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MICROTUS POPULATION BIOLOGY: DEMOGRAPHIC CHANGES IN FLUCTUATING POPULATIONS OF *M. OCHROGASTER* AND *M. PENNSYLVANICUS* IN SOUTHERN INDIANA.

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Abstract. *Microtus pennsylvanicus* and *M. ochrogaster* are sympatric in southern Indiana grasslands. From June 1965 to August 1967 four populations were live trapped, three of them in 0.8-hectare (2-acre) outdoor pens. Both species increased during 1965 and reached peak densities in summer 1966. *Microtus ochrogaster* declined abruptly that fall and remained low; *M. pennsylvanicus* declined the following spring.

One of the fenced populations increased to a density about three times that of its unfenced control. By early fall 1966 it had nearly destroyed its food resources and then suffered a severe decline associated with obvious overgrazing and starvation. No such overgrazing has been seen on any unfenced grasslands in this area. Dispersal is probably necessary for normal population regulation in these voles, since fenced populations seem unable to regulate their density below the limit set by starvation.

Both species bred extensively in the winter of 1965–66 during the phase of population increase. There was little or no breeding during the winter after the peak.

Survival of females in the trappable population of both species was high and relatively constant until the end of the cycle. In males, periods of low survival punctuated the increase and peak phases, and these periods of low male survival did not occur at the same time in the two *Microtus* species. Some mortality processes are thus highly specific for sex and species. In the fenced populations survival rates were very high and no sporadic male losses occurred.

Increasing and peak populations of *M. pennsylvanicus* and *M. ochrogaster* are characterized by adults of large body size. During the increase and peak phases some voles stopped growing at low weights (30–40 g) while others reached high asymptotic weights (45–55 g).

The demography of these *Microtus* species in southern Indiana is similar to that of other cyclic voles and lemmings in temperate and arctic areas.

The natural regulation of animal numbers can be studied most clearly in populations which show large changes in abundance (Chitty 1960) and these populations are also well suited to studies in population genetics (Birch 1960; Ford 1964). Unfortunately the population biology of few organisms has been studied from a unified viewpoint: ecologists usually neglect *quality* for *quantity,* and geneticists usually do their studies in an ecological vacuum. The purpose of this series of papers is to summarize our continuing studies on the interrelationships of quantity and quality in field populations of voles (*Microtus*).

We have begun this search by asking whether genetic changes play any part in causing periodic fluctuations in numbers of small rodents (Chitty 1964). Many species of *Microtus* as well as other microtines show these periodic fluctuations or "cycles," and no satisfactory explanation is currently available for these changes (Krebs 1964, 1966). In this first paper we consider the demographic aspects of periodic fluctuations for *Microtus pennsylvanicus* and *Microtus ochrogaster* in southern Indiana. We are particularly concerned here with mortality patterns determined from live-trapping data, and we report on three experimentally manipulated populations.

Methods

These studies were carried out on abandoned pastures in southern Indiana. The main study area is located 11.3 km (7 miles) east of Bloomington on the Grasslands Research Area of Indiana University. A large grassland area which had not been cultivated for 6 years prior to the start of these studies was subdivided into four grids (Fig. 1). Three of these grids were fenced with 6.3-mm (¼-inch) mesh hardware cloth extending 0.6 m into the ground and 0.6 m above ground, capped with an inverted V of aluminum. These fences were nearly 100% effective in preventing immigration or emigration. Occasionally a mole would burrow under the fence, which would enable a few mice to escape. Since we were trapping the grassland area around these fences, we probably detected most of these individuals. Fifteen escapees were picked up during this study, which involved about 2,900 individuals in the fenced populations.

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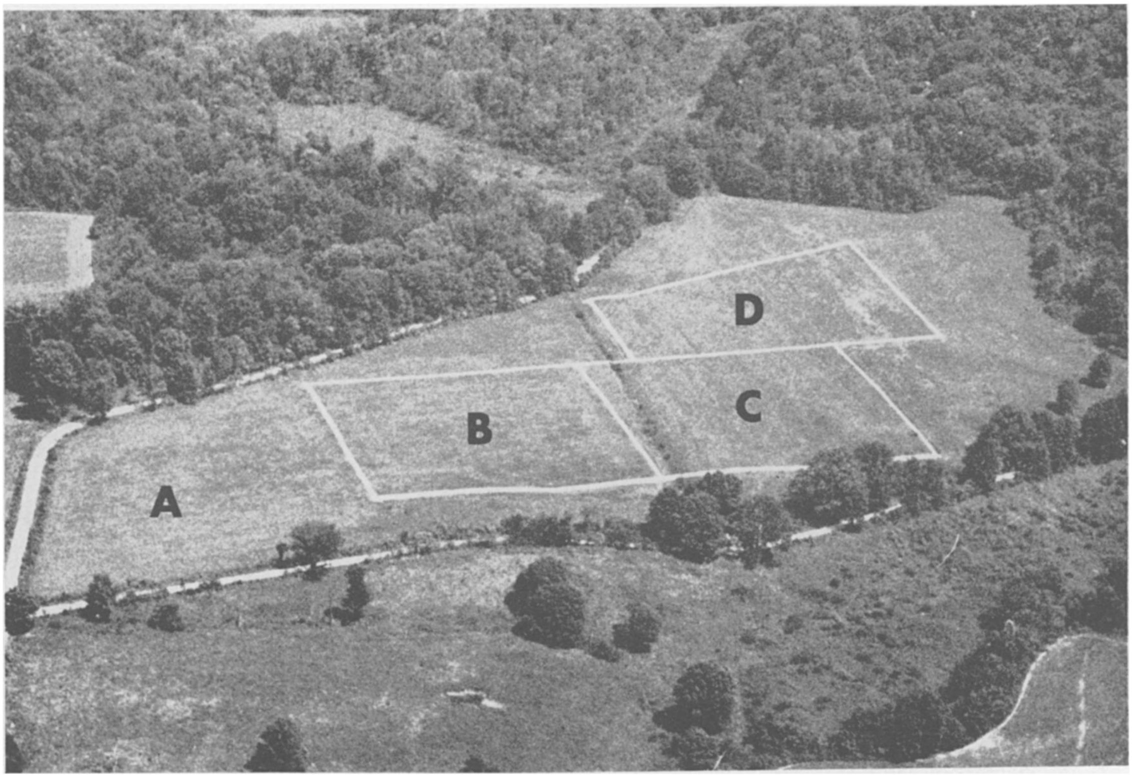

FIG. 1. Aerial view of the four live-trapping grids. Sides of square grids are 91.5 m (300 ft).

These four areas were covered by a checkerboard of points spaced 7.6 m (25 ft) apart. Each grid was 10 by 10, except grid D, which was made slightly irregular to follow habitat boundaries. Each area was live trapped with 100 Longworth live traps on a biweekly schedule. More traps (to a maximum of 200) were made available as population densities increased. These live traps were left permanently on the trapping areas, locked open when not in use, and each was covered with a heavy board. Traps were placed anywhere in the general vicinity of the trap point where sign of vole activity could be found. Crimped oats and cotton were placed in each trap when set. Trapping was done for 2 days every second week. Traps were set in the afternoon, checked the following morning and again in the afternoon, and locked during the third check on the next morning. During the summer, traps were opened overnight only, to prevent mortality from the heat. Using these techniques we avoided almost all trap mortality, and have been able to follow these populations year round.

Upon first capture each vole was tagged with a lettered and numbered fingerling fish tag in the right ear. The following data were also recorded at each capture: species; location on grid; weight; sex; for males, position of testes; and for females, vagina perforate or not, nipples small, medium or large, and pubic symphysis closed, slightly open, or open. We weighed the mice to the nearest gram using specially constructed spring scales; mice were suspended by their tails with alligator clips for weighing.

Few voles lost their ear tags, and such individuals could usually be identified by their location, size, and sex, and the appropriate synonymy noted. Seven of 325 *M. ochrogaster* and 25 of 492 *M. pennsylvanicus* lost ear tags on grid A.

Data were punched on IBM cards and we did the entire analysis on a CDC 3600 computer at the Indiana University Research Computing Center, using a series of programs described by Krebs (1967).

WEATHER

Southern Indiana has a typical continental climate with large seasonal temperature fluctuations and abundant rainfall scattered evenly through the year. Table 1 summarizes some weather data for the area of study. Temperature has been recorded since July 1965 by a recording hygrothermograph situated on the study area in a screened shelter 10.2 cm (4 in.) off the ground. A recording rain gauge was installed in the study area in May 1967.

TABLE 1. Weather data, 1965–67

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean Temperature (°C)[b]												
1965	-1.2[a]	0.6[a]	2.1[a]	13.5[a]	20.5[a]	21.6[a]	22.3	21.1	19.2	11.7	7.0	4.1
1966	-2.3	-0.1	6.1	10.7	13.3	19.8	23.8	21.1	16.0	10.3	5.9	0.8
1967	0.9	-1.7	7.1	13.1	15.2	22.5	22.6	20.9	16.7	11.4	4.6	-0.1
Precipitation (mm)[b]												
1965	74[a]	112[a]	55[a]	117[a]	72[a]	65[a]	98[a]	163[a]	157[a]	28[a]	16[a]	64[a]
1966	60[a]	79[a]	22[a]	130[a]	69[a]	69[a]	115[a]	76[a]	132[a]	30[a]	123[a]	149[a]
1967	31[a]	64[a]	98[a]	93[a]	116	55	143	74	49	131	56	162
Hours of sunshine[c]												
1965	171	207	161	199	340	337	355	303	223	225	135	103
1966	142	120	192	141	296	305	316	258	226	222	85	66
1967	101	156	159	205	231	245	252	310	236	143	100	82
Mean soil temperature at 10.2 cm (4 in.)[d]												
1965	3.4	2.4	3.1	11.3	19.8	22.7	24.3	23.7	20.2	13.4	9.3	4.9
1966	2.2	0.8	5.8	8.7	15.7	21.5	26.7	24.3	21.0	13.9	9.8	5.2
1967	4.0	3.1	8.2	13.3	18.1	23.6	24.4	23.5	20.1	14.5	8.2	6.0

[a] Data from Bloomington I.U. Station.

[b] Temperature and precipitation recorded on Grasslands Research Area unless otherwise indicated.

[c] Recorded at Indianapolis, Indiana.

[d] Recorded at Dubois Southern Indiana Forage Farm under fescue sod.

At the present time we do not know which, if any, of the many variables of weather are significant to vole populations, but because some weather variations probably have population effects, we describe in a general manner the climatic regime.

Snow is not uncommon during the winter in southern Indiana but it rarely stays on the ground for more than a few days before melting. We have not missed one weekly trapping in three winters because of snow. From about December to April the soil is usually saturated with moisture and because of poorly drained soils on the study area, local flooding occurs after heavy rains. Voles probably live in surface nests during these months, and we have been unable to find any evidence that local floodings produce any substantial mortality in the trappable population.

Yearly differences in the weather of this area (Table 1) are small compared with the seasonal changes. Spring 1965 was warmer than average, and fall 1966, cooler than average. Fall 1965 was particularly dry while late fall 1966 was very wet. Hours of sunshine show a general trend: 1965 > 1966 > 1967. This is true for both summer and winter periods. Soil temperatures provide a crude measure more relevant to the microclimate of a vole. They are surprising mainly in the summer maxima which reached 30°C (86°F) in 1965 and 1967 and 33°C (91°F) in 1966. July 1966 showed particularly high soil temperatures. To reach a mean soil temperature of 21°C (70°F) or less a vole must burrow to 51 cm (20 in.) or more during July and August.

VEGETATION

The study area shown in Figure 1 was part of the soil-bank grassland program and consequently was not disturbed from fall 1959 onward. Dominant plants for the four trapping areas are given in Table 2. The fence row almost on the boundary between grids B and C (see Fig. 1) divides this area into two parts which differ in cultivation history. Grids A and B are very similar, dominated by fescue (*Festuca* sp.). Grids C and D are also similar to one another, but are dominated by orchard grass (*Dactylis glomerata*). These and other grasses present were planted and are not natural stands. The fields tend to be rapidly colonized by small tree seedlings. Our only disturbance to the vegetation during this study has been to cut out these small trees.

Both species of *Microtus* occupy a great diversity of grass and weed communities in our study area (see Keller and Krebs MS, in prep. for more details), and the vegetational differences between the four trapping areas reported here are minor in comparison with this habitat spectrum.

POPULATION DENSITY

Enumeration technique

We have abandoned attempting to estimate population density by capture-recapture techniques because of nonrandom sampling (see Krebs 1966 for a discussion of this problem) and instead rely on complete enumeration of the trappable population by intensive live trapping. Note that

TABLE 2. Dominant plants on the four live-trapping grids. + = common; ++ = abundant; +++ = very abundant

Species	Grid A	Grid B	Grid C	Grid D
Festuca sp.	+++	+++	+	+
Dactylis glomerata			++	+++
Agrostis sp.				+
Solidago altissima	++	+++	+++	+++
Solidago temuifolia	+		+	
Solidago juncea		+	+	++
Veronia altissima			+	
Aster sp.	+	+	++	+++
Eragrostis alba				+
Campsis radicans				+
Asclepias syriaca	+	+	+	+
Rubus sp.				+
Chyrsanthemum leucanthemum		+	+	+
Prunella vulgaris				+
Ambrosia artemisiifolia	+	+	+	+
Eupetorium rugosum	+			
Carex sp.	+			
Helenium flexuosum			+	+
Circium sp.			+	+
Solanum carolinense		+	+	+
Rosa sp.			+	+
Desmodium sp.		+	+	+
Plantago lanceolata			+	
Achillea millefolium				+
Pycnanthemum flexuosum			+	+
Convolvulus sepium		+		+
Rhus radicans			+	+
Trifolium pretense			+	+
Melilotus spp.			++	+

the population referred to here is the trappable population. Voles are on the average about 25 g and about 4–6 weeks old when first caught in our traps; females are caught at slightly lighter weights than males.

Microtus ochrogaster is much more "trappable" than *M. pennsylvanicus*. Two types of data illustrate this. Table 3 gives estimates of "trappability" obtained by comparing the actual catch in each trapping period of 2 days with the number of voles known to be alive on the area. These estimates were summed over 4-month periods. They are maximum values because the numbers known alive are minimal estimates, but the error here is believed to be small. Table 3 shows with one possible exception no differential trappability of the two sexes. Finally, these data show that *M. pennsylvanicus* become relatively untrappable during the summer. This is striking particularly when new areas are live trapped in the summer; it may be possible then to catch only a few voles of this species in live traps even during the peak summer.

Additional information on relative trappability is given in Table 4 which chronicles four complete removals of voles from fenced grids. All these removals were begun during the summer when *M. pennsylvanicus* is least trappable, and this tends to maximize the differences between the two species. Many of the *M. pennsylvanicus* caught several weeks after the start of removal were young animals just entering the trappable population. Consequently "trappability" as measured in Table 3 cannot be applied to these series directly. These complete-removal observations indicate clearly that *M. ochrogaster* is more easily trapped out of an area than is *M. pennsylvanicus.*

We believe that we can enumerate at each trapping period about 90% of the *M. ochrogaster* on an area and about 75% of the *M. pennsylvanicus* (50% in summer). By repeating these enumerations at 2-week intervals we can obtain a reasonably precise description of demographic trends.

Experimental manipulations

Each of the four areas live trapped was subject to a different experimental treatment, as follows:

grid A control, unfenced
grid B unmanipulated, fenced
grid C cropped of adults, fenced
grid D introduction experiment, fenced

Each of these grids occupied about 0.8 hectares (2 acres). None of these treatments were done in replicate at this stage because of the prohibitive

TABLE 3. Trappability of *Microtus pennsylvanicus* and *M. ochrogaster* on grid A. Trappability is measured by the percentage of mice known to be alive which were actually caught

Period	*Microtus pennsylvanicus*				*Microtus ochrogaster*			
	Males		Females		Males		Females	
	N[a]	trappability	N	trappability	N	trappability	N	trappability
Oct.–Jan. 1965–66	231	64.1%	277	82.3%	79	92.4%	85	91.8%
Feb.–May 1966	427	75.4%	417	74.6%	113	96.5%	153	93.5%
June–Sept. 1966	238	57.6%	403	56.8%	297	92.9%	286	93.0%
Oct.–Jan. 1966–67	296	72.0%	362	72.1%	107	97.2%	128	92.2%
Feb.–May 1967	216	81.5%	260	86.2%	28	96.4%	19	100.0%

[a] N = number of mice known to be alive on the area at the time sampled, summed over the indicated time period.

TABLE 4. Complete removal of voles from fenced areas. Dates are start of removal live trapping. Asterisks in each series mark the division between initial trapping on the normal 2-days-a-week schedule and terminal trapping on a 7-days-a-week schedule

	Weeks after start of removal													Total no. voles removed
Grid D July 26, 1965	0	2	4	6	8	10	12	14	16	18	20	22		
M. ochrogaster	6	1	1	2	0	0	0	0	0	0*	0	0		10
M. pennsylvanicus	3	0	1	5	4	18	3	5	1	1*	0	0		41
Grid P July 17, 1967	0	2	3	4	5	6								
M. ochrogaster	38	18*	0	0	0	0								56
M. pennsylvanicus	2	3*	12	5	1	0								23
Grid C July 10, 1967	0	2	3	4	5	6	7	8	9	10	11	12	13	
M. ochrogaster	21	5*	2	0	0	0	0	0	0	0	0	0	0	28
M. pennsylvanicus	0	4*	7	8	12	4	2	4	2	2	1	1	0	47
Grid D[a] July 10, 1967	0	2	3	4	5	6	7							
M. ochrogaster	28	14*	3	3	1	0	0							49

[a] Single species population.

amount of work involved and because we believe that any interesting results should be replicated at a later date.

Grid B was set up to measure the effects of fencing per se on the population. We must determine what size of area is a "universe" to a vole population, and this size of pen (91.5 m by 91.5 m) is at least an order of magnitude larger than any previously tried (cf. van Wijngaarden 1960; Clarke 1955). Nothing was done to the population in this grid; we merely fenced in the voles already resident on the area.

Grid C was designed to test Chitty's (1960) suggestion that a cropped population should remain in the phase of increase. This experiment has previously been attempted by Smyth (1968) and Krebs (1966) and failed in both cases, because of induced immigration into the cropped area. The cropping procedure was irregular. We began removing one half of all voles above 30 g every time we trapped, keeping species and sexes tallied separately. This was apparently an excessive removal rate and we lowered it later to one-third of all voles above 30 g during each trapping period. When population size became very small we stopped cropping altogether to avoid extinction. We attempted to keep the two species in roughly equal numbers, so that sometimes we cropped one species but not the other.

Grid D was used to explore the general question of what happens if one removes a sample of voles from another population and seeds them into a vacant area. This can be viewed as one possible technique for producing expanding populations out of phase with the surrounding areas. A pilot experiment of this type was tried by Krebs (1966, p. 248). Grid D was trapped out in the summer and fall of 1965 and then seeded on February 22, 1966 with 18 *M. ochrogaster* (4 ♂♂, 14 ♀♀) taken from a field which was at peak density just south of Yellowwood Lake (4.8 km NE of study area). This grid thus differs from the other three in being a single-species population.

The populations on grids B, C, and D were removed beginning July 10, 1967, and this set of experiments was terminated.

Results

Grid A.—Microtus pennsylvanicus began increasing in summer 1965 as this study began (Fig. 2). The explosive increase in the summer and fall of 1965 (15% per week) tapered to a slower increase rate (5% per week) during the winter

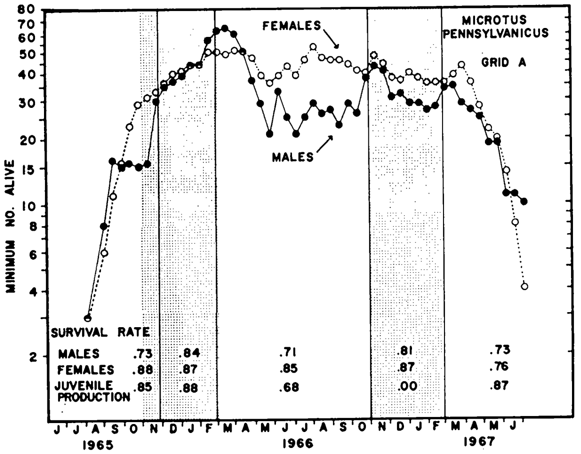

FIG. 2. Population changes in *Microtus pennsylvanicus* on unfenced grid A, 1965–67. Vertical lines mark divisions between "summer" and "winter" breeding periods. Winter months (November to February) are shaded. Survival rates are mean survival per 14 days for the five periods. Juvenile production is the mean number of young recruited per lactation (cf. Table 8).

1965–66. The number of males declined markedly during early spring of the peak year 1966, falling 14% per week during April and May, and then remaining virtually stationary until October 1966, when an abrupt rise in the number of males partly offset the spring drop. Females showed neither the sharp spring drop in numbers nor the autumn rise found in males. The winter of 1966–67 was another period of stationary numbers, but a sharp decline began in late March 1967 in both sexes (8–9% per week decline). This decline was not excessively prolonged or severe, and numbers had begun recovering again in late summer 1967.

Microtus ochrogaster also began increasing in summer 1965 (Fig. 3), but the rate of increase was lower, averaging about 4% per week in summer 1965 and winter 1965–66. This slow increase was accompanied by many reversals and the whole increase phase was very irregular compared with that in *M. pennsylvanicus*. The peak phase was short, July to early October 1966, and an extremely rapid decline began in early October 1966 (38% per week) and by early December the population was reduced to very low numbers. This decline in *M. ochrogaster* occurred while *M. pennsylvanicus* on the same area remained at peak numbers. The slight recovery which occurred at the end of this decline in December 1966 was produced by the immigration of unmarked subadult and adult voles. During the rest of winter 1966–67 numbers were low and stationary. A further decline occurred in April 1967 and only a few individuals were present through summer 1967.

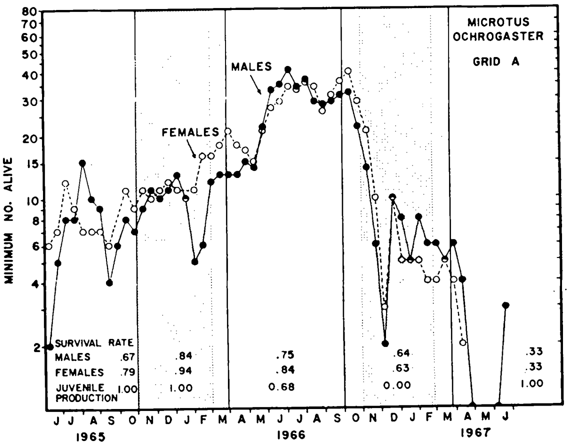

FIG. 3. Population changes in *Microtus ochrogaster* on unfenced grid A, 1965–67. Vertical lines mark divisions between "summer" and "winter" breeding periods. Winter months (November to February) are shaded. Survival rates are mean survival per 14 days for the five periods. Juvenile production is the mean number of young recruited per lactation (cf. Table 8).

Both species were thus in phase, reaching peak populations in the same year, 1966. In *M. ochrogaster* the increase was less intense and more prolonged and the decline much earlier and more severe, compared with that in *M. pennsylvanicus* living on the same area.

Grid B.—These fenced but otherwise unmanipulated populations also began to increase in summer 1965. *Microtus pennsylvanicus* increased during this time at a rate slightly higher than did grid A (Fig. 4), but the differences in density between grids A and B were small through winter 1965–66. Then in the spring of the peak year densities on these two areas diverged sharply, grid A remaining constant and grid B increasing to very high numbers by August 1966. Over four times as many *M. pennsylvanicus* were present on grid B as on grid A during late summer 1966. This high density in the fenced area B resulted in severe overgrazing, even during the growing season, and by late September much of the grass was grazed to ground level. During October and November 1966 this population declined at an average rate of 18% per week, from 292 voles to 55. During this decline some vegetation recovery occurred, and through the remainder of winter 1966–67 numbers fell much more slowly. This slow fall continued through the spring and early summer of 1967, with only a slight recovery being made in July as the experiment was terminated.

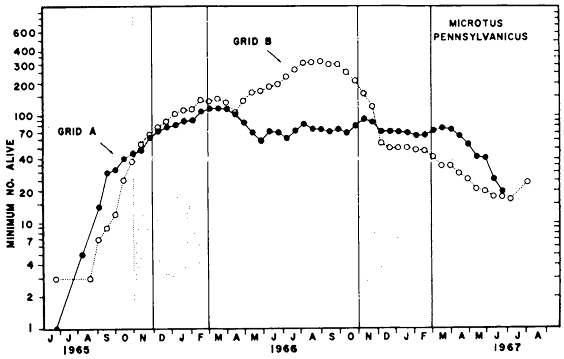

FIG. 4. Population changes in *M. pennsylvanicus* on fenced grid B contrasted with those on unfenced grid A, 1965–67.

Microtus ochrogaster numbers on grid B also diverged sharply from those on grid A (Fig. 5). From low numbers in summer 1965 the grid B population increased rapidly to a peak in February 1966 at an average rate of 9% per week, over twice the rate of increase of grid A. Numbers fell slowly from February to June 1966 and then rose sharply back to about the same level by September 1966. During October and November 1966 this population declined at an average rate of 11% per

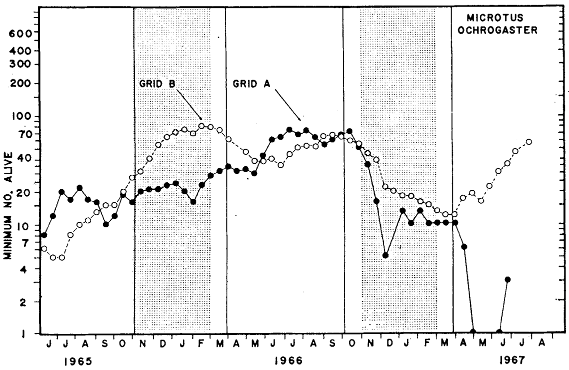

FIG. 5. Population changes in *M. ochrogaster* on fenced grid B contrasted with those on unfenced grid A, 1965–67.

week, from 64 voles to 22. This decline coincided with the *M. pennsylvanicus* decline and severe overgrazing. During the rest of the winter of 1966–67 numbers continued to fall, but began recovering again in spring 1967 at an increase rate of 11% per week, similar to the population trend 2 years previous. Peak densities of *M. ochrogaster* were nearly identical on grids A and B.

Fencing the grid B population thus produced higher rates of population increase than occurred on unfenced grid A. This resulted in *M. pennsylvanicus* reaching a density level on grid B about four times that on grid A, severe overgrazing, and a sharp population drop. Such high density, and associated overgrazing, has not been encountered anywhere in a natural population during this study. Thus simply fencing a population of these voles has serious repercussions on population density regulation.

Grid C.—The fence effect described above for grid B unfortunately confounds the interpretation of population density changes associated with cropping this fenced population. Figure 6 shows population changes in the grid C population of *M. pennsylvanicus*. Unfortunately we overestimated what peak density to expect on grid A and while we thought we were cropping the population around a low level of 40–60 voles, this turned out to be nearly peak densities in these populations. This experiment thus inadvertently became a cropping experiment on a high-density population rather than on a low- to moderate-density one. Differences between grids C and A are shown more clearly in Figure 7, which plots the rate of population density increase against time. This shows that grid C consistently maintained much higher increase rates through the autumn of 1966, when cropping was stopped for the winter. A temporary renewal of heavy cropping in March 1967 also seemed to stimulate population growth of the remainder in spring 1967.

Microtus ochrogaster was also cropped on grid

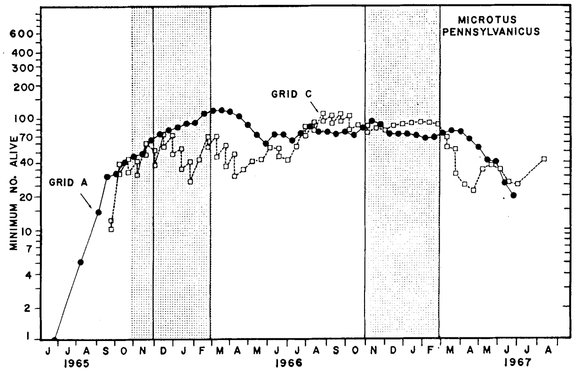

FIG. 6. Population changes in *M. pennsylvanicus* on fenced grid C, contrasted with those on unfenced grid A, 1965–67. Vertical drops in population curve represent cropping of adult voles.

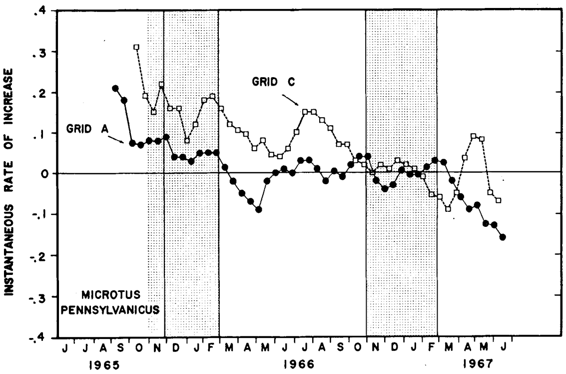

FIG. 7. Instantaneous rates of population increase in *M. pennsylvanicus* on fenced and cropped grid C, 1965–67, contrasted with those on unfenced grid A. Curves smoothed by three-point running average.

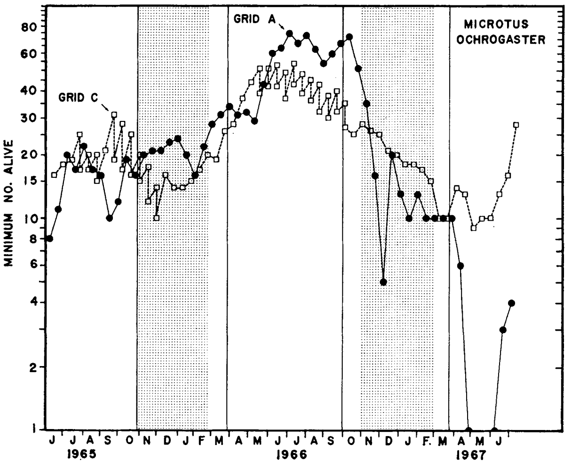

FIG. 8. Population changes in *M. ochrogaster* on fenced grid C, contrasted with those on unfenced grid A, 1965–67. Vertical drops in population curve represent cropping of adult voles.

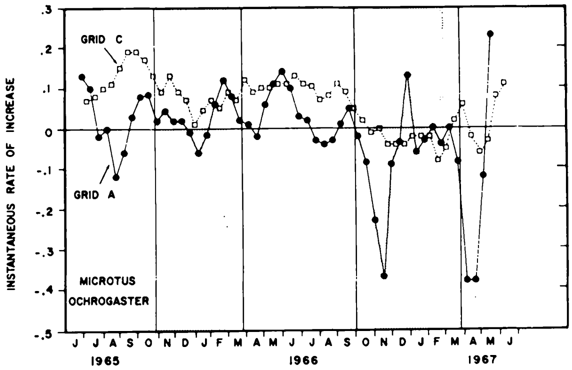

FIG. 9. Instantaneous rates of population increase in *M. ochrogaster* on fenced and cropped grid C, 1965–67, contrasted with those on unfenced grid A. Curves smoothed by three-point running average.

C with the same problems just described (Fig. 8). Figure 9 shows that this cropped population maintained higher rates of population increase on the average than grid A. The grid C population did not suffer the catastrophic decline in fall 1966 which occurred on grid A, but it decreased steadily through the winter of 1966–67. Some recovery occurred in spring 1967 on grid C and this experiment was then terminated.

Cropping these populations at relatively high densities in a fenced area thus resulted in an increased rate of population growth which strongly compensated for the continual removals.

Grid D.—The single species population of *M. ochrogaster* which was introduced into this vacant grid on February 22, 1966 increased very rapidly from the initial 18 colonizers (Fig. 10). From March to May 1966 this population increased about 23% per week and from June to September about 7% per week, reaching an extreme density just over 494 per hectare (200 per acre) in October and November 1966, 7 months after the introduction. This population remained very high through December and January, and began to decline in February 1967. The decline accelerated during March 1967 and reached a maximum rate for 2 weeks in mid-March when 54% of the population was disappearing per week (117 voles present on March 6 to 24 voles on March 20). This decline was associated with overgrazing of the habitat which was unable to support such a high vole density during the nongrowing season. A heavy wet snow during the second week of March may have helped to accelerate the decline. After falling to a low of 11 voles in early April 1967, this population began to increase in April and increased steadily at an average rate of 14% per week until the experiment was terminated on July 10, 1967.

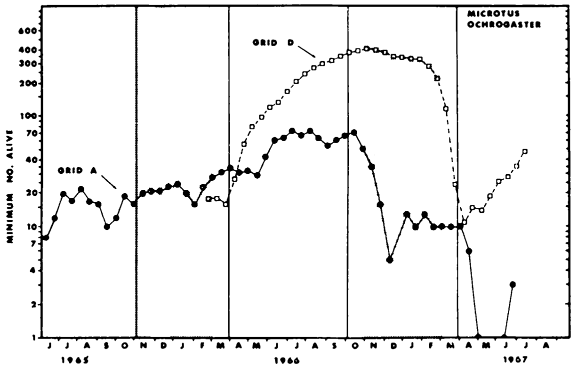

FIG. 10. Population changes in *M. ochrogaster* on grid D contrasted with those on unfenced grid A, 1965–67. Eighteen voles were introduced into vacant grid D on February 22, 1966.

The peak density of *M. ochrogaster* on grid D was almost equal to peak density of both *Microtus* species combined on grid B. The peak reached on grid D was over five times as high as that reached on grid A by *M. ochrogaster* (Fig. 10).

REPRODUCTION

Reproductive changes are assessed most accurately by a detailed autopsy program, and we report on this in another paper (Keller and Krebs MS in prep.). Only a crude measure of reproductive activity is obtained by recording the external appearance of live-trapped voles and we confine ourselves here to interpretations of gross changes in reproduction. We use the position of the testes as an index of reproductive condition in the males. The size of the nipples is an index of lactation for females, and the pubic symphysis of females becomes open for a few days before and after parturition. Females were recorded as obviously pregnant if they showed a bulging abdomen while being suspended for weighing. Probably only the last week of pregnancy could be detected this way.

Length of breeding season

The annual cycle of breeding in temperate zone *Microtus* can be divided into two segments, here called "summer" and "winter." The best variable to use for determining the breeding activity of a population is probably the percentage of females with medium to large nipples ("lactating"). This criterion will underestimate the start of active breeding by about 3 weeks, the length of the gestation period, and the following data are corrected for this time lag.

The summer 1965 breeding season tapered off by November for *M. ochrogaster* (Fig. 11) and by December for *M. pennsylvanicus* (Fig. 12). Breeding continued at a reduced rate throughout the winter of 1965–66 in both species, and picked up again in early March 1966 for *M. pennsylvani-*

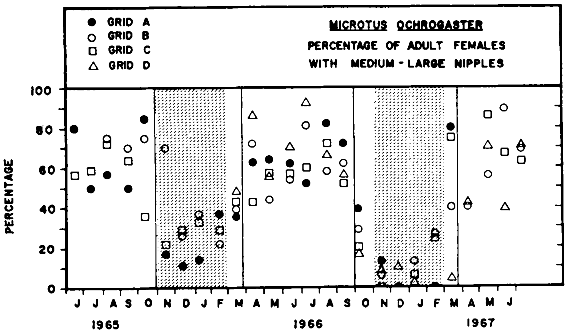

FIG. 11. Monthly percentages of "lactating" adult females in *M. ochrogaster* on all grids, 1965–67.

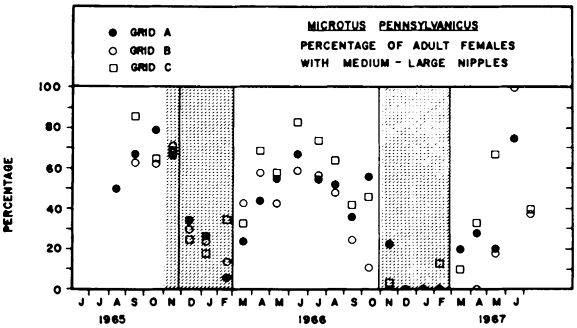

FIG. 12. Monthly percentages of "lactating" adult females in *M. pennsylvanicus* on all grids, 1965–67.

cus and late March for *M. ochrogaster*. Breeding continued through the peak summer of 1966 until late September for *M. ochrogaster* and late October for *M. pennsylvanicus*. In both species summer breeding began to fall off about 1 month earlier in the peak year 1966 than in the increase year 1965.

During the winter of 1966–67 female *M. pennsylvanicus* went completely out of breeding condition, but a few *M. ochrogaster* females remained in breeding condition. In *M. pennsylvanicus,* breeding resumed in late February and early March 1967, about the same time as the preceding year. In *M. ochrogaster* the normal level of breeding resumed in mid- to late-March 1967, similar to the previous year. There was little difference between the various grid populations in the timing of breeding seasons. In particular, the effects of fencing the B, C, and D populations and cropping the C populations have not changed the length of breeding seasons in any significant amount.

Two effects, in summary, are notable: (1) summer breeding ended about one month earlier in peak populations than in increasing populations; (2) extensive winter breeding occurred only during the winter of population increase and not during the winter following the peak.

Intensity of breeding

Major changes in the weight at sexual maturity, pregnancy rates, or prenatal mortality should register in at least some of the external sexual characteristics recorded in this live-trapping study. Data on these characteristics have been summed over summer and winter breeding periods delimited in Figures 11–12. These breeding periods are marked on all time-series figures in this paper, and are referred to as follows: period I—summer 1965; period II—winter 1965–66; period III—summer 1966; period IV—winter 1966–67; and period V—summer 1967.

Table 5 gives the various measures of breeding performance on both species for each live-trap grid. Data on the condition of the vaginal opening are not given because of the great variability found in this character and because it did not seem to respond closely to changes in reproductive performance. Chi-square analyses were employed in order to test: (i) for homogeneity among grids within periods (e.g. are the percentages of scrotal males significantly different between grids A, B, and C for summer 1965 in *M. ochrogaster?*) ; and (ii) for homogeneity among years (summers) within grids (e.g. are the percentages of scrotal males significantly different for grid A between summer 1965, summer 1966, and summer 1967 in *M. ochrogaster?*).

The reproductive data for *M. ochrogaster* are almost completely homogeneous. Of the 25 comparisons between grids, only 3 are significant. The winter 1966–67 data on nipple size are significantly heterogeneous ($P < .01$) but this is produced by the heterogeneity in March 1967 between grids (see Fig. 11). Two sets of the percentage of pregnancy data are also heterogeneous: winter 1965–66 and summer 1966, both because

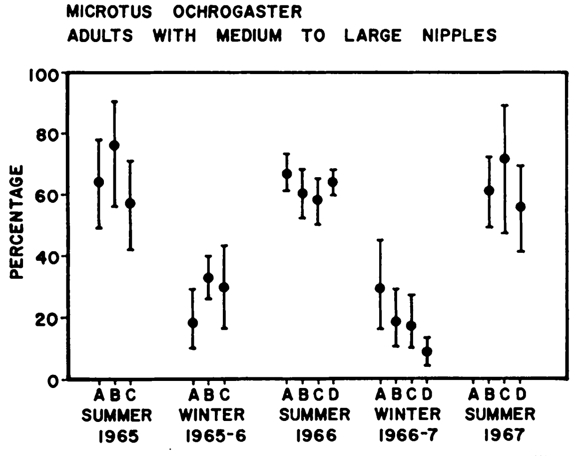

FIG. 13. Seasonal means for the percentage of "lactating" adult females in *M. ochrogaster,* 1965–67. Vertical limits represent 95% confidence intervals.

TABLE 5. Intensity of breeding as measured by external characteristics for all populations, 1965–67. Data are the proportions of appropriate individuals falling into each category,[a] summed over the entire breeding season. (Sample size in parentheses)

Season and group	*Microtus pennsylvanicus*			*Microtus ochrogaster*			
	Grid A	Grid B	Grid C	Grid A	Grid B	Grid C	Grid D
Summer 1965							
Testes scrotal							
Adults[b]	1.00 (74)	.98 (40)	.81 (26)	.93 (41)	.95 (59)	.92 (52)	—
Subadults[b]	.03 (40)	.23 (35)	.16 (19)	.60 (25)	.50 (10)	.56 (41)	—
Nipples medium to large							
Adults	.67 (129)	.64 (58)	.74 (53)	.64 (50)	.76 (29)	.57 (63)	—
Public symphysis open							
Adults[c]	.30	.35	.23	.16	.38	.21	—
Obviously pregnant							
Adults[c]	.16	.29	.13	.24	.34	.32	—
Winter 1965-66							
Testes scrotal							
Adults	.70 (84)	.61 (138)	.60 (106)	.73 (67)	.78 (214)	.64 (75)	—
Subadults	.06 (34)	.00 (52)	.04 (48)	.09 (23)	.17 (53)	.17 (23)	—
Nipples medium to large							
Adults	.24 (108)	.22 (97)	.30 (96)	.18 (82)	.33 (218)	.30 (61)	—
Public symphysis open							
Adults[c]	.21	.10	.12	.07	.12	.12	—
Obviously pregnant							
Adults[c]	.07	.12	.15	.02	.17	.26	—
Summer 1966							
Testes scrotal							
Adults	.98 (354)	.96 (502)	.95 (237)	.98 (252)	.95 (204)	.98 (157)	.96 (805)
Subadults	.25 (68)	.22 (582)	.21 (141)	.43 (75)	.54 (76)	.53 (87)	.43 (204)
Nipples medium to large							
Adults	.44 (431)	.44 (641)	.61 (296)	.67 (273)	.61 (223)	.58 (188)	.64 (831)
Pubic symphysis open							
Adults[c]	.27	.17	.16	.19	.18	.16	.17
Obviously pregnant							
Adults[c]	.10	.12	.14	.12	.30	.22	.27
Winter 1966-67							
Testes scrotal							
Adults	.46 (56)	.06 (16)	.35 (106)	.62 (37)	.60 (102)	.58 (69)	.62 (572)
Subadults	.07 (125)	.03 (157)	.00 (99)	.25 (79)	.15 (33)	.11 (27)	.17 (241)
Nipples medium to large							
Adults	.10 (61)	.00 (10)	.03 (58)	.29 (45)	.18 (83)	.17 (101)	.08 (1272)
Pubic symphysis open							
Adults[c]	.05	.00	.00	.04	.00	.02	.02
Obviously pregnant							
Adults[c]	.02	.00	.00	.00	.01	.04	.04
Summer 1967							
Testes scrotal							
Adults	.93 (122)	.91 (35)	.93 (60)	.60 (5)	.89 (37)	1.00 (8)	.96 (23)
Subadults	.37 (38)	.52 (25)	.46 (26)	.50 (10)	.68 (44)	.46 (37)	.48 (42)
Nipples medium to large							
Adults	.23 (123)	.31 (32)	.37 (67)	1.00 (4)	.61 (92)	.71 (21)	.56 (61)
Pubic symphysis open							
Adults[c]	.15	.16	.05	.00	.11	.00	.05
Obviously pregnant							
Adults[c]	.09	.06	.05	.50	.10	.14	.18

[a] For example, in the second column of the second row, 23% (0.23) of the 35 subadult males had scrotal testes.
[b] Adults defined as 34 g or heavier; subadults, 22–33 g.
[c] These are the same females as in the nipple-size category preceding, hence, sample size is the same.

of the very low pregnancy rate for grid A. This apparent difference between grid A and the other areas is not substantiated in either the nipple size data (Fig. 13) or the pubic symphysis data; it may represent a bias in judging which females are "obviously pregnant."

In contrast to this, the *M. pennsylvanicus* reproductive data are quite heterogeneous. The principal effect of significance is a general trend toward lower reproductive performance in the series of summers: 1965 > 1966 > 1967. This effect occurs on all grids and is significant in most of the characteristics measured. The percentage of adults with scrotal testes decreases from 1965 to 1967, while that of subadults increases over this time. The percentages of females with me-

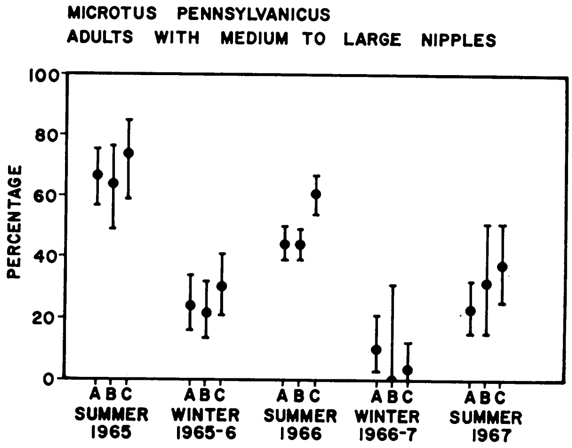

FIG. 14. Seasonal means for the percentage of "lactating" adult females in *M. pennsylvanicus,* 1965–67. Vertical limits represent 95% confidence intervals.

dium to large nipples (Fig. 14), with open pubic symphysis, and obviously pregnant, all decrease from 1965 to 1967. This unanimity of change suggests a significant decline in total reproductive output from the increase summer of 1965 to the peak summer of 1966 to the decline summer of 1967.

Differences between grids which are significant are listed below for *M. pennsylvanicus:*

Characteristic	Time period	Reason
Testes—adults	Summer 1965	grid C low
Testes—subadults	Winter 1966–67	grid B low
Nipple size	Summer 1965	grid A low
Pubic symphysis	Winter 1966–67	grid A high
	Summer 1966	grid C high
	Winter 1965–66	grid A high
	Summer 1966	grid A high

These differences are not all readily explained. The low percentage of scrotal adults in grid B during the winter of 1966–67 followed the period of habitat destruction and malnutrition. Possibly the other differences are consequences of the same causes which produced the general decline in reproductive output from 1965 to 1967.

To summarize, total reproductive intensity during the summer breeding season, as measured by crude external sexual characteristics, seemed constant and independent of the population trends in *M. ochrogaster.* In *M. pennsylvanicus* there was a generalized trend toward lower reproductive effort in the sequence of summers 1965 > 1966 > 1967, corresponding with the increase, peak, and decline phases of the cycle. Reproductive changes were similar in both fenced and unfenced populations.

MORTALITY

Mortality in a live-trapping study is equated with disappearance from the trappable population and thus includes emigration. We are interested here in temporal changes in survival rates, measured by direct enumeration. Two components are discussed: survival in the trappable population; and early juvenile survival.

Survival in the trappable population

Survival rates enumerated in the trappable population refer mainly to the adult and subadult components of the population.

Do adults, subadults, and juveniles caught in live traps have the same survival rates? We know that survival rates are different between males and females (see below) and hence we segregate sexes in this analysis. Tables 6 and 7 give the mean survival rates for these weight groups in the two *Microtus* species. These survival rates are summed over whole seasons to provide these data, and an individual vole is tallied each time it is trapped.

Data on the juvenile weight class (< 22 g) are very few and inadequate for detailed analysis. We concentrate here on the subadult (22–33 g) and adult (> 33 g) groups. If we look for heterogeneity in these two groups for each season and each grid separately, we find no significant differences in *M. ochrogaster* except for grid A, summer 1966, when the survival rate of subadult males was significantly lower than that of adult males. In *M. pennsylvanicus* most of the six heterogeneous groups are in summer 1966, where all the females and the grid B and grid C males showed subadult survival rates significantly below adult survival rates. The same occurred in *M. pennsylvanicus* females on grid A in summer 1965. These differences range from about .05 to .21 in magnitude, and average .13 per 2 weeks.

We conclude that subadult males and females of *M. pennsylvanicus* did have lower survival rates than adults particularly during the summer breeding season when densities were high. In winter survival rates were always similar for adults and subadults in both *Microtus* species. In summer survival of *M. ochrogaster* subadult males may be reduced compared with that of adult males, but no clear evidence for this can be seen in subadult females.

Figure 15 presents total survival rates for *M. pennsylvanicus* on grid A. Two points are shown: (1) female survival rates were high, relatively constant, and independent of density until spring 1967 when the population declined; and (2) male survival rates were highly variable, showing periods of very poor survival sporadically through-

TABLE 6. *Microtus pennsylvanicus* minimum survival rates per 14 days. (Sample size in parentheses)

Season and Group	Males Grid A	Males Grid B	Males Grid C	Females Grid A	Females Grid B	Females Grid C
Summer 1965						
Adults	.77 (68)	.85 (39)	.93 (15)	.93 (110)	.93 (58)	.91 (32)
Subadults	.62 (26)	.89 (35)	.82 (17)	.57 (21)	.94 (33)	.93 (14)
Juveniles	.60 (5)	–	.64 (11)	1.00 (6)	.75 (4)	1.00 (6)
Winter 1965-66						
Adults	.87 (86)	.89 (135)	.88 (58)	.88 (106)	.89 (93)	.95 (60)
Subadults	.81 (47)	.88 (52)	.88 (43)	.89 (57)	.92 (85)	.92 (49)
Juveniles	.67 (6)	1.00 (8)	.89 (9)	.60 (10)	1.00 (11)	1.00 (5)
Summer 1966						
Adults	.73 (339)	.81 (587)	.86 (169)	.87 (410)	.86 (790)	.91 (224)
Subadults	.63 (60)	.76 (608)	.68 (128)	.78 (94)	.76 (626)	.70 (141)
Juveniles	.45 (11)	.86 (76)	.78 (9)	.83 (12)	.79 (169)	.77 (13)
Winter 1966-67						
Adults	.77 (65)	.55 (22)	.93 (75)	.87 (77)	.67 (18)	.82 (45)
Subadults	.85 (127)	.68 (212)	.87 (93)	.88 (144)	.66 (224)	.95 (163)
Juveniles	.63 (19)	.23 (13)	–	.84 (25)	.66 (32)	1.00 (3)
Summer 1967						
Adults	.73 (118)	.80 (30)	.67 (66)	.77 (122)	.68 (25)	.84 (61)
Subadults	.69 (32)	.73 (22)	.57 (23)	.78 (87)	.87 (53)	.74 (50)
Juveniles	.82 (11)	–	.80 (10)	.43 (7)	1.00 (9)	.77 (13)

TABLE 7. *Microtus ochrogaster* minimum survival rates per 14 days. (Sample size in parentheses)

Season and Group	Males Grid A	Males Grid B	Males Grid C	Males Grid D	Females Grid A	Females Grid B	Females Grid C	Females Grid D
Summer 1965								
Adults	.79 (34)	.98 (47)	.97 (32)	–	.80 (44)	.96 (23)	.98 (43)	–
Subadults	.58 (24)	.87 (8)	.86 (36)	–	.69 (16)	1.00 (7)	1.00 (15)	–
Juveniles	.14 (7)	–	1.00 (5)	–	.71 (7)	–	1.00 (6)	–
Winter 1965—66								
Adults	.86 (73)	.88 (222)	.93 (56)	–	.92 (87)	.91 (22[illegible])	.92 (47)	–
Subadults	.79 (24)	.76 (55)	.89 (18)	–	1.00 (31)	.89 (54)	.83 (12)	–
Juveniles	.67 (3)	.64 (11)	1.00 (4)	–	1.00 (3)	.73 (11)	1.00 (8)	–
Summer 1966								
Adults	.83 (234)	.91 (181)	.91 (129)	.94 (661)	.87 (248)	.87 (197)	.96 (147)	.94 (717)
Subadults	.47 (66)	.82 (65)	.90 (83)	.97 (177)	.78 (50)	.81 (47)	.91 (68)	.95 (157)
Juveniles	.82 (17)	.91 (22)	.90 (19)	.94 (32)	.74 (19)	1.00 (9)	.90 (30)	.86 (49)
Winter 1966—67								
Adults	.65 (51)	.82 (120)	.90 (63)	.90 (1491)[a]	.69 (65)	.89 (99)	.93 (91)	.93 (1114)[a]
Subadults	.62 (84)	.75 (44)	.83 (24)	.96 (124)[a]	.66 (86)	.83 (93)	.83 (42)	.95 (350)[a]
Juveniles	.90 (10)	.67 (3)	1.00 (2)	1.00 (11)[a]	.64 (11)	1.00 (5)	.50 (2)	.92 (12)[a]
Summer 1967								
Adults	.60 (5)	.95 (19)	.80 (5)	1.00 (9)	.25 (4)	.94 (68)	.68 (19)	.81 (43)
Subadults	.13 (8)	.82 (34)	.87 (30)	.90 (31)	.50 (2)	.81 (26)	.80 (20)	.84 (25)
Juveniles	.50 (2)	.93 (15)	.86 (7)	.88 (8)	–	1.00 (7)	1.00 (4)	.92 (13)

[a] The period of population decline from February 6 to April 8, 1967 excluded from these totals. For this decline period survival rates were: adult males, .51 (209); subadult males, .54 (44); adult females, .59 (261); and subadult females, .59 (90).

out the cycle. These periods of poor male survival were reflected in some of the density changes (Fig. 2), e.g. October–November 1965, April–May 1966. Note that the low survival rate in early December 1966 in both sexes was a result of fox (*Urocyon cineroargenteus*) depredation on the live traps during a trapping period. The male survival rates are not well correlated with female survival rates (r = .37, n = 46) and consequently the loss process must be sex selective.

Total survival rates for *M. ochrogaster* on grid A are shown in Figure 16. Except for a period in July 1965 female survival rates again tended to be high and fairly constant, while male survival

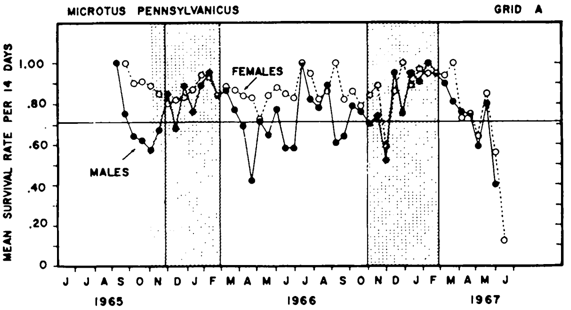

FIG. 15. Mean survival rate per 14 days for male and female *M. pennsylvanicus* on unfenced grid A, 1965–67. Horizontal line is an arbitrary division at a survival rate of 0.71; survival rates below this line represent losses of more than 50% of the population every 4 weeks.

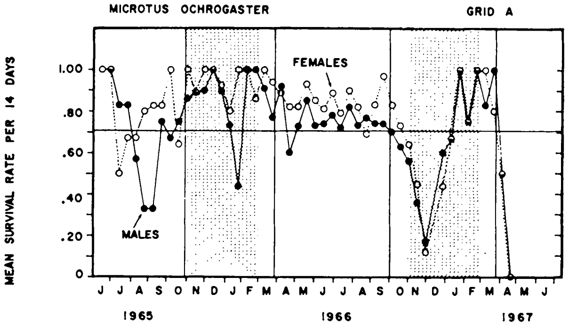

FIG. 16. Mean survival rate per 14 days for male and female *M. ochrogaster* on unfenced grid A, 1965–67. Horizontal line is an arbitrary division at a survival rate of 0.71; survival rates below this line represent losses of more than 50% of the population every 4 weeks.

rates showed three periods of very poor survival in 1965 and early 1966. Both sexes showed greatly reduced survival rates during the population decline in fall 1966 (cf. Fig. 3). Correlation between male and female survival rates in this population of *M. ochrogaster* is good ($r = .73$, $n = 55$), and this reflects principally the correspondence found during the decline phase. There is no correlation between the survival rates of these two *Microtus* species living side by side on the same area ($r = .19$, $n = 44$). The large decline in *M. ochrogaster* during fall 1966 was not reflected in the survival rates of *M. pennsylvanicus*. None of the sporadic periods of low survival in *M. pennsylvanicus* males corresponds with similar type of periods in *M. ochrogaster* males. *From this we conclude that the factors causing low survival rates in these vole populations are species specific, and within a species, often sex specific.*

Tables 6 and 7 show how fencing affected survival on grids B, C, and D. The fenced populations all had higher survival rates, often approaching 100%, during the increase and early peak phase in *M. pennsylvanicus* and throughout this study in *M. ochrogaster*. This effect seemed to begin as soon as the fence was set out in June 1965. Associated with this high survival in the fenced populations is the absence of sporadic periods of high mortality in males, as shown by the unfenced populations. On grid B there were no periods of high mortality during the increase and peak phases until the habitat destruction in fall 1966 caused reduced survival. On grid D exactly the same pattern emerged—continuous high survival in both sexes until the habitat became seriously damaged and then a population decline with low survival rates. Both *Microtus* species seemed to respond quickly after these habitat destructions, since on grids B and D, the survival rates of these species were similar in the summer before the habitat destruction and in the summer after.

The effect on survival of cropping the grid C population cannot be clearly dissociated from the fence effect. Both species maintained very high survival rates on this area, *M. ochrogaster* throughout the study and *M. pennsylvanicus* through the winter of 1966–67. Survival deteriorated in *M. pennsylvanicus* during the period of high density in August–September 1966 and again in the spring and summer of 1967 after a winter of high density and good survival.

Most instances of low male survival in these two species were apparently not selective for a particular weight group. There are however times when mortality seems to fall heavily and selectively on subadults of one sex but not on adults of the same sex or either group of the opposite sex. For example, during November and December 1965 *M. pennsylvanicus* subadult females on grid A showed low survival rates while adult females had high survival rates. During June and July 1966 *M. ochrogaster* subadult males on grid A had a very low survival rate while adult males and females and subadult females had high survival rates (Fig. 17). We can detect no clear pattern in when and where to expect this weight-group specific mortality to occur. This type of mortality was much less common in the enclosed populations (B, C, and D) of both species.

To summarize, survival in the trappable population of both species on unfenced grid A tended to be high and relatively constant in females throughout the cycle until the decline, while in males sporadic periods of low survival punctuated both the increase and peak phases. Survival rates did not correlate between the two species living side by side on the same area. In the fenced populations survival rates were very high in both

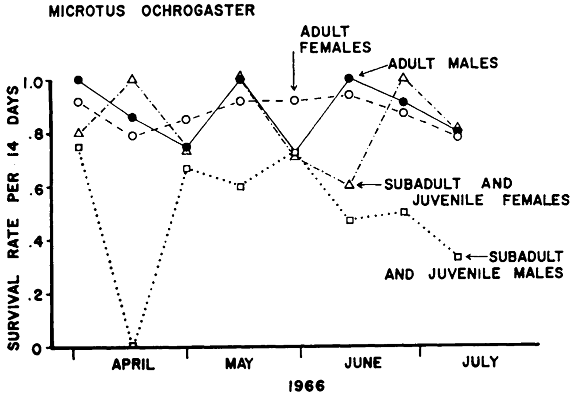

FIG. 17. Minimum survival rates per 14 days for *Microtus ochrogaster* sex and weight groups during an episode of selective high mortality, grid A.

sexes and no sporadic periods of low survival occurred in males.

Early juvenile survival

Since few juveniles are caught in live traps, direct observations on survival during the possibly critical period from weaning to reaching trappable size at approximately 25 g (from about 2 to 6 weeks of age) are rare. We attempt to measure survival in this period by an index relating recruitment of young into the trappable population to the number of possibly lactating females (Krebs 1966):

$$\text{index}_t = \frac{\text{no. new voles less than 30 g in week } t}{\text{no. females with medium-large nipples caught in week } (t\text{-}4)}$$

Because of our high trapping intensity we feel that changes in this index provide a reasonably reliable indicator of large changes in early juvenile survival.

Table 8 gives the mean indices for both species, and from these data we make three points. First, early juvenile survival was apparently reduced about 20–30% during the peak summer on grid A, but was otherwise the same during the increase summer of 1965 and the decline summer of 1967 in both species. Thus the population decline was not associated with poor early juvenile survival. Second, the cropped grid C population of both species showed very high juvenile survival indices, at times twice as high as those on uncropped and unfenced grid A. Third, the fenced grid B population had even higher indices than grid C for *M. pennsylvanicus* during the summers of 1965 and 1966. The index remained high during the summer of 1966 on grid B and this was the main reason why this population reached a very high density in fall 1966 (Fig. 4). In contrast, *M. ochrogaster* on grid B did not show indices any higher than those found on unfenced grid A. Even during the rapid population increase in 1965 on grid B (Fig. 5) *M. ochrogaster* did not have higher indices of early juvenile survival, and this suggests that population density changes are not closely correlated with the early juvenile survival rate in this species. On grid B the low index of summer 1966 in *M. ochrogaster* resulted in a peak population on grid B which did not differ greatly from that on grid A. Finally, the introduced grid-D *M. ochrogaster* population had very good early juvenile survival for the first 3 months, but this

TABLE 8. Mean indices[a] of early juvenile survival. Ranges are based on samples including three or more females

		Grid A		Grid B		Grid C		Grid D	
Species	Season	Mean	Range	Mean	Range	Mean	Range	Mean	Range
M. pennsylvanicus	Summer 1965	0.9	0.5–1.2	2.4	1.5–2.5	1.2	0.8–1.5	–	–
	Winter 1965-66	0.9	0.4–2.0	1.5	1.2–2.5	2.5	1.3–4.5	–	–
	Summer 1966	0.7	0.0–2.2	1.5	0.8–3.7	1.0	0.1–3.0	–	–
	Winter 1966-67	..	–	–	–	1.4[b]	0.5–1.6	–	–
	Summer 1967	0.9	0.3–1.7	0.7	–	1.3	0.0–2.2	–	–
M. ochrogaster	Summer 1965	1.0	0.2–1.7	0.6	–	1.5	0.8–2.0	–	–
	Winter 1965-66	1.0	–	1.0	0.4–3.0	2.1	–	–	–
	Summer 1966	0.7	0.1–2.0	0.5	0.1–1.1	1.2	0.6–2.2	1.7	1.2-3.8 (March to May)
								0.4	0.3–0.6 (June to Sept.)
	Winter 1966-67	–	–	–	–	–	–	0.4	0.1–0.6
	Summer 1967	1.0	–	1.0	0.5–2.2	1.3	–	1.8	0.3–2.7

[a] No. of young trapped per lactating female.
[b] Early winter breeding only, Nov. 1 to Dec. 17, 1966.

quickly deteriorated to poor juvenile survival once high density was reached. In spite of the low indices during the summer and fall of 1966, this grid D population continued to increase until November 1966.

To summarize, the survival of voles between weaning and trappable size (c. 25 g) does not seem to be correlated closely with population density changes. A high rate of early juvenile survival is not necessary for rapid increase, and a low rate is not sufficient to cause a decline.

GROWTH

Growth rates of voles are highly variable and provide a further index of conditions within the population. Three aspects of growth are considered here: Individual growth rates for body weight; body weight distributions; and individual growth curves.

Growth rates

Growth rates were calculated as instantaneous relative growth rates in per cent increase per day. Only male voles caught at 2- or 4-week intervals were used. Data for each 4-week period were condensed by the use of linear regression between mean body weight and growth rate for each time period. These regressions change from month to month in slope and elevation. A single representative growth rate was calculated from each regression by adjusting the growth rate to a hypothetical 35-g vole. These adjusted mean growth rates seem to describe adequately the pattern of growth changes in these populations.

Adjusted growth rates for *M. ochrogaster* are shown in Figure 18 and for *M. pennsylvanicus* in Figure 19. Two general points are shown by these figures: (1) growth rates were much lower during the winter 1966–67 than the previous winter 1965–66; and (2) spring growth rates were lower in 1967 than in 1966 when the populations were at peak densities. More specific changes for each grid are summarized as follows:

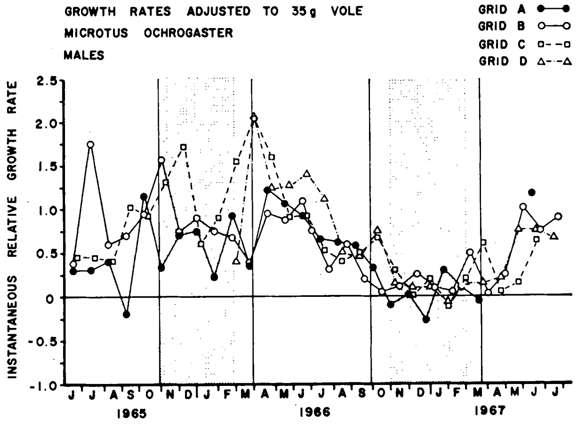

FIG. 18. Growth rate changes in *Microtus ochrogaster* males, 1965–67. Data grouped into 4-week periods, and adjusted by regression to a standard 35-g vole.

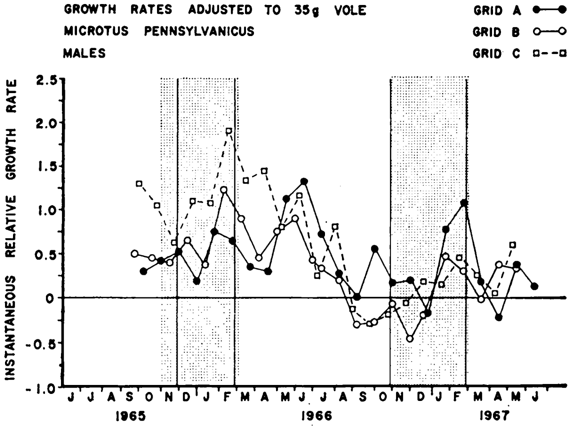

FIG. 19. Growth rate changes in *Microtus pennsylvanicus* males, 1965–67. Data grouped into 4-week periods, and adjusted by regression to a standard 35-g vole.

Grid A.—Growth rates were low in *M. ochrogaster* during summer 1965 as the increase phase began but they remained moderate to low through the following winter when winter breeding occurred. High growth rates in both species were reached in spring and early summer of 1966, the peak phase, but these fell off steadily through the summer and fall to values near zero in the winter of 1966–67. *M. ochrogaster* retained near-zero growth rates through this winter, after the population declined, and the few animals present in midsummer 1967 had high growth rates at that time. *Microtus pennsylvanicus* showed an anomalous spurt of growth during January and February 1967, just before the population began to decline, but these high growth rates were not sustained into the spring of 1967 and growth was particularly poor from March to June during the population decline.

Grid B.—During the rapid increase of *M. ochrogaster* on this fenced area, growth rates were typically greater than those on grid A. This trend is reversed in summer 1966 when grid B voles showed slightly lower growth rates than those of grid A. During the winter of 1966–67 after the catastrophic decline associated with habitat destruction, growth rates of *M. ochrogaster* were very low, but perhaps slightly above those of grid A animals. Spring 1967 growth rates were very low but high growth rates returned by early summer as this population began increasing again. *Microtus pennsylvanicus* growth rates on this grid were slightly above those of grid A during winter 1965–66 and spring 1966 when this population was increasing rapidly. By July 1966 a rapid deterioration in growth began which culminated in negative growth rates during fall 1966 when the catastrophic population decline occurred. Growth rates remained negative through early winter but recovered to a moderate level in January and February 1967. Spring growth was poor in 1967 and the population continued its decline.

Grid C.—Cropping this population seemed to produce a substantial increase in growth rates until both species reached relatively high densities in late spring 1966. After this point growth rates were not unusually high or particularly different from those on other grids.

Grid D.—This introduced *M. ochrogaster* population had very high growth rates during its rapid population expansion from March to July 1966. In spite of its very high density from August 1966 to February 1967, growth rates were not unusually low but similar to those of grid A voles. After the catastrophic population decline in March–April 1967, when growth rates remained very low, the population began to increase in May and growth rates returned to a moderately high level.

Thus there is a general pattern of high growth rates associated with periods of population increase. Winter growth rates were good during the period of winter breeding but near zero during the following winter, after the peak, when no significant breeding occurred.

Body weight distributions

Figures 20 and 21 show the monthly body weight distributions for males of the two species. The trapping period closest to the middle of the month was utilized for these data. These figures show strikingly the change in maximum size over the population cycle—increasing and peak populations are characterized by adults of large body size. In *M. ochrogaster* (Fig. 21) there were almost no voles above 40 g except during the increase and peak phases. In *M. pennsylvanicus* (Fig. 20) there were many voles above 46 g during the increase and peak. These large animals disappeared during the winter of 1966–67 after the peak. A sudden spurt of growth (Fig. 19) in early spring 1967 produced March weight distributions which essentially were identical with those of the previous March. But as the population declined these large males were eliminated and almost no large voles were seen during summer 1967.

We do not present data here for the other grid populations. They were very similar to the grid A data just presented, except that neither grid B nor grid C *M. pennsylvanicus* populations showed the large-sized voles that occurred on grid A during spring 1967.

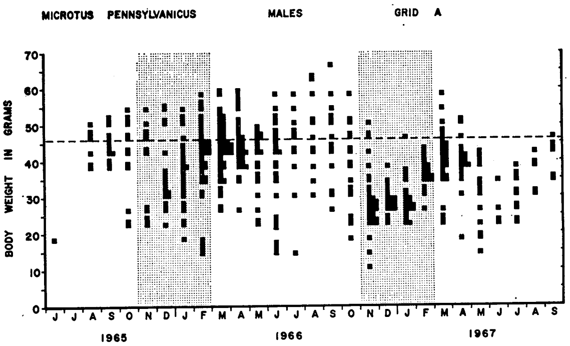

FIG. 20. Body weight distributions of *Microtus pennsylvanicus* males from grid A, 1965–67. Each small square represents one vole. Data grouped into 4-g intervals.

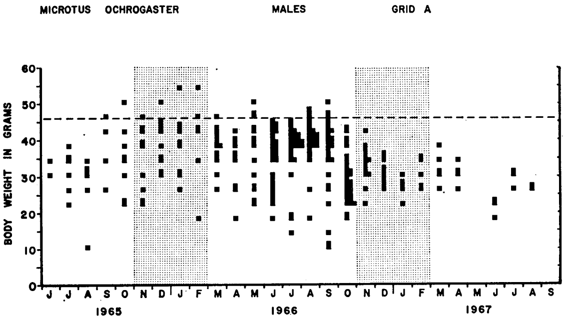

FIG. 21. Body weight distributions of *Microtus ochrogaster* males from grid A, 1965–67. Each small square represents one vole. Data grouped into 4-g intervals.

Peak and expanding populations of *M. ochrogaster* and *M. pennsylvanicus* thus seem to be characterized by adult males of large size in much the same manner as other cyclic microtines (Krebs 1964, p. 51).

Growth curves

An explanation of why some phases of the cycle have larger sized adults must ultimately come down to an analysis of individual voles and their course of growth. The difficulty here is that relatively few voles live long enough and are recaptured often enough to provide a detailed growth curve. Some selected cases from grid A for both species are shown in Figure 22.

Two general observations may be made from these data and that of other individuals not given here. First, many of the large-sized adults were already large when first captured (e.g. A-57, A-52; Fig. 22). Data on the earlier growth of these voles would be most desirable. A few cases of growth from subadult size to large-sized adults are available (A-166, A-131) to suggest that these large voles are not just very old ones. Second,

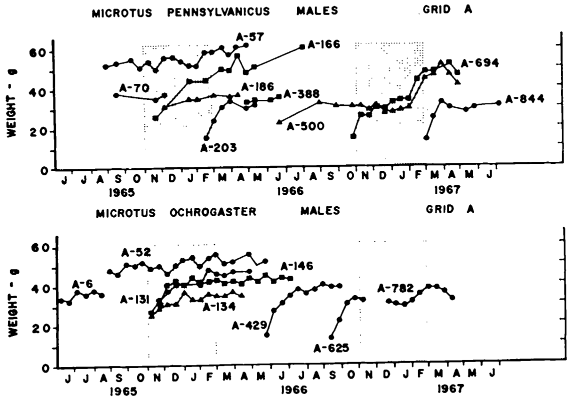

FIG. 22. Selected growth curves for individual male *Microtus pennsylvanicus* and *M. ochrogaster* from grid A, 1965–67.

many animals reach stable asymptotes of weight (A-186, A-134) at small adult body size. In many cases these individuals stopped growth when other voles are growing at moderate to high rates (cf. Figs. 18, 19). Some cases of stable asymptotes occurred at the end of the 1966 growing season in *M. pennsylvanicus* and low body weights were retained over the winter of 1966–67 (e.g. A-500) when growth rates were nearly zero. Some of these overwintered small *M. pennsylvanicus* increased to high body weights in early spring 1967 (A-500, A-694). One juvenile *M. pennsylvanicus* born in spring 1967 during the population decline seemed to stop growing at a very low body weight. Very few *M. ochrogaster* were caught in 1967 and growth data after the population decline were few.

Thus we conclude that, although many voles do not survive long enough to reach their full adult size, some voles do reach asymptotic weights and these asymptotes may be at a range of values from small to large body size.

DISCUSSION

Two difficulties plague studies of small mammal populations and decrease the utility of much of the research reported in the literature. First, reasonably accurate census information at closely spaced intervals is a prerequisite for discussions of population processes. Yet many workers continue to sample at monthly intervals or longer, using estimation procedures like the Lincoln Index without any attention to the assumptions involved. Second, studies which escape the first problem often fail to achieve the transition from a simple description of demographic changes to testing postulated causal relationships. The converse of this second difficulty is also common. Many of the hypotheses proposed to explain population changes in small rodents are argued on the basis of more or less detailed information on the supposed causal factor and very little data on the population processes which require explanation.

The outcome of this is the current situation in which the number of theories proposed to explain population fluctuations in rodents is larger than the number of good descriptions of the variations in birth, death, and growth rates which accompany the population density changes. We will consider here demographic events in *Microtus pennsylvanicus* and *M. ochrogaster* populations. This is part of a continuing effort to provide a descriptive background of periodic fluctuations in rodents and to test causal hypotheses (Krebs 1964, 1966).

Population density

Unfenced populations.—*Microtus pennsylvanicus* is widely believed to undergo periodic fluctuations throughout its range, but few data are available which show the detailed pattern of density changes in this species. Hamilton (1937), the basic reference for this vole, described a pattern of slow buildup in his New York populations over 2 years and then a rapid decline over apparently a few months in the spring. The explosive increase found in the present study was not found in Hamilton's populations. Golley (1961) followed density changes in a *M. pennsylvanicus* population in southern Michigan for 1 year, apparently during the increase and early peak phases of the cycle. His population changes closely resemble ours for grid A (Fig. 2) for the first half of the cycle. Highest density was reached in February 1957, 136–148 per hectare (55–60 per acre) (Golley 1961, Fig. 1). Getz (1960) also followed *M. pennsylvanicus* population changes in southern Michigan for 1 year, apparently during a phase of low numbers. His populations did not exceed 17 per hectare (7 per acre) in one area and 62 per hectare (25 per acre) in another area and showed an annual cycle of summer increase and winter decrease in numbers. Bole (1939) recorded *M. pennsylvanicus* densities in rich meadows in the Cleveland area between a high of 210 per hectare (85 per acre) and a low of 35 per hectare (14 per acre) over 4 years.

Microtus ochrogaster population changes are less well documented than those of *M. pennsylvanicus*. Martin (1956) and Fitch (1957) have reported on populations of this vole in eastern Kansas for a 4-year period. Population changes reported by these authors are similar to those described here (Fig. 3), including a slow and somewhat erratic approach to peak densities [approximately 334–358 per hectare (135–145 per acre), Martin 1956, Fig. 5], a short peak phase, a decline beginning in the fall of the peak year, and a gradual decrease to very low numbers by fall of the following year. Unfortunately these Kansas data are confounded with successional changes in the habitat, severe flooding and later drought conditions of unknown relevance.

Peak densities for our undisturbed populations were about 136–148 per hectare (55–60 per acre) for *Microtus pennsylvanicus* and 86–99 per hectare (35–40 per acre) for *M. ochrogaster*. These are considerably below estimated peak densities given by Hamilton (1937) for *M. pennsylvanicus* (395–568 per hectare or 160–230 per acre) and by Martin (1956) for *M. ochrogaster* (361 per hectare or 146 per acre). There is unfortunately no way to determine the reliability of these literature estimates, and Aumann's (1965) acceptance of *Microtus* densities reported in the literature requires a faith in the reliability of these estimates which we do not have. Combined peak densities of these southern Indiana *Microtus* were about one-third those of *M. californicus* populations (Krebs 1966) and were only two to three times greater than those of lemmings (Krebs 1964). These Indiana *Microtus* reached densities about one-half to one-third those of Lake Vyrnwy *M. agrestis* populations in Britain (Chitty 1952), and approximately the same densities as Wytham *M. agrestis* populations (Chitty and Phipps 1966).

The possibility of competition between these two *Microtus* species cannot be discounted. The very high density reached by *M. ochrogaster* alone on grid D might suggest that this species does better in the absence of *M. pennsylvanicus*. The comparison of grids B and D thus supports a *prima facie* case for some competition. Unfortunately this comparison is confounded with the "fence-effect," and this competition may only be noticeable at very high densities. If competition were strong, we would expect these two species to fluctuate 1–2 years out of phase, but this does not necessarily happen. Habitat segregation does not seem to occur in this study area. Other grasslands in this area may support pure or mixed populations of these two species (Keller and Krebs MS in prep.), and further work is needed to determine whether pure species populations are a result of habitat unsuitability, inadequate dispersal, or competitive exclusion.

Fenced populations—The "fence-effect" described previously is not a new effect. Similar demographic effects have been described by Clarke (1955), Louch (1956), and van Wijngaarden (1960) for *Microtus* populations in small enclosures. We have merely extended this observation to a universe approximately 80–600 times larger than those previously used. This raises the vexing question of how large an area would be required before normal population processes could operate to regulate density. These enclosed populations are essentially islands, and consequently these results impinge on the problem of why species on islands are often more abundant than they are on the mainland (cf. MacArthur and Wilson 1967).

We consider two mechanisms which might produce this "fence-effect." First, predation. If the fence prevents predators from preying on the enclosed population, then we might attribute this effect to reduced predation pressure. We can see no evidence from our field observations to support this idea. The following predators seemed to have free access to these fenced areas: Red-tailed Hawks (*Buteo jamaicensis*), owls, foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), feral cats (*Felis domesticus*), and dogs (*Canis familiaris*). The fence prevents most snakes and weasels (*Mustela frenata*) from entering, but weasels are not common in this area (we catch them in our Longworth traps when they are present) and the snakes in these open fields do not subsist on mice [neither the copperhead (*Agcistrodon contortrix*) nor the rattlesnake (*Crotalus horridus*) have been taken on the Grassland Research Area]. Both grids B and D had resident shrew (*Blarina brevicauda*) populations but shrews did not seem to be more or less abundant inside the fenced areas compared with outside. Thus we can see no clear indication that this "fence-effect" is caused by predation.

Second, dispersal. The fence clearly prevents all immigration and emigration. In the absence of dispersal, the fenced populations did not regulate their densities below the level set by food supply, and they overgrazed the habitat. This suggests that *dispersal is somehow necessary for normal population regulation in these voles.* This dispersal effect may be simply a net movement of "surplus" voles away from the live trapping area. This implies that there must be a continual overproduction of voles, providing "surplus" animals, at least in the increase and peak phases, and these voles must be continually moving into and out of any arbitrarily defined grid area which is unfenced. We infer from the differences between our fenced and unfenced grids that this "surplus" group does not normally accumulate anywhere and must therefore suffer a very high mortality rate, perhaps by eventually moving off into woodland areas (Fig. 1). This is essentially the suggestion made by Andrzejewski (1962) (see discussion in Krebs 1966, p. 268).

The mechanism which causes dispersal must involve some form of aggressive behavior. Data from our fenced populations suggest that the behavioral interactions which produce these "surplus" voles are not sufficiently strong to cause death in these *Microtus,* and when the "resident" and "surplus" voles are forced to remain together, no high mortality ensues in either sex. Note that crowding per se with all its possible physiological effects (Christian and Davis 1964) was not sufficient in either grid B or grid D to stop the population from increasing to the point of food shortage.

Many authors have talked about the possible role of dispersal in population regulation (e.g. Lidicker 1962; Howard 1960; Murray 1967) but no one has set up adequate experimental studies to investigate dispersal. The first difficulty is to devise a rigorous operational definition of a dispersing animal. Not every unmarked adult animal which appears on a sampling area can be automatically assumed to be a disperser. Probably two techniques would be most useful for recognizing dispersing voles: (1) providing vacant areas from which there is a continual removal of immigrants; and (2) devising exit doors for fenced populations. These would allow one to determine the populational attributes of dispersers. Further information could then be obtained on the genetic, physiological, and behavioral characteristics of individual dispersers to see if they are a random sample of the resident population.

Reproduction

We review reproductive changes in these *Microtus* in detail in a later paper (Keller and Krebs MS in prep.) and here we point out only the great similarity between reproductive changes recorded here and those found in cycling lemming populations in northern Canada (Krebs 1964) and cyclic red-backed vole populations in Finland (Kalela 1957).

Mortality

No data are available in the literature for *Microtus pennsylvanicus* giving changes in survival rates over several years. Getz (1960) estimated an average survival of 12% for the first month of life for *M. pennsylvanicus* in southern Michigan. Golley (1961) suggested about 10% survival during the first month for this species. These estimates are slightly below our crude estimate of 18% survival from birth to recruitment into the trappable population (0.9 recruits per lactation, average litter size 5, grid A, Table 8). Getz (1960) estimated mean lifespan of about 8 weeks in both sexes during his 1-year study. This is considerably less than the mean expectation of life at first capture for *M. pennsylvanicus* found in this study (grid A):

	Increasing and peak	Declining
Males	9–13 weeks	6 weeks
Females	17–21 weeks	7 weeks

This lends further support to the suggestion that Getz was sampling populations in the low phase of the cycle. Note that the mean expectation of life is not very biologically meaningful in this situation of large changes in week-to-week survival rates of males.

Martin (1956) suggested that *Microtus ochrogaster* born during the fall and winter months had a higher expectation of life (4–5 months) than those born during the spring and summer (1–2 months). The major part of his fall-winter cohorts were voles born during the increase phase of the cycle, and most of the spring-summer cohorts were voles born during the peak and decline phases. These results seem to agree with our data on mean expectation of life at first capture (grid A):

	Increasing and peak	Declining
Males	8–11 weeks	5–6 weeks
Females	16–18 weeks	5–8 weeks

The sporadic episodes of high losses found especially in males were also found in *Microtus agrestis* populations by Chitty and Phipps (1966). However, the pattern of these episodes differed somewhat. We found little evidence of sporadic losses in females, contrary to the findings for *M. agrestis,* and we also found no difference in the timing of high losses in the two sexes when the population declined. Chitty and Phipps (1966) suggested that these sudden losses were caused by intraspecific strife, and it is difficult to attribute them to conventional agents of loss particularly in the mixed species populations we have studied. The absence of these high-loss periods in the fenced populations suggests that they are associated with periods of dispersal.

The very high losses which occur between birth and recruitment into the trappable population (about 80% in *M. ochrogaster* and 85% in *M. pennsylvanicus*) seem to be a constant part of the demography of these voles. Population trends in unfenced areas thus do not depend on variations in this high loss of young juveniles, and the aspects of mortality that are demographically more significant involve the trappable (mainly adult and subadult) segment of the population. Krebs (1966) reached the same conclusion for *Microtus californicus* populations.

Growth

These *Microtus* populations show the same sequence of changes in mean body size recorded for other cyclic microtines by Chitty and Chitty (1962), Kalela (1957), and Krebs (1964, 1966). Growth rates are higher in increasing and peak populations of both *Microtus pennsylvanicus* (Fig. 19) and *M. ochrogaster* (Fig. 18). The size variations shown by these two *Microtus* species seem to be the result of variable asymptotic size limits for individual voles. Some individuals grow rapidly and continue growing to large adult size, others grow rapidly and stop growth at small adult size. Growth is clearly associated with breeding seasons, and winter breeding during the increase phase of the cycle is closely linked with good winter growth.

Conclusions

We have presented the demography of *Microtus pennsylvanicus* and *M. ochrogaster* populations in southern Indiana through approximately one cycle of abundance. The results are similar to those described for *Microtus agrestis* by Chitty and coworkers in Britain, for *Lemmus trimucronatus* and *Dicrostonyx groenlandicus* in the central Canadian arctic (Krebs 1964), for *Clethrionomys rufocanus* in Finland by Kalela (1957), and for *Microtus californicus* by Krebs (1966). The demography of these species is not identical but the similarities are very great in view of the obvious differences in life history and in the environmental conditions from tundra to temperate grasslands. Thus winter breeding, which is an important part of the increase phase in lemmings and also in *M. pennsylvanicus* and *M. ochrogaster,* is not involved in *Clethrionomys rufocanus* fluctuations (Kalela 1957). The mechanisms by which total reproductive output is raised in the phase of cyclic increase may not be identical in all populations.

Speculation about whether all cyclic small rodents have a similar mechanism preventing unlimited increase or whether several mechanisms might be involved is seriously hampered by the absence of a single instance of cyclic population changes which can be explained. What ecological parameters must be measured to allow us to predict subsequent population events? No one yet has been able to find any variables which provide the required predictive insight into these population fluctuations. We report here the necessary demographic background to achieving an adequate explanation. Whatever mechanism one proposes must produce the demographic syndrome we have just described in detail.

We will consider in a second paper (Tamarin and Krebs 1969) genetic changes at the transfer in locus in the populations described above and will show that there are genetic events associated with these demographic changes. In a third paper (Keller and Krebs, MS in prep.) we will trace the detailed changes in reproduction in other local populations of these two *Microtus* species. In a fourth paper (Krebs MS in prep.) behavioral changes in male activity and aggressiveness will be examined and the demographic events will be shown to be associated with changes in male aggressive behavior.

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