2.93 ± .32	2.32 ± .17					
11 Feb.-8 March	15-18	0.89 ± .12	1.45 ± .15	2.67 ± .31					
11 Mar.-5 Apr.	19-22	0.88 ± .10	2.18 ± .18	2.98 ± .26					
8 Apr.-3 May	23-26	0.77 ± .12	1.34 ± .14	2.88 ± .71					
6 May-31 May	27-30	0.40 ± .13	0.94 ± .16	1.18 ± .38					
3 June-28 June	31-34	—	0.77 ± .11	1.05 ± .28					
1 July-26 July	35-38	—	1.03 ± .08	0.98 ± .09					
29 July-23 Aug.	39-42	—	0.02 ± .06	0.25 ± .10	0.22 ± .09				
26 Aug.-20 Sept.	43-46		−0.18 ± .04	−0.02 ± .07	−0.20 ± .07	0.74 ± .72			
23 Sept.-18 Oct.	47-50		0.17 ± .04	0.22 ± .08	0.15 ± .06	0.09 ±1.18			
21 Oct.-15 Nov.	51-54		0.08 ± .06	0.52 ± .12	0.19 ± .14	1.77 ±1.54			
18 Nov.-13 Dec.	55-58		0.43 ± .12	0.29 ± .22	0.71 ± .19	0.19 ± .30		3.42 ± .37	
16 Dec.-10 Jan.	59-62		0.47 ± .15	0.67 ± .11	0.28 ± .16	0.83 ± .24		2.95 ± .25	
1964									
13 Jan.-7 Feb.	63-66		1.30 ± .50	0.39 ± .19	0.76 ± .13	0.80 ± .67	3.90 ±3.88	3.14 ± .28	0.87 ± .26
10 Feb.-6 March	67-70		4.05 ± .34	3.10 ± .36	0.99 ± .33	0.52 ± .34	—	2.97 ± .24	0.30 ± .26
9 Mar.-3 Apr.	71-74		3.29 ± .34	2.40 ± .17	2.70 ± .32	—	—	3.64 ± .38	1.44 ± .22
6 Apr.-1 May	75-78		1.98 ± .34	1.75 ± .17	1.96 ± .27	—	0.88 ± .16	1.84 ± .19	1.66 ± .42
4 May-29 May	79-82		2.12 ± .22	1.74 ± .15	1.36 ± .23	0.59 ± .24	0.50 ± .24	1.32 ± .20	0.82 ± .21
1 June-26 June	83-86		1.48 ± .19	1.97 ± .21	1.51 ± .29	—	—	0.51 ± .25	0.72 ± .19
29 June-24 July	87-90		1.11 ± .17	1.23 ± .13	0.61 ± .40	—	—	−0.17 ± .66	0.69 ± .13

they were in the expanding 1963 population on this area.

BODY WEIGHT DISTRIBUTIONS

Body weight distributions are a composite produced by many factors, only one of which is growth rates. These distributions have been used extensively in analyzing small mammal populations, principally because they are relatively easy to obtain. The body weight distribution is produced by an interaction of growth rates, mortality rates, and recruitment rates for the trappable population. I shall deal here only with male weights obtained from live trapping; snap trapping samples would probably have other biases in capture.

Table 14 gives the body weight distributions and mean weights for males from all the populations during this study. These data are spaced at 5-6 week intervals and consequently only a portion of the total data for males is included here. It is impossible to distinguish different generations of mice on the basis of weight except for a few weeks at the start of the breeding season.

At the beginning of the study the Parr Field

population had more large males than either of the Tilden populations. This difference continued until January 1963, but began to disappear in February and March so that by early April the Parr Field and Tilden weight distributions were very similar. During May and June these positions were reversed, so that by July the Parr Field population, which was declining rapidly, consisted almost entirely of small juveniles, while the Tilden populations still had many large males. The two expanding Tilden populations did not differ greatly during 1962-3 in spite of the intensive cropping of the Experimental, and the Tilden Control reached the same top-heavy type weight distribution in early June 1963 that the Parr Field had reached in early December 1962.

The large mice gradually disappeared during the dry season and the September weight distributions are very similar on the Tilden areas and RFS 3. The Tilden Experimental population was depressed slightly below the others at this time because of the continual removal of males ≥ 40 g.

In October 1963, just after the first autumn rains, some striking differences began to appear. The RFS 4 population, which unlike all others had apparently been breeding during the dry season, had a few very heavy males, which made the weight distribution resemble in general that found the previous year at the Parr Field. The RFS 3 population began increasing in average weight first in late October, the Tilden Control began next in early December, and the Tilden Experimental population began last in early January.

The RFS 6 population in mid-November 1963 consisted of males larger than those of any of the

TABLE 14. Body weight distributions and mean body weights for male *Microtus* on the live trapping areas, 1962-4. All distribution data given in percentages. All weights in grams.

	12-23 Nov. 1962			3-14 Dec.			7-18 Jan. 1963			11-22 Feb.			18-29 March			22 Apr.-3 May		
Weight Group	RP[a]	TC	TE	RP	TC	TE	RP	TC	TE	RP	TC	TE	RP	TC	TE	RP	TC	TE
10—			9	2		3					1		1	1			1	
14—			6	0		0		5	2	1	0		1	1	2		2	
18—	6		3	0	4	3	1	2	2	2	0		1	0	2		2	
22—	3	13	3	4	4	8	4	3	2	3	0	2	5	3	2	7	2	7
26—	3	7	14	4	18	8	6	0	6	9	1	0	5	7	3	15	1	2
30—	11	27	17	4	7	22	7	3	0	10	1	5	7	3	3	15	4	2
34—	8	3	0	2	20	16	7	3	12	12	6	5	13	3	12	19	6	2
38—	6	0	0	9	13	5	4	5	6	2	4	10	5	6	11	4	5	7
42—	6	13	0	4	9	11	4	7	18	5	15	12	5	6	11	1	10	19
46—	6	10	6	7	18	14	4	14	12	7	7	14	5	8	14	6	13	14
50—	14	20	9	7	5	5	13	32	16	10	14	10	7	8	11	2	11	10
54—	17	3	17	9	2	3	14	17	14	18	26	17	16	21	15	9	20	19
58—	11	3	6	13		0	4	5	6	5	8	10	7	14	6	6	12	10
62—	8		11	15		3	13	3	2	10	10	14	12	9	5	7	8	7
66—	3			19			7			4	4		7	9	5	3	3	
70—				0			4			1	1		2			4	2	
74—				2			3			1			2			1		
78—							1											
N	36	30	35	54	55	37	69	59	49	94	72	58	101	87	65	99	104	42
$\bar{x}$	46.3	39.1	39.9	52.5	37.7	36.9	50.2	47.0	44.6	45.9	51.2	49.6	47.7	49.6	46.3	42.1	48.6	47.4
SE	2.3	2.0	3.0	2.0	1.2	1.7	1.8	1.5	1.5	1.5	1.2	1.3	1.5	1.5	1.4	1.5	1.2	1.6

	27 May-7 June			1-12 July			5-16 Aug.			9-20 Sept.			14-25 October 1963			
Weight Group	RP	TC	TE	RP	TC	TE	TC	TE	RFS 3	TC	TE	RFS 3	TC	TE	RFS 3	RFS 4
10—		1		6	1											
14—		0	2	19	1											
18—		0	2	13	4	1	1	6			2					
22—	14	7	4	25	3	4	1	5		2	3					
26—	2	2	0	6	9	14	3	5	2	8	17	4	4	8		
30—	10	5	4	13	24	16	19	13	13	39	40	42	21	37	23	
34—	10	2	8	0	12	5	10	20	33	14	18	12	26	23	18	
38—	12	2	10	0	16	31	32	29	37	29	14	36	38	25	27	11
42—	17	4	8	6	2	5	11	9	7	5	6	2	8	3	23	0
46—	5	7	2	13	7	9	6	2	2	1	0	0	3	3	5	0
50—	14	9	10		6	5	9	7	2	2	1	4	1		0	0
54—	3	14	24		4	1	2	1	0	1					5	0
58—	5	14	8		9	5	3	1	0							22
62—	3	17	8		1	0	2	1	2							33
66—	0	4	8		0	1	1		0							0
70—	5	9	4		2		1		2							22
74—		2														0
78—																11
N	59	81	51	16	139	74	157	134	46	169	124	50	157	118	22	9
$\bar{x}$	42.8	52.7	49.5	26.0	39.0	38.7	40.8	37.1	39.1	35.1	33.0	36.1	36.7	34.9	39.1	63.1
SE	1.7	1.6	1.9	2.9	1.0	1.1	0.7	0.7	1.1	0.4	0.5	0.8	0.3	0.4	1.3	3.7

Weight Group	18-29 November 1963					23 Dec.-3 January 1964						27 January-7 February					
	TC	TE	RFS3	RFS4	RFS6	TC	TE	RFS 3	RFS 4	RFS 6	FP	TC	TE	RFS 3	RFS 4	RFS 6	FP
10—				10	20												
14—			5	0	10			5									
18—			0	0	0			0		25						18	17
22—		3	5	0	0			5		0						12	0
26—	7	29	0	0	0		5	10		0						6	0
30—	13	38	5	0	10		29	5	20	0			7			12	0
34—	26	18	10	0	0	25	33	19	0	33	28		0	9		6	0
38—	46	12	20	0	0	19	19	19	0	17	14	17	7	45		0	0
42—	2		10	10	0	25	14	10	20	8	0	17	21	18	40	24	0
46—	7		15	10	0	19		14	0	8	14	17	29	18	0	6	17
50—			25	40	0	13		14	40	0	0	17	29	0	0	0	33
54—			5	20	30				0	0	14	17	0	0	40	6	0
58—				0	10				20	8	0	0	7	9	20	6	17
62—				10	0						0	17				6	17
66—					10						28						
70—					0												
74—					10												
N	46	34	20	10	10	16	21	21	5	12	7	6	14	11	5	17	6
$\bar{x}$	37.2	31.7	41.8	48.3	44.2	42.8	35.7	38.6	47.8	35.7	50.3	50.5	46.9	43.6	50.8	36.8	49.2
SE	0.7	0.6	2.3	4.3	7.5	1.3	0.9	2.1	5.0	3.3	6.0	3.4	1.8	2.1	3.2	3.5	6.4

Weight Group	2-13 March 1964					6-17 April 1964					11-22 May 1964				
	TC	TE	RFS 3	RFS 6	FP	TC	TE	RFS 3	RFS 6	FP	TC	TE	RFS 3	RFS 6	FP
10—			7					4	5			2			
14—	9		7	7			2	4	5			0	5		3
18—	18		0	0			2	0	18			2	0		0
22—	9		0	0		9	6	7	5	6		7	5		8
26—	0	10	7	14		0	12	15	11	6	9	12	5	15	16
30—	0	0	0	14	15	0	8	7	11	13	9	12	10	23	3
34—	0	14	14	7	15	9	10	0	11	6	18	12	15	15	5
38—	0	10	0	36	0	0	14	7	11	0	14	9	10	15	3
42—	0	14	14	0	8	9	2	4	8	0	5	14	10	23	5
46—	0	5	7	0	8	0	12	19	8	6	14	12	10	0	8
50—	0	14	7	0	15	27	6	11	3	13	5	7	10	8	8
54—	27	14	7	7	23	18	18	4	0	0	9	5	5		3
58—	18	14	14	7	0	9	6	11	3	19	5	5	0		5
62—	18	0	0	0	0	18	2	4	0	6	9	2	15		14
66—		5	14	0	8			4	3	6	5				8
70—				7	8					13					5
74—										0					3
78—										0					3
82—										6					
N	11	21	14	14	13	11	50	27	38	16	22	43	20	13	37
$\bar{x}$	44.2	46.9	44.4	39.5	49.0	50.6	41.5	41.7	32.2	52.9	44.6	39.2	42.5	37.2	47.5
SE	6.2	2.4	4.8	3.8	3.5	3.5	1.8	3.0	2.1	4.6	2.7	1.7	3.1	2.0	3.0

Weight Group	15-26 June 1964					20-31 July 1964				
	TC	TE	RFS 3	RFS 6	FP	TC	TE	RFS 3	RFS 6	FP
10—		3			2		4			
14—		0			5		1			2
18—		3			5		1			2
22—	8	18			2		7			5
26—	8	15	9		19	5	9			5
30—	4	12	0		12	5	4	17		5
34—	8	6	9	10	9	10	10	0	20	15
38—	13	6	18	40	12	7	16	33	80	22
42—	4	9	27	20	9	10	9	17		8
46—	8	6	18	10	5	19	20	17		8
50—	25	6	0	10	0	26	10	0		7
54—	8	9	9	10	5	7	6	17		7
58—	13	3	0		7	7	3			7
62—		3	9		7	5				7
66—					0					
70—					0					
74—					0					
78—					2					
N	24	33	11	10	43	42	70	6	5	59
$\bar{x}$	44.2	36.4	44.6	43.6	38.8	47.1	39.4	42.8	38.6	42.3
SE	2.4	2.3	3.1	1.8	2.4	1.4	1.4	3.3	1.0	1.5

[a]Abbreviations for areas: RP = Richmond Parr Field; TC = Tilden Control; TE = Tilden Experimental; RFS = Richmond Field Station areas; FP = Richmond Ford Plant.

other areas. There is a close tie-in between the loss of the heavy males on RFS 4 in late October and early November and the appearance of heavy males on RFS 6 at the same time. Between 28 October and 29 November five male *Microtus* (53-70 g) were known to have moved from RFS 4 to RFS 6. These large males disappeared quickly from the RFS 6 population, and throughout the breeding season

TABLE 15. Body weight distributions for *Microtus* removed to laboratory from Tilden Park, 11 November 1963-24 January 1964, and simultaneous weight distributions for mice remaining on the Tilden areas. All distribution data given in percentages.

(1) *MALES*:

Weight Group	11-15 Nov. 1963				25-29 November				9-13 December				23-27 December			
	Lab TC[a]	Lab TE	Field TC	Field TE	Lab TC	Lab TE	Field TC	Field TE	Lab TC	Lab TE	Field TC	Field TE	Lab TC	Lab TE	Field TC	Field TE
10—																
14—																
18—																
22—			1					3								
26—			7	6			7	29				25				5
30—		17	25	31		11	13	38			4	42				29
34—	67	44	41	34		6	26	18		6	4	33			25	33
38—	33	39	21	29		33	46	12		28	65			6	19	19
42—			4			11	2			6	13			17	25	14
46—			1		100	28	7		67	22	9			11	19	
50—						6			33	17	4		33	17	13	
54—						6				17				22		
58—										6			67	17		
62—														0		
66—														11		
70—																
N	3	18	85	87	3	18	46	34	3	18	23	12	3	18	16	21

Weight Group	6-10 Jan. 1964				20-24 January				(2) *FEMALES*: 11-15 Nov. 1963				25-29 November			
	Lab TC	Lab TE	Field TC	Field TE	Lab TC	Lab TE	Field TC	Field TE	Lab TC	Lab TE	Field TC	Field TE	Lab TC	Lab TE	Field TC	Field TE
10—																
14—																
18—																
22—											1	4				3
26—										28	7	29		28	37	66
30—				31				19	100	8	25	38		12	41	30
34—			18	31			8	31		52	41	25		12	10	2
38—		6	18	19		11	17	25		12	21	4		36	12	
42—		17	29	13		11	25	19			4		100	4		
46—		11	12	6		17	33	6			1			8		
50—	33	28	12		33	11	8									
54—		11	12			22	8									
58—		0				0										
62—	67	11			33	6										
66—		11			33	17										
70—		6				6										
N	3	18	17	16	3	18	12	16	1	25	70	107	1	25	49	61

Weight Group	9-13 December				23-27 December				6-10 January 1964				20-24 January			
	Lab TC	Lab TE	Field TC	Field TE	Lab TC	Lab TE	Field TC	Field TE	Lab TC	Lab TE	Field TC	Field TE	Lab TC	Lab TE	Field TC	Field TE
10—																
14—																
18—																
22—				8				13				3				
26—		8	28	48			26	29			7	18				18
30—		8	38	28		20	39	39		16	33	50		12	25	42
34—		24	25	12		8	22	16		8	47	24		12	50	24
38—		28	6	4		20	9	3		16	13	3		20	25	9
42—	100	24	0		100	24	0			28		3		32		6
46—		8	3			12	4		100	16			100	8		
50—						16				16				16		
54—																
N	1	25	32	25	1	25	23	38	1	25	15	38	1	25	12	33

[a] TC = Tilden Control, TE = Tilden Experimental.

1963-4 scarcely any males on RFS 6 exceeded 66 g.

The absence of effective recruitment during December 1963 and January 1964 shows clearly in the body weight distributions for the Tilden areas, RFS 3, and RFS 4, in marked contrast to the heavy representation of juveniles in the RFS 6 samples at this time.

The Tilden Experimental mice stayed consistently below the weights of Tilden Control animals during the breeding season 1963-4. At times a maximum of 63% of the Control males were above 54 g, while 33% was the maximum achieved above this weight by Experimental males. The body weights of both Tilden areas in 1963-4 were consistently below those on the same areas in 1962-3 when these populations were increasing to a peak.

The most striking weight distributions in 1964 were those for the Ford Plant. By April the Ford Plant males had achieved a weight distribution characterized by large animals and clearly distinct from all the other populations. These differences were further accentuated in May and June but began to disappear in July as the dry season progressed. The two largest males recorded in this study were an 85 g male on this area in early April 1964 and an 84 g male on the Parr Field in January 1963.

Peak and expanding populations of *Microtus californicus* thus seem to be characterized by adult males of large body size in much the same manner as other cyclic microtines like *Microtus agrestis* (Chitty and Chitty, 1962b) and lemmings (Krebs, 1964).

GROWTH EXPERIMENT ON TILDEN *Microtus*

From 11-15 November 1963 47 *Microtus* were brought into the laboratory from Tilden Park. Four of these were captured next to the Control grid and the other 43 were animals removed from the Experimental area. These mice were all placed in individual cages and provided with commercial rat pellets, carrots, and water *ad lib*, and occasionally with lettuce or oats. The purpose of this experiment was to compare the growth of animals kept under conditions of isolation and abundant food in the laboratory with that of animals living under field conditions in declining populations. The same type of experiment has been done by Newson and Chitty (1962) on *M. agrestis*.

Table 15 gives the body weight distributions for mice brought into the laboratory and followed at two week intervals from 11 November 1963 to 24 January 1964, and the corresponding weight distributions for mice remaining on the field areas. There was little growth in the field animals over this period of 2½ months. The Tilden Experimental population was cropped of heavier animals until 29 November, hence it has a weight distribution shifted below that of the Control. Some of the Microtus brought into the laboratory in November increased rapidly in weight; others remained stationary or increased slowly, and every range of intermediate between these extremes was found. The results was that for males and females the weight distribution of the laboratory animals spread out, with the minimum staying about at the minimum weight of the field animals while the maximum weight of the laboratory *Microtus* greatly exceeded that of the field animals on either grid. Even after growth began to accelerate in the field during February 1964 none of the males in the field ever reached the maximum weights attained in the laboratory mice by late December.

Some *Microtus* on these Tilden areas must therefore have had a capacity for rapid growth in autumn in 1963, but no rapid growth was observed at this time in the field. There might be two explanations for this: (1) the types of animals which were capable of rapid growth were eliminated selectively in the field populations after mid-November; or (2) the types capable of rapid growth remained in these populations throughout the fall and early winter, being prevented from growing by some ecological or behavioral factor(s). The first suggestion could be tested directly by removing samples at intervals through the fall and winter and comparing them. Unfortunately this was not done here. However, in the Tilden Experimental population there was little mortality over this period in the field, and this suggests that selective elimination is not the major factor causing the observed low growth rates at this time.

Most of the mice brought into the laboratory came into breeding condition within 1-3 weeks of confinement, earlier than females in the field on both Tilden areas and earlier than males on the Experimental. Not a single mouse of the original 47 died in captivity during the 2½ months of this experiment.

Thus *Microtus* taken from the declining Tilden populations and placed in the laboratory in isolation and with superabundant food showed growth rates varying from almost zero to high levels. Declining mice left in the field all showed very low growth rates. This poor growth in the field was probably caused by some factor restraining growth, rather than by selective elimination of those individuals which do grow.

MOVEMENTS AND DISPERSAL

Movements of mice are not easily studied by live trapping procedures because of the unknown elements involved in the interaction between mouse and trap. The relation between trap-revealed movements and actual movements is consequently difficult to evaluate. Dispersal movements, particularly from one live trapping area to another, give a rough index of how much long range movement must be occurring. Recent interest in this area has been focused on the suggestion of Andrzejewski (1962) that a small mammal population consists of a migratory fraction and a resident fraction, both about equal in size under some conditions (Andrzejewski and Wierzbowska, 1961).

TABLE 16. Mean length of movements between trapping periods for adult and subadult males and females, and 95% confidence limits for these estimates. Movements were measured from first capture point of trapping period t to first capture point of trapping period $t + 1$.

	Adult Males			Subadult Males			Adult Females			Subadult Females		
	N	$\bar{x}$	95% C.L.	N	$\bar{x}$	95% C.L.	N	$\bar{x}$	95% C.L.	N	$\bar{x}$	95% C.L.
Tilden Control												
Breeding 1962-3	577	26.8	24.7–28.9	126	32.3	24.1–40.5	928	15.7	14.7–16.7	263	20.6	17.6–23.6
Non-Breeding 1963		—		717	21.6	19.8–23.3		—		601	22.4	20.6–24.2
Breeding 1963-4	137	45.5	38.5–52.5	56	37.5	26.7–48.2	116	23.1	19.0–27.2	141	35.5	29.0–42.0
Tilden Experimental												
Breeding 1962-3		—		68	44.4	34.6–54.2		—		201	25.4	22.1–28.8
Non-Breeding 1963		—		369	21.2	18.4–23.9		—		447	18.7	16.5–20.9
Breeding 1963-4	155	39.8	34.6–45.0	136	35.1	28.9–41.3	316	15.9	13.5–18.3	339	22.1	19.1–25.2
Richmond Parr												
Breeding 1962-3	405	26.2	23.3–29.0	113	32.4	24.3–40.5	777	15.3	13.9–16.6	263	19.8	16.6–22.9
RFS 3												
Non-Breeding 1963		—		189	21.0	17.3–24.7		—		197	16.0	13.6–18.4
Breeding 1963-4	115	40.5	36.2–44.7	79	34.4	27.7–41.1	125	19.4	16.1–22.7	138	24.5	20.0–29.0
RFS 4												
Breeding 1963-4	57	39.5	32.5–46.5		—		83	21.5	17.1–26.0	24	24.1	15.7–32.5
RFS 6												
Breeding 1963-4	56	53.0	44.7–61.2	54	42.5	33.7–51.2	108	31.4	26.3–36.5	65	30.9	25.0–36.8
Richmond Ford Plant												
Breeding 1964	50	51.2	37.0–65.4	20	73.1	43.7–102.4	77	29.1	23.1–35.2	28	35.7	25.0–46.4
Correlation between mean length of movement and population density (log scale)		−0.60			−0.12			−0.50			−0.46	

MOVEMENTS

Movements recorded on individuals *within* a single three-day trapping period will not be analyzed here because they are too much affected by population density in relation to trap density, trap response of individuals, and other variables. Only movements recorded on individuals *between* adjacent trapping periods will be analyzed (first capture point of one period to first capture point of the next). These movements will be used as an index of home range size. Like other species of *Microtus* (e.g. Godfrey, 1954), *M. californicus* individuals seem to remain on a restricted area throughout their residence on the live trapping area. Major shifts of home ranges if they occur usually result in the animal's disappearance from the grid.

There are many biological difficulties in interpreting trap-revealed movements of small mammals (cf. Brown, 1956; Chitty, 1937; Brant, 1962; and others). In addition there are several statistical problems which are not easily resolved. Not all lengths of movements are possible with a grid-trapping system, and furthermore the distribution of movements is highly skewed with many small movements and few large ones. Fortunately most of my samples are large and the standard statistical procedures for estimation may be used with only a small error because of the central limit theorem (Ostle, 1963, p. 92).

Table 16 gives the mean length of movements recorded between trapping periods for subadults and adult males and females of the seven populations from which extensive data were available. Movement data were discarded if the interval between captures was more than four weeks. Adult and subadult movements were separated by the weight of the animals at the first capture (if between 26-39 g it was classed as a subadult). There was no indication of significant trends in movements within each breeding and non-breeding season, and consequently movements were pooled in all groups for the whole breeding season and similarly for the whole non-breeding season. Correlation coefficients were calculated between the population density and the mean length of movement recorded for the various sex and age groups. These data are also given in Table 16. The data were grouped into four week intervals and all areas were combined to get these correlations.

Six points may be noted from these movement data. (1) During the breeding season males always averaged longer movements between captures than females. In the non-breeding season this was not the case. Movements were shorter in the non-breeding season and did not differ between the sexes. (2) Subadult males were unique in showing a little variation in their movements during the different breeding seasons. Movements seemed to be nearly the same in this group on all areas and in sparse

and dense populations. In the non-breeding season subadult males seemed to range only about half as far as breeding season subadults. (3) Adult males during the breeding season moved about considerably less in dense populations, such as the Tilden Control in 1962-3, compared with sparse populations. (4) Movements in females were also affected by density changes. Subadult females seemed to range slightly more than adult animals. With the exception of the Tilden Experimental in 1963-4, both adult and subadult females moved longer distances in sparse populations. (5) Cropping the Tilden Experimental population during the 1962-3 may have increased movements slightly in subadult males and females, when compared with Tilden Control, but the differences are not significant. (6) The RFS 6 population which was supplied with supplemental food showed large average movements in all groups.

DISPERSAL

The close proximity of the live trapping areas in Tilden Park, the Parr Field-Ford Plant area, and at the Richmond Field Station made it possible to detect many inter-grid movements and thus to obtain a crude estimate of long range dispersal.

TILDEN AREA:

The Tilden Control and Experimental areas were separated by 300 feet of grassland habitat broken only by two fire trails. The Experimental area was heavily cropped of adult mice from November 1962 to November 1963, and the heavy immigration of adult mice into this area raises the question of where these animals were coming from.

There was surprisingly little movement between the Control and the Experimental grids during this period of heavy cropping. Only two subadult females tagged on the Control turned up on the Experimental area, both moving during June 1963. In addition two *Microtus* moved from the Control area to the area live-trapped by O. P. Pearson, about 400 feet to the north of the Control. These were an adult male in February 1963 and a subadult female in August 1963. There was thus little long range movement between these areas during the 1962-3 increase and peak population. In particular the large number of immigrants entering the Experimental area must have come from the area immediately adjacent to this grid, since none were drawn from the Control quadrat 300 feet distant.

There was considerably more movement between grids in 1964 after cropping was discontinued and densities were lower. Two mice moved from the Control to the Experimental during 1964 and three moved in the opposite direction. A subadult female moved from the Control to the Experimental in late May 1964 and a subadult male moved the same way in mid-June. An adult male moved from the Experimental to the Control in early March, and adult female in April, and a subadult male in July. In neither breeding season was there any evidence of a migratory group of *Microtus* moving through the resident population in the manner proposed by Andrzejewski (1962).

RICHMOND PARR FIELD-FORD PLANT:

The presence of a very high density *Microtus* population on the Parr Field in late 1962 and early 1963 coupled with the very low density Ford Plant population immediately adjacent presented a unique situation to study dispersal in this species. Unfortunately intensive trapping of the Ford Plant was not begun until May 1963 and so our information is somewhat incomplete. From the density estimates (Fig. 1) something must have severely restricted dispersal into the Ford Plant area at least until March or April.

A total of 126 *Microtus* were tagged on the Parr Field and later caught on the Ford Plant grid, which began 50 feet away. This is 11.4% of the 1098 mice tagged on the Parr Field between November 1962 and July 1963. A total of 55 males and 71 females were known to have moved from the Parr Field to the Ford Plant from late December to mid-May. The majority (64%) of these emigrants were last caught on the Parr Field between 11 February and 15 March. It is difficult to pinpoint the major time of emigration since the Ford Plant was not trapped heavily until early May and many animals may have been present on this grid for several weeks before they were caught. For this reason the time of last capture on the Parr Field is probably a closer estimate of actual emigration time than the time of first capture on the Ford Plant.

There was no clear indication of much immigration into the Ford Plant area before February 1963. Only 8 of the 30 *Microtus* caught on this area in January and February were animals tagged on the Parr Field. The wave of immigrants which colonized the Ford Plant in late February and March produced a substantial increase in population density on this area. This wave of immigration coincided with the time of highest numbers on the Parr Field and the beginning of the decline (Fig. 1).

The true number of mice moving from the Parr Field to the Ford Plant area was undoubtedly greater than the 126 animals we observed, but it was probably not more than twice this figure. The majority of the *Microtus* on the Parr Field must have lived and died more or less *in situ*. The proportion on male to female emigrants was not significantly different from the proportion of the sexes in the whole population. Finally, no *Microtus* were caught which had moved in the reverse direction from the Ford Plant grid to the Parr Field until late May 1963. Between 20 May and 21 June three adult males and three subadult females moved in this direction.

Four points should be noted to summarize this situation: (1) in spite of the proximity of a dense population in the heavily exploited Parr Field habitat to a sparse population in the unexploited Ford

Plant area, there was little emigration from the Parr Field during the period of population increase (November to February); (2) as the Parr Field population reached a peak and began its decline during February and March emigration increased sharply in both sexes; about 10-20% of all the Parr Field animals emigrated to the Ford Plant; (3) both sexes seemed to emigrate in the same proportion as they were present in the Parr Field population; and (4) no movements were recorded in the opposite direction from the Ford Plant to the Parr Field until late May when the densities of the two areas had equalized.

RICHMOND FIELD STATION:

The spacing and arrangement of the live trapping grids at the Richmond Field Station allowed us to record many dispersal movements between areas. A total of 29 movements between grids were recorded from July 1963 to August 1964. The bulk of these occurred in two groups. Eleven *Microtus* (6 ♂, 5 ♀) moved from RFS 4 to the RFS 6 food grid in the fall of 1963. Most of these movements occurred between late October and late November at the time when the grass was sprouting and artificial food was set out on RFS 6.

The second main exodus occurred from late March to early May 1964 when 8 mice (3 ♂, 5 ♀) moved in the reverse direction from RFS 6 to RFS 4. This exodus coincided with the time of highest density on the RFS 6 area and the beginning of the decline. During the same time three *Microtus* moved from RFS 6 to RFS 3 and two additional mice from RFS 6 to RFS 5. During this period there were 127 known losses on RFS 6, and hence at least 10% of the known losses were caused by animals dispersing from the area. It is unlikely that we missed many animals which dispersed since the live trapping areas occupied almost all of the suitable habitat in the area and these were trapped intensively by DeLong and myself throughout this period.

Very few *Microtus* left RFS 3 during the study. Only four mice from RFS 3 were found on the other grids—two females moved to RFS 5 between November and January, and two males moved to RFS 4, one in October and the other in January. Again I could find no evidence of a "migrant" fraction of the population.

The conclusions from these Richmond Field Station grids support those gathered on the other Richmond and Tilden areas. Dispersal of individual *Microtus* from one area to another was not very common under natural conditions. The majority of individuals seemed to live and die in a quite restricted area. Changes in survival rates as measured by live trapping were thus primarily a function of changes in mortality rather than dispersal. None of the declines I observed could be attributed to a mass dispersal of animals from the study area. Under some conditions dispersal would occur but density was not the major determining factor. Emigration was most common when populations were reaching a "peak" and beginning to decline, whether this "peak" was at a low or at a high density, and immigration was heavy into the Tilden Experimental area while cropping was carried out.

On the other hand, dispersal on a small scale may still be very important in determining population changes. The addition of only a few individuals to a sparse population may be an important event in population ecology as it in population genetics, if it should turn out that these animals which disperse are not a random sample of the population (Lidicker, 1962).

DISCUSSION

Periodic fluctuations in population size are widely believed to be most violent in the arctic and subarctic regions of the northern hemisphere. This is usually explained on the basis of the relatively simple arctic ecosystems (e.g. Dymond, 1947; Odum, 1959; Margalef, 1963). Nevertheless, *Microtus californicus* populations in central California show periodic fluctuations superficially similar to the 3-4 year lemming cycle of the tundra, even though they live in a Mediterranean climate in a complex grassland ecosystem (Pearson, 1964). The magnitude of the *Microtus* fluctuations reported here is greater than those reported for more northerly microtines by Thompson (1955), Pitelka (1958), Kalela (1957), and Krebs (1964). The idea that periodic fluctuations became more marked as one moves north must be abandoned as far as comparisons between species are concerned. Whether an intensive study of the dynamics of single species would show significant changes from south to north remains to be seen.

Do these populations which fluctuate periodically have a common method of population control, a common set of necessary factors preventing unlimited increase? At first sight this would seem to be highly unlikely. These populations include many different species of mammals and birds, living in a wide variety of ecosystems. Nevertheless, Chitty (1960, 1964) has presented some reasons why we should consider the possibility of a common explanation, and Krebs (1964, p. 51) has also discussed this point. We will proceed, in the manner of the statistical null hypothesis, by assuming a common explanation until there is good evidence to the contrary.

What type of differences do we observe between these different species? Unfortunately, we have little information on the critical demographic parameters in species which show periodic fluctuations. I have previously reviewed this subject with reference to lemmings (Krebs, 1964), and I would like to discuss here the demography of *Microtus californicus* fluctuations and to compare this information with what has been described in other species.

POPULATION CHANGES

Hoffman (1958) and Marsh (1962) carried out intensive studies on *M. californicus* populations.

Unfortunately Hoffmann's information on population changes was based on snap-trapping of only three lines at intervals of about 2-4 months, and hence gives only a crude measure of population changes. I question his conclusion that populations of this species tend to return to the same population level before the start of each breeding season. This conclusion does not agree with my results or with those of Marsh (1962).

Marsh (1962) described population changes on an area in Tilden Park from 1958-61 and on Brooks Island from 1959-61. The Brooks Island area was just being colonized by *Microtus* when Marsh did his work (see Lidicker and Anderson, 1962) and the population changes recorded are somewhat confounded with this colonization. His Tilden population remained very low during 1959, but began increasing during the spring of 1960, apparently increasing throughout the summer and fall of 1960 and the winter and spring of 1961 to a density of about 100-200 per acre, in a manner strongly suggestive of the Tilden Control population during 1962-3.

There are almost no accurate descriptions of population declines in this species. Brant (1962) described a decline in *Microtus* in Tilden Park which began in November 1951 and ended in March 1952. However, the densities he described were extremely low (1-25 per acre), and this seems to be an example of the type of decline observed on RFS 4 during 1963-4. Declines measured by snap-trapping alone could give very inaccurate estimates because of the change in movement patterns from breeding to non-breeding season (see above). Pearson (1964) reports a decline from Tilden Park which extended from July 1961 to March 1962 with census estimates at six-week intervals. This decline in general followed the same pattern established for the Tilden Control. Unfortunately Pearson estimated his densities by the Lincoln Index, which probably underestimates population size, and by snap-trapping indices, which must be strongly affected by variations in movements. The trends he described must therefore be considered as only approximate and the absolute density figures somewhat suspect. Cook (1959) described a decline in the same area during the summer and fall of 1955 which again seemed to follow the Tilden Control pattern.

No one has yet described a breeding season decline in *M. californicus* like that observed on the Parr Field and Ford Plant in the spring of 1963. These breeding season declines are clearly more difficult to understand than the non-breeding season declines. There is a whole host of mortality factors including predation, malnutrition, disease, and others, which must continually reduce the population in the absence of breeding. If all we see in a species are non-breeding season declines, we may be tempted to suggest that these conventional mortality factors are sufficient to explain the population changes.

Chitty and Chitty (1962a) have described a variety of patterns of population change in *Microtus agrestis*. Events in *M. californicus* cycles seem more condensed than those for *M. agrestis*. The increase and peak phase may both be compressed into one year, as in lemmings (Krebs, 1964), and in one case (Parr Field) the increase, peak, and decline all occurred within one year. The declines on the Tilden areas and RFS 3 seemed analogous to Chitty's Type H decline.

There is little information on the phase of low numbers, which may extend for as long as three years in *M. californicus* (Pearson, 1963), or be as short as six months (cf. Pearson, 1964, and this study). The RFS 4, RFS 5, and RFS 6 populations are examples of populations in this phase. Characteristically these populations increased for a part of the breeding season and then suffered a breeding season decline, so that if one sampled these populations at long term intervals it would appear that nothing was changing.

The great variety of population changes illustrated in Fig. 1 may at first sight be discouraging to someone who is looking for a unified explanation of cyclic changes. The population changes were different on every grid studied, even those at the Richmond Field Station only a few feet apart. Why this is so is not known at present, and in particular whether numerous causal factors must be invoked to explain this variety of changes is not known.

REPRODUCTIVE CHANGES

Greenwald (1957) found *M. californicus* breeding throughout the year with a reduced pregnancy rate during the summer dry season. He found differences in weight at maturity in females, length of breeding season, and litter size between the two years of his study, but he was uncertain whether these were caused by weather differences between the years or by population changes. Unfortunately Greenwald had no accurate information on density changes. Hoffmann (1958) also studied reproduction in this species and concluded that there was little variation in reproductive parameters compared with large variations in population density. His samples however were 1-4 months apart and were adequate to pick up only very large changes in reproductive parameters if they occurred. Unfortunately he had no data on the population decline in *M. californicus*, which might have altered his conclusions. His observation that weight at sexual maturity did not vary from year to year should be reexamined with more complete data and the more refined statistical technique of Leslie, Perry, and Watson (1945).

Brant (1962) found *M. californicus* breeding mainly in the summer dry season, in complete contradiction to both Hoffmann and Greenwald. Marsh (1962) also reported breeding during the dry season. In this study *Microtus* apparently bred during the dry season in 1962 on the Tilden areas and the Parr Field, and there was definite breeding on RFS 4 throughout the 1963 dry season. This anomaly

of breeding during the dry season is directly comparable to winter breeding in lemmings (Koshkina and Khalansky, 1962; Krebs, 1964) and in *Clethrionomys* (Newson, 1963), and perhaps is even more remarkable in view of the extremely adverse environmental features of the dry season. Dry season breeding sometimes presaged a population increase (e.g. Marsh, 1962; Tilden Control), and sometimes was of no great consequence (Brant, 1962; RFS 4). There are no records of extensive dry season breeding in dense populations.

Marsh (1962) seems to have been the first to recognize that certain breeding season did not begin promptly at the first autumn rains but were delayed 5-8 weeks. Lidicker (pers. comm.) has also pointed this out. No one apparently has suggested that this delay in the onset of breeding may be related to the periodic fluctuations in population size in this species. The delay in breeding was most conspicuous in the declining Tilden populations in 1963-4. The RFS 3 population which was also declining at this time showed little delay in the onset of breeding, but in effect differed little from the Tilden areas because the November to January recruitment from this breeding was very poor.

The close of the breeding season in these voles must be affected to some degree by the spring weather, principally by rainfall variations, as Greenwald (1957) suggests. Unless several different populations are under observations at once, it may be impossible to observe differences in this variable, which may be related to cyclic phase. Declining or low populations in this study seemed to stop breeding slightly earlier than increasing or peak populations.

There are two striking changes in the length of breeding season in *M. californicus* which must be explained: first, breeding may occur with good recruitment during the dry season in some years, while in other years it is virtually absent; and second, the onset of breeding in some years is delayed 5-10 weeks after the grass has sprouted. I suggest that both these changes are associated with cyclic phase in the same way that analogous changes in length of breeding season are in lemmings (Krebs, 1964).

These data on *Microtus californicus* seem to lend additional support to the idea that periodic fluctuations are associated with specific variations in some reproductive parameters such as length of breeding season. These changes in reproductive parameters are not necessarily of great importance in determining density changes but they are important symptoms of what is going on in the population. Unfortunately most workers assessing reproductive changes in relation to density changes (e.g. Patric, 1962) work with data so confounded with variation in weight and parity of the animals, time of year, age at maturity, and trapping technique, that valid conclusions about the relationship of reproductive changes to population changes are impossible.

MORTALITY CHANGES

There are few data available on mortality changes in *M. californicus*. Hoffmann (1958) drew some conclusions on mortality patterns in this species from an analysis of sex and age distributions of snap-trapped animals. He did not have enough data to pinpoint the mortality changes which he thought must control population density in this species. March (1962) concluded that density in these voles was controlled by mortality in the summer and autumn.

It is axiomatic that the less there is known about a problem, the simpler its solution appears. Nowhere is this more evident than in the analysis of cyclic mortality changes. Many ideas on "crash" declines are based on an extremely simple view of cyclic mortality, one involving a sudden heavy mortality affecting all sex and age groups alike over a short time period. Other workers (e.g. Green and Evans, 1940) suggest that there is a critical stage in the life cycle which is mainly affected and thus causes these declines. The mortality picture which has emerged from this study does not fit either of these pictures. All sex and age groups seemed adversely affected in low or declining populations, and periods of heavy mortality occurred at different times in these groups. Weanling and early juvenile mortality, which has been suggested as the critical mortality change by some authors (e.g. Hoffmann, 1958), did not appear to be related to periodic fluctuations in M. *californicas*. Populations would increase in some cases when early juvenile mortality was high and decrease when this mortality was low.

My results are also at odds with Marsh's (1962) suggestion that density was controlled in this species by mortality in the summer and autumn. The Richmond Parr Field and RFS 6 populations, for example, do not follow this pattern. One of the more persistent fallacies in population ecology is that the problem of regulation can be discussed in the either-or terms or reproduction and mortality (Lack, 1954; Southern, 1959). It is unlikely that we will find any simplicity at this level of analysis, so that we can say, for example, that population a, b, and c are regulated by reproductive changes and populations x, y, and z by mortality changes. Both factors are involved in the control of California vole populations, as they were with lemming populations (Krebs, 1964), and simplicity must be sought at a deeper level of analysis.

The most extensive information on cyclic mortality is that for *Microtus agrestis* assembled by Chitty (1952, and later papers) and his coworkers in England. The mortality schedule of this species can be summarized as follows: (1) mortality rates during most of the winter (non-breeding season) are low and similar in all phases of the cycle; (2) mortality rates increase markedly in late winter or early spring; this mortality may occur before the breeding season begins or just after it starts; it may occur at

a different time in males and in females; this heavy spring mortality occurs at least in peak and declining populations and is more severe in the latter; (3) summer mortality rates are low for adults in the peak year; juveniles may suffer heavy mortality in the early part of the peak breeding season, but they invariably survive poorly in declining populations.

The mortality schedule of *M. californicus* is similar in some respects to that of *M. agrestis*. The decline showed by the Tilden Control and RFS 3 populations from October 1963 to February 1964 resembled the spring mortality of *M. agrestis*, although it was very prolonged. None of these declines however showed any differences in timing between the sexes. Mortality rates were low in adults of both species during the breeding season of the peak year.

The major difference between these species seems to be in juvenile mortality. Low and declining *M. californicus* populations are characterized by poor survival in all sex and weight groups of the trappable population; conversely peak and expending populations are characterized by high survival in all classes, including the juveniles. These changes in survival of the trappable population in *M. californicus* are the major changes correlated with the density changes. Weanling and early juvenile survival in the California voles does not seem to be involved in the cyclic changes, contrary to what Godfrey (1955) found in *M. agrestis*. I have found some expanding populations with very poor survival rates for early juveniles, and other declining populations with very good rates.

These differences in early juvenile survival may be partly a result of differences in the age at first capture of juveniles. If young mice were trapped at an earlier age, part of the mortality which I class as weanling and early juveniles mortality in *M. californicus* would be a part of juvenile mortality in the trappable population. Another reason for the observed differences in juvenile survival might be the different types of declines (Krebs, 1964, p. 55). Godfrey (1955) was describing a Type G (no recovery) decline, while my data for the Tilden Control refer to a Type H (some recovery) decline (see Chitty and Chitty, 1962a, Fig. 1).

To summarize: the main feature of the mortality schedule of *M. californicus* and probably other cyclic microtines is high survival of all sex and age groups of the trappable population during the expanding and peak phases, and low survival of all these groups during the declining and low phases. Survival of animals during the weanling stage and shortly thereafter may show exactly the reverse pattern and need not bear any constant relationship to survival in the trappable population. The crucial changes in survival in this species seem to occur after the animals have reached trappable size.

GROWTH

The variations in body weight which accompany these fluctuations (Chitty and Chitty, 1962b) may possibly hold the key to an understanding of these cycles. It is unlikely that body weight *per se* in an important factor; rather it is probably a superficial index of more fundamental changes in the population.

High body weights are characteristically associated with peak populations of a great variety of microtines (Krebs, 1964), including *M. californicus*. There are three mechanisms which could account for this: (1) individuals might have higher growth rates in peak populations; (2) growth rates might be similar in all phases of the cycle but individuals in peak populations might continue growing longer to a higher asymptotic weight; or (3) growth rates might be similar in all phases of the cycle but more individuals might survive in peak populations to reach maximum size, and so give a higher mean body weight.

Growth rates were not higher in peak populations during this study. In fact the highest growth rates observed were in the low RFS 6 population which was fed (Krebs and DeLong, 1965). The growth rates of males above 50 g did not differ among the various populations, and there is consequently no evidence for the second explanation of a variable asymptote. Most of the variation in mean body weights described here can be attributed to variations in survival rate. Low body weights in declining and low populations were the results of the short duration of life characteristic of this cycle phase. If this relation between body weights and mortality is added to the observation that growth in *M. californicus* occurs only during the breeding season, we have an explanation of changes in body weight for these populations. Most changes in body weight can be completely reduced to changes in the two primary factors of reproduction and mortality. The only exception to this generalization was the RFS 3 population which showed low growth rates from November 1963 to January 1964, a period of high survival and reproductive activity in this declining population.

Does this explanation apply to other cyclic microtines? Chitty and Chitty (1962b) have described in detail body weight changes in *M. agrestis*, and their results do not agree entirely with this explanation. Body weights in over-wintered *M. agrestis* may remain low during the breeding season in some declines (cf. Chitty and Chitty, 1962b, Table 1, 1949 decline). This suggests either low growth rates in some declines of this species, or a lower asymptotic weight. I concluded from a study of lemmings (Krebs, 1964, p. 61) that the growth rates of individuals varied over the cycle and that this produced the body weight changes. This is probably not true if one restricts the analysis of growth rates to the breeding season only. Clearly there were differences in growth rates in this study between November 1962 and November 1963 on the Tilden Control, but the major reason for this was the lack of breeding

in 1963. I doubt that there are any cyclic variations in growth rates independent of reproductive changes.

MOVEMENTS AND DISPERSAL

Andrzejewski (1962) has argued in a series of papers that small mammal populations consist of two parts, residents and transients (Andrzejewski and Wierzbowska, 1961; Andrzejewski and Wroclawek, 1962; Andrzejewski, 1963). This suggestion had been made earlier by Evans (1942) and Kalela (1954). The observation that a large fraction of live trapped mice are caught only once has been the main source for this idea. If an exponential curve is fitted to the number of animals known to be alive 1, 2, 3, . . . t time units after first capture, and if this is extrapolated back to the time of first capture, the estimated number of animals caught is always very much less than the actual number caught (Andrzejewski and Wierzbowska, 1961). Andrzejewski (1962) claims that the difference between the estimated and the observed numbers represents the migratory fraction of the population, animals which are moving through the live-trapping area. This 'excess' number of animals caught but once is explained more simply by the fact that the numbers known to be alive after 2, 3, or more trapping periods are not independent random samples, since all the mice present are not caught each time (see also Holgate, 1964). There is no evidence that rodent populations can be divided into resident and transient groups, and the population changes which Andrzejewski (1963) attributed to movements and dispersal are more properly analyzed as changes in reproduction or mortality.

Dispersal of mice in this study was not very common with the exception of the cropped Tilden Experimental population. Stickel (1946) found that removal of *Peromyscus leucopus* from a central one-acre plot caused the surrounding mice to shift into the vacant area. Andrzejewski and Wroclawek (1962) in a similar type of removal experiment with *Apodemus agrarius, A. flavicollis,* and *Clethrionomys glareolus* concluded that the trapped out area was repopulated by mice from the migratory sector of the population, not from the resident mice on an adjacent grid. Unfortunately they give no information on the size or age distribution of the colonizing animals; perhaps the immigrants were largely young unmarked individuals which could have come from the control grid. The experimental design of Stickel (1946) with the removal grid completely surrounded by the control grid is clearly superior to that used by Andrzejewski in which the control bordered the removal grid on one side only.

FACTORS REGULATING *Microtus californicus* POPULATIONS

The changes that occur in *M. californicus* populations are similar to those known in lemmings and other cyclic microtines which have been studied intensively (Chitty, 1964; Krebs, 1964). Major changes occur not only in mortality but also in reproduction, and it is these specific changes which remain to be explained adequately.

I would like to discuss three conventional explanations proposed for microtine fluctuations with particular reference to *M. californicus,* and then consider possible self-regulatory mechanisms which may be operating in these populations.

FOOD:

Marsh (1962) concluded that density was controlled in *M. californicus* populations by mortality in the summer and fall, mediated by the food supply during this period. There is no doubt that the dry season is the critical food season for these mice, and a number may die because of these harsh conditions. However, we have shown elsewhere that the RFS 6 population decreased to virtual extinction during the latter part of the growing season in the presence of supplemental grain and natural food (Krebs and DeLong, 1965). It seems unlikely that any of the declines observed in this study was caused by food shortage. Also, some populations, such as the Parr Field 1962 population and the Tilden population described by Marsh (1962), increased during the dry season, when the food supply is supposedly minimal in quantity and succulence.

DISEASE:

There was little evidence of widespread epidemic disease in any of the populations studied. Mice rarely died in the traps, even though they often had to remain overnight in them. In addition samples from all these areas were regularly removed to the laboratory to study aggressive behavior. In only one case did we get any heavy laboratory mortality among these animals. Eleven *Microtus* were brought in from the Richmond Parr Field on 4 July 1963, and all of these died in the laboratory within five days (all in separate cages). Autopsies were made on four of these by the State Department of Public Health in Berkeley but only an enteric streptococcus could be isloated from the blood and visceral organs. Twelve mice from this population were brought into the laboratory in late May and eight more in early June without any mortality. The "big-foot" infection (cf. Bell, Owen, and Jellison, 1958) was found in only a few isolated individuals.

Only a few carcasses were discovered on all the areas during the various population declines. The largest numbers were found on the Richmond Parr Field and Ford Plant areas during June and July 1963. While setting the live traps at this time one would find about 5-10 carcasses less than one week old.

Murray (1965) has presented recent evidence that periodic declines in *Microtus montanus* can occur with very little associated disease. In other declines with the same species Kartman, Prince, and Quan (1959) found tularemia epizootics widespread, particularly in very dense populations. Perhaps the

terminal decline on the Richmond areas in June and July 1963 was produced by an epidemic. House mice (*Mus musculus*) on this area suffered a catastrophic decline at the same time as the terminal *Microtus* decline (DeLong, 1965). This was the only *Microtus* mortality in this study which could be associated with a possible epizootic and the evidence is all indirect.

PREDATION:

Pearson (1964) suggested that carnivores ate 88% of the *Microtus californicus* on a 35 acre field in Tilden Park during the peak summer, fall, and winter of 1961-2. About 3800 *Microtus* were recovered in carnivore droppings from June 1961 to February 1962. Two questions are raised by this work: first, how accurate are these estimates; and second, is predation an adequate explanation for the observed population changes?

There are two sources of error which greatly affect these estimates. The primary estimate of 4400 *Microtus* on the 35 acre area (126 per acre) may be a gross underestimate of the true numbers. In this study I enumerated densities in excess of 260 per acre in 1963 on the Tilden Control grid, which immediatedly adjoins this 35 acre area Pearson has studied. I suspect that I caught ⅔ of the individuals in this particular situation. If these 1963 densities were roughly equivalent to the 1961 densities on this area, Pearson's estimated 126 per acre may be only ½ or even ⅓ the true density. Only 22% of the tagged *Microtus* which disappeared from Pearson's live trapping grid were later found in carnivore scats, and I suspect this figure is closer to the true mortality than the previous 88% estimate.

Another less serious source of error is the edge-effect of collecting carnivore droppings from the fire trails on the border of the 35 acre study area. A "border-strip" should be added to the area to compensate for this, just as is commonly done in live trapping studies. This applied only to one side of Pearson's study area, since three sides were bounded by unsuitable habitats.

The second question is, given that predators have killed a substantial if undefined proportion of *Microtus*, whether this mortality is an adequate explanation for the observed population changes. I do not think it is an adequate explanation for three reasons. First, we must explain reproductive changes as well as mortality changes in these populations, and it is unlikely that any variation in predation could produce the delay in breeding characteristic of declining populations, or the dry season breeding found at times of expanding populations. Second, there was only a slight amount of predation in both the Richmond Field Station and the Richmond Parr Field-Ford Plant areas, yet these areas also showed fluctuations in *Microtus* numbers. Third, differences between the nearly adjacent Tilden Control and Experimental areas in 1963 and 1964 cannot be explained by predation.

Predation, especially by efficient carnivores like feral house cats, is probably an important density-dependent mortality factor in fluctuating *M. californicus* populations. However, it is probably not an essential part of these periodic fluctuations, which seem to go on equally well without heavy predation. (Chitty, 1960; Krebs, 1964).

SELF-REGULATORY MECHANISMS:

The changes which occurred in the parameters of these *Microtus* populations can not be readily understood by looking for correlated changes in food supply, disease incidence, or predator pressure. Self-regulatory mechanisms may thus be involved. By these I mean changes in quality or phenotypic fitness of individuals as density changes. These changes in quality, described elegantly in one particular case by Wellington (1964 and earlier) for the western tent caterpillar, operate in conjunction with extrinsic variables such as food supply and predation to stop population growth. They do not operate independently of the external environment, but cooperatively. They involve the organism side of the *individual organism—environmental factors* duet which fixes birth and death rates in the population (Chitty, 1955).

A self-regulatory mechanism could be either genetic or phenotypic in its operation. Both types might involve physiological or behavioral changes in the animals, and to investigate these in this particular situation we would have to answer two questions: (1) are there physiological or behavioral changes in individuals over the population cycle?; (2) if so, are these changes necessary causes of the cycle? If any changes can be described, we must determine whether or not they have a genetic basis.

Christian and Davis (1964) support a phenotypic hypothesis of self-regulation by a behavioral-endocrine feedback system, elicited by "social pressure" and operating principally through the pituitary-adrenocortical axis. No evidence for the changes postulated by Christian has been found in three intensive field studies on cyclic small mammals (Mullen, 1964; Krebs, 1964; Chitty, 1961); and, although Christian and Davis (1964) present several reasons why these data may be unreliable, there are no data from field populations which corroborate this hypothesis.

Chitty (1960, 1964) supports a genotypic hypothesis of self-regulation, and no one as yet has obtained the relevant evidence to corroborate this suggestion. Chitty argues that interactions between individuals, if they have anything like the strong physiological effects described by Christian and Davis (1964) for laboratory situations, should have a selective effect in field populations. We should thus consider the possibility that a genetic polymorphism has been evolved to offset these effects of interactions.

No attempt was made in this study to test either of these hypotheses critically, and there is no point

in arguing which (if either) fits my data better. An attempt was made by M. Tamura to describe possible variations in aggressive behavior of male *M. californicus* from the populations I studied. This is one aspect of a long term attempt to evaluate these two competing hypotheses of self-regulation, and unfortunately the results must be published elsewhere (Tamura, in prep.). These populations of the California vole may be self-regulatory, but I do not have the critical evidence that this is in fact the case. Only the failure to explain the observed demographic changes by conventional extrinsic agents supports this view, but this negative evidence is very weak substance on which to base any conclusions about regulation.

CONCLUSION

Two points have emerged from this work. First, periodic fluctuations in *Microtus californicus* in central California are similar in many ways to fluctuations of lemmings in northern Canada and field voles in Britian. Second, the details of population changes in this species are extremely variable from one area to the next. Some populations increased systematically during the breeding season, while others increased only in spurts. Males at times suffered heavy mortality for a short period, while females at the same time had low mortality. Whatever is causing these demographic changes must be highly labile and discriminatory.

Finally, a start has been made on an experimental analysis of these periodic fluctuations. The 1964 Richmond Ford Plant experiment suggests that expanding populations could be produced more or less at will on natural areas. It is unlikely that much more will be achieved in solving this problem of periodic fluctuations without a vigorous experimental attack on natural populations.

SUMMARY

1. Eight populations of the California field mouse were studied near Berkeley, California, from September 1962 to September 1964. About 21,000 captures were recorded on nearly 7000 mice by live trapping these areas, usually at two-week intervals.
2. Population size could not be estimated by the usual capture-recapture techniques because sampling was non-random both between marked and unmarked animals and within the marked segment. The populations were estimated by direct enumeration.
3. Densities varied between less than 1 per acre to at least 325 per acre on one area. Expanding populations seemed to begin increasing during the dry season and to continue throughout the next growing season to reach peak densities by the next spring or summer.
4. Two types of declines could be distinguished. Some populations began to decline during the middle of the plant growing season while breeding was still in progress. Other populations declined during the non-breeding season, principally in fall and winter.
5. Three experiments were done:
   (a) The Tilden Experimental population was cropped of adult mice from November 1962 to November 1963 in an attempt to test Chitty's (1960) suggestion that cropping could maintain the population continuously in the expanding phase of the cycle. A heavy immigration rate completely offset this cropping experiment, and although 1758 adult *Microtus* were removed from this two-acre area during the year, the Experimental population continued to increase by immigration to reach a peak at the same time as the Tilden Control.
   (b) Seven pairs of mice removed from an expanding population were introduced into the Richmond Ford Plant area in January 1964 to see if an expanding population could be produced experimentally by artificial immigration. This area had suffered a catastrophic decline in the summer of 1963 and very few mice were on the area at the time of the introduction. The response to this introduction was striking, and the population reached about 300 per acre in August 1964.
   (c) The low RFS 6 population was provided with supplemental food from October 1963 to September 1964 in an attempt to see if superabundant food was sufficient to produce an expanding population. The population increased irregularly to a moderate density, but it then declined through the last part of the breeding season and became virtually extinct during the dry season.
6. The major reproductive changes were in the length of breeding season. Expanding populations seemed to reproduce effectively during the dry season, while declining populations usually did not begin breeding until 5-10 weeks after the first autumn rains.
7. Expectation of life was higher in males and females of all trappable age groups in expanding populations, when compared with low or declining populations. Removing the adults from the Tilden Experimental raised survival rates of subadults and juveniles 5-10%, but providing supplemental food for the low RFS 6 population did not increase survival rates of any age group to the high levels found in expanding populations.
8. Weanling and early juvenile mortality was not clearly related to the population changes. Some expanding populations had poor survival in this group and some low populations had very good survival. Survival of this group was not related to

survival in the trappable segment of the population.

9. Survival rates were extremely variable in sparse populations. This resulted in sudden spurts of population growth, which sometimes occurred at different times for males and females. During the breeding season females always survived better than males, but the survival rate of the two sexes was equal in the non-breeding season.
10. Populations which declined during the breeding season also showed reduced individual growth rates during these declines. The highest sustained growth rates were those of the RFS 6 population provided with supplemental food. Cropping the Tilden Experimental population also increased growth rates. Growth rates during the breeding season were as good in the Tilden Control population during the peak year as during the decline.
11. Peak and expanding populations of *Microtus californicus* were characterized by adult males of large body size in the same way as other cyclic microtines. High body weights in these populations can usually be explained by two factors: growth which occurs only during the breeding season, and low mortality rates which are found only in peak and expanding populations.
12. Forty-seven *Microtus* brought in from the declining Tilden areas in November 1963 grew at rates which varied from almost zero to high levels when kept in isolation with superabundant food. Animals in the field at this time all grew slowly.
13. Males averaged longer movements between trapping periods than females. Movements in subadult males were unique in being nearly the same on all areas and in sparse and dense populations. Other groups tended to move about more in sparse populations.
14. Dispersal between live trapping areas was very low. Only two animals moved the 300 feet from the Tilden Control to the Experimental during the cropping experiment, and the immigrants to this area must have come from the immediate surroundings. Most individuals seemed to live and die in a quite restricted area, although dispersal was more common in sparse populations. There was no evidence of a transient, migratory population of mice on any of the areas.
15. Food shortage did not appear to be a necessary condition for the demographic changes described here. Epidemic disease may have caused the terminal part of one decline, but evidence is indirect. No other declines could be associated with disease. Predation may have caused considerable mortality on the Tilden areas, particularly in the dry season after the peak, but the Richmond areas suffered very little predation. There is no evidence of predation either preventing these microtine populations from expanding or causing them to decline and remain at low numbers.
16. Self-regulatory mechanisms may be responsible for these demographic changes but no direct evidence of phenotypic or genotypic changes in fitness was obtained in this study.
17. Periodic fluctuations of *Microtus californicus* in central California are similar in many ways to fluctuations of lemmings in northern Canada and field voles in Britain. These broad similarities are recognizable even though the details of population changes in this species are extremely variable from one area to the next.

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