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Vole population fluctuations:

factors affecting peak densities and intervals between peaks

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Factors associated with initiation of population cycles of *Microtus ochrogaster* and *M. pennsylvanicus* were studied in alfalfa, bluegrass and tallgrass habitats for 25 years. For both species, increased survival appeared to be the most important factor associated with initiation of a population cycle during a given year. There was no difference in reproduction the previous winter or during spring (both species) and autumn (*M. ochrogaster*) of cycle and non-cycle years. Weather differences, including episodes of extreme conditions, were not associated with cycle and non-cycle years. There was no indication that cyclic phenomena were a result of habitat degradation owing to high densities during peak phases. We found no relationship between peak densities and rate of decline, length and extent of the decline, population density during the subsequent trough, or the interval until the next cycle. Population cycles appeared to be initiated by relaxation of predation pressure which occurred erratically across years.

Key words: meadow vole, Microtus *ochrogaster*, *Microtus pennsylvanicus*, population cycles, prairie vole

Populations of most arvicoline (microtine) rodents have been observed to undergo high amplitude fluctuations in numbers. Some fluctuations are erratic or annual, while other populations appear to fluctuate periodically at 2-5 year intervals, i.e., display population cycles (Krebs et al. 1969; Krebs and Myers 1974; Taitt and Krebs 1985; Krebs 1996; Bjørnstad et al. 1998). The reality of population cycles remains unresolved (Batzli 1996). A species may display different patterns of fluctuation among sites and among years within the same site (Marcström et al. 1990). Neither is there convincing evidence

that different species undergo synchronous fluctuations in the same site (Krebs et al. 1969).

Irrespective of the nature of the fluctuations, the fact remains that many species of arvicoline rodents undergo some sort of high amplitude fluctuations in numbers. Two basic questions that must be addressed to understand population cycles are: (1) Why do populations display very high amplitude fluctuations some years and not others? (2) Why are some fluctuations annual and others more long term? To answer the first question we need to know the demographic variables responsible for rapid population growth some years, but not others.

The following factors have been proposed to initiate population cycles (Krebs et al. 1969; Krebs and Myers 1974; Gaines and Rose 1976; Pinter 1988; Batzli 1992; Boonstra et al. 1998; Oli and Dobson 1999, 2001): (1) High levels of winter breeding preceding the peak year (this simply raises the question of why reproduction is high some winters and not others). (2) An earlier than normal beginning of breeding during cycle years (raising the question of why breeding begins earlier in some years than others). (3) Reduction in predation pressure that allows the population to grow. (4) Favorable weather conditions during cycle years as contrasted to non-cycle years, when weather stresses suppress population growth. (5) Early age at first reproduction during cycle years and delayed breeding during non-cycle years (again, raising the question as to what is responsible for such variation).

With respect to whether fluctuations are annual or multi-annual, 2 questions must be answered: (1) What factors determine the length of the interval between cycles? (2) Is there a relationship between peak densities and inter-peak intervals? Factors affecting the interval between peak densities may include: (1) Delayed density-dependent

recovery of the habitat from effects of the previous peak density (Batzli 1992; Agrell et al. 1995). (2) Delayed density-dependent effects of the peak density on quality of the animals (Christian 1971, 1980; Norrdahl and Korpimäki 2002). (3) Delayed predator-prey effects on mortality of voles (Körpimaki and Norrdhal 1991; Klemola et al. 2000).

During the course of a 25-year study of population demography of the prairie vole, *Microtus ochrogaster*, and the meadow vole, *M. pennsylvanicus* (Getz et al. 2001) we obtained data relevant to the above questions. Data were obtained from 3 habitats in which there were a total of 30 population cycles of *M. ochrogaster* and 14 cycles of *M. pennsylvanicus*. Another 9 population cycles of *M. ochrogaster* and 6 of *M. pennsylvanicus* were observed in other sites during the course of the study; these were not included in the present analyses, but provided additional information as to timing of population peaks and declines.

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). Populations of *M. ochrogaster* and *M. pennsylvanicus* were monitored in 3 habitats: restored tallgrass prairie (March 1972--May 1997), bluegrass, *Poa pratensis* (January 1972--May 1997) and alfalfa, *Medicago sativa* (May 1972--May 1997). We have described the study sites in detail elsewhere (Getz et al. 1979, 1987, 2001), and thus provide only brief descriptions here.

We trapped sites in 2 restored tallgrass prairies, 1 located in Trelease Prairie, the other in Phillips Tract. Relative abundances of plants in Trelease Prairie were as follow: big bluestem, *Andropogon gerardii* (17%); bush clover, *Lespedeza cuneata* (16%); ironweed, *Vernonia* (12%); Indian grass, *Sorghastrum nutans* (10%); approximately 20 additional species with relative abundances of <10% (Getz et al. 1979).

Lindroth and Batzli (1984) recorded relative abundances of the most prominent plant species in the Phillips Tract prairie: *A. gerardii* (38%); *L. cuneata* (25%); Beard tongue foxglove, *Penstemon digitalis* (16%); and *S. nutans* (19%). All other species represented <1% relative abundance. Both prairies were burned during the spring at 3-4-year intervals to control invading shrubs and trees.

Four bluegrass study sites were established within a former bluegrass pasture located in Phillips Tract. The pasture was released from grazing in June 1971; dense vegetative cover existed by autumn 1971. Relative abundances of plants during that period were: *P. pratensis* (70%); dandelion, *Taraxacum officinale* (14%); 25 other species with relative abundances of $\leq$10% (Getz et al. 1979). To suppress invading forbs, shrubs and trees, the bluegrass sites were mowed about 25 cm above the surface during late summer every 2-3 years. The entire area was mowed at the same time.

Two adjacent sites with *M. sativa* were trapped during the study. A site was trapped until the *M. sativa* began to be crowded out by invading forbs and grasses. One year before trapping was terminated in that 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, common plants (in addition to

alfalfa) included: *P. pratensis*; goldenrod, *Solidago*; timothy, *Phleum pratense*; brome grass, *Bromus inermis*; clover, *Trifolium repens* and *T. pratense*; and plantain, *Plantago*. A series of 3-m wide strips were mowed (every 3rd strip) 25 cm above the surface periodically each summer to control invading weedy forbs and promote new growth of *M. sativa*. The first strips usually were mowed in early June; mowing normally stopped in mid September. The subsequent strips were not mowed until vegetation in the previously mowed strips was nearly full-grown. Times of mowing were spaced so that at least two-thirds of the field had vegetative cover at all times.

Procedures

A grid system with 10-m intervals was established in all study sites. One wooden multiple-capture live-trap (Burt 1940) was placed at each station. Each month a 2-day prebaiting period was followed by a 3-day trapping session. Cracked corn was used for prebaiting and as bait in traps. We used vegetation or aluminum shields to protect traps from the sun during summer. Wooden traps provided ample insulation in winter so nesting material was not placed in the traps at any time. We estimated trap mortality to be <0.5%.

Traps were set in the afternoon and checked at about 0800 h and 1500 h on the following 3 days. All animals were toe-clipped, $\leq$2 toes on each foot, at 1st capture 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.

Species, grid station, individual indentification, 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 were recorded at each capture.

Data analysis

Demography.--Density of voles for each trapping session was estimated based on the minimum number known to be alive (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 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. Further, since we utilized prebaited multiple-capture live-traps checked twice daily for 3 days each session, our capture efficiency was very high. Of animals estimated to be present, 92% of the *M. ochrogaster* and 91% of the *M. pennsylvanicus* were captured each session.

A population cycle was presumed to have occurred when population fluctuations exceeded the following densities: *M. ochrogaster*—alfalfa, 75/ha; bluegrass, 35/ha; tallgrass, 30/ha. *M. pennsylvanicus*—alfalfa and bluegrass 25/ha (*M. pennsylvanicus* was acyclic in tallgrass; Getz et al. 2001). Each cycle included trough, increase, peak, and decline phases. For both species the beginning and end of each phase for each cycle was arbitrarily determined, based on major inflections in population change for that phase and cycle. Most population fluctuations of *M. ochrogaster* were distinct entities with well-defined phases and a peak typically of one month. Population cycles of *M. pennsylvanicus*, on the other hand, were much more irregular, with fluctuating densities within the phases. The peak often was represented by a period of fluctuating high densities with a "spike" in density somewhere within the period. Our delineation of the phases for *M. pennsylvanicus* is therefore less precise than for *M. ochrogaster*.

In our analyses we focus on demographic variables deemed most important with respect to population demography, i.e., survival (total population, adult and young), persistence of young on the study site and proportion adult females that were reproductive. Survival was calculated as the proportion of animals present 1 month that survived to the next month ("monthly survival"). Persistence of animals first captured as young ($\leq$ 29g), and presumed to have been born on the study site since the last trapping session, was estimated as the time elapsed from the month they were first captured until they disappeared from the site. For reproductive comparisons, we calculated the proportion of adult ($\geq$30 g) females recorded as reproductive for each month.

Initiation of population cycles.--The following comparisons were made: (1) Proportion reproductive females the winter prior to cycle

and non-cycle years. (2) Survival and reproduction during the typical period of increase (*M. ochrogaster*, summer (June-August) and autumn (September-November); *M. pennsylvanicus*, spring (March-May) and summer for cycle and non-cycle years. (3) Survival and reproduction during the trough and the following increase for cycle years

Habitat degradation.--In this paper we also evaluate the potential effects of the peak density on habitat quality (degradation) and timing of the subsequent population cycle. For this we correlated peak density with the following (based on the stated assumptions): (1) Length of the decline; the shorter the decline, the greater has been the degradation of the habitat at the peak density. (2) Rate of decline; the more rapid the decline, the greater has been the degradation of habitat quality at the peak density. (3) Extent of decline; the greater the drop in numbers, the greater has been habitat degradation at the peak density. (4) Length of the subsequent trough; the longer the time before the next population increase begins, the greater has been habitat degradation at the peak density, i.e., longer recovery time required.

Influence of weather on population cycles.--Weather data were compiled 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.

To estimate responses of *M. ochrogaster* to weather,deviations in temperature and precipitation from the previous 30-year means were calculated for the 4-month periods of March-June and July-October each year. These periods were selected as the times when weather could have the greatest impact on population cycles (Fig. 1) by creating conditions favoring or suppressing initiation of the increase phase (March-June) and maintenance, enhancement or disruption of the increase

phase (July-October). Comparisons were made between years with and without population cycles.

Mean monthly temperatures may not be the only factor exerting a negative impact on population growth. Episodes of unusually extreme conditions, even if of relatively short duration, have the potential to adversely affect population growth (e.g., reducing survival and reproduction), in effect, "nipping in the bud" population growth (Pinter 1988). We, therefore, identified periods of subzero ($\leq$-1 C) temperatures during March-April, the period prior to the time of initiation of population increases, and temperatures $\geq$28 C during July-August, the typical period when population increases were beginning to gain momentum during a cycle year. For episodes of extreme temperatures during these 2-month periods, we compiled the number of such episodes, their average length and mean temperatures. We compared data for cycle and non-cycle years in alfalfa and bluegrass; there were too few *M. ochrogaster* cycles in tallgrass for analysis. We also compared the amount of rain during March-April that might have contributed to the stress of low temperature episodes.

There were only 5 *M. pennsylvanicus* population cycles in alfalfa and the timing of the increase phases of these cycles was erratic (Fig.2). We did not attempt correlations with beginning of an increase and weather conditions for this population. However, 6 of the increases of *M. pennsylvanicus* populations in bluegrass included the months of March-June (Fig. 2). We therefore compared deviations in March-June temperature and precipitation from the 30-year means for cycle and non-cycle years. We also compiled episodes of subzero (^{0}C) temperatures during March-April, the period prior to the initiation of population increases and compared them for cycle and non-cycle years.

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 independent-sample t-tests, and assess the associations between variables using the Pearson's correlation analyses. Degrees of freedom (*d.f.*) for "persistence of young on study sites" are actual numbers of individuals involved; all other *d.f.* represent number of months of data. When degrees of freedom for *t*-tests are given in whole numbers, variances are equal (Levene's test for equality of variances). When variances were not equal, *d.f.* is given to 1 decimal place. SPSS 10.0.7 for Macintosh (SPSS, Inc. 2001) was used for all statistical analyses.

Results

Microtus ochrogaster

Timing of phases.--In general, the increase phase of *M. ochrogaster* population cycles in alfalfa began late spring and summer (April, 2 cycles; May, 3; June, 1; July, 3; August, 1; September, 2; November, 1; Fig. 1); the mean time of beginning of the increase was the third week in June. Increases began about two months later in bluegrass (March, 1 cycle; May 1; June, 1; July, 1; August, 1; September, 4; October, 2; November 1). Two increases, each, in tallgrass began in September and November; the fifth began in March (Fig. 1).

Most population cycles of *M. ochrogaster* in both alfalfa and bluegrass peaked in autumn-early winter (Alfalfa: July, 1 cycle; September, 1; October, 2; November, 4; December, 2; January, 2;

February, 1. Bluegrass: April, 1 cycle; October, 1; November, 5; December, 2; January, 2; February, 1). Population peaks in tallgrass occurred in December, January (2 cycles) and 1 each in April and June.

Of the 13 population cycles in alfalfa, 11 of the peaks were only 1 month in duration, with a marked decline in population density the month following the peak (Fig. 1). The 1972 cycle peak lasted 3 months and the 1987 peak, 2 months. As in alfalfa, 10 of the 12 population cycles in bluegrass peaked for only 1 month (Fig. 1). The 1982 peak was 2 months long. Population density was high during December 1982-December 1983; there was no conspicuously distinct peak month. Peak periods in tallgrass were somewhat longer: 1973 and 1983 peaks were 3 months, each; 1985, 2 months; 1988 and 1989, 1 month each.

Initiation of population cycles.--The proportion of adult females that were reproductive did not differ during winters preceding a population cycle and those of non-cycle years (Alfalfa: 0.37 ± 0.05 and 0.45 ± 0.05, respectively; t = 1.153, *d.f.* = 55, P = 0 .254. Bluegrass: 0.57 ± 0.07 and 0.42 ± 0.08, respectively; t = 1.547, *d.f.* = 47, P = 0.129. Tallgrass: 0.52 ± 0.11 and 0.55 ± 0.11, respectively; t = 0.066, *d.f.* = 28.8, P = 0.948).

Of the 30 population cycles recorded for *M. ochrogaster* in the three habitats during the main study, 3 were preceded by higher than average winter reproduction. Only 3 of the 44 total "non-cycle periods" (for all 3 habitats) were preceded by higher than normal reproduction.

Survival (total population) was significantly greater in both alfalfa and bluegrass during summer and autumn (typical period of population growth) of cycle years as contrasted to non-cycle years (Alfalfa: 0.76 ± 0.02 and 0.44 ± 0.04, respectively; t = 6.964, *d.f.* = 82.8, $P < 0.001$. Bluegrass: 0.47 ± 0.01 and 0.36 ± 0.02, respectively;

t = 2.12, $d.f.$ = 117, P = 0.036). Persistence of young born during summer and autumn was greater during cycle than non-cycle years in both alfalfa and bluegrass (Alfalfa: 2.2 ± 0.1 and 1.7 ± 0.1 months, respectively; t = 3.733, $d.f.$ = 225.2, P = 0.001. Bluegrass: 2.1 ± 0.1 and 1.7 ± 0.1 months, respectively; t = 2.997, d$.f.$ = 119.2, P = 0.003). There were too few cycles in tallgrass for such analysis,

Survival (total population, adult and young) and persistence of young on the study site increased significantly in both alfalfa and bluegrass as the population entered the increase phase, as compared to during the preceding trough (Table 1).

The proportion of females that were reproductive were similar during summer and autumn of cycle and non-cycle years (Alfalfa: 0.88 ± 0.04 and 0.87 ± 0.02, respectively; t = 0.214, $d.f.$ = 50.2, P = 0.831. Bluegrass: 0.88 ± 0.04 and 0.85 ± 0.02, respectively; t = 0.489, $d.f.$ = 96, P = 0.626). The proportion of females that were reproductive did not differ between the trough and increase phases in alfalfa and bluegrass, while significantly fewer females were reproductive during the increase than the trough in tallgrass (Table 1).

Because of the few population cycles in tallgrass, comparisons of weather conditions and population cycles were limited to alfalfa and bluegrass populations. There was no relationship between March-June temperature conditions with respect to whether a population cycle occurred (Table 2). Nor was there a difference in precipitation during March-June of cyclic and non cyclic years. July-October temperatures were significantly higher during non cycle than cycle years in alfalfa, but not in bluegrass (Table 2). July-October precipitation was higher during years of population cycles than during non-cyclic years. However, owing to wide year-to-year variation, only differences for the bluegrass population were statistically significant (Table 2).

Episodes of temperature extremes during March-April (temperatures ≤1C) and July-August (temperatures ≥28 C) did not differ markedly between cycle and non cycle years in either alfalfa or bluegrass populations. During March-April of cycle years in alfalfa, there were an average of 2.9 ± 0.4 episodes of 2.5 ± 0.5 days each with an average temperature of —2.3 ± 0.2C; during non cycle years there were 2.3 ± 0.4 episodes of 2.9 ± 0.4 days, with an average temperature of —3.0 ± 0.3C. During March-April of cycle years in bluegrass there were 2.2 ± 0.5 episodes of 2.6 ± 0.5 days each with an average temperature of —2.1 ± 0.2C; during non cycle years there were 2.7 ± 0.3 episodes of 2.7 ± 0.3 days with an average temperature of —2.9 ± 0.3C.

Likewise, during July-August, there was little difference in the episodes of exceptionally high temperatures between cycle and non cycle years. During July-August of cycle years in alfalfa, there were an average of 0.8 ± 0.3 episodes of 1.7 ± 0.3 days each, with an average temperature of 28.7 ± 0.2C, while during non cycle years there were 2.5 ± 0.7 episodes of 2.5 ± 0.3 days, with an average temperature of 28.9 ± 0.2C. During July-August of cycle years in bluegrass there were 1.0 ± 0.4 episodes of 2.1 ± 0.3 days each with an average temperature of 28.7 ± 0.2C; during non cycle years there were 1.9 ± 0.5 episodes of 2.4 ± 0.4 days with an average temperature of 29.0 ± 0.2C.

Effects of peak densities on habitat quality.--Peak densities and length of the decline were not correlated in either alfalfa (r = 0.266, n = 13, P = 0.381) or bluegrass (r = 0.413, n = 11, P = 0.207). In alfalfa peak density was not correlated with rate of decline (r = -0.082, n = 13, P = 0.790) or total decline in numbers (r = 0.073, n = 13, P = 0.812). There was a marginally negative correlation between rate of decline and length of the decline phase (r = -0.550, n = 13, P = 0.051). Likewise, in bluegrass, peak density was not correlated with

rate of decline (r = -0. 427, n = 10, P = 0.218) or total decline in numbers (r = -0.362, n = 10, P = 0.304). There was, however, a significant negative correlation between rate of decline and length of the decline in bluegrass (r = -0.760, n = 10, P = 0.011).

None of the decline comparisons with peak densities in tallgrass was significant (length of decline: r = -0.759, n = 5, P = 0.137; rate of decline: r = -0.428, n = 5, P = 0.473; total numbers: r = -0.283, n = 5, P = 0.644; rate of decline in relation to length of the decline: r = -0.796, n = 5, P = 0.107)

Length of the subsequent trough was not correlated with peak densities (Alfalfa, r = -0.527, n = 12, P = 0.078; Bluegrass, r = 0.228, n = 11, P = 0.501). Nor was there a correlation between peak densities and mean population densities during the subsequent trough in either alfalfa (r = 0.313; n = 11; P = 0.348) or bluegrass (r = 0.453, n = 9, P = 0.220). Population fluctuations in tallgrass were too erratic for comparison of length of trough in relation to peak densities (Fig. 1). One of the 2 highest peak densities was followed by a low phase of only 3 months, while the other very high peak was followed by a low phase of at least 85 months (through the end of the study). Lower peaks were followed by low phases of up to 120 months (Fig. 1).

Microtus pennsylvanicus

Timing of phases.--Time of initiation of the increase phase was more variable for *M. pennsylvanicus* than for *M. ochrogaster* in both alfalfa (March, 1 cycle; April, 1; May, 2; September, 1) and bluegrass (1 each, February, April, June, July, October and 2 each, March and September) (Fig. 2). Population peaks in alfalfa, 1 each, occurred in May, June, July, September, and November. Peak densities also occurred

erratically in bluegrass: February, 1 peak; June, 3: July, 2; August, 1; November, 2.

Factors associated with cycle years.--The proportion of adult females that were reproductive did not differ during the winters preceding cycle and non-cycle years (Alfalfa: 0.38 ± 0.13 and 0.62 ± 0.15, respectively; t = 1.184, *d.f.* = 16, P = 0.254; Bluegrass: 0.31 ± 0.07 and 0.18 ± 0.08, respectively; t = 1.546, *d.f.* = 39, P = 0.126). Only 2 of the 14 cycles were preceded by higher than average winter reproduction; none of the 31 "non-cycle periods" were preceded by higher than average reproduction.

Total population survival was significantly greater during spring-summer (typical period of population growth) of cycle as contrasted to non-cycle years (alfalfa and bluegrass combined because of small sample sizes): 0.63 ± 0.02 and 0.45 ± 0.03, respectively; t = 5.160, *d.f.* = 148.1, P = < 0.001). Total population survival in both alfalfa and bluegrass and survival of young in bluegrass increased between the trough and increase phases, as did persistence of young in bluegrass (Table 3). Persistence of young in alfalfa and bluegrass, combined, was greater during spring and summer of cycle years than non-cycle years (2.4 ± 0.1 and 1.4 ± 0.1 months, respectively; t = 5.018, *d.f.* = 132.9, P < 0.001).

There was no difference in the proportion of females reproductive during spring-summer of cycle and non-cycle years (0.68 ± 0.03 and 0.73 ± 0.04, respectively; t = 0.327, *d.f.* = 108.1, P = 0.175). Likewise, there was no difference in proportion of females reproductive between the trough and increase in either habitat (Table 3).

There was no difference in temperature deviations from the 30-year means during March-June of cycle and non-cycle years in bluegrass (+0.6 ± 0.2 C and +0.7 ± 0.5 C, respectively; t = 0.173, *d.f.* = 10, P =

0.866). Likewise, there was no difference in deviations in precipitation from the 30-year means during March-June of cycle and non-cycle years (-0.7 ± 1.9 cm and +2.9 ± 6.1 cm, respectively; t = 0.570, *d.f.* = 10, P = 0.581). Episodes of unusually low temperatures during March-April were similar during cycle and non-cycle years (3.4 ± 0.6 episodes of 2.3 ± 0.4 days each, average temperature of —3.0 ± 0.5 C and 2.1 ± 0.3 episodes of 3.2 ± 0.6 days, average temperature of —3.0 ± 0.4 C, respectively). There were too few cycles in alfalfa for analysis.

Effects of peak densities on habitat quality.--Population fluctuations were too erratic and peak densities did not vary sufficiently in alfalfa for analysis of effects of peak densities on habitat quality. In bluegrass there was no correlation between peak density and rate of decline (r = -0.624, n = 8, P = 0.098) or length of the decline (r = -0.610, n = 8, P = 0.108). Although peak density was correlated with extent of decline (r = -0.884, n = 8, P = 0.004), there was no relationship between peak density and length of the following trough in bluegrass (r = -0.043, n = 9, P = 0.913).

Discussion

By definition, multi-annual population cycles of arvicoline rodents are characterized by high amplitude ($\geq$ 10-fold) fluctuations in population density that occur at $\geq$2, most commonly 3-4, year intervals (Krebs and Myers 1974; Taitt and Krebs 1985; Krebs 1996; Oli and Dobson 1999). Getz et al. (In Review a) concluded length of the increase period was responsible for variation in amplitudes of fluctuation of *Microtus ochrogaster* and *M. pennsylvanicus*. In this analysis, we addressed 2 aspects of demography regarding population peaks: (1) Why

high amplitude fluctuations some years and not others and (2) why multiple-year intervals between population peaks.

Our results indicate that, among the demographic variables considered, the only demographic change consistently associated with initiation of a population cycle of both *M. ochrogaster* and *M. pennsylvanicus* in a given year was greater survival, including persistence of young on the study site. Survival was significantly greater during periods typical of population growth (spring-summer, *M. pennsylvanicus*; summer-autumn, *M. ochrogaster*) during years with a population cycle than during non-cycle years. Further, survival and persistence of young generally were greater during the increase than during the previous low phase during cycle years. In contrast, the proportion of females reproductive during the typical period of increase did not differ between cycle and non-cycle years or during the increase in comparison to the previous low density period of cycle years. Neither was there a correlation between breeding during the winter and whether a population increase occurred the following year. Early age at first reproduction has been suggested to be an important demographic determinant of the initiation of a population cycle (Oli and Dobson 1999, 2001), but our data did not allow a rigorous test of this idea.

There was no significant variation in weather conditions between cycle and non-cycle years during the period prior to (*M. ochrogaster*) and during (both species) the time the increase typically occurred. Neither were there episodes of extreme weather conditions during non-cycle years that might have suppressed a population increase.

Previous studies that have investigated the factors influencing the interval between population cycles have been inconclusive (Boonstra et al. 1998). Reduction in habitat quality owing to high population

densities has been proposed, but evidence for such a reduction is mainly from manipulative studies in which predators were excluded (Klemola et al. 2000) or emigration prevented (Krebs et al. 1973), resulting in exceptionally high population densities. When less drastic impacts on the vegetation were recorded, effects on nutrient quality of the vegetation were not observed (Agrell et al. 1995; Klemola et al. 2000). Norrdahl and Korpimäki (2002) concluded a time lag in recovery of the quality of voles from effects of previous high densities represented indirect effects from changes in the biotic environment rather than direct effects on individuals. They observed a 12-month time lag in recovery of individual quality, an interval much longer than the life span of most animals in the population. Saucey (1984) concluded delayed density-dependent factors appeared to fit a predator-prey model rather than habitat degradation.

We found no consistent correlation between peak population densities and indicators of habitat degradation that would account for the interval between population increases. Rate and length of the decline were not correlated with peak densities in *M. ochrogaster*. Only exent of declines of *M. pennsylvanicus*, but not *M. ochrogaster,* were positively correlated with peak densities. Likewise, there was no correlation between peak densities and length of time until the subsequent population increase. Based on these results and our qualitative observations during the study, we conclude that there was no significant habitat degradation during population peaks or that the magnitude of such was not related to population density at the peak. Neither direct effects nor indirect effects (habitat degradation) on quality of the animals appeared to account for the delay in the next population increase.

Variation in predation pressure appears to influence whether a population cycle occurs during a given year and the length of the interval between population peaks. Elsewhere (Getz et al. In Review a,b) we conclude that variation in predation pressure is the primary factor responsible for the amplitude of population fluctuation and cessation of population growth of most cycles of *M. ochrogaster*, but not *M. pennsylvanicus*. For cycles peaking in autumn-winter, a winter density-independent decline in reproduction contributed to cessation of growth and the decline phase of both species.

Korpimäki and Norrdhal (1991) concluded that whereas resident generalist predators tend to dampen population fluctuations and reduce the probability of population cycles, resident specialists may deepen and prolong population lows and generate multi-annual cycles (Hanski et al. 1991; Graham and Lambin 2002). Nomadic specialists, on the other hand, dampen fluctuations by rapidly responding to sites with high population densities. Lin and Batzli (1995) listed 21 potential predators of voles in our study sites. Of those listed, only the least weasel (*Mustela nivalis*) is considered a specialist predator on voles (Pearson 1985). Although feral cats (*Felis silvestris*) utilize a variety of prey during spring-autumn, voles most likely constitute the predominant prey during autumn-winter (Lin and Batzli 1995). Of 8 raptors common in the area, only 1, the rough-legged hawk (*Buteo lagopus*), is migratory, appearing in our study region in November and leaving in early spring. This species is a specialist predator on voles and can be considered nomadic in that it can select high density sites for foraging. Five species of snakes are common on the study sites, but are active only from early spring-early autumn.

Although we did not monitor *M. nivalis* populations, we frequently caught individuals in our vole live-traps, providing an indication of

weasel presence in our study sites. These captures were almost always during times when vole population densities were high. If *M. nivalis* were the primary predator on voles and displayed delayed density-dependent effects on vole populations, we would have observed synchrony among the contiguous vole populations. This was observed for *M. ochrogaster*. However, populations of *M. pennsylanicus* did not display synchrony among the 3 habitats. Thus, *M. nivalis* may be a factor in maintaining low population densities of *M. ochrogaster*, but not of *M. pennsylvanicus*.

Although *Buteo lagopus* may have a role in initiating a decline phase (Getz et al. In Review a), it would not play a role in maintaining lengthy low periods. They would migrate north before an increase phase would be initiated and arrive back after an increase either had been prevented by other predators or had already been initiated and the population achieving a relatively high density.

Felis silvestris most likely are nomadic in their hunting, and their presence is not entirely density-dependent. Numbers in a given area at a given time often reflect the varying numbers of cats maintained at nearby houses or farmsteads. We presume most would spend much of the time feeding in vole habitats near their shelter, whether it be homesteads or forest stands, even when population densities were low (George, 1974, Warner 1985). Thus, cats would tend to hold down population density during the low period.

Resident generalist predators are the most likely sources of mortality maintaining low population densities (Hanski et al. 1991). While snakes are not a major predator on adult voles (Lin and Batzli 1995), Getz et al. (2000, In Review a) suggested snakes play a major role in suppressing population increases in *M. ochrogaster* through predation on nestlings. Other resident predators would exert varying

predation pressure on vole populations during spring-autumn. Further, predator-prey interactions of the various species would vary among habitats. Predation effectiveness varies with hunting ability and habitat conditions (cover) and ability of prey to avoid predators (variable prey risk).

The impact of individual species of predators would vary from year to year since numbers of each are controlled by different factors. Some years one or more species may be responsible for suppressing population growth, while others would be involved other years. Given the erratic nature of such events, population cycles would be expected to be erratic in nature, with no typical predator-prey cycle, and thus no distinct predictable interval between cycles. This is what we observed with respect to population fluctuations of both species of voles over the 25 years of our study. Although the role of predation in population cycles of arvicoline rodents has been controversial (e.g., Korpimäki and Norrdahl 1998; Graham and Lambin 2002), our results indicate that predation plays an important role in the dynamics of our study populations.

Acknowledgements

The study was supported in part by grants NSF DEB 78-25864 and NIH HD 09328 and by the University of Illinois School of Life Sciences and Graduate College Research Board. We thank the following individuals for their assistance with the field work: L. Verner, R. Cole, B. Klatt, R. Lindroth, D. Tazik, P. Mankin, T. Pizzuto, M. Snarski, S. Buck, K. Gubista, S. Vanthernout, M. Schmierbach, D. Avalos, L. Schiller, J. Edgington, B. Frase, and the 1,063 undergraduate “mouseketeers” without whose extra hands in the field the

study would not have been possible. C. Haun, M. Thompson and M. Snarski entered the data sets into the computer.

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Table 1. Comparison of demographic variables during the trough and the subsequent increase phase of *Microtus ochrogaster* population cycles. Survival: proportion (mean ± SE) of individuals surviving to next month. Persistence: number of months (mean ± SE) individuals first captured as young animals remained on the study site. Reproductive: proportion (mean ± SE) of adult females reproductive each month. Sample sizes are given in parentheses; sample sizes for persistence data are total number of individuals, for other variables, sample sizes are number of months of data included in each sample. Two sample t-tests were used to test for differences in each variable between trough and increase phase. Values with a single asterisk (*) indicate significant difference at $P < 0.01$; those with double asterisks (**) indicate significant difference at $P < 0.001$.

	Alfalfa		Bluegrass		
	Trough	Increase	Trough	Increase	
Survival					
Total	0.513 ± .025**	0.686 ± .016**	0.387 ± .030**	0.594 ± .025**	0.3(
	(147)	(65)	(128)	(48)	
Adults	0.445 ± .028**	0.638 ± .018**	0.428 ± .036**	0.571 ± .029**	0.4{
	(132)	(67)	(90)	(47)	

Table 1 (Cont.)

Young	0.235 ± .033**	0.538 ± .030**	0.199 ± .034**	0.384 ± .044**	0.25
	(82)	(62)	(64)	(39)	
Persistence	1.96 ± .08*	2.15 ± *	1.66 ± .10**	2.19 ± .06**	1.4
	(479)	(1529)	(183)	(744)	
Reproductive	0.775 ± .028	0.818 ± .023	0.800 ± .033	0.766 ± .035	0.7
	(75)	(19)	(90)	(47)	

Table 2. Effects of weather conditions on initiation and maintenance of population cycles of *Microtus ochrogaster*. Deviations from the previous 30-year averages of mean monthly temperatures (^{o}C) and total precipitation (cm) for the four month periods, March-June and July-October. Number of years are given in parentheses, and ranges are given below each value. Values of t-statistic (2-sample t-tests) and observed significance level (*P*-value) also are given for each comparison.

	March-June		July-October	
	Cycle years	Non cycle years	Cycle years	Non cycl
Alfalfa				
Temperature	+0.4 (13)	+0.3 (12)	-0.6 (13)	+0.1
	-1.0 to +2.3	-1.8 to +2.8	-1.8 to +0.1	-1.1 t
	t = 0.39, *d.f.* = 23, P = 0.702		t = 2.75, *d.f.* = 17.1, P	
Precipitation	+3.7 (13)	+3.1 (12)	+7.6 (13)	+2.9
	-4.7 to +19.7	-19.8 to +24.6	-8.2 to +39.8	-12.0 t
	t = 0.13, *d.f.* = 16.4, P = 0.897		t = 0.93, *d.f.* = 22.9, P	
Bluegrass				
Temperature	+0.6 (12)	+4.0 (12)	-0.3 (13)	+0.1
	-1.0 to +2.8	-1.8 to +2.5	-0.9 to +1.5	-1.8 t
	t = 1.199, *d.f.* = 23, P = 0.243		t = 0.104, *d.f.* = 23, P =	
Precipitation	+0.1 (13)	+2.8 (12)	+11.5 (13)	-0.3
	-5.8 to +19.7	-19.8 to 24.6	-12.0 to +17.2	-4.3 to
	t = 0.271, *d.f.* = 23, P = 0.789		t = 2.655, *d.f.* = 23. P =	

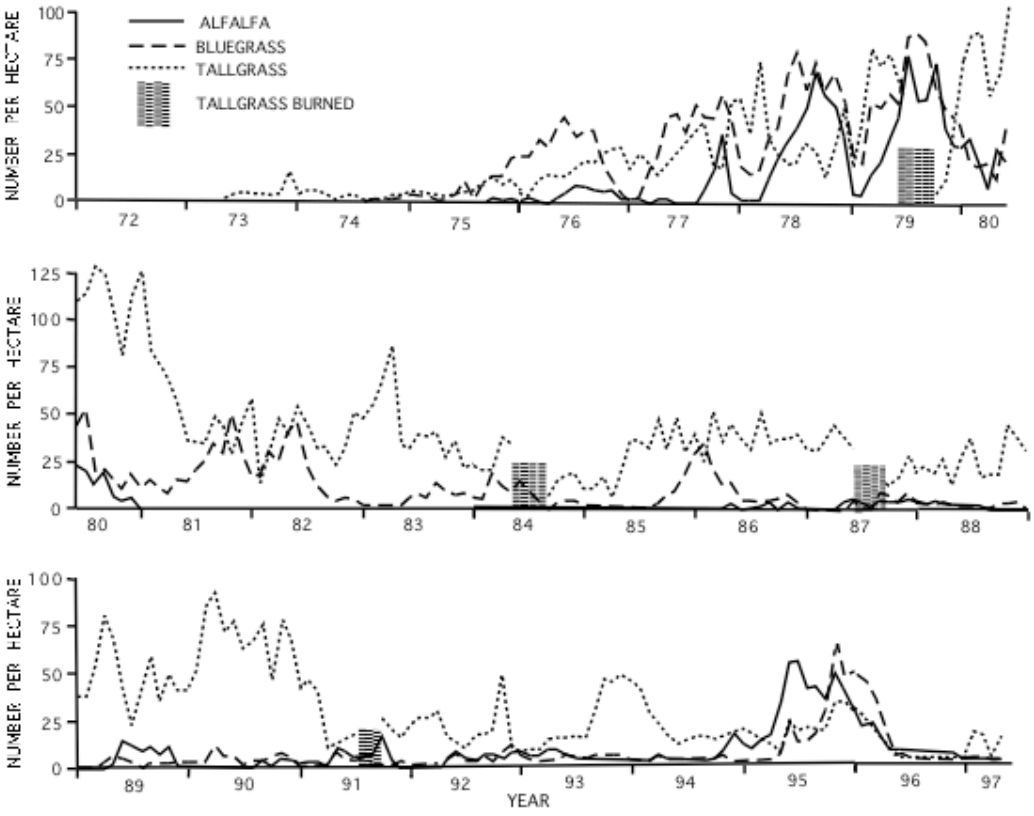
Table 3. Comparison of demographic variables during the trough and the subsequent increase phase of *Microtus pennsylvanicus* population cycles. Two sample t-tests were used to test for differences in each variable between trough and increase phase. Values with a single asterisk (*) indicate significant difference at $P < 0.01$; those with double asterisk (**) indicate significant difference at $P < 0.001$. See Table 1 for details of variables.

	Alfalfa		Bluegrass	
	Trough	Increase	Trough	Increase
Survival				
Total	0.421 ± .033**	0.546 ± .034**	0.437 ± .034**	0.588 ± .020**
	(85)	(20)	(103)	(44)
Adults	0.348 ± .043	0.478 ± .054	0.571 ± .039	0.535 ± .025
	(50)	(20)	(57)	(41)
Young	0.390 ± .172	0.410 ± .078	0.194 ± .052**	0.462 ± .044**
	(5)	(18)	(38)	(35)
Persistence	1.78 ± .24	1.89 ± .18	1.69 ± .18**	2.55 ± .13**
	(46)	(73)	(80)	(315)
Reproductive	0.810 ± .043	0.787 ± .035	0.625 ± .050	0.650 ± .045
	(47)	(20)	(71)	(43)

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.


ALFALFA
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TALLGRASS BURNED
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