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POPULATION DYNAMICS OF *MICROTUS OCHROGASTER* IN EASTERN KANSAS[1]

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Abstract. Four eastern Kansas populations of the prairie vole, *Microtus ochrogaster*, were live trapped from 1970–73 to gain insight into the population regulation of this species. All four populations exhibited a 2-yr cycle in numbers with peak densities generally occurring in June 1972. Peak densities were followed by a decline in numbers, a recovery, and a population crash in spring 1973.

Reproductive parameters changed dramatically as density rose and fell. The summer breeding season in the crash year of 1973 was shortened by at least 3 mo. A reduction in breeding activity occurred during the summer of every year of the study. The highest amount of reproduction occurred during the spring and fall. More voles were breeding during the winter before the peak year (1971–72) than during either the preceding or succeeding winters. There was no deviation from a sex ratio of 1 in the populations.

Mortality rates had a strong impact on changes in numbers. Survival rates of juveniles and subadults in the population were significantly lower than adults in the summer breeding season. Adults survived better during winter than during summer. Survival of ♂♂ and ♀♀ was correlated and was relatively low during episodes of decreasing density. The survival of voles between weaning and trappable size was high during periods of increasing density and low during periods of declining density.

A multiple regression analysis was performed to determine the relative usefulness of four demographic variables in predicting mean rate of population increase. The analysis indicated that early juvenile and ♀ survival are the best predictors of population growth.

Growth of voles in the populations was assessed from body weight distributions and instantaneous growth rate per body weight. There was no shift in body weight toward heavier animals in peak populations and instantaneous growth rates were erratic.

Finally, inconsistencies in these results compared with other microtine studies, such as the short peak phase, lack of a well-defined breeding season, a summer breeding depression, and the absence of a shift towards heavier animals in the peak phase, are discussed in relation to a single or multifactor hypothesis for explaining population cycles.

Key words: Demography; Kansas; Microtus; *population cycles; population regulation; Rodentia.*

INTRODUCTION

Populations of microtine rodents undergo periodic fluctuations or cycles in population density every 2–4 yr. The repeating sequence of demographic events (increase phase, peak phase, decline phase, and a phase of low density) of population cycles offers a unique opportunity to study population regulation. Although population fluctuation in voles and lemmings is a widely recognized phenomenon, there is little agreement on the mechanisms causing population cycles. The regularity of population cycles has prompted some investigators to suggest a single causal mechanism (Chitty 1952, Krebs et al. 1973) while Lidicker (1973) has proposed that, depending on the species and geographical location, several factors may be involved. Lidicker has argued that the regularity of population cycles may be misleading, since rarely has a given species been studied through two successive cycles. Furthermore, it is often difficult to make meaningful comparisons among microtine studies due to different methodologies in collecting and analyzing data. Thus, even successive studies at a given locality may not be directly comparable.

The purpose of the present study is to monitor changes in density, reproduction, and survival in four eastern Kansas populations of the prairie vole, *Microtus ochrogaster*, to gain some insight into the population regulation of this species. If there are a substantial number of inconsistencies in how these demographic parameters change over a population fluctuation compared to previous studies, then a more holistic approach to population cycles would be justified in the future. In addition, the demographic data are being used for a study of the ecological genetics of *Microtus ochrogaster*, which will be reported in the future by M. S. Gaines and R. K. Rose.

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TABLE 1. Climatological data from 1970–1973 on main study area

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Mean temperature (°C)												
1970											4.7	1.5
1971	–4.0	–3.1	4.8	13.3	16.2	24.4	22.8	23.1	21.7	16.0	7.0	1.9
1972	–3.4	–0.2	7.0	12.1	16.8	23.2	23.5	23.6	20.5	11.8	4.6	–2.2
1973	–2.9	0.6	8.3	11.3	15.8	22.8	24.9					
Precipitation (mm)												
1970											26	34
1971	42	55	18	28	91	76	129	36	55	70	54	41
1972	3	19	20	69	115	71	156	153	178	72	97	60
1973	100	16	346	59	164	33	259					

MATERIALS AND METHODS

Four live-trapped grids (A, B, C, and D) used in the study were located 11 km northeast of Lawrence, Kansas (*see* Rose 1974, Fig. 1 for aerial photograph). Grids A, B, and D were all within 1.2 km of one another while grid C was 3.6 km from the main study area. Grid A was the same area (quarry field) used by Martin (1956) in his study of *M. ochrogaster.* We began trapping grids A, B, and D in November 1970, while trapping on Grid C was initiated in June 1971. Trapping on all grids was terminated in July 1973. The grids consisted of 100 trapping stations spaced 7.6 m apart. Each grid was 0.8 ha. One Longworth live trap covered with a board was placed in the general vicinity of each station where signs of vole activity could be found. Traps on each grid were checked on a biweekly schedule. The area of the grids and trapping schedule were designed after Krebs et al. (1969) to standardize the demographic data.

At first capture, voles were marked with lettered and numbered fingerling fish tags in the right ear. The following data were recorded for each vole during a trapping period: location on grid, weight to heaviest g, position of testes (scrotal or abdominal) for males, condition of vagina (perforate or not perforate), nipple size (small, medium, or large) and condition of pubic symphysis (closed, slightly open, or open) for females. Each newly tagged vole was bled through the suborbital sinus for a genetic study. During the course of this study 108 of over 3,000 voles marked lost their ear tags. Individuals with lost ear tags were synonymized with the appropriate tag number based on sex, weight, genotype, and location on the grid. All data were punched into cards and analyzed at the University of Kansas Computation Center using programs described by Krebs (1967).

Microtus ochrogaster was the most abundant small mammal species on all grids. The southern bog lemming, *Synaptomys cooperi,* occurred at moderate densities on grids A and B. Other mammal species live-trapped in this study in order of decreasing occurrence were: *Sigmodon hispidus* (hispid cotton rat), *Reithrodontomys megalotis* (western harvest mouse), *Peromyscus maniculatus* (prairie deer mouse), *Blarina brevicauda* (short-tailed shrew), *Reithrodontomys montanus* (plains harvest mouse), *Zapus hudsonius* (meadow jumping mouse), *Cryptotis parva* (least shrew), and *Microtus pinetorum* (pine vole).

CLIMATE AND VEGETATION

Lawrence, Kansas is situated near the western edge of the eastern hardwood forest at 38° 58′ latitude and 95° 16′ longitude with an elevation of 305 m. Lawrence has a typical continental climate with large seasonal fluctuations in temperature and large monthly variations in rainfall. Temperature and rainfall were measured on the main study area with a recording hygrothermograph (Table 1).

The annual differences in temperature during the 3 yr of the study were small compared to seasonal variation. The winter of 1970–71 was colder than the two successive winters. Soils were rarely frozen for longer than 2 wk and snow usually melted within a few days.

Rainfall varied greatly from month to month but most of the precipitation occurred in the summer as a result of thunderstorm activity. Both 1972 and 1973 were wetter than 1971. Occasionally there was flooding on some of the grids during the summer months but we have no evidence that local flooding caused increased mortality of the trappable voles. No protracted period of drought occurred during the study.

All four grids were situated in abandoned fields dominated by cultivated brome grass (*Bromus inermis*). Common plant species on each grid are presented in Table 2. Plant species diversity on the grids increased as follows: C < D < B < A.

TABLE 2. Common plant species on grids A, B, C, and D. + = common; ++ = moderately abundant; +++ = very abundant

Species	Grid A	B	C	D
Bromus sp.	+++	+++	+++	+++
Agrostis sp.		++	+	++
Andropogon sp.	+	+		
Eragrostis spectabilis		+	+	++
Ambrosia artemisiifolia	+	+	+	
Symphoricarpos orbiculatus	++	++		+
Rosa setigera	+	+		
Solanum carolinense		+	+	+
Solidago sp.	+		+	
Gleditsia triacanthos	+	+		+
Maclura pomifera	++	+		+

RESULTS

Density changes

Population densities were obtained by enumeration of voles in the trappable population. Enumeration of the trappable population is an effective technique for estimating density only if there is a high probability of recapturing animals. We checked trapping efficiency by comparing the number of animals captured in each trapping period with the number of voles known to be alive. These data summed over seasons are presented in Table 3. The winter months are designated as November–February and the summer months are designated as March–October. There are only four cases where the trappability is < 75% (grid A, males, winter 1970–71; grid A, females, summer 1971; grid B, males, winter 1970–71; and grid B, males, summer 1971). We tested for differential trappability between males and females with a chi-square analysis. The percentage recapture of males and females known to be alive was compared on each grid for each season. There were statistically significant differences in trappability between males and females in 6 of the 23 possible comparisons ($p < .05$). There is no apparent trend in differential trappability by sex (Table 3). Overall, we believe our results are comparable to Krebs et al. (1969) who found enumeration to be 90–95% efficient.

Grid A.—The population was stable in numbers on this grid (30–40 voles) during the first 4 mo of the study (Fig. 1). Numbers began to decline from March through May 1971 with a mean r (instantaneous rate of increase) of –.05 ± .01 (SE) per week. Numbers were low through the summer 1971 (9–13 voles) but started increasing in the fall 1971. The population continued to increase through the winter 1971–72 with a mean r of .08 ± .01 (SE) per week and reached a peak density of 92 voles in June 1972. There was a decline in numbers during the late summer and fall 1972, followed by a recovery during the following winter and spring. The population declined precipitously during the summer 1973 with a mean r of –0.14 ± .05 (SE) per week. At the end of the study in July 1973 only three animals were present on the grid.

Grid B.—Population density of this grid was higher than grid A at the start of the study (Fig. 2). The population declined during the winter 1970–71 with a mean r of –.08 ± .02 (SE) per week and remained at low numbers during the summer and fall 1971. A rapid phase of population growth began in July 1971 and proceeded increasing with a mean r of .09 ± .01 (SE) per week during the winter 1971–72. The population reached a peak density of 73 voles in June 1972. The density remained high through summer and fall 1972. The population began declining in January 1973 and proceeded through the following spring with a mean r of –.07 ± .01 (SE) per week.

Grid C.—This grid had a population of 20 voles when we began trapping in August 1971 (Fig. 3). After a slight decline in density during the early fall, numbers increased through the winter of 1971–72 with a mean r of .07 ± .03 (SE) per week and reached a peak density of 75 voles in February 1972. Numbers remained high until June 1972 and then declined during the summer and fall 1972 with a mean r of –.08 ± .02 (SE) per week. There was

TABLE 3. Percentage recapture of *Microtus ochrogaster* known to be alive. Numbers in parentheses represent number known to be alive on areas summed over seasons (winter, November–February; summer, March–October). Boldface indicate statistically significant differences between ♂♂ and ♀♀ ($p < .05$) during a season

Season	Grid A ♂♂	Grid A ♀♀	Grid B ♂♂	Grid B ♀♀	Grid C ♂♂	Grid C ♀♀	Grid D ♂♂	Grid D ♀♀
Winter 1970–71	**60.0**(145)	**77.8**(153)	72.6(113)	79.8(114)	—	—	91.5(82)	91.5(94)
Summer 1971	**77.3**(97)	**56.8**(139)	73.3(30)	92.1(38)	93.2(59)	80.6(72)	80.6(72)	82.7(81)
Winter 1971–72	**76.0**(288)	**87.3**(261)	93.8(130)	97.1(105)	75.3(243)	83.0(230)	90.2(153)	88.2(170)
Summer 1972	**87.6**(327)	**80.4**(382)	**79.4**(350)	**86.1**(374)	**95.6**(203)	**86.3**(234)	87.5(216)	89.3(215)
Winter 1972–73	80.9(251)	81.5(270)	80.7(249)	86.7(203)	84.6(65)	88.1(59)	86.2(65)	87.3(71)
Summer 1973	89.9(159)	89.0(154)	94.1(68)	89.2(93)	93.9(33)	96.1(26)	94.2(86)	98.6(70)

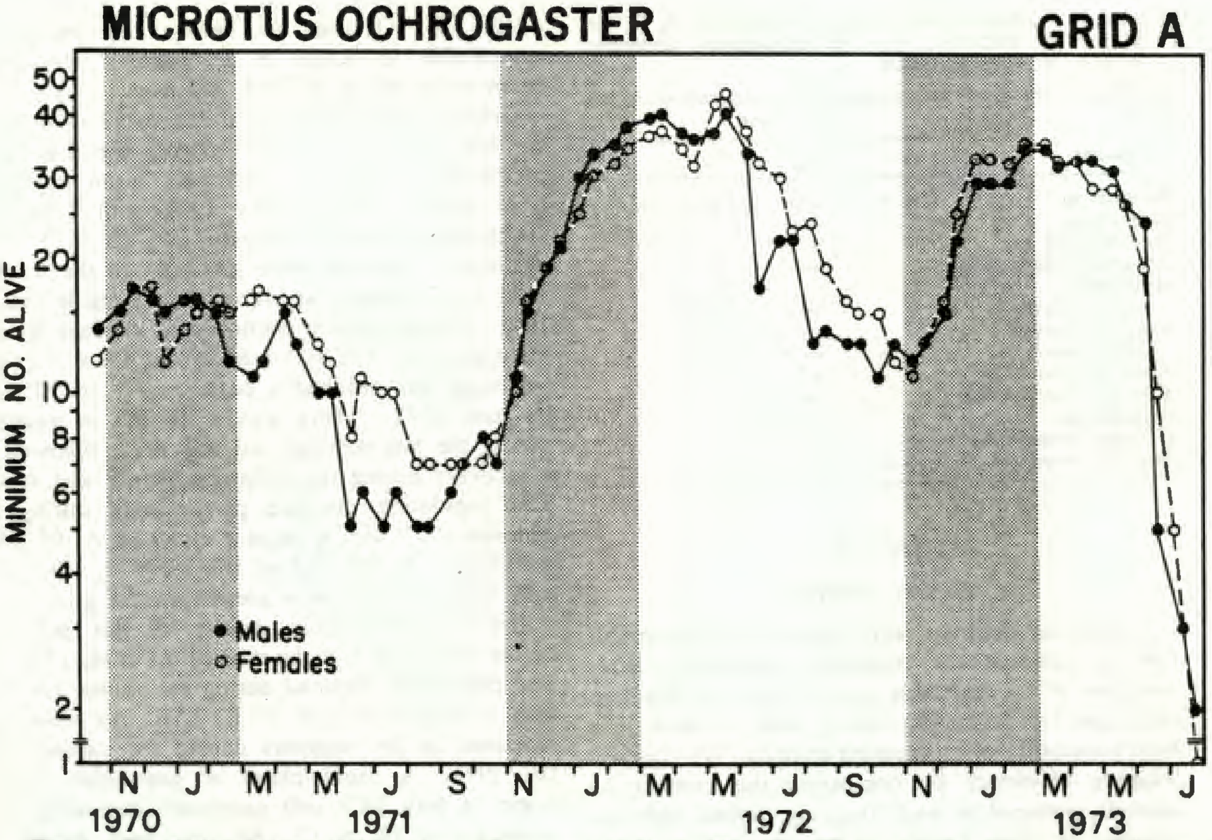

FIG. 1. Population density of *Microtus ochrogaster* on grid A, 1970–73. Winter months (November–February) are shaded.

some recovery during the winter 1972–73, but by late spring the population was in a low density phase. The density data on grid C were less reliable than the other grids because there was high mortality in the trappable vole population due to a coyote (*Canis latrans*) eating trapped voles from June to October 1972.

Grid D.—Vole densities were high (75) at the start of the study (Fig. 4). There was a precipitous crash in numbers from November 1970 to January 1971. During this period the mean r per week was −.11 ± .05 (SE). Numbers remained low from February to March and started increasing in April 1971. The population increased through November 1971 with a mean r of .14 ± .05 (SE) per week. There was a slight decline in numbers followed by a recovery in May 1972. A peak density of 51 voles was reached in June 1972. There was a general decline in numbers during the remainder of the study punctuated with short periods of increasing density.

In summary, grids B, C, and D had a 2-yr cycle in density with the peak phase generally occurring in June 1972. Grid C was slightly out of phase with peak densities occurring in February 1972 and numbers remaining high until June 1972. Grid A also tended to exhibit a 2-yr cycle. However, since numbers in summer 1971 were not as low as other grids, it could be argued that the cycle on grid A was longer than 2 yr, assuming the summer 1971 was not a low phase. Peak densities on grids A, B, and D were followed by a decline in numbers, a recovery, and a population crash in spring 1973. The population on grid C declined after the peak, but never recovered to the same extent as the other grids. In July 1973 at the end of the study all grids were at low densities (3–8 per grid).

Reproduction

Reproductive changes reported here are based on external reproductive characteristics. Testes position was used as an index of breeding activity in males. Three parameters were used in females: (1) condition of vagina—perforate when breeding; (2) amount of lactation tissue—nipples medium or large when lactating; (3) condition of pubic symphysis—open 3 days before and after parturition. In addition, females with bulging abdomens were recorded as pregnant. Although these external reproductive parameters are not as reliable as detailed autopsy data, they serve our purpose in presenting a general overview of reproductive changes occurring during a population cycle. It is anticipated that a more de-

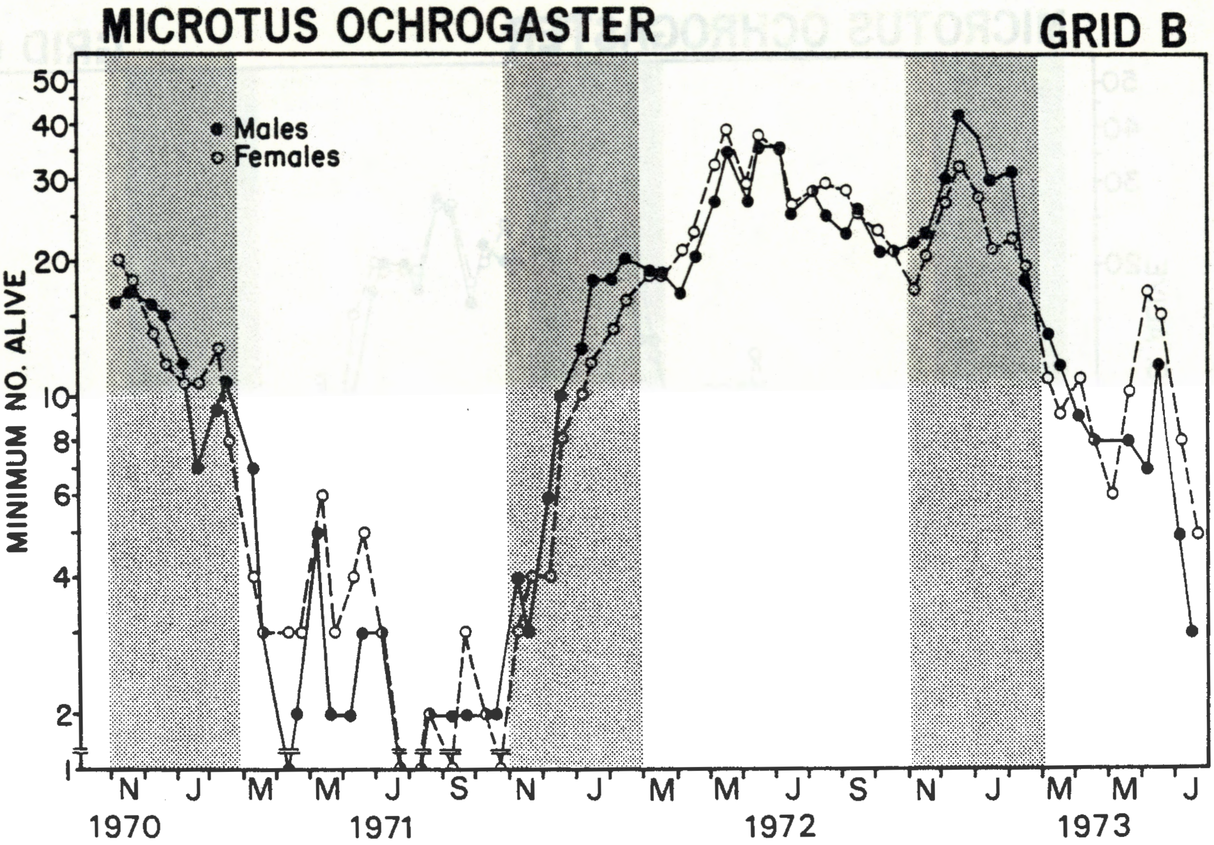

FIG. 2. Population density of *Microtus ochrogaster* on grid B, 1970–73.

tailed account of reproductive changes based on autopsy data will be reported elsewhere by R. K. Rose and M. S. Gaines. The annual breeding cycle of *M. ochrogaster* has been arbitrarily divided into winter (November–February) and summer (March–October) months. The most reliable index of breeding activity of all the parameters listed above is lactation (Krebs et al. 1969). We plotted the percentage of adults with medium or large nipples on all four grids during each month in an attempt to discern any general pattern in breeding activity (Fig. 5). Voles weighing 34 g or heavier were arbitrarily defined as adults based on autopsy data (Rose 1974), which indicated that 33 g is the median age of sexual maturity. An adjustment of 3 wk from the onset of breeding activity to the appearance of voles with medium to large nipples was made to compensate for the 21-day gestation period.

Several facts are evident in Fig. 5. First, there was low breeding activity during the winter 1970–71 and winter 1972–73, whereas there was a higher incidence of breeding during the winter 1971–72 just before the peak year. Second, the summer breeding season in 1973 following the peak year was shortened by at least 3 mo. There was a noticeable decline in breeding during May 1973, followed by virtually no breeding in June and July 1973 on all grids. Additional data collected from August through October 1973 indicated that voles were still not in breeding condition. Third, there was a depression in breeding during the summer (June, July, or August) of each year on most grids.

The data for different reproductive parameters were pooled over seasons for each grid (Table 4). Chi-square analyses were performed on reproductive data to test the following: (1) homogeneity among grids in the same season; (2) homogeneity among seasons on the same grid; and (3) homogeneity for the same season over years on each grid (e.g., grid A—summer 1971, summer 1972, and summer 1973). Eight of the 24 comparisons (6 seasons, 4 parameters) among grids were statistically significant ($p < .05$). Most of the heterogeneity occurred during the summer 1971 in which testes position, nipple size, and condition of the pubic symphysis were significantly different ($p < .05$) among the four grids. This heterogeneity was due to a higher incidence of breeding activity on grid C. There is no obvious explanation to account for this result. There was a considerable amount of heterogeneity in reproductive data among seasons on the same grid. The following comparisons were significantly heterogenous ($p < .05$) among seasons: grid A—testes position, nipple size, and condition of pubic sym-

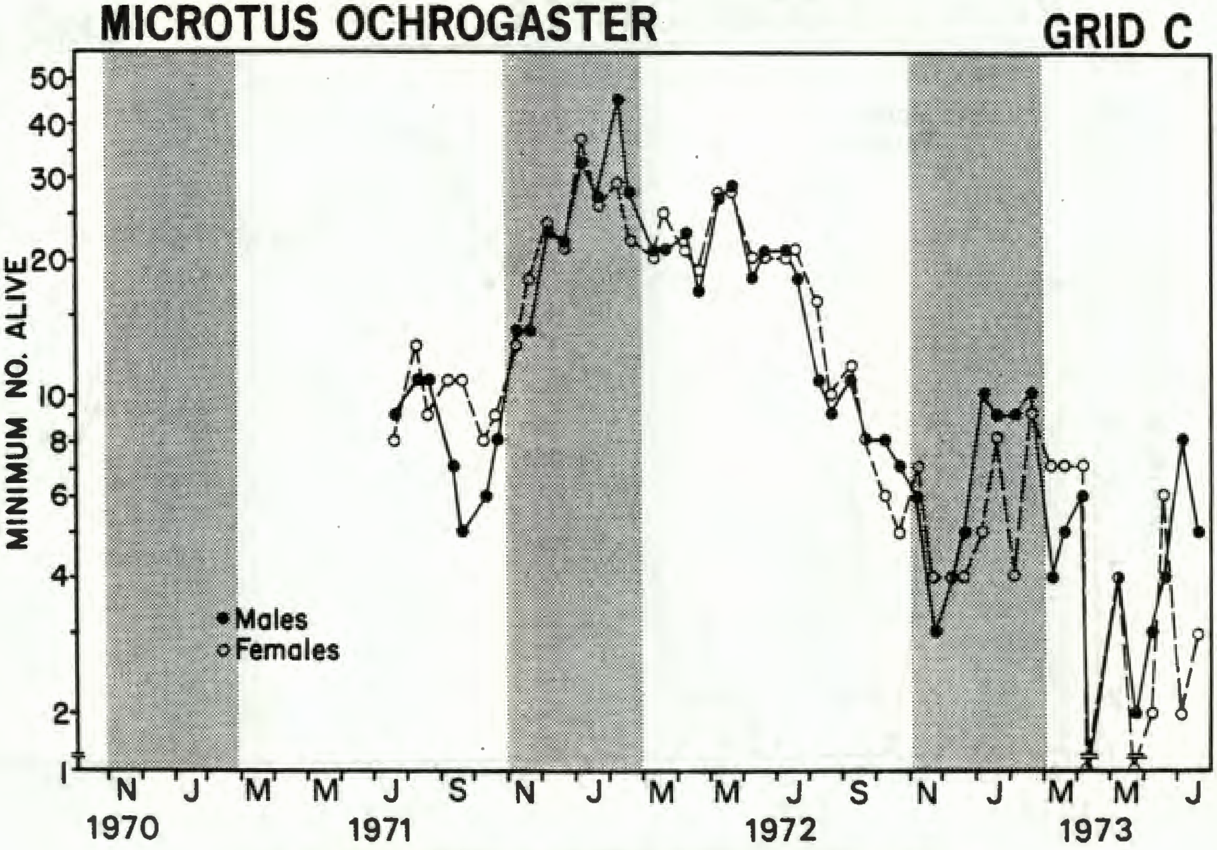

FIG. 3. Population density of *Microtus ochrogaster* on grid C, 1971–73.

physis; grid B—testes position and nipple size; grid C—testes position, nipple size, condition of pubic symphysis, and pregnancy rates; and grid D—testes position and nipple size. The nipple size data were used to test for heterogeneity in breeding activity for the same season over different years. There was statistically significant heterogeneity in breeding activity among the three winter breeding seasons on grids B and D ($p < .01$). Differences in breeding activity among the winter breeding seasons on grids A and C approached statistical significance ($p < .10$). There were no statistically significant differences among the summer breeding seasons on any grid. The heterogeneity we observed among winter seasons on the grids indicate that changes in breeding activity were not just seasonal.

Several trends in reproductive activity are apparent from Table 4. First, there was a higher incidence of breeding activity during summer periods than in winter periods. Second, there was a higher incidence of breeding in the winter 1971–72 compared to the two other winter periods based on all reproductive parameters.

In summary, data on external reproductive parameters indicated that summer breeding in 1973 was shortened by at least 3 mo. A reduction in breeding activity occurred during the summer of every year of the study. We found statistically significant heterogeneity in reproductive parameters on the same grid over different seasons with a trend towards highest reproductive activity during the summer breeding season. In addition, the winter before the peak year had the highest level of breeding activity compared to the preceding and succeeding winters.

Sex ratios

Deviations from a sex ratio of 1 could affect population density. Populations with a higher percentage of females may have a higher reproductive output and thus higher rates of increase than populations with an excess of males or with equal sex ratios. Several studies on *Microtus californicus* populations (Greenwald 1957, Hoffmann 1958, Batzli and Pitelka 1971, Lidicker 1973) indicate that sex ratios are disturbed in favor of females during the breeding season. Martin (1956) reported a consistent deficiency of males in *M. ochrogaster* populations from eastern Kansas. Myers and Krebs (1971*a*) studying *M. ochrogaster* and *Microtus pennsylvanicus* from southern Indiana found a deficiency of males in the resident trappable population, but the number

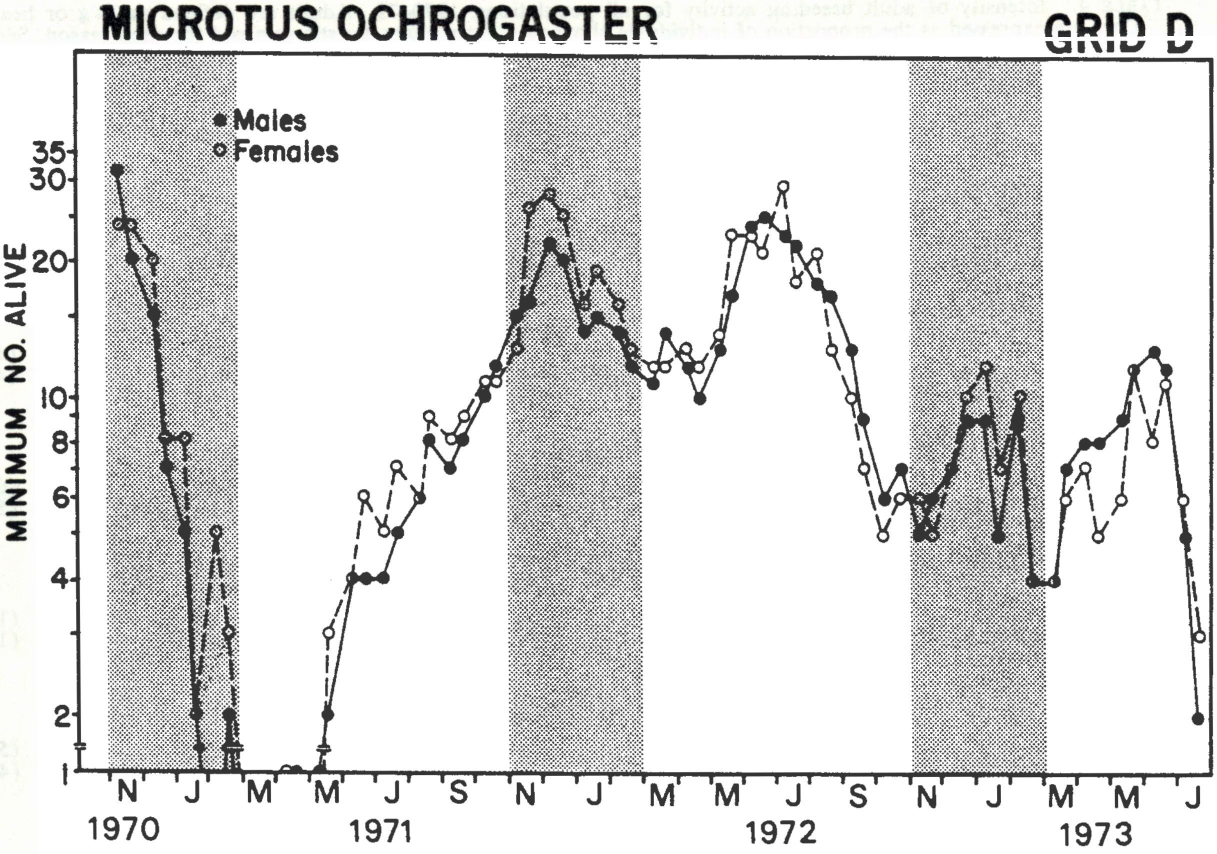

FIG. 4. Population density of *Microtus ochrogaster* on grid D, 1970–73.

of recruits over a long period of time showed an excess of males.

We pooled sex ratios for each trapping period over seasons for each grid. The sex ratios of resident animals and new recruits were analyzed separately. A chi-square homogeneity test indicated that there were no significant differences in sex ratios for either residents or recruits among seasons on any grid. Sex ratios were pooled over the entire study for each grid. There were no significant deviations from a sex ratio of 1 in residents or recruits on any grid. The data were pooled for all grids and again there were no significant deviations from a sex ratio of 1.

Mortality

We measured mortality in the trappable population from minimum survival rates per 14 days. In addition, an index of early juvenile survival was calculated from the ratio of the number of juveniles recruited into the population to the number of lactating adults. Since Krebs et al. (1969) found that survival rates of males and females were not correlated, we analyzed the sexes separately.

Survival of the trappable population.—Survival rates of the trappable population summed over seasons on each grid are presented in Table 5. We first tested for heterogeneity in survival rates among three weight classes (adults [$\geqslant$ 34 g], subadults [22–33 g], and juveniles [$<$ 22 g]) during each season for each grid using a chi-square homogeneity test. For example, do adults, subadults, and juveniles on grid A have the same survival rates during the winter 1970–71? Survival rates among age groups were significantly heterogenous ($p < .05$) for the following season and grids: grid A, males—summers 1971 and 1972; grid A, females—summers 1971, 1972, and 1973; grid B, males—summer 1972 and winter 1972–73; grid B, females—summer 1972; grid C, males—summers 1971 and 1972; grid C, females—summers 1971 and 1972; grid D, males—summers 1972 and 1973; grid D, females—summers 1971 and 1973. In all cases where survival rates were significantly heterogenous among age classes, juveniles and subadults had lower survival than adults for both males and females. Most of the statistically significant differences occurred during the summer breeding season.

We also tested for heterogeneity among survival rates for each age class over seasons on the same grid. For example, do adult males on grid A have the same survival rates over all seasons? Fifteen

TABLE 4. Intensity of adult breeding activity for all populations, 1970–73. Adults are defined as 34 g or heavier. Data are expressed as the proportion of individuals showing a given characteristic summed for each season. Sample sizes are in parentheses. Sample sizes for public symphysis open and obviously pregnant are same as nipple category

Season and group	Grid A	B	C	D
Winter 1970–71				
Testes scrotal	.84 (62)	.82 (52)	----	.83 (63)
Nipples medium to large	.21 (40)	.18 (41)	----	.18 (33)
Pubic symphysis open	.03	.06	----	.09
Obviously pregnant	.00	.00	----	.03
Summer 1971				
Testes scrotal	.88 (57)	.94 (34)	1.00 (48)	.95 (43)
Nipples medium to large	.50 (92)	.46 (35)	.82 (49)	.58 (48)
Pubic symphysis open	.12	.14	.37	.27
Obviously pregnant	.02	.09	.16	.13
Winter 1971–72				
Testes scrotal	.93 (148)	.85 (66)	.94 (109)	.94 (69)
Nipples medium to large	.36 (125)	.50 (54)	.41 (110)	.56 (54)
Pubic symphysis open	.10	.13	.06	.19
Obviously pregnant	.02	.06	.09	.09
Summer 1972				
Testes scrotal	1.00 (180)	.99 (172)	1.00 (121)	1.00 (102)
Nipples medium to large	.50 (212)	.59 (222)	.69 (156)	.54 (111)
Pubic symphysis open	.13	.19	.24	.21
Obviously pregnant	.06	.09	.22	.08
Winter 1972–73				
Testes scrotal	.92 (167)	.93 (155)	.97 (35)	.92 (50)
Nipples medium to large	.29 (176)	.51 (134)	.25 (36)	.38 (48)
Pubic symphysis open	.07	.16	.03	.13
Obviously pregnant	.03	.06	.06	.08
Summer 1973				
Testes scrotal	.75 (53)	.91 (33)	1.00 (8)	.94 (35)
Nipples medium to large	.66 (67)	.69 (42)	.60 (16)	.71 (42)
Pubic symphysis open	.21	.14	.20	.29
Obviously pregnant	.09	.12	.20	.17

of the 24 possible comparisons of each age group on the same grid over different seasons (4 grids, 3 age groups, 2 sexes) were significantly heterogenous ($p < .05$). All comparisons of survival rates among the juvenile and subadult age groups were not significant. The heterogeneity observed in adult males and females was due to higher survival rates in the winter breeding seasons compared to the summer breeding seasons. There were no statistically significant differences between adult males and adult females on each grid within the same season.

Finally, we determined whether changes in survival rates were seasonal by testing for heterogeneity in adult males and females among the same breeding seasons over different years on each grid (i.e., grid A—summer 1971, summer 1972, and summer 1973). The following grids had statistically significant differences ($p < .01$) in adult survival rates for the breeding seasons indicated: grid A—males, winter; grid B—males, winter and summer; grid B—females, winter and summer; and grid C—females, summer. There was a trend on all grids for adult males and females to have higher survival rates in the winter of the peak year (1971–72) compared to the preceding and succeeding winters. These results suggest that changes in survival rates cannot be explained seasonally.

Survival rates for *M. ochrogaster* on grid A over a density cycle are presented in Fig. 6. Patterns in male and female survival rates in this population are similar to those found on other grids. Two points can be made from the data: (1) male and female survival rates were significantly correlated ($r = .54$, $N = 69$, $p < .01$) and (2) survival rates of males and females were relatively low during periods of decreasing density.

Early juvenile survival.—We estimated survival during the period from weaning until voles reached a trappable size ($\approx$ 25 g) using an index (Krebs and Delong 1965) which relates the recruitment of young voles into the population to the number of lactating females. The index can be expressed as

$$\text{index of early juvenile survival at time } t = \frac{\text{no. new voles} < 30 \text{ g in wk } t}{\text{no. females with medium to large nipples caught in wk } t\text{-}4}$$

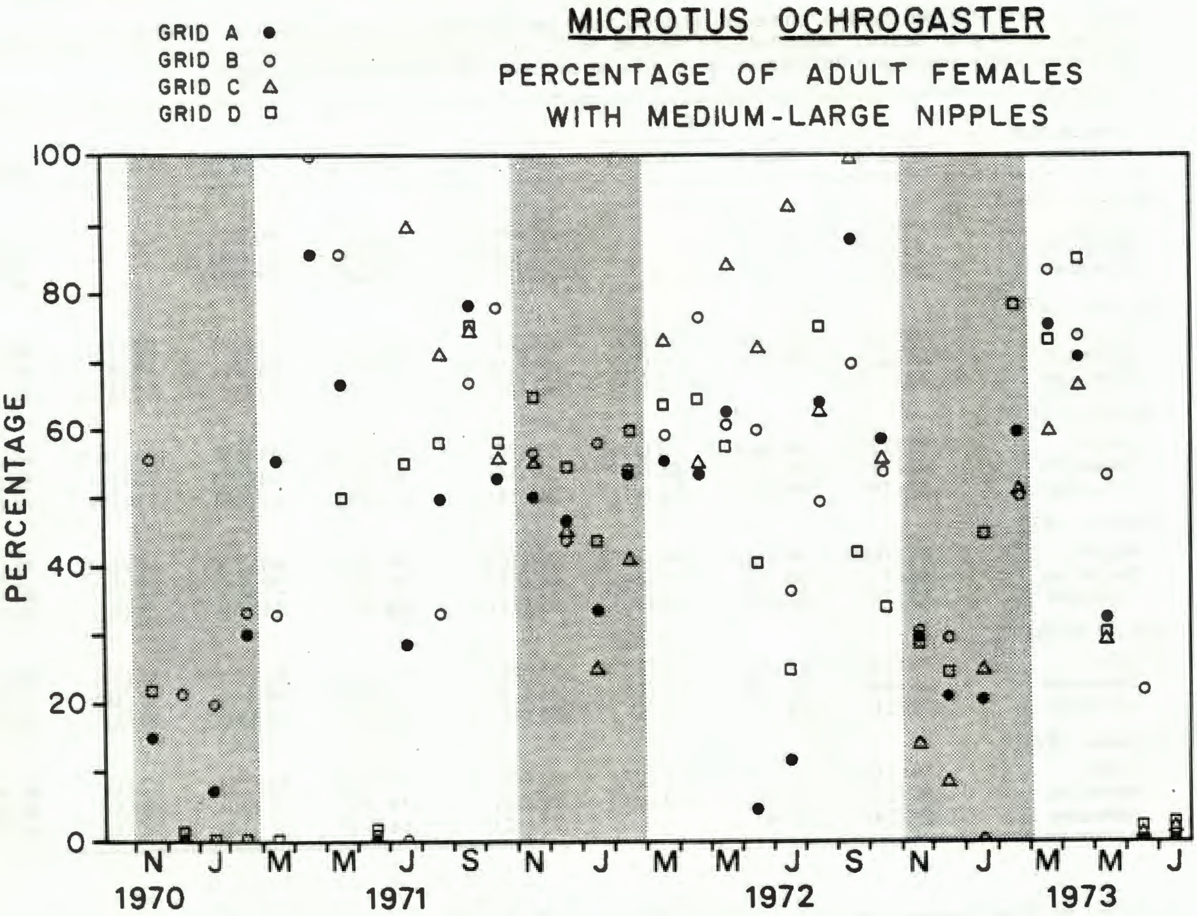

FIG. 5. Monthly percentages of lactating adult females *in Microtus ochrogaster* on all grids, 1970–73.

This index could be misleading if litter size varied with season. Unfortunately, we do not have complete autopsy data over the entire study (Rose 1974) and will assume litter size is constant.

The mean indices of early juvenile survival for all grids summed for each season are presented in Table 6. Early juvenile survival was highest on all grids during the winter 1971–72 when populations were increasing. Periods of decreasing density were generally characterized by low juvenile survival. For example, juvenile survival on grid A during the increase phase in winter 1971–72 was three times higher than during the precipitous decline in summer 1973. Similarly, there was low juvenile survival during the rapid decline on grid D in winter 1970–71 as well as during the decline in summer 1973. The population on grid C, slightly out of phase with the other grids, experienced a population decline in summer 1972 which was also accompanied with low juvenile survival.

We assessed the relative usefulness of four demographic variables, index of early juvenile survival, male survival rate, female survival rate, and percent of females lactating, in predicting mean rate of increase of the population by multiple regression analysis. All variables were mean values for summer and winter breeding seasons for each grid. Table 7 indicates that the index of early juvenile survival and female survival rates are the best predictors of population growth. Male survival rate and percent females lactating are not needed for predicting population growth. These results are consistent with those of Krebs (1971) which indicated that the index of early juvenile survival explained the most variation in mean rate of population growth in *M. ochrogaster* populations from southern Indiana.

To summarize, survival rates of juveniles and subadults in the trappable population were signficantly lower than those of adults of both sexes in the summer breeding season. There was significant heterogeneity in survival rates of adults of both sexes over seasons on each grid. Survival rates of adults during the winter breeding season tended to be higher than in the summer breeding season. Survival rates of males and females were correlated and were relatively low during episodes of decreasing density. The

TABLE 5. *Microtus ochrogaster* minimum survival rates per 14 days. Sample sizes are in parentheses. Adults are defined as 34 g or heavier; subadults are defined as 22 to 33 g; juveniles are defined as < 22 g. Boldface indicate statistically significant differences ($p < .05$) in survival rates among weight classes

Season and group	♂♂				♀♀			
	Grid A	Grid B	Grid C	Grid D	Grid A	Grid B	Grid C	Grid D
Winter 1970–71								
Adults	.90 (59)	.67 (52)	—	.57 (46)	.92 (51)	.60 (47)	—	.55 (33)
Subadults	.93 (15)	.82 (17)	—	.56 (25)	.74 (38)	.81 (31)	—	.88 (43)
Juveniles	.80 (5)	.50 (2)	—	.50 (2)	1.00 (4)	.57 (7)	—	.86 (7)
Summer 1971								
Adults	**.72** (44)	.63 (16)	.72 (32)	**.85** (34)	**.76** (67)	.71 (24)	**.83** (36)	**.88** (40)
Subadults	**.45** (22)	.00 (4)	.20 (5)	**.40** (10)	**.80** (15)	.78 (9)	**.17** (6)	**.50** (12)
Juveniles	**.62** (13)	—	.18 (11)	**.67** (3)	**.36** (14)	.25 (4)	**.13** (8)	**.33** (3)
Winter 1971–72								
Adults	.95 (120)	.94 (64)	.70 (106)	.72 (78)	.95 (106)	.93 (55)	.75 (103)	.66 (62)
Subadults	.92 (73)	.84 (31)	.65 (46)	.58 (36)	.94 (71)	.94 (17)	.77 (53)	.65 (57)
Juveniles	.93 (30)	.90 (10)	.65 (17)	1.00 (16)	.19 (22)	.93 (14)	.75 (16)	.84 (32)
Summer 1972								
Adults	**.81** (182)	**.80** (186)	.64 (135)	**.70** (105)	**.81** (214)	**.83** (238)	**.68** (162)	.71 (112)
Subadults	**.44** (57)	**.50** (64)	.33 (45)	**.60** (68)	**.77** (57)	**.57** (54)	**.49** (39)	.63 (46)
Juveniles	**.45** (75)	**.67** (46)	.46 (30)	**.42** (19)	**.44** (63)	**.51** (45)	**.29** (21)	.58 (33)
Winter 1972–73								
Adults	.86 (132)	**.74** (127)	.63 (30)	.51 (35)	.91 (131)	.81 (100)	.54 (37)	.53 (34)
Subadults	.86 (36)	**.87** (46)	.45 (20)	.45 (11)	.92 (49)	.69 (45)	.30 (10)	.29 (21)
Juveniles	.76 (21)	**.61** (23)	.60 (5)	.75 (4)	.87 (23)	.74 (34)	.20 (5)	.50 (6)
Summer 1973								
Adults	.73 (110)	.60 (50)	.41 (17)	.72 (43)	**.76** (125)	.63 (52)	.37 (19)	**.82** (45)
Subadults	.56 (25)	.46 (13)	.40 (10)	.71 (24)	**.38** (13)	.75 (20)	.40 (5)	**.63** (8)
Juveniles	.67 (24)	.50 (8)	—	.75 (12)	**.64** (14)	.57 (14)	.00 (3)	**.08** (12)

survival of voles between weaning and trappable size was high during periods of increasing density and low during periods of declining density.

Growth

The growth of voles has been previously shown to be closely integrated with the demographic machinery of the population. Krebs et al. (1969) found that *M. ochrogaster* and *M. pennsylvanicus* from increasing and peak populations have higher body weights than voles from declining populations. In this study two approaches were used to assess growth in the population: (1) body weight distributions, and (2) instantaneous growth rate per body weight. Only males were used in the analysis to avoid the confounding effect of pregnancy.

Body weight distributions of males on each grid were plotted as in Fig. 20 and 21 of Krebs et al. (1969). Contrary to the prairie voles in southern Indiana, we found no evidence of a shift in body weight toward heavier animals in peak populations. These observations were supported by additional body weight data of both males and females in several localities in the Lawrence area (Rose 1974, Fig. 3).

Instantaneous relative growth rates were calculated using the method described by Krebs et al. (1969). Data for voles caught at 4-wk intervals were condensed into a single value by the use of a linear regression between body weight and growth rate for each 4-wk period. Instantaneous growth rates for each grid population are presented in Fig. 7. Growth rates on all four grids were relatively high during November and December 1971, and gradually declined during the spring 1972. There was a burst of growth on all grids during June and July 1972 concomitant with peak densities. A decrease in growth was observed on all grids in late summer and early fall 1972, followed by another sporadic burst of growth in November and December 1972. Growth rates on most grids with the exception of grid B remained relatively high during the population decline in late spring 1973.

In summary, growth rates were erratic with substantial amounts of growth occurring during the winter 1971–72, the summer 1972 when populations reached peak densities, and in the winter 1972–73. The population decline was accompanied with high growth rates. Thus, there was no apparent association between growth and density.

DISCUSSION

There has been a considerable amount of disagreement over the last 50 yr about the causal

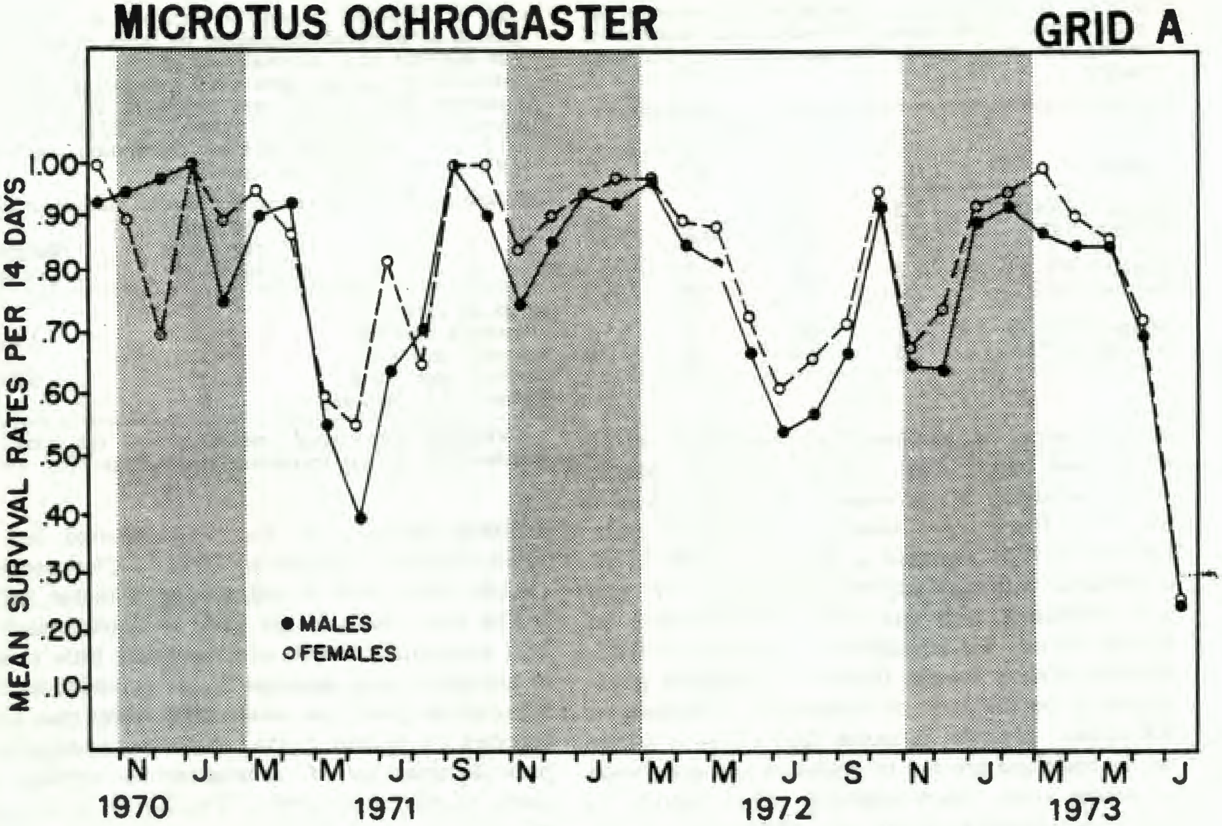

FIG. 6. Mean survival rate per 14 days for male and female *Microtus ochrogaster* on grid A, 1970–73.

mechanism for population cycles. Extrinsic factors such as predation, food, weather, and disease have all been suggested as the cause for population cycles. In addition, two self-regulatory hypotheses have been proposed: a stress hypothesis and a genetic-behavioral hypothesis coupled with dispersal. Krebs and Myers (1974) give an excellent review of the evidence for each of these hypotheses. An assumption common to all of these hypotheses is that a single factor is responsible for population cycles. Thus, populations of lemmings in Point Barrow, Alaska, and *Microtus ochrogaster* in southern Indiana and eastern Kansas "are all marching to the same drummer." Recently, Bunnell (1972) and Lidicker (1973) have favored a multifactor approach by considering population cycles in a community context. There are several reasons why a single factor hypothesis is more appealing than the multifactor approach. First, a single factor hypothesis leads to testable predictions. If we assume that the causes for population cycles are different, any multifactor hypothesis we adopt is untestable in different geographic localities, or for that matter cannot be tested over two successive cycles in the same locality. Secondly, a syndrome of demographic events has been associated with population cycles (Chitty 1952, Krebs 1964, Krebs 1966, Krebs et al. 1969, Krebs and Myers 1974). Such regularity is difficult to explain with a multifactor approach. Lidicker (1973) argues that the regularity of demographic changes may be misleading since rarely has a population been studied through two successive cycles.

Here, the use of the same methods as Krebs et al. (1969) allows us to compare data for both studies. We have found Kansas prairie voles to differ in several ways from the attributes of cycling microtine rodents (Krebs and Myers 1974) and from prairie voles in southern Indiana. We believe it is instructive to investigate contradictions to the current dogma on population cycles and attempt to explain why these inconsistencies occur.

Density changes

Length of the cycle.—Microtine population cycles are typically 3–4 yr in duration but cycles of 2, 5, and 6 yr are common (Krebs and Myers 1974). *Microtus ochrogaster* populations in this study typically exhibited a 2-yr cycle with peak densities occurring in late spring and early summer. However, this statement must be qualified since the ultimate length of the cycle will depend on the length of the phase of low numbers. *Microtus ochrogaster* and *M.*

TABLE 6. Indices of early juvenile survival summed for each season. Each index represents total number of young per total number of lactating ♀♀ for each season

	Grid			
Season	A	B	C	D
Winter 1970–71	1.2	1.0	—	0.7
Summer 1971	0.9	0.9	0.8	1.5
Winter 1971–72	1.8	1.3	1.2	1.7
Summer 1972	1.1	0.9	0.7	1.3
Winter 1972–73	1.1	0.9	1.0	1.3
Summer 1973	0.5	0.9	1.3	0.8

pennsylvanicus in southern Indiana (Krebs et al. 1969) also had a 2-yr cycle in numbers. Martin (1956) studying *M. ochrogaster* in eastern Kansas for 2.5 yr found no evidence of a population cycle. Lidicker (1973) reported a quasi-2-yr cycle in *M. californicus* with regularly recurring peaks every year and alternating high and low winter densities on Brooks Island. He considers the most obvious difference between Brooks Island and mainland populations to be the lack of mammalian predators on the island. Lidicker proposes that a 3–4-yr cycles on the mainland are due to predation and emigration of young voles, which together reduce density to very low numbers during the population decline. This extreme reduction in numbers results in a longer recovery period, consequently lengthening the duration of the cycle. Lidicker suggests that shorter cycles of 2 yr would be generated without the involvement of mammalian predators. He also superimposes interacting density dependent and independent factors to explain the 2-yr cycle. Although Lidicker's hypothesis is difficult to test due to its complexity, we can comment on the role of predation in the 2-yr cycle of *M. ochrogaster* in eastern Kansas. We have observed a number of mammalian predators in the vicinity of our grids such as coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and feral cats (*Felis domesticus*), all of which have been reported to eat *Microtus* (Martin 1956). Thus, there is no paucity of mammalian predators on the study area, yet *M. ochrogaster* has a 2-yr cycle in eastern Kansas.

Regularity of the cycle.—Density estimates for grids A, B, C, and D (Fig. 1–4) suggest that the increase phase of the cycle was least variable, among replicates, whereas the decline phase was most variable. The increase phase of the cycle lasted 1 yr on most grids with highest numbers being attained in June 1972. Several studies on *Microtus* cycles also indicate that the population increase is characterized by a rapid explosion in numbers which occupies 1 yr or less (Chitty and Chitty 1962, Krebs et al. 1969). However, a more gradual increase in numbers lasting 2 yr has been reported for *M. pennsylvanicus* (Hamilton 1937), *Clethrionomys* (Fuller 1969), and *M. californicus* (Lidicker 1973).

TABLE 7. Multiple regression analysis of population growth in *Microtus ochrogaster* on index of early juvenile survival (X_1), survival rate of ♂♂ (X_2) survival rate of ♀♀ (X_3) and percent ♀♀ lactating (X_4). The equation that is the best predictor of population growth is $Y = 0.220X_1 + 0.400X_3 - 0.515$ ($F_{2, 20} = 13.5$, $p < .01$). The multiple correlation coefficient (R) = .76. NS = not significant

	Multiple regression coefficient	Relative importance[a]
Index of early juvenile survival	0.233	1.0
Survival rate (♂♂)	NS	—
Survival rate (♀♀)	0.477	0.94
Percent ♀♀ lactating	NS	—

[a] Relative importance measured by the ratio of standardized partial regression coefficients (Zar 1974).

The peak phase of the cycle is characterized by high population density with relatively little change in numbers. Peak densities in our populations (51–92 voles per grid) are considerably lower than those reported by Martin (1956) but are comparable to peak densities for *M. ochrogaster* in southern Indiana (Krebs et al. 1969). The length of the peak phase in our study was short, and varied from 5 mo on grid C (February 1972–June 1972) to 8 mo on grid B (June 1972–January 1973). The peak phases on grids A and D were not as well defined. High numbers on both grids were followed by a decline and subsequent recovery period. Similar patterns of declines followed by a recovery in the peak year have been found in *Lemmus trimucronatus* (Krebs 1964) and *M. agrestis* (Chitty and Chitty 1962). Although Krebs and co-workers (Krebs et al. 1969, Gaines and Krebs 1971, Myers and Krebs 1975*b*) found declines and subsequent recoveries during the peak year in *M. pennsylvanicus* populations, they rarely observed this pattern of density change in *M. ochrogaster* whose peak phase was short and difficult to define.

The decline phase of the cycle is most variable. Three types of declines have been recognized (Chitty 1952) and are summarized by Krebs and Myers (1974): (1) Type H decline—the most gradual with numbers diminishing over 2 yr and with some recovery during the breeding season; (2) Type G decline—a gradual decline with no recovery during the breeding season. The decline takes a year or less; and (3) Type M decline—dramatic crash in numbers occurring over a short time period. The population on grid A had an H decline. There was a decline in numbers after the peak in June 1972, a recovery through the winter of 1972–73, and then a population crash in the spring 1973. This type of

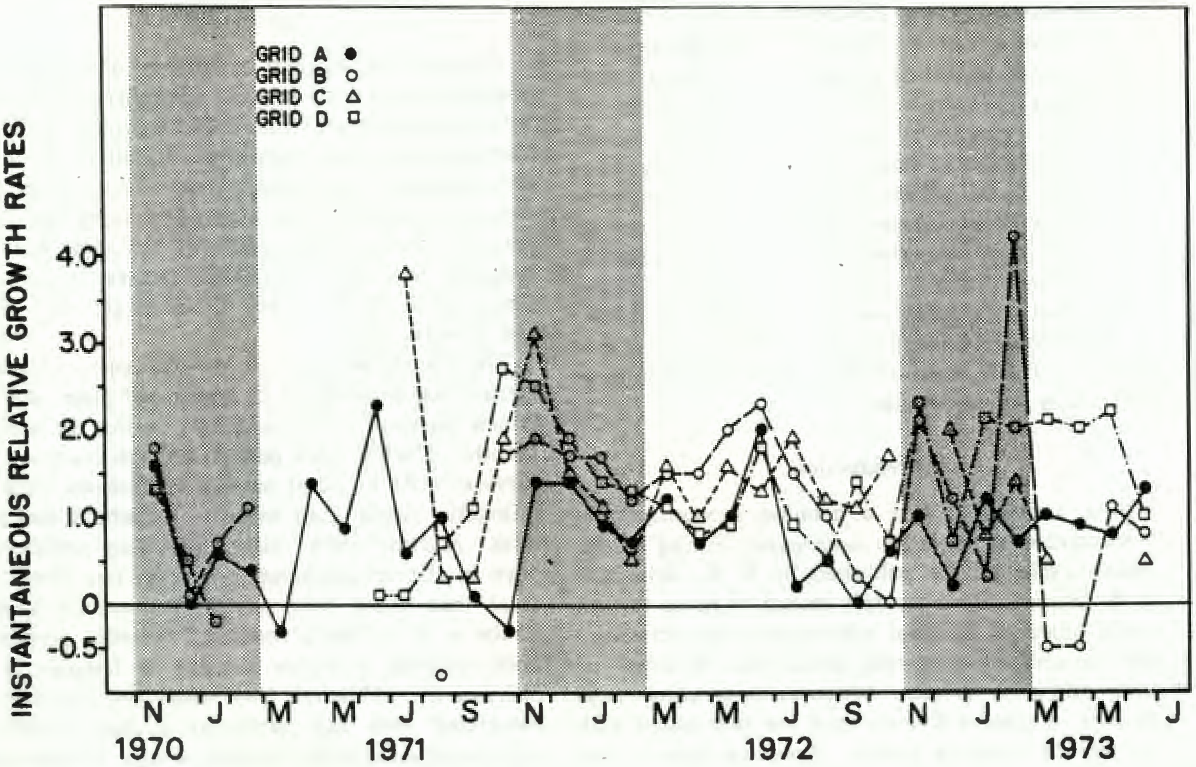

FIG. 7. Growth rate in *Microtus ochrogaster* males on all grids, 1970–73. Data grouped into 4-wk periods, and adjusted by regressions to a standard 35-g vole.

decline, where numbers after the recovery are equal to peak densities, may lead to the conclusion that populations are not cycling. Grids B and D also exhibited a type H decline, since there was some recovery during the breeding season in late spring 1973. Grid C exhibited a type G decline with numbers dropping steadily from June 1972 through June 1973. However, there was some predation of the trappable population on grid C through this period which may have contributed to this pattern of decline. Interestingly, the composite density curve of Rose (1974, Fig. 2) produced by pooling biweekly samples from five removal-trapping grids closely approximates the curve from grid C. This supports the notion that removing voles from a declining population may convert an H decline into a G decline.

It is difficult to explain the variation in the patterns of declines in densities among grids. Grid A has a unique decline with a decrease in density to low levels followed by a recovery in numbers equalling peak density. One possible explanation for this decline is the lower intensity of breeding coupled with lower survival during June and July 1973 on grid A (see Fig. 5 and 6) compared to the other grids. High intensity of summer breeding in 1971 may also be responsible for the earlier peak on grid C.

The phase of low numbers of a population cycle is difficult to define. Some populations may decline and remain at low numbers for 1–3 yr, whereas other populations may go directly from a decline to an increase phase (Myers and Krebs 1971*b*). Since only a few descriptions of populations at low numbers are available (Getz 1960, Pearson 1963, Krebs 1966), there is no a priori criteria for determining whether a cycle is in a low phase. This in turn may lead to difficulties in determining the length of the cycle. For example, numbers on grids B and D were very low in the summers of 1971 and 1973 (3–7 voles), which led us to conclude there was a 2-yr cycle. The population on grid A had moderately low densities (10–13 voles) in the summer 1971 compared to July 1973 (one vole) or the summer lows on grids B and D. If summer 1971 on grid A is considered to be a low phase, the population had a 2-yr cycle. However, an argument could be made for a longer cycle on grid A if summer 1971 was not a low phase. Furthermore, if we consider the period from August–November 1971 as a low phase on grid A, we would conclude the population exhibited an annual cycle. Our point is that until a priori criteria are established as to what constitutes a low phase, the data can be made to fit any length of cycle we choose.

The major feature of the density changes described for *M. ochrogaster* in this study that distinguished it from other microtine cycles is the typically short peak phase. Martin (1956) and Fitch (1957) observed brief periods of high numbers in *M. ochrogaster* populations in eastern Kansas. Similarly, there was a short peak phase observed in *M. ochrogaster* populations from southern Indiana (Krebs et al. 1969). In contrast, other species such as *Lemmus trimucronatus* (Krebs 1964), *M. agrestis* (Chitty 1952), and *M. pennsylvanicus* (Krebs et al. 1969) all have well-defined peak phases which last a year or more. There is no obvious explanation for these differences among species.

Reproduction

It is anticipated that a detailed account of reproductive changes in *M. ochrogaster* during a population cycle will be published by R. K. Rose and M. S. Gaines. Here we only intend to make several points based on external reproductive characteristics that are contradictory with similar data obtained for other microtine species. *Microtus ochrogaster* populations in eastern Kansas bred the year-round with no distinct breeding season. Breeding activity was reduced each winter except in the peak year and there was little or no breeding in July and August. These observations do not support the data of Fitch (1957) who found little evidence of winter breeding in Kansas voles, based on obvious pregnancies. He also observed a reduction of breeding in the summer months which he attributed to drought. Krebs et al. (1969) reported that *M. ochrogaster* and *M. pennsylvanicus* populations in southern Indiana had a distinct breeding season with the highest incidence of breeding occurring in the summer months. They did not observe a summer depression in breeding as exhibited by Kansas voles. These inconsistencies between the Indiana and Kansas studies may be related to climatic differences between the two areas.

Sex ratios

Our results demonstrating equal sex ratios are inconsistent with other studies on population fluctuations of small rodents which report an excess of males in the trappable population. Williams (1966) has suggested that deviations in sex ratios can act to regulate density in a population out of equilibrium with itself. We do not know of any studies that have demonstrated a correlation between sex ratios and population density. Even if there were a positive correlation between these two variables, it would be difficult to distinguish between cause and effect. It would be interesting to perturb sex ratios in favor of males or females in natural populations of voles and determine its effect on density.

Mortality

The data we obtained on survival of the trappable population and early juvenile mortality are consistent with other studies of microtine populations. During increasing and peak densities, mortality was low in the trappable population, whereas during declining densities, mortality was high. The same association between mortality and phase of the cycle has been reported for other microtine species (Chitty and Chitty 1962, Krebs 1966, Krebs et al. 1969, Batzli and Pitelka 1971).

The population cycle of *M. ochrogaster* in eastern Kansas was punctuated by periods of poor male and female survival which occurred during the summer months. During these periods of high mortality, the survival rates of adult males and females were significantly higher than those of subadults and juveniles. Martin (1956) also found that prairie voles born in the spring–summer months had lower survival than those born in the fall–winter months. Krebs et al. (1969) observed sporadic periods of poor survival in males but not in females in *M. ochrogaster*. Although poor male survival was not associated with any particular season, statistically significant differences between adults and subadults in the summer months agree with our results.

Our data on early juvenile survival indicate consistently high mortality of voles from parturition until recruitment into the trappable population throughout the cycle. Krebs et al. (1969) estimated early juvenile losses to be as high as 80%. Since this mortality was a constant part of the demography of Indiana voles, Krebs and co-workers suggested that mortality of the trappable population plays a greater role than early juvenile survival in determining density changes. Our results indicate that although there was high early juvenile mortality in all phases of the cycle, the greatest losses generally occurred during periods of declining densities. In light of these data, early juvenile survival may have a critical role in the demography of fluctuating vole populations. Therefore, it is essential that techniques are developed to measure early juvenile survival more accurately.

Growth

Previous studies of fluctuating populations of microtine rodents indicate that high body weights are characteristic of peak densities (Kalela 1957, Chitty and Chitty 1962, Krebs 1964, Batzli and Pitelka 1971, Krebs et al. 1973). However, Kansas prairie voles did not exhibit this trend. Before the discrepancy can be explained, we must consider how high body weight animals can be produced in the peak phase of the population cycle. Krebs and Myers (1974) give three possible explanations for heavy animals in peak years which are not mutually exclusive. First, survival may be higher during the increase and peak phase resulting in older and heavier animals. Although we found that survival was higher when density was increasing, we have no information on the age structure of the populations. Most of the data that have been accumulated from other studies (Chitty 1952, Krebs 1964) suggest that heavy animals in the increase and peak phases are the same ages as lighter animals in the decline phase. Second, voles may grow faster in the increase and peak phase. Our data on instantaneous growth rates do not show a trend towards increased growth rates during the increase and peak phases (Fig. 7). Thus, there is no reason to expect voles of heavy weight in the peak phase based on growth rates. Third, growth rates of young voles may be constant but will show an asymptote at heavier weights in peak years. This could be tested with a large cohort of voles that are captured each trapping period over a long timespan. Small sample sizes prohibited us from testing this hypothesis.

Body length is another index of growth that may be a better measure than body weight since it reflects skeletal development. It is interesting to note that when we measured body length of voles from a circuit of live traps in the Lawrence area, we found a trend towards longer males and females during the peak phase (Rose 1974, Fig. 4).

Single factor vs. multifactor hypotheses

Our results on the dynamics of *M. ochrogaster* populations in eastern Kansas generally are in agreement with other studies on microtine rodents. However, some of our observations such as the short peak phase, lack of a well-defined breeding season, summer breeding depression, the absence of a shift towards heavier animals in the peak phase, and equal sex ratios are inconsistent with the current dogma. The question that emerges is: do these inconsistencies negate a single factor hypothesis in favor of a multifactor hypothesis in explaining the cause for population cycles?

We agree with Lidicker (1973) that microtine populations have to be considered in the context of the community in which they occur. The interactions between environmental factors and the population may change population densities. The demographic patterns exhibited by *M. ochrogaster* may represent in an evolutionary sense a composite of the patterns found in *M. californicus*, a dry-adapted species, and *M. pennsylvanicus*, a cold-adapted species. *Microtus californicus* is a species that has adapted to midsummer drought, whereas *M. pennsylvanicus* is faced with the obstacles presented by harsh winters. Although eastern Kansas experiences only occasional droughts in summer, from central Kansas to the foothills of the Rocky Mountains the average rainfall is 25–40 cm with predictable droughts in midsummer. The summer breeding depression in *M. ochrogaster* may be an adaptation to the central plains, whereas the midwinter breeding depression may be an adjustment to severe winters that are similarly experienced by *M. pennsylvanicus*. The short peak phase may also be related to the unpredictability of summer drought conditions in eastern Kansas. The theory of *r*- and *K*-selection states that species (*r*-strategists) in unpredictable environments put more energy into reproduction at the expense of competitive ability, whereas species (*K*-strategists) in predictable environments put more energy into efficient utilization of resources at the expense of reproduction (Abrahamson and Gadgil 1973). If *M. ochrogaster* is more of a *r*-strategist than *M. californicus* and *M. pennsylvanicus*, we would predict a shorter peak phase for the former due to poor intraspecific competitive ability at high densities. The absence of high body weights could be a cause or an effect of the short peak phase.

The inconsistencies we found in the demography of *M. ochrogaster* compared to previous studies indicate that the demographic processes contributing to population cycles are more complicated than has been previously assumed. However, a multifactor hypothesis is not entirely satisfactory in explaining population cycles. Although environmental interactions may explain some of the anomalies we observed, they cannot account for the syndrome of demographic events that are associated with population cycles in a variety of species over different geographic localities.

Perhaps the single factor and multifactor approaches to population cycles can be reconciled by arranging small mammals on a continuum from those species that exhibit short-term annual cycles, such as *Peromyscus maniculatus* (Sadleir 1965) and *Sigmodon hispidus* (Joule and Cameron 1975), to those that have long-term cycles which are found in microtine rodents (Krebs et al. 1973). Superimposed on the superannual cycles are factors that affect the demography in the same manner as in annual cycling species. These factors could be abiotic (temperature, humidity, and rainfall) or biotic (competition and predation). They would also be multifactorial in that many are dependent on the community in which the population occurs. The summer breeding depression observed in this study is an example of an annual event superimposed on a superannual cycle. It is interesting to note that populations of *Sigmodon hispidus* in eastern Kansas, a species that has an annual cycle, also exhibit a summer breeding depression (L. R. McClenaghan and M. S. Gaines, *personal observation*). We believe that underlying long-term population cycles is some basic mechanism. Furthermore, it is becoming increasingly apparent that dispersal may be the mechanism of population regulation in cycling species (Myers and Krebs 1971*b*, Garten and Smith 1974, Lidicker 1975, Joule and Cameron 1975, Krebs et al. 1976). It is significant that dispersal plays a major role in the population regulation of superannual cycling rodent species (Krebs et al. 1976) as well as annual cycling species (Garten and Smith 1974).

We have three recommendations for future research on population cycles. First, a detailed comparison must be made between demographic patterns found in annual cycling species and those found in superannual cycling species. A survey of this kind which could be accomplished with the existing literature would at the very least provide a baseline for a continuum of demographic changes exhibited by annual and superannual cycling species. Second, a multivariate approach should be taken to determine which factors are closely associated with the demography of superannual cycling species. A multivariate analysis will not show cause and effect, but will determine: (1) the degree of correlation among factors; (2) which factors explain the most variation in demographic parameters; and (3) whether different factors are operating annually or superannually. Perturbation experiments could then be performed with a given factor or a pair of factors to test for causal relationships with demography. The major drawback of this approach is that although abiotic factors are the easiest to quantify, they may be least important to the demography of the species. Third, since dispersal is the prime candidate for a necessary factor for population cycles, more work needs to be done on other species to test the generality of the qualitative differences that have been found between residents and dispersers (see Myers and Krebs 1971*b*). Most of the studies on dispersal have utilized vacuum grids. Animals are continuously removed from an area and all new animals appearing on the area are defined as dispersers. Other methods should be devised to monitor dispersal more accurately. Ultimately, we would like to know what factors are triggering dispersal and what happens to dispersers after they leave the population.

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