

Vole population dynamics: factors affecting amplitudes of fluctuation

Lowell L. Getz, Joyce E. Hofmann, Betty McGuire, and Madan K. Oli

L. L. Getz, Dept of Animal Biology, Univ. Illinois, 505 S. Goodwin Ave., Urbana, IL 61801, USA (L-GETZ@life.uiuc.edu). – J. E. Hofmann, Illinois Natural History Survey, 607 E. Peabody Dr., Champaign, IL 81820, USA. – B. McGuire, Department of Biological Sciences, Smith College, Northampton, MA 01063, USA. – M. K. Oli, Dept of Wildlife Ecology and Conservation, 110 Newins-Ziegler Hall, University of Florida, Gainesville, FL 32611, USA.

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Oikos

Factors affecting amplitudes of fluctuation during 39 population cycles of *Microtus ochrogaster* and 20 cycles of *M. pennsylvanicus* were studied in alfalfa, bluegrass and tallgrass habitats over a 25-year period. Thirty-two of the 39 *M. ochrogaster* population cycles peaked in autumn or winter. Variation in peak densities appeared to be related primarily to length of the increase period. Peak densities and amplitudes of fluctuation were not correlated with initial population densities, rate of increase, length of the reproductive period, survival rates, proportion of reproductive females, or body mass during the increase phase. Cessation of growth of *M. ochrogaster* populations that peaked in autumn-winter resulted from a combination of a density-dependent reduction in survival and a density-independent reduction in reproduction during the winter. Cessation of growth of *M. ochrogaster* populations peaking during spring-summer resulted from density-dependent reduction in survival; reproduction remained high during the increase through the peak and decline. Density-dependent predation appears to be the primary mortality factor stopping population growth of *M. ochrogaster*. Nine *M. pennsylvanicus* cycles peaked during November-February, and 11 peaked during June-September. No single factor was consistently associated with stoppage of population growth for *M. pennsylvanicus*. A marked decline in reproduction was associated with stoppage of population growth in six of the *M. pennsylvanicus* cycles that peaked during autumn-winter and in three that peaked during June-September

Two criteria must be met for population fluctuations of arvicoline (microtine) rodents to be classified as multi-annual: (1) intervals between population peaks should be >2 yrs. (2) amplitudes of fluctuation (the difference between peak and trough densities) must be ≥ 10 -fold (Krebs and Myers 1974, Taitt and Krebs 1985, Krebs 1996). Thus, if we are to understand causation of multi-annual population cycles we must identify the factors that influence length of interval between cycles, and determine the circumstances under which populations achieve unusually high densities some years and not others (Krebs 1996). We concluded elsewhere (Getz et al. In Review a) that relaxation of predation pressure is the primary factor responsible for initiation of population cycles and determining intervals between peaks in our study populations. In this paper we evaluate factors affecting peak densities, amplitudes of fluctuation and cessation of population growth.

Population cycles that reach a peak in autumn or winter in temperate regions do so at the onset of potentially adverse environmental conditions which may negatively impact habitat quality (decline in food and cover) and the animals themselves (e.g., an increased stress response, which could affect survival and reproduction; Christian 1980). In addition, extrinsic environmental stresses may reinforce intrinsic density-dependent factors, leading to more pronounced reductions in survival and reproduction. Batzli (1992) proposed seasonal changes in demographic variables, especially reproduction, to be responsible for seasonal patterns in population density. Differences in density-independent extrinsic factors, e.g., weather extremes, also may result in variation in population density from one year to the next.

Density-dependent factors may impact population changes through increased mortality and decreased reproduction. If no delay is involved, negative feed-backs tend to stabilize population density by dampening fluctuations (Hanski et al. 1993, Ostfeld et al. 1993, Ostfeld and Canham 1995). If delayed effects are involved, however, such factors may increase amplitudes of fluctuation (Saucey 1984).

Getz et al. (In Review b) show that survival rates of *M. ochrogaster* and *M. pennsylvanicus* generally do not vary significantly between autumn (typically the period of increase of most *M. ochrogaster* and some *M. pennsylvanicus* populations) and winter (when decline phases often occur), but that reproduction generally drops from high to low levels from autumn to winter. However, the analyses were general in nature and did not specifically examine factors influencing amplitudes of fluctuation and cessation of population growth.

In this paper, we use data from a 25-yr study (Getz et al. 2001) to investigate factors influencing peak densities, amplitudes of fluctuation and cessation of population growth in the prairie vole, *Microtus ochrogaster*, and the meadow vole, *M. pennsylvanicus*, in three habitats (alfalfa, bluegrass and tallgrass prairie). Data were obtained from a total of 30 population cycles of *M. ochrogaster* and 14 cycles of *M. pennsylvanicus* at our main study sites. Another nine population cycles of *M. ochrogaster* and six of *M. pennsylvanicus* were observed in other sites monitored for shorter periods than in the long-term study. Thus, we had sufficient phase-specific data to allow investigation of the factors that might influence amplitudes of fluctuation and cessation of population growth in our study populations.

Methods

Study sites

The study sites were located in the University of Illinois Biological Research Area ("Phillips Tract") and Trelease Prairie, both 6 km NE of Urbana, Illinois (40°15'N, 88°28'W). We monitored populations of *M. ochrogaster* in restored tallgrass prairie (March 1972--May 1997), bluegrass, *Poa pratensis* (January 1972--May 1997), and alfalfa, *Medicago sativa* (May 1972--May 1997) habitats. We have described the study sites in considerable detail elsewhere (Getz et al. 1979, 1987, 2001) and thus limit our descriptions here.

We trapped study sites in two restored tallgrass prairies: one located in Trelease Prairie, the other in the nearby Phillips Tract. The predominant plant species in Trelease Prairie included big bluestem, *Andropogon gerardii* (17%), bush clover, *Lespedeza cuneata* (16%), ironweed, *Vernonia* (12%), Indian grass, *Sorghastrum nutans* (10%), and another 15 species in which each constituted <10 % of the total plant abundance (Getz et al. 1979). The most prominent plant species in the Phillips Tract site were *A. gerardii*, (38%), *L. cuneata* (25%), Beard tongue foxglove, *Penstemon digitalis* (16%), and *S. nutans* (19%). All other species represented <1% relative abundance (Lindroth and Batzli 1984).

Both prairies were burned during the spring every 3-4years to control invading shrubs and trees. We trapped sites in one or both of the two tallgrass prairies, depending upon requirements of the overall study at the time; vole populations fluctuated in synchrony in the two tallgrass areas (Getz and Hofmann 1999). During the course of the overall study, additional tallgrass study sites within Trelease and Phillip Tract were trapped for several years as a part of another study. Data from these study sites, where appropriate, were included in the analyses.

The bluegrass study sites were established within a former *P. pratensis* pasture located in Phillips Tract. The main plant species at these sites were bluegrass (70%) dandelion, *Taraxacum officinale* (14%) and about 25 other species with relative abundance of <10% (Getz et al. 1979). To reduce successional changes, especially those involving invading forbs, shrubs and trees, bluegrass sites were mowed in their entirety during late summer every 2-3 years. A bluegrass site, with vegetation characteristics similar to those above, was trapped for 10 years as part of another study. Where appropriate, data from the latter site have been included in the analyses.

Two adjacent *M. sativa* sites in Phillips Tract were trapped. These sites were separated by a 10-m closely mown strip. A site was trapped until invading forbs and grasses began to crowd out the *M. sativa*. One year before trapping was terminated in one site, the other was planted to *M. sativa* so that the plants would be fully developed when trapping commenced. Initially, *M. sativa* comprised 75% of the vegetation in each site. During the last year of usage, other common plants included: *P. pratensis*; goldenrod, *Solidago*; timothy, *Phleum pratense*; brome grass, *Bromus inermis*; clover, *Trifolium repens* and *T. pratense*; and plantain, *Plantago*. Periodically each summer, a series of 3-m wide strips was mowed (25 cm above the surface) to control invading weedy forbs and to promote new growth of *M. sativa*. The schedule of mowing was such that at least two-thirds of the field had vegetative cover at all times. Even in the mown strips, live vegetation and recently mown litter provided surface cover.

Trapping procedures

We established a grid system with 10-m intervals in all study sites, and placed one wooden multiple-capture live-trap (Burt 1940) at each

station. Each month we pre-baited for 2 days and then trapped for 3 days; cracked corn was used for prebaiting and as bait in the traps. During the summer we covered traps with vegetation or aluminum shields to prevent exposure of captured animals to high temperatures. At no time did we provide nesting material in the traps; the wooden traps provided ample insulation in the winter. Trap mortality during the 25-year study was less than 0.5%.

We set traps in the afternoon and checked them at approximately 0800h and 1500h for the following 3 d. At first capture, we toe-clipped all animals (≤ 2 toes on each foot) for individual identification. Although toe clipping no longer is a recommended method of marking animals, during most of the time of the study few alternative methods were available. Ear tags were available, but owing to frequent loss of tags, toe clipping was deemed a more effective means of marking individuals. The field protocol, including use of toe clipping, was reviewed periodically by the University of Illinois Laboratory Animal Resource Committee throughout the study. The committee approved the field protocol, based on University and Federal guidelines, as well as those recommended by the American Society of Mammalogists, in effect at the time.

At each capture we recorded species, grid station, individual identification, sex, reproductive condition (males: testes abdominal or descended; females: vulva open or closed, pregnant, as determined by palpation, or lactating), and body mass to the nearest 1 g. For analysis, we considered animals that weighed ≤ 29 g as young and those weighing ≥ 30 g as adult.

Data analysis

Peak densities.--Population density for each trapping session was estimated using the minimum number known to be alive method (MNA; Krebs 1966, 1999). Previously marked individuals not captured in a given trapping session, but trapped in a subsequent session, were considered to have been present during the sessions in which they were not captured. Although the Jolly-Seber index is recommended for estimating population density (Efford 1992), at least 10 individuals must be trapped each session in order to obtain reasonable estimates (Pollock, et al. 1990). During months voles were present in the study sites, 10 or fewer *M. ochrogaster* were trapped 26%, 52% and 62% percent of trapping sessions in alfalfa, bluegrass, and tallgrass, respectively. Ten or fewer *M. pennsylvanicus* were trapped 55% of the sessions in alfalfa, 46% in bluegrass, and 24% in tallgrass. Since the same index should be used throughout, we felt justified in using MNA. Because we utilized prebaited multiple-capture live-traps, checked twice daily for 3 days each session, our capture efficiency was very high. Of the animals estimated to be present, 92% of the *M. ochrogaster* and 91% of the *M. pennsylvanicus* were actually captured each session.

We used correlation analysis to estimate the influence of the following variables on peak densities and amplitudes of fluctuation (based on the indicated presumptions): (1) Population density at the beginning of the increase phase. Reasonably high quality habitat conditions would maintain high population densities during the trough, which, in turn, could lead to higher densities at the subsequent peak and higher amplitudes of fluctuation. (2) How soon in the year the increase phase begins. If population growth stops about the same time each year because of seasonal effects on survival and reproduction and if rates of increase do not vary, then an earlier start of the increase phase will result in higher peak densities and amplitudes of

fluctuation. (3) Length of the increase phase. Given a constant rate of increase, the longer that conditions remain favorable for population growth the higher will be the peak densities and amplitudes of fluctuation. (4) Length of the reproductive period (period with >60% of the females reproductive). The longer reproduction remains high and is not off-set by mortality, the higher the peak densities and amplitudes of fluctuation.

Exceptionally favorable habitat conditions during the increase phase of a cycle may also influence peak densities and amplitudes of fluctuation. We therefore examined correlations between peak densities and amplitudes of fluctuation and the following increase phase factors that may be associated with habitat quality: (1) rate of increase [$N(t+1)/N(t)$], (2) survival, (3) reproduction, and (4) body mass of adult males (Getz et al. In Review b). Higher rates of survival and greater proportions of reproductive females would result in higher peak densities. Body mass is an indication of quality of the animals, which in turn, is an indication of habitat quality. We compared body mass only of adult males (≥ 30 g) to avoid bias from variation in the proportion of population comprised of young animals and from variation in reproductive status of females. We recognize that during the winter, body mass of some adult males dropped below 30 g, perhaps resulting in a slight, but not critical, bias during this period.

The influence of weather conditions on *M. ochrogaster* population growth was evaluated for peak densities in alfalfa and bluegrass; there were too few population cycles in tallgrass for analysis. Peak densities were grouped as low (alfalfa, <100/ha; bluegrass, < 35/ha), intermediate (alfalfa, 101-199/ha; bluegrass, 36-99/ha), and high (alfalfa, >200/ha; bluegrass, >100/ha). Deviations in mean monthly temperatures and total precipitation from the previous 30-year means

were calculated for March-June and July-October each year. These periods were selected as the times when weather extremes could have the greatest impact on population cycles (Fig. 1). More specifically, extreme weather might either trigger or suppress initiation of a cycle (March-June) or maintain, enhance or dampen the increase phase of a cycle (July-October). Monthly weather data were also examined for the years population peaks were unusually low (alfalfa, <86/ha; bluegrass, <28/ha) to determine if there were episodes of extreme temperature or precipitation that might have impacted population growth. There was insufficient variation in peak population densities of *M. pennsylvanicus* in alfalfa and bluegrass to warrant such analyses.

Weather data were obtained from the Illinois State Water Survey climatological records. The weather station was located on the campus of the University of Illinois, approximately 10 km from the study sites.

Cessation of growth.--For *M. ochrogaster*, density-independent seasonal impacts on survival and reproduction were examined by comparing monthly survival of adults and young and proportion of adult females pregnant during September-November (autumn) and December-February (winter) for cycle years (that is, when peaks occurred October-February) with non cycle years. Because of the greater inconsistencies in timing of the population cycles of *M. pennsylvanicus* with respect to seasons, we did not compare autumn-winter variations in survival and reproduction for this species.

Density effects for both species were analyzed by comparing demographic variables three months prior to the peak, the peak month and the three months following the peak. Data for cycles peaking in spring-summer and autumn-winter were analyzed separately. The one

population cycle of *M. ochrogaster* in alfalfa that peaked in summer (July 1976) was combined with the five tallgrass population cycles that peaked in spring or summer for analysis. Owing to the irregular configuration of the phases of the cycle in *M. pennsylvanicus*, we also examined individual cycles of this species in an effort to determine what variables might have stopped population growth.

Some cycles were not suitable for analyses. We excluded cycles in which the increase phase was short (≤ 2 months) or the entire period of high density was long (≥ 5 months) with irregular fluctuations that made it difficult to determine the peak month. All 13 population cycles of *M. ochrogaster* in alfalfa were suitable for analysis. In bluegrass sites, 16 of the 17 cycles of *M. ochrogaster* peaked during October-February, and were suitable for analyses. Four of the eight population cycles of *M. ochrogaster* in tallgrass that peaked in April and July were also suitable. Because of marked demographic differences among populations in *M. ochrogaster* (Getz et al. In Review c), data for the three habitats were analyzed separately, except as noted above for cycles peaking in spring-summer. Only one of the *M. pennsylvanicus* cycles (alfalfa) was not suitable for analysis. There were no differences in peak densities or amplitudes of fluctuation of *M. pennsylvanicus* populations in alfalfa and bluegrass (Getz et al. In Review c), and thus data from the two habitats were combined for analysis.

Survival was calculated for adults and young. Survival estimates were based on animals present the month of record that survived until the next month. Estimates of reproduction were proportion of adult females that were pregnant during a given month. We used pregnancy because it is a conservative indicator of reproductive condition at a specific time. We did not consider condition of the vulva or nipples

because animals with open vulvas may not have mated, and there is a lag time following cessation of lactation during which the nipples remain large. These latter instances may result in animals being wrongly classified as reproductive.

Increased nestling survival has been identified as a major factor involved in initiation of population cycles of *M. ochrogaster* (Getz et al. 2000), but the role of nestling survival on the initiation or continuation of the decline phase has not been tested. Data from the current study appear adequate to examine the role of nestling survival in stoppage of population growth and initiation of a decline.

The index of nestling survival was derived from the number of juveniles (≤ 20 g) present one month divided by the number of pregnant females present the previous month. We assumed that survivors of young born to females pregnant one trapping session would be out of the nest and captured as juveniles during the following monthly trapping. We also assumed that litter size did not vary significantly with season or phase of the population cycle (Keller and Gaines 1970, Getz et al. 2000). This obviously is a crude index of nestling survival because some pregnant females may have been missed in a given month and some surviving young born to advanced pregnant females may have exceeded 20 g before the next trapping period. Accordingly, we limited our estimates to periods with at least five pregnant females. For these comparisons, we included the three months preceding the peak, the peak and the first month of the decline. There were too few pregnant females present the second and third months of the decline for analysis. We also compared nestling survival during the months of August-December to test for seasonal changes that might affect nestling survival. Likewise, too few pregnant females were present in January and February for analysis of nestling survival during these two winter

months. Because too few *M. pennsylvanicus* females were pregnant most months we did not derive an index of nestling survival for this species.

Episodes of adverse weather conditions may result in increased mortality sufficient to stop population growth and trigger a decline. We examined weather data for evidence of weather episodes that may have contributed to the stoppage of population growth and initiation of population declines.

Statistical analyses

Because most of the variables did not meet the requirements for normality (population densities and demographic variables were non normal at the 0.05 level; Kolmogorov-Smirnov test; Zar 1999), all variables were log-transformed. Variables that included "zeros" were log (X+1)-transformed because logarithm of zero is not defined. This allowed us to test for differences using analysis of variance (ANOVA), independent-sample t-tests or Pearson's correlation coefficient procedures, where appropriate. One-way ANOVAs were followed by Tukey's honestly significant difference (HSD) post-hoc multiple comparisons. Sample sizes represent number of months of data. When degrees of freedom (df) for t-tests are given in whole numbers, variances were equal (Levene's test for equality of variances). When variances were not equal, df is given to one decimal place. We used SPSS 10.0.7 for Macintosh (SPSS, Inc. 2001) for all statistical analyses.

Results

Microtus ochrogaster

Population cycles

Twenty-five *M. ochrogaster* population cycles in the main study sites peaked during October-February; three peaks occurred in spring (bluegrass: April 1977; tallgrass: April 1973, April 1983) and two in the summer (alfalfa: July 1976; tallgrass: June 1985). In the other study sites, six cycles in bluegrass peaked during autumn or winter; one in tallgrass peaked in the winter and two in summer. Thus, of a total of 39 population cycles of *M. ochrogaster*, 32 peaked from October to February. Five of the seven spring-summer peaks were in tallgrass, three of which peaked the same month (June 1985) in three different tallgrass sites.

Peak densities and amplitudes of fluctuation

Length of the increase phase in alfalfa was positively correlated with both the subsequent peak density and amplitude of fluctuation (Table 1). None of the correlations between any of the other demographic variables and either peak density or amplitude of fluctuation was significant.

Population density at the beginning of the increase phase in bluegrass was positively correlated with the subsequent peak density and amplitude of fluctuation (Table 1). As in alfalfa, length of the increase phase was positively correlated with both peak density and with amplitude of fluctuation (Table 1). Length of the reproductive period was also positively correlated with peak densities and amplitudes of fluctuation (Table 1). Survival during the increase was significantly correlated with and peak densities and amplitudes of fluctuation in bluegrass (Table 1). Correlations between all other demographic variables and either peak density or amplitude of fluctuation were not significant (Table 1).

Beginning population density in tallgrass was correlated with peak densities, but not amplitudes of fluctuation (Table 1). The

proportion of females reproductive was positively correlated with both peak densities and amplitudes of fluctuation, as was body mass of adult males during the increase (Table 1). None of the other correlations between demographic variables and either peak density or amplitude of fluctuation was significant (Table 1).

There was no consistent relationship between temperature and precipitation conditions during March-June and July-October of cycle years that would explain unusually high peaks of *M. ochrogaster* (Table 2).

Cessation of population growth

Adult survival of *M. ochrogaster* in alfalfa remained high during September and October of cycle years with peaks in autumn-winter, began to decline in November, and dropped a total of 29% by the end of the winter months (Table 3). Seasonal analysis of demographic data revealed that adult survival was significantly greater during September-November (autumn) than during December-February (winter) in both cycle ($t=4.39$, $df=63.9$, $P<0.001$) and non cycle years ($t=2.72$, $df=55$, $P<0.001$). In bluegrass, adult survival declined 36% during the decline and was lower during winters than autumn only during cycle years ($t=4.14$, $df=88$, $P<0.001$); non cycle years: ($t=1.62$, $df=116$, $P=0.109$). Survival of adults did not differ during winters of cycle and non cycle years (alfalfa: 0.385 ± 0.039 and 0.303 ± 0.062 , respectively; $t=1.48$, $df=64$, $P=0.144$; bluegrass: 0.341 ± 0.037 and 0.301 ± 0.042 ; $t=1.00$, $df=102$, $P=0.321$).

Survival of young did not differ during September-November and December-February of cycle and non cycle years in alfalfa (Table 4). When the data were grouped by season, survival of young in alfalfa was greater during autumn than winter of cycle years ($t=2.98$, $df=71$,

$P=0.004$), but was greater during winter than autumn of non cycle years ($t=3.87$, $df=54$, $P<0.001$; Table 4). Survival of young in bluegrass did not differ during autumn and winter of cycle ($t=0.83$, $df=81$, $P=0.408$) and non cycle years ($t=0.58$, $df=82$, $P=0.563$). Nor was there a difference in survival of young during winters of cycle and non cycle years (alfalfa: 0.333 ± 0.037 and 0.360 ± 0.084 , respectively; $t=0.04$, $df=28.9$, $P=0.970$; bluegrass: 0.337 ± 0.041 and 0.300 ± 0.049 ; $t=0.87$, $df=88$, $P=0.385$).

Adult survival of *M. ochrogaster* was high during the increase to the peak (months P-3 to P-1) in alfalfa, began dropping at the peak (Pk), and became significantly lower than during the increase in the first and second months of the decline (Table 5). A similar trend was observed in bluegrass, but the difference did not become significant until the second month of the decline. Survival of young dropped markedly, beginning at the peak in alfalfa, but survival did not change from the increase through the decline in bluegrass (Table 5). The data were also grouped as pre-peak, peak and post-peak months for analysis. Post-peak survival was significantly lower for adults in alfalfa ($F=25.84$, $df=2,85$, $P<0.001$) and bluegrass ($F=13.33$, $df=2,102$, $P<0.001$) and for young in alfalfa ($F=8.32$, $df=2,82$, $P=0.001$), but not in bluegrass ($F=0.50$, $df=2,91$, $P=0.607$).

Indices of nestling survival (all cycles in alfalfa and bluegrass pooled) dropped gradually from August through October, and more steeply in November and December (1.07 ± 0.25 , 0.85 ± 0.13 , 0.82 ± 0.16 , 0.60 ± 0.18 , and 0.45 ± 0.16 , respectively); the differences approached significance ($F=2.32$, $df=4,109$, $P=0.061$). Indices of nestling survival were higher during the three months preceding the peak (1.07 ± 0.20 , 0.92 ± 0.19 and 0.79 ± 0.14 , respectively) than at the peak (0.32 ± 0.07 ; $F=3.914$, $df=81$, $P=0.012$). Nestling survival indices during months P-3 and P-2 were

significantly different from those during peak (Tukey's HSD test, $P < 0.05$). Too few pregnant females were present for post-peak analysis.

Survival of adults did not differ among the individual months (P-3 through P + 3) for the cycles that peaked during spring and summer ($F = 2.03$, $df = 6, 35$, $P = 0.087$). When the data were grouped as pre-peak, peak and post-peak, however, adult survival was significantly lower at and following the peak ($F = 5.59$, $df = 2, 39$, $P = 0.007$). Survival of young differed among months during P-3 through P+3, with generally higher survival during the pre-peak months than at the peak or during the post-peak months (Table 5). When grouped as to pre peak, peak and post peak, the differences in survival of young were significant ($F = 9.08$, $df = 2, 30$, $P < 0.001$, respectively).

Because of small sample sizes, data for comparisons of nestling survival indices for population cycles peaking during spring-summer, were grouped as to the three pre-peak months and the peak with the first month of the decline. The differences were significant (1.48 ± 0.40 and 0.63 ± 0.12 , respectively; $t = 2.124$, $df = 19$, $P = 0.047$). There were sharp declines in the proportion of females pregnant, beginning in late autumn and continuing the rest of the winter during both cycle and non cycle years in alfalfa and bluegrass (Table 6). When data were grouped by season, the proportion of females that were pregnant was significantly lower during winter than autumn in both habitats for cycle years (alfalfa: $t = 9.26$, $df = 73$, $P < 0.001$; bluegrass: $t = 9.90$, $df = 5.7$, $P < 0.001$) and non cycle years (alfalfa: $t = 4.29$, $df = 48$, $P < 0.001$; bluegrass: $t = 3.13$, $df = 86$, $P = 0.002$). There was no difference in the proportion of females pregnant in winters of cycle years and non cycle years in alfalfa (0.111 ± 0.220 and 0.181 ± 0.040 ; $t = 1.57$, $df = 57$, $P = 0.121$). In bluegrass, the proportion of pregnant females was lower during the

winter of cycle than non cycle years (0.062 ± 0.018 and 0.181 ± 0.047 ; $t=2.28$, $df=55.1$, $P=0.027$).

Cycles that peaked in autumn-winter were characterized by a major decline in the proportion of females pregnant during the peak month and the three months following the peak in comparison to the three months preceding the peak in both alfalfa ($F=19.85$, $df=2,85$, $P<0.001$) and bluegrass ($F=33.77$, $df=2,97$, $P<0.001$) (Table 7). When populations peaked in summer, however, there was no difference in the proportion of females pregnant during the three months preceding the peak, the peak month, and the three months following the peak ($F=1.01$, $df=2,37$, $P=0.373$) (Table 7).

There was a period of low temperatures or heavy rain preceding cessation of growth of only 2 of the 13 peaks in alfalfa; these extreme weather events might have contributed to the cessation of population growth. Two weeks prior to the January 1985 peak, there was a 3-day period with an average temperature of -20.0°C . Immediately following the November 1985 alfalfa trapping session (the peak month for that cycle) there was a 2-day period of heavy rain (total of 7.3 cm) with mean temperatures of 13.5°C . No other peak was preceded by episodes of extreme weather events.

Cessation of population growth of one population cycle in bluegrass was preceded by unusually low temperatures: December 1973, 3-day mean of -18.5°C . There was no period of exceptionally high rainfall the month preceding any of the peaks.

An episode of unusual weather conditions was associated with stoppage of growth for four of the five population cycles in tallgrass: April 1973 peak, 10.3 cm of rain during a 5-day period in April; August 1985, the entire month of July was very hot (mean temperature of 26.3°C , 7.4°C above average) and dry (5.4 cm below average precipitation);

February 1988, temperatures during a 7-day period in early January, -13.2°C; January 1990, temperatures during an 11-day period in mid December 1989 averaged -18.3°C.

Although survival during the month of the extreme weather was much lower for six of the seven episodes from all three habitats, as described above (an average of 24% lower), such effects would have contributed to the cessation of growth of only six of the 39 population cycles observed in this study.

Microtus pennsylvanicus

Population cycles

Of the 15 population cycles recorded for *M. pennsylvanicus* in bluegrass, nine peaked in winter and six in June-September. All five cycles in alfalfa peaked during summer.

Peak densities and amplitudes of fluctuation

The correlation between length of the reproductive period and peak densities and amplitudes of fluctuation in alfalfa approached significance (Table 8).

There were too few population fluctuations of *M. pennsylvanicus* in alfalfa suitable for rate of increase analyses. Beginning of the increase phase was too variable for analysis of relationship between beginning of the increase and peak densities or amplitudes of fluctuation. None of the correlations between all other demographic variables and either peak density or amplitude of fluctuation was significant (Table 8).

Initial population density in bluegrass was correlated with peak density, but not amplitudes of fluctuation (table 8). Correlations between all other demographic variables and either peak density or amplitude of fluctuation were not significant (Table 8).

Cessation of population growth

Neither survival nor the proportion of pregnant females differed among the months prior to and following the peak (Table 9, 10).

When data for the cycles were grouped as to pre-peak, peak and post-peak, survival of adults and young and reproduction did not differ during the three months prior to the peak, at the peak, and the three months following the peak for years populations peaked June-September and November-February (Table 9, 10).

Population cycles of *M. pennsylvanicus* were irregular in respect of configuration of the phases of the cycle (Fig. 2). The increase phase often included one or more months of declines in density before reaching the peak. Further, many peak periods were essentially more than two months of fluctuating, relatively high densities with a one month "spike" of higher density sometime during this period, which we designated at the actual peak. Declines also often included reverses of one or two months before eventually declining to the trough. When the cycles were combined for analysis, these erratic fluctuations during the increase and decline may have masked any general differences that might have existed between the pre-peak months, the peak and the post-peak months. An inspection of individual population cycles provides more details as to possible reasons for stoppage of growth of *M. pennsylvanicus* populations.

Seasonal decline in reproduction during winter appeared to have contributed to the stoppage of growth of the five of the seven cycles peaking in November and December. In one of the two cycles peaking in January-February, reproduction had already stopped prior to the peak, with a 30% drop in adult survival associated with stoppage of

population growth. The other cycle involved only a very small spike (6/ha) in density during a relatively modest peak period (22-35/ha).

Cessation of growth appeared to result from a marked decline in reproduction in three of nine populations that peaked June-September in alfalfa and bluegrass (declines of 35%, 36% and 66% from the peak). Cessation of growth in another resulted from a 33% decline in adult survival. Stoppage of growth of a fifth resulted from a combination of decreased survival (40%) and reproduction (18%) following the peak. The remaining four cycles, two in bluegrass that peaked in June 1976 and August 1979 and two in alfalfa peaking in July 1979 and June 1995, all had irregular increases and declines, with no obvious change in survival or reproduction associated with stoppage of growth.

There was no unusual weather event associated with cessation of population growth of the five alfalfa cycles. Episodes of extreme weather events could have contributed to the stoppage of growth of only four of the 15 population cycles in the bluegrass: July 1980 peak, a 14-day period of very high temperatures (average 28.4°C) and no rainfall; February 1980 peak, a 6-day period of very low temperatures, -12.2°C; December 1977 peak, 6-day period of -17.7°C temperatures; February 1986 peak, 6-day period of -17.4°C temperatures. Survival was lower (25%) during the month of weather extremes only for the December 1977 stoppage.

Discussion

Two aspects of population demography determine amplitudes of fluctuation in arvicoline rodents: (1) population growth during the increase phase and (2) timing of cessation of growth and initiation of a decline in population density. Interaction of these two phenomena result in population densities rising to very high peaks some years,

while achieving only modest densities in other years. The ultimate questions, however, are: (1) What demographic variables drive the increase phase differently some years? and (2) What variables change to stop population growth?

Batzli (1992) and Lin and Batzli (2001) summarized factors potentially affecting demographic variables that result in variation in population growth, including habitat quality (cover and food), predation pressure and weather conditions. Neither the timing of the increase phase nor population density at the beginning of the increase phase were primary determinants of peak densities or amplitudes of fluctuation in our study. We found that only length of the period of increase was consistently correlated with peak densities and amplitudes of fluctuation.

Although among-habitat differences in population fluctuations of *M. ochrogaster* may have resulted from differences in habitat quality (Getz et al. In Review c), the present analysis indicated that temporal variation in within-habitat quality was not a factor affecting peak densities or amplitudes of fluctuations during a population cycle. If habitat quality had been involved in peak densities and amplitudes of fluctuation, then we should have seen either higher rates of increase, greater survival, greater body mass (an indicator of better quality animals), or greater proportions of reproductive females during those years in which population cycles achieved higher densities. Instead, we found only length of the reproductive period and survival in bluegrass and proportion of reproductive females in tallgrass to be positively correlated with peak densities and amplitudes of fluctuation. We did not detect a relationship between weather conditions during the increase phase and peak densities and amplitudes of fluctuation.

If peak densities are dependent upon length of the increase phase and not upon variation in demographic variables during the increase, then changes in factors that stop population growth and their timing become a major determinant of the magnitude of population fluctuations. Cessation of population growth and initiation of the decline phase result from increased mortality and decreased reproduction; emigration does not appear to be an important factor in stopping population growth (Krebs and Myers 1974, Gaines and McClenaghan 1980, Verner and Getz 1985, Lidicker and Stenseth 1992). Increased mortality and decreased reproduction may result from effects of density-independent factors (e.g., adverse weather conditions) as well as density-dependent factors (e.g., predation, quality of the animals; Christian 1971, 1980, Saucy 1984, Krebs 1996).

Thirty-two of the 39 population cycles of *M. ochrogaster* in our study sites peaked and declined during autumn-winter. There was no evidence, however, that a winter decline in survival was responsible for cessation of population growth (Getz et al. In Review b). In the present analysis, only adults in alfalfa displayed a winter decline in survival. Adult male body mass was significantly lower following the peak, whether the population peaked in spring-summer or autumn-winter, indicating lesser quality animals during the decline (Getz et al. In Review c). There was no winter decline in body mass in either alfalfa or bluegrass populations in those years when populations were not declining. These observations suggest that lower body mass, and perhaps quality of animals, resulted from the effects of density, and not season.

The presumption that lesser quality animals (based only on lower body mass) is a response to population density in *M. ochrogaster* is not entirely consistent with changes in survival following a peak. In the

present study, there was decreased survival of adults in alfalfa during winters of both cycle and non cycle years, while body mass was lower only during winters following population peaks (Getz et al. In review c). Survival of adults in bluegrass, on the other hand, was less during winter than autumn only during cycle years, when body mass was also lower.

Significantly fewer female *M. ochrogaster* were pregnant during winter than during autumn in alfalfa and bluegrass during both cycle and non cycle years. There was no difference in the proportion of pregnant females in alfalfa during winters of cycle and non cycle years, although fewer females in bluegrass were pregnant during the winter of cycle than non cycle years. The proportion of females pregnant did not differ during the increase and decline phases of population cycles that peaked and declined in spring-summer. Thus, while winter reduction in reproduction (Getz et al. In Review b) most likely contributed to declines of *M. ochrogaster* population cycles that peaked in autumn-winter, such changes do not appear to be the primary cause of cessation of population growth. Further, episodes of weather stress were not associated with cessation of population growth in *M. ochrogaster*.

From these observations, we conclude that increased mortality from density-dependent predation is the most likely cause of cessation of population growth and decline in numbers of *M. ochrogaster*. We further suggest that such effects of predation are erratic with respect to their magnitude and timing.

Resident specialist and nomadic generalist predators have the potential to display density-dependent responses to prey populations, resulting in cessation of population growth (Korpimäki and Norrdahl 1991, 1998, Erlinge, et al. 1983, Hanski et al. 1991). Lin and Batzli

(1995) listed 21 potential predators of voles in our study sites. Of these, only the least weasel (*Mustela nivalis*) is considered a specialist predator on voles throughout the year (Pearson 1985). Another common predator, the feral cat (*Felis silvestris*), utilizes a variety of prey during spring-autumn, but may concentrate on voles during late autumn-winter (Lin and Batzli 1995). Numbers of cats in a given area at a given time, however, reflect varying numbers of cats maintained at nearby houses or farmsteads and are not necessarily density-dependent in respect to vole population densities.

One winter resident migratory raptor, the rough-legged hawk (*Buteo lagopus*), is a potential specialist predator on voles in our study region. Migratory raptors may act as nomadic predators by selecting high density vole populations on which to feed while on their winter grounds. The remainder of the predators listed by Lin and Batzli (1995) are essentially nomadic generalists.

Lin and Batzli (1995) listed five species of snakes (western fox snake, *Elaphe vulpina*; black rat snake, *E. obsoleta*; eastern yellow-bellied racer, *Coluber constrictor*; eastern milk snake, *Lampropeltis triangulum*; prairie king snake, *L. calligaster*) as potential predators on voles in our study sites. Although these snakes feed on voles, they would have hibernated at least a month prior to the cessation of population cycles peaking in autumn-winter. Lin and Batzli (1995) and Getz et al. (In Review a) further concluded that snake predation was a minor source of mortality in vole populations. Thus, it is most likely that snakes would not be major contributors even to cessation of increases of population cycles that peaked in spring-summer.

We did not formally monitor fluctuations in numbers of predators or predation pressure on our study sites. However, we frequently caught individuals of *M. nivalis* in our vole live-traps, providing a

general indication of their presence in our study sites. These captures were almost always during times when vole densities were high.

Rough-legged Hawks begin arriving in east-central Illinois in November, about the time of most peaks of *M. ochrogaster* population cycles, and remain until early spring. Christmas bird count data for our region indicate that numbers of Rough-legged Hawks vary at least 12-fold among winters (summarized in *American Birds* for years 1972-1996). We did not maintain records of sightings on our study areas, but at least a few individuals were observed in and around the study sites most winters. By the time Rough-legged Hawks migrated north in spring, the decline phase normally had run its course.

Differential density-dependent effects of the remaining six mammalian predators (raccoon, *Procyon lotor*; red fox, *Vulpes vulpes*; gray fox, *Urocyon cinereoargenteus*; coyote, *Canis latrans*; long-tailed weasel, *Mustela frenata*; mink, *M. vison*) and seven raptors (American Kestrel, *Falco sparverius*; Northern Harrier, *Circus cyaneus*; Red-tailed Hawk, *Buteo jamaicensis*; Barn Owl, *Tyto alba*; Eastern Screech Owl, *Otus asio*; Short-eared Owl, *Asio flammeus*; Great-horned Owl, *Bubo virginianus*) may be involved in cessation of population growth of *M. ochrogaster* cycles.

The impact of individual predator species would vary from year to year because numbers of each are controlled by different factors. Some years one or more species, acting alone or in concert, may be responsible for suppressing population growth, while others may be involved in other years. Given the independent nature of population fluctuations and mortality effects of each predator species, population densities and amplitudes of fluctuation of voles would be expected to be erratic in nature, with no distinct predictable peak densities or amplitudes of fluctuation. This is what we observed with respect to

population fluctuations of *M. ochrogaster* over the 25 years of our study.

Nine of the 19 population fluctuations of *M. pennsylvanicus* analyzed in this study peaked during autumn-winter, the remaining 10 peaked in spring-summer. Except for a positive correlation between beginning density and peak densities in bluegrass, timing of the start of the increase phase, population density at the start of the increase and length of the increase period were not correlated with either peak densities or amplitudes of fluctuation. There was no correlation between demographic variables during the increase and peak densities or amplitudes of fluctuation of *M. pennsylvanicus*. Neither was there any indication of involvement of weather conditions that were related to peak densities achieved. For populations peaking in November-December, winter reduction in reproduction appeared to be the primary factor responsible for cessation of population growth. Further, in four of nine cycles peaking in June-September, a decline in reproduction was involved in stoppage of population growth. A decline in survival may have contributed to stoppage of growth of one cycle that peaked in winter and of two that peaked in July-September. These findings for the most part, however, are based on changes involving only one or two months at the peak or the month following the peak and did not continue throughout the decline, as was typical of *M. ochrogaster*. That no one factor appeared responsible for population growth or its cessation is consistent with the erratic nature of the occurrence and amplitudes of fluctuation of *M. pennsylvanicus* populations in our study sites.

We conclude that predation, enhanced by winter reduction in reproduction, was responsible for stopping population growth and driving the decline phase of populations of *M. ochrogaster* that peak in autumn-winter. Density-dependent mortality from a variety of predators

appeared responsible for cessation of growth of the few populations of *M. ochrogaster* that peaked in spring-summer; changes in reproduction were not involved. While factors involved in stoppage of growth of populations of *M. pennsylvanicus* were more varied than those of *M. ochrogaster*, decreased reproduction appeared to be the most prevalent cause. Because most *M. pennsylvanicus* population cycles peak and decline during spring-summer, seasonal effects on reproduction (Getz et al. In Review b) are not a primary factor in cessation of population growth of this species. We suggest that intrinsic density-dependent effects might influence reproduction in *M. pennsylvanicus* populations.

Phase-related changes in age at maturity have been suggested to be important determinants of amplitudes of fluctuations (Oli and Dobson 1999, 2001), but we could not test this idea for either species in the present study.

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References

- Batzli, G. O. 1992. Dynamics of small mammal populations: a review. – In: McCullough, D. R., and Barrett, R. H. (eds.), *Wildlife 2001: populations*. Elsevier Applied Science, New York, pp. 831-850.
- Burt, W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. – *Univ. Mich. Mus. Zool. Misc. Publ.* 45: 1-58.
- Christian, J. J. 1971. Population density and reproductive efficiency. – *Biol. Reprod.* 4:248-294.
- Christian, J. J. 1980. Endocrine factors in population regulation. – In: Cohen, M. N., Malpass, R. S., and Klein, H. G. (eds.), *Biosocial mechanisms of population regulation*. Yale Univ. Press, New Haven, CT, pp. 367-380.
- Efford, M. 1992. Comment-revised estimates of the bias in minimum number alive estimator. – *Can. J. Zool.* 70: 628-631.
- Erlinge, S., Goransson, G., Hansson, L., Hogstedt, G., Liberg, O., Nilsson, I. N., Schantz, T., and Sylven, M. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. – *Oikos* 40: 36-52.
- Gaines, M. S. and McClenaghan, L. R., Jr. 1980. Dispersal in small mammals. – *Ann. Rev. Ecol. Syst.* 11: 163-196.
- Getz, L. L., Cole, F. R., Verner, L., Hofmann, J. E., and Avalos, D. 1979. Comparisons of population demography of *Microtus ochrogaster* and *M. pennsylvanicus*. – *Acta Theriol.* 24: 319-349.
- Getz, L. L., Hofmann, J. E., Klatt, B. J., Verner, L., Cole, F. R., and Lindroth, R. L. 1987. Fourteen years of population fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus* in east central Illinois. – *Can. J. Zool.* 65: 1317-1325.

- Getz, L. L., and Hofmann, J. E. 1999. Diversity and stability of small mammals in tallgrass prairie habitat in central Illinois, USA. - *Oikos* 85:356-363.
- Getz, L. L., Simms, L. E., and McGuire, B. 2000. Nestling survival and population cycles in the prairie vole, *Microtus ochrogaster*. - *Can. J. Zool.* 78: 1723-1731.
- Getz, L. L., Hofmann, J. E., McGuire, B., and Dolan, T. W., III. 2001. Twenty-five years of population fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus* in three habitats in east-central Illinois. - *J. Mammal.* 82: 22-34.
- Getz, L. L., Hofmann, J. E., McGuire, B., and Oli, M. K. In Review a. Vole population fluctuations: factors affecting peak densities and intervals between peaks. - *J. Mammal.*
- Getz, L. L., Hofmann, J. E., McGuire, B., and Oli, M. K. In Review b. Habitat-specific demography of sympatric vole populations. - *Can. J. Zool.*
- Getz, L. L., Hofmann, J. E., McGuire, B. and Oli, M. K. In Review c. Demography of fluctuating vole populations: are changes in demographic variables consistent across individual cycles, habitats and species? - *Ecology*
- Hanski, I., Hansson, L., and Henttonen, H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. - *J. Anim. Ecol.* 60: 353-367.
- Hanski, I. P., Turchin, P., Korpimäki, E., and Henttonen, H. 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. - *Nature* 364: 232-235.
- Keller, B. L., and Krebs, C. J. 1970. Microtine population biology III. Reproductive changes in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus* in southern Indiana. - *Ecol. Monogr.* 40: 263-294.

- Korpimäki, E., and Norrdahl, K. 1991. Do breeding nomadic avian predators dampen population fluctuations of small mammals? - *Oikos* 62: 195-208.
- Korpimäki, E., and Norrdahl, K. 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. - *Ecology* 79: 2448-2455.
- Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. - *Ecol. Monogr.* 36: 239-273.
- Krebs, C. J. 1996. Population cycles revisited. - *J. Mammal.* 77:8-24.
- Krebs, C.J. 1999. *Ecological methodology*. Addison-Welsey, New York, New York.
- Krebs, C. J., and Myers, J. H. 1974. Population cycles in small mammals. - *Adv. Ecol. Res.* 8: 267-399.
- Lidicker, W. Z., Jr., and Stenseth, N. C. 1992. To disperse or not to disperse: who does and why? - In: Stenseth, N. C. and Lidicker, W. Z. (eds.). *Animal dispersal: small mammals as a model*. Chapman and Hall, New York, N. Y., pp. 21-36.
- Lin, Y. K., and Batzli, G. O. 1995. Predation on voles: an experimental approach. - *J. Mammal.* 76: 1003-1012.
- Lin, Y. K., and Batzli, G. O. 2001. The influence of habitat quality on dispersal, demography and population dynamics of voles. - *Ecol. Monogr.* 71: 245-275.
- Lindroth, R. L., and Batzli, G. O. 1984. Food habits of the meadow vole (*Microtus pennsylvanicus*) in bluegrass and prairie habitats. - *J. Mammal.* 65: 600-606.
- Oli, M. K., and Dobson, F. S. 1999. Population cycles in small mammals: the role of age at sexual maturity. - *Oikos* 86: 557-566.
- Oli, M. K., and Dobson, F. S. 2001. Population cycles in small mammals: the \square -hypothesis. - *J. Mammal.* 82: 573-581.

- Ostfeld, R. S., Canham, C. D., and Pugh, S. R. 1993. Intrinsic density-dependent regulation of vole populations. - *Nature*, London 366: 259-261
- Ostfeld, R. S., and Canham, C. D. 1995. Density-dependent processes in meadow voles: an experimental approach. - *Ecology* 76: 521-532.
- Pearson, O. P. 1985. Predation. - In: Tamarin, R. H. (ed.), *Biology of New World *Microtus**. Spec. Publ. Am. Soc. Mammal. 8: 535-566.
- Pollock, K. H., Nichols, J. D., Brownie, C., and Hines, J. E. 1990. Statistical inference for capture-recapture experiments. - *Wildl. Monogr.* 107: 1-97.
- Saucey, F. 1984. Density dependence in time series of the fossorial form of the water vole, *Arovicola terrestris*. - *Oikos* 71: 381-392.
- SPSS, Inc. 2001. SPSS 10.0.7 for Macintosh. Chicago, Illinois
- Taitt, M. J., and Krebs, C. J. 1985. Population dynamics and cycles. - In: Tamarin, R. H. (ed.), *Biology of New World *Microtus**. Spec. Publ. Am. Soc. Mammal. 8: 567-620.
- Verner, L., and Getz, L. L. 1985. Significance of dispersal in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus*. - *J. Mammal.* 66: 338-347.
- Zar, J. H. 1999. *Biostatistical analysis*. 4th Ed. Prentice Hall. Upper Saddle River, New Jersey.

Table 1. Correlation of various demographic variables with peak density and amplitudes of fluctuation of *Microtus ochrogaster* in three habitats. r , Peterson's correlation coefficient; N , number of population cycles; P , significance of the correlation.

<u>Demographic variables</u>	<u>Peak density</u>			<u>Amplitude</u>		
	<u>r</u>	<u>N</u>	<u>P</u>	<u>r</u>	<u>N</u>	<u>P</u>
<u>Alfalfa</u>						
<u>Initial population density</u>	<u>0.562</u>	<u>12</u>	<u>0.057</u>	<u>0.438</u>	<u>12</u>	<u>0.15</u>
<u>Timing of increase</u>	<u>-0.288</u>	<u>13</u>	<u>0.340</u>	<u>0.272</u>	<u>12</u>	<u>0.35</u>
<u>Length of increase</u>	<u>0.695</u>	<u>12</u>	<u>0.012</u>	<u>0.764</u>	<u>12</u>	<u>0.00</u>
<u>Length of reproductive period</u>	<u>0.314</u>	<u>13</u>	<u>0.296</u>	<u>0.229</u>	<u>12</u>	<u>0.47</u>
<u>Rate of increase</u>	<u>0.474</u>	<u>13</u>	<u>0.102</u>	<u>0.346</u>	<u>13</u>	<u>0.24</u>
<u>Survival rates</u>	<u>0.110</u>	<u>13</u>	<u>0.721</u>	<u>0.109</u>	<u>13</u>	<u>0.51</u>
<u>Proportion females reproductive</u>	<u>0.201</u>	<u>13</u>	<u>0.511</u>	<u>0.224</u>	<u>13</u>	<u>0.46</u>
<u>Male body mass during increase</u>	<u>0.456</u>	<u>13</u>	<u>0.118</u>	<u>0.469</u>	<u>12</u>	<u>0.12</u>
<u>Bluegrass</u>						
<u>Initial population density</u>	<u>0.696</u>	<u>17</u>	<u>0.002</u>	<u>0.566</u>	<u>17</u>	<u>0.01</u>
<u>Timing of increase</u>	<u>-0.226</u>	<u>17</u>	<u>0.384</u>	<u>-0.272</u>	<u>17</u>	<u>0.25</u>
<u>Length of increase</u>	<u>0.724</u>	<u>17</u>	<u>0.001</u>	<u>0.727</u>	<u>17</u>	<u>0.00</u>
<u>Length of reproductive period</u>	<u>0.651</u>	<u>17</u>	<u>0.005</u>	<u>0.626</u>	<u>17</u>	<u>0.00</u>
<u>Rate of increase</u>	<u>-0.452</u>	<u>17</u>	<u>0.068</u>	<u>-0.355</u>	<u>17</u>	<u>0.16</u>
<u>Survival rates</u>	<u>0.552</u>	<u>17</u>	<u>0.021</u>	<u>0.594</u>	<u>17</u>	<u>0.01</u>
<u>Proportion females reproductive</u>	<u>-0.160</u>	<u>17</u>	<u>0.540</u>	<u>-0.248</u>	<u>17</u>	<u>0.33</u>
<u>Male body mass during increase</u>	<u>0.440</u>	<u>17</u>	<u>0.077</u>	<u>0.463</u>	<u>17</u>	<u>0.06</u>

Table 1 (Cont.)

<u>Tallgrass</u>						
<u>Initial population density</u>	<u>0.723</u>	<u>8</u>	<u>0.043</u>	<u>0.646</u>	<u>8</u>	<u>0.08</u>
<u>Timing of increase</u>	<u>-0.651</u>	<u>8</u>	<u>0.080</u>	<u>-0.643</u>	<u>8</u>	<u>0.08</u>
<u>Length of increase</u>	<u>0.441</u>	<u>8</u>	<u>0.274</u>	<u>0.491</u>	<u>8</u>	<u>0.21</u>
<u>Length of reproductive period</u>	<u>0.616</u>	<u>8</u>	<u>0.103</u>	<u>0.612</u>	<u>8</u>	<u>0.10</u>
<u>Rate of increase</u>	<u>-0.221</u>	<u>8</u>	<u>0.598</u>	<u>-0.258</u>	<u>8</u>	<u>0.53</u>
<u>Survival rates</u>	<u>0.595</u>	<u>8</u>	<u>0.120</u>	<u>0.584</u>	<u>8</u>	<u>0.12</u>
<u>Proportion females reproductive</u>	<u>0.704</u>	<u>8</u>	<u>0.052</u>	<u>0.741</u>	<u>8</u>	<u>0.03</u>
<u>Male body mass during increase</u>	<u>0.904</u>	<u>8</u>	<u>0.002</u>	<u>0.936</u>	<u>8</u>	<u>0.00</u>
<u>All sites</u>						
<u>Initial population density</u>	<u>0.601</u>	<u>37</u>	<u><0.001</u>	<u>0.519</u>	<u>37</u>	<u>0.00</u>
<u>Timing of increase</u>	<u>-0.194</u>	<u>37</u>	<u>0.251</u>	<u>-0.213</u>	<u>37</u>	<u>0.20</u>
<u>Length of increase</u>	<u>0.642</u>	<u>37</u>	<u><0.001</u>	<u>0.669</u>	<u>37</u>	<u><0.0</u>
<u>Length of reproductive period</u>	<u>0.728</u>	<u>37</u>	<u><0.001</u>	<u>0.712</u>	<u>37</u>	<u><0.0</u>
<u>Rate of increase</u>	<u>-0.365</u>	<u>37</u>	<u>0.026</u>	<u>-0.314</u>	<u>37</u>	<u>0.05</u>
<u>Survival rates</u>	<u>0.506</u>	<u>37</u>	<u>0.001</u>	<u>0.499</u>	<u>37</u>	<u>0.00</u>
<u>Proportion females reproductive</u>	<u>0.236</u>	<u>37</u>	<u>0.5160</u>	<u>0.203</u>	<u>37</u>	<u>0.22</u>
<u>Male body mass during increase</u>	<u>0.456</u>	<u>37</u>	<u>0.118</u>	<u>0.469</u>	<u>137</u>	<u>0.12</u>

Table 3. Survival rates (mean + SE) of adult *Microtus ochrogaster* during autumn (September–November) and winter (December–February). Survival rate was estimated as the proportion surviving to the next month. Values of F-statistic, degrees of freedom (number of months included in sample), and observed significance level (*P*) for one-way ANOVA comparing survival among the months are also given. Values within a column with different superscripts differ significantly at the 0.05 level (Tukey's HSD test).

<u>Month</u>	<u>Alfalfa</u>		<u>Bluegrass</u>	
	<u>Cycle years</u>	<u>Noncycle years</u>	<u>Cycle years</u>	<u>Noncycle years</u>
<u>September</u>	<u>0.638 + 0.037^a</u>	<u>0.474 + 0.107^a</u>	<u>0.542 + 0.066^{ab}</u>	<u>0.296 + 0.06</u>
<u>October</u>	<u>0.611 + 0.055^{ab}</u>	<u>0.535 + 0.127^a</u>	<u>0.615 + 0.042^a</u>	<u>0.380 + 0.08</u>
<u>November</u>	<u>0.525 + 0.052^{abc}</u>	<u>0.575 + 0.091^a</u>	<u>0.457 + 0.048^{abc}</u>	<u>0.546 + 0.08</u>
<u>December</u>	<u>0.431 + 0.078^{abc}</u>	<u>0.287 + 0.107^a</u>	<u>0.380 + 0.062^{bc}</u>	<u>0.380 + 0.07</u>
<u>January</u>	<u>0.382 + 0.075^{bc}</u>	<u>0.358 + 0.120^a</u>	<u>0.386 + 0.056^{abc}</u>	<u>0.293 + 0.07</u>
<u>February</u>	<u>0.347 + 0.052^c</u>	<u>0.250 + 0.078^a</u>	<u>0.257 + 0.072^c</u>	<u>0.225 + 0.06</u>
<u>F; df</u>	<u>4.23; 5,69</u>	<u>1.55; 5,51</u>	<u>5.01; 5,84</u>	<u>1.67; 6,11</u>
<u>P</u>	<u>0.0021</u>	<u>0.1904</u>	<u>0.0005</u>	<u>0.1357</u>

Table 4. Survival rates (mean + SE) of young (< 29 g) *Microtus ochrogaster* during autumn (September-November) and winter (December-February). See Table 3 for statistics.

<u>Month</u>	<u>Alfalfa</u>		<u>Bluegrass</u>	
	<u>Cycle years</u>	<u>Noncycle years</u>	<u>Cycle years</u>	<u>Noncycle years</u>
<u>September</u>	<u>0.478 + 0.078^a</u>	<u>0.160 + 0.096^a</u>	<u>0.310 + 0.091^{ab}</u>	<u>0.349 + 0.141^a</u>
<u>October</u>	<u>0.527 + 0.071^a</u>	<u>0.254 + 0.062^a</u>	<u>0.371 + 0.062^{ab}</u>	<u>0.364 + 0.136^a</u>
<u>November</u>	<u>0.484 + 0.060^a</u>	<u>0.325 + 0.064^a</u>	<u>0.460 + 0.038^a</u>	<u>0.351 + 0.092^a</u>
<u>December</u>	<u>0.321 + 0.059^a</u>	<u>0.306 + 0.137^a</u>	<u>0.397 + 0.063^{ab}</u>	<u>0.302 + 0.078^a</u>
<u>January</u>	<u>0.304 + 0.052^a</u>	<u>0.434 + 0.156^a</u>	<u>0.386 + 0.056^{ab}</u>	<u>0.338 + 0.085^a</u>
<u>February</u>	<u>0.372 + 0.084^a</u>	<u>0.333 + 0.118^a</u>	<u>0.186 + 0.056^b</u>	<u>0.228 + 0.083^a</u>
<u>F; df</u>	<u>1.83; 5,67</u>	<u>0.50; 5,32</u>	<u>2.23; 5,79</u>	<u>0.16; 5,78</u>
<u>P</u>	<u>0.1195</u>	<u>0.7771</u>	<u>0.0589</u>	<u>0.9766</u>

Table 5. Survival (mean + SE) of *Microtus ochrogaster* the three months prior to the peak (P-3 to P-1), peak and three months following the peak (P+1 to P+3) during cycles that peak during autumn-winter and spring-summer. See Table 3 for statistics.

	<u>Autumn-winter peaks</u>			
	<u>Alfalfa</u>		<u>Bluegrass</u>	
	<u>Adult survival</u>	<u>Young survival</u>	<u>Adult survival</u>	<u>Young survival</u>
<u>Peak -3</u>	<u>0.673 + 0.043^a</u>	<u>0.485 + 0.064^{ab}</u>	<u>0.571 + 0.069^{ab}</u>	<u>0.410 + 0.124^a</u>
<u>Peak -2</u>	<u>0.682 + 0.033^a</u>	<u>0.562 + 0.075^a</u>	<u>0.589 + 0.069^a</u>	<u>0.324 + 0.078^a</u>
<u>Peak -1</u>	<u>0.661 + 0.035^a</u>	<u>0.550 + 0.064^a</u>	<u>0.605 + 0.044^a</u>	<u>0.421 + 0.057^a</u>
<u>Peak</u>	<u>0.495 + 0.037^{ab}</u>	<u>0.400 + 0.031^{ab}</u>	<u>0.411 + 0.045^{abc}</u>	<u>0.406 + 0.045^a</u>
<u>Peak +1</u>	<u>0.301 + 0.048^b</u>	<u>0.251 + 0.033^b</u>	<u>0.378 + 0.046^{abc}</u>	<u>0.343 + 0.048^a</u>
<u>Peak +2</u>	<u>0.301 + 0.060^b</u>	<u>0.356 + 0.093^{ab}</u>	<u>0.332 + 0.055^{bc}</u>	<u>0.462 + 0.072^a</u>
<u>Peak +3</u>	<u>0.504 + 0.074^b</u>	<u>0.373 + 0.085^{ab}</u>	<u>0.308 + 0.078^c</u>	<u>0.192 + 0.063^a</u>
<u>F; df</u>	<u>11.35; 6,81</u>	<u>3.12; 6,78</u>	<u>4.59; 6,98</u>	<u>1.67; 6,87</u>
<u>P</u>	<u>< 0.0001</u>	<u>0.0086</u>	<u>0.0004</u>	<u>0.1379</u>

Table 6. Proportion of adult female *Microtus ochrogaster* that were pregnant during autumn (September–November) and winter (December–February). See Table 3 for statistics.

<u>Month</u>	<u>Alfalfa</u>		<u>Bluegrass</u>	
	<u>Cycle years</u>	<u>Noncycle years</u>	<u>Cycle years</u>	<u>Noncycle years</u>
<u>September</u>	<u>0.551 + 0.026^a</u>	<u>0.475 + 0.138^{ab}</u>	<u>0.445 + 0.061^a</u>	<u>0.179 + 0.065^{bc}</u>
<u>October</u>	<u>0.490 + 0.039^a</u>	<u>0.620 + 0.105^a</u>	<u>0.430 + 0.034^a</u>	<u>0.590 + 0.096^a</u>
<u>November</u>	<u>0.269 + 0.035^b</u>	<u>0.478 + 0.100^{ab}</u>	<u>0.273 + 0.044^b</u>	<u>0.388 + 0.082^{ab}</u>
<u>December</u>	<u>0.154 + 0.039^{bc}</u>	<u>0.205 + 0.052^{ab}</u>	<u>0.095 + 0.035^c</u>	<u>0.305 + 0.090^{abc}</u>
<u>January</u>	<u>0.078 + 0.027^c</u>	<u>0.184 + 0.085^b</u>	<u>0.076 + 0.037^c</u>	<u>0.137 + 0.055^{bc}</u>
<u>February</u>	<u>0.096 + 0.045^c</u>	<u>0.138 + 0.087^b</u>	<u>0.015 + 0.009^c</u>	<u>0.014 + 0.014^c</u>
<u>F; df</u>	<u>28.70; 5,69</u>	<u>3.87; 5,44</u>	<u>24.58; 5,79</u>	<u>6.10; 5,82</u>
<u>P</u>	<u>< 0.0001</u>	<u>0.0054</u>	<u>< 0.0001</u>	<u>< 0.0001</u>

Table 7. Proportion of adult female *Microtus ochrogaster* pregnant the three months prior to the peak (P-3 to P-1), peak and three months following the peak (P+1 to P+3) during cycles that peak during autumn/winter and spring/summer (five of the six spring/summer peaks were in tallgrass; the other in alfalfa). See Table 3 for statistics.

<u>Month</u>	<u>Winter/autumn peaks</u>		<u>Spring/summer peaks</u>
	<u>Alfalfa</u>	<u>Bluegrass</u>	
<u>Peak -3</u>	<u>0.448 + 0.046^a</u>	<u>0.451 + 0.061^a</u>	<u>0.106 + 0.074^b</u>
<u>Peak -2</u>	<u>0.426 + 0.032^a</u>	<u>0.394 + 0.056^{ab}</u>	<u>0.552 + 0.149^a</u>
<u>Peak -1</u>	<u>0.398 + 0.055^{ab}</u>	<u>0.365 + 0.043^{ab}</u>	<u>0.454 + 0.080^a</u>
<u>Peak</u>	<u>0.245 + 0.053^{ab}</u>	<u>0.235 + 0.050^{bc}</u>	<u>0.484 + 0.064^a</u>
<u>Peak +1</u>	<u>0.147 + 0.052^c</u>	<u>0.125 + 0.040^{cd}</u>	<u>0.580 + 0.057^a</u>
<u>Peak +2</u>	<u>0.122 + 0.055^c</u>	<u>0.036 + 0.019^d</u>	<u>0.489 + 0.092^a</u>
<u>Peak +3</u>	<u>0.222 + 0.074^{bc}</u>	<u>0.113 + 0.052^{cd}</u>	<u>0.365 + 0.114^{ab}</u>
<u>F; df</u>	<u>6.84; 6,81</u>	<u>11.82; 6,91</u>	<u>2.93; 6,33</u>
<u>P</u>	<u>< 0.0001</u>	<u><0.0001</u>	<u>0.0211</u>

Table. 8. Correlation of various demographic variables with peak density and amplitudes of fluctuation of *Microtus pennsylvanicus* in three habitats. r , Peterson's correlation coefficient; N , number of population cycles; P , significance of the correlation.

<u>Demographic variables</u>	<u>Peak density</u>			<u>r</u>
	<u>r</u>	<u>N</u>	<u>P</u>	
<u>Alfalfa</u>				
<u>Initial population density</u>	<u>0.295</u>	<u>5</u>	<u>0.630</u>	<u>0.457</u>
<u>Length of increase</u>	<u>0.845</u>	<u>5</u>	<u>0.072</u>	<u>0.024</u>
<u>Length of reproductive period</u>	<u>0.862</u>	<u>5</u>	<u>0.060</u>	<u>0.857</u>
<u>Survival rates</u>	<u>0.234</u>	<u>5</u>	<u>0.705</u>	<u>-0.02</u>
<u>Proportion females reproductive</u>	<u>-0.464</u>	<u>5</u>	<u>0.431</u>	<u>-0.63</u>
<u>Male body mass during increase</u>	<u>-0.104</u>	<u>5</u>	<u>0.868</u>	<u>-0.32</u>

Table 8 (Cont.)

<u>Bluegrass</u>				
<u>Initial population density</u>	<u>0.634</u>	<u>15</u>	<u>0.011</u>	<u>0.127</u>
<u>Length of increase</u>	<u>-0.215</u>	<u>15</u>	<u>0.441</u>	<u>0.130</u>
<u>Length of reproductive period</u>	<u>-0.108</u>	<u>15</u>	<u>0.701</u>	<u>0.004</u>
<u>Rate of increase</u>	<u>-0.024</u>	<u>15</u>	<u>0.932</u>	<u>0.316</u>
<u>Survival rates</u>	<u>0.313</u>	<u>15</u>	<u>0.257</u>	<u>0.243</u>
<u>Proportion females reproductive</u>	<u>0.142</u>	<u>15</u>	<u>0.613</u>	<u>0.017</u>
<u>Male body mass during increase</u>	<u>0.022</u>	<u>15</u>	<u>0.939</u>	<u>0.029</u>

Table 9. Survival (mean + SE) of *Microtus pennsylvanicus* the three months prior to the peak (P-3 to P-1), peak and three months following the peak (P+1 to P+3) during cycles that peak during autumn/winter and spring/summer. See Table 3 for statistics.

<u>Month</u>	<u>Autumn-winter peaks</u>		<u>Spring-summer peaks</u>	
	<u>Adult</u>	<u>Young</u>	<u>Adults</u>	<u>Young</u>
<u>Peak -3</u>	<u>0.372 + 0.096^a</u>	<u>0.633 + 0.153^a</u>	<u>0.545 + 0.089^a</u>	<u>0.595 + 0.</u>
<u>Peak -2</u>	<u>0.438 + 0.098^a</u>	<u>0.250 + 0.144^a</u>	<u>0.640 + 0.070^a</u>	<u>0.486 + 0.</u>
<u>Peak -1</u>	<u>0.425 + 0.097^a</u>	<u>0.295 + 0.093^a</u>	<u>0.563 + 0.062^a</u>	<u>0.414 + 0.</u>
<u>Peak</u>	<u>0.419 + 0.038^a</u>	<u>0.298 + 0.074^a</u>	<u>0.567 + 0.060^a</u>	<u>0.459 + 0.</u>
<u>Peak +1</u>	<u>0.327 + 0.087^a</u>	<u>0.550 + 0.047^a</u>	<u>0.537 + 0.056^a</u>	<u>0.517 + 0.</u>
<u>Peak +2</u>	<u>0.440 + 0.103^a</u>	<u>0.458 + 0.034^a</u>	<u>0.580 + 0.094^a</u>	<u>0.286 + 0.</u>
<u>Peak +3</u>	<u>0.373 + 0.030^a</u>	<u>0.439 + 0.037^a</u>	<u>0.414 + 0.074^a</u>	<u>0.238 + 0.</u>
<u>F; df</u>	<u>0.24; 6,49</u>	<u>2.59; 6,36</u>	<u>0.93; 6,41</u>	<u>1.42; 6,36</u>
<u>P</u>	<u>0.9626</u>	<u>0.0347</u>	<u>0.4813</u>	<u>0.2375</u>

Table 10. Proportion of adult female *Microtus pennsylvanicus* pregnant the three months prior to the peak (P-3 to P-1), peak and three months following the peak (P+1 to P+3) during cycles that peak during autumn-winter and spring-summer. See Table 3 for statistics.

<u>Month</u>	<u>Autumn-winter peaks</u>	<u>Spring-summer peaks</u>
<u>Peak -3</u>	<u>0.020 + 0.020^a</u>	<u>0.354 + 0.076^a</u>
<u>Peak -2</u>	<u>0.293 + 0.112^a</u>	<u>0.329 + 0.071^a</u>
<u>Peak -1</u>	<u>0.257 + 0.078^a</u>	<u>0.225 + 0.054^a</u>
<u>Peak</u>	<u>0.100 + 0.041^a</u>	<u>0.125 + 0.058^a</u>
<u>Peak +1</u>	<u>0.056 + 0.042^a</u>	<u>0.250 + 0.071^a</u>
<u>Peak +2</u>	<u>0.042 + 0.042^a</u>	<u>0.242 + 0.106^a</u>
<u>Peak +3</u>	<u>0.188 + 0.073^a</u>	<u>0.399 + 0.116^a</u>
<u>F; df</u>	<u>2.79; 6,49</u>	<u>1.37; 4,42</u>
<u>P</u>	<u>0.0204</u>	<u>0.2504</u>

Figure legends

Fig. 1. Densities of *Microtus ochrogaster* in 3 habitats in east-central Illinois; populations were monitored at monthly intervals.

Fig. 2. Densities of *Microtus pennsylvanicus* in 3 habitats in east-central Illinois. Populations were monitored at monthly intervals.

