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Demography of fluctuating vole populations: Are changes in demographic variables consistent across individual cycles, habitats and species?

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Abstract. We analyzed monthly survival rates, persistence of young, reproduction, recruitment of young, immigration rates, body mass, and sex ratio for fluctuating sympatric populations of *Microtus ochrogaster* and *M. pennsylvanicus* in alfalfa, bluegrass and tallgrass over 25 years. *M. ochrogaster* underwent 13 population cycles in alfalfa, 12 in bluegrass and five in tallgrass. *M. pennsylvanicus* displayed five cycles in alfalfa, nine in bluegrass and was acyclic in tallgrass. Among the demographic variables considered, only increased survival and persistence of young were associated consistently with the increase phase of population cycles in both species. Survival rates, persistence of young and reproduction of *M. ochrogaster* were lower during the decline than during the increase phase in alfalfa and bluegrass, but not in tallgrass. There were no demographic differences between the decline and increase phases for *M. pennsylvanicus* in either alfalfa or bluegrass. Most differences in demographic variables within phases among habitats involved survival and explained among-habitat demographic differences of each species. Differences in demographic variables within phases between species also mainly involved survival; these differences were consistent with differences in demography of the two species in alfalfa. Overall, our data indicate that changes in survival were most important in determining patterns of fluctuation in our study populations.

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

Introduction

Many species of arvicoline (microtine) rodents undergo high-amplitude fluctuations in abundance. Some populations fluctuate erratically and some annually, while others appear to undergo multi-annual “population cycles” with peak densities typically occurring at 3-4-year intervals (Krebs and Myers 1974, Taitt and Krebs 1985, Krebs 1996).

Considerable variation has been observed in the configuration of population fluctuations among species and among populations of the same species (Bjørnstad et al. 1998, Krebs and Myers 1974, Saitoh et al. 1998). Within a species, populations occupying different habitats in the same region may display erratic, annual or multi-annual fluctuations (Taitt and Krebs 1985, Lidicker 1988). Populations of a species within the same site may display annual fluctuations at some times and multi-annual cycles at other times (Marcström et al. 1990). Species with similar habitat requirements may display different cyclic phenomena, and species with different requirements may display similar cycles in the same site (Krebs et al. 1969, Taitt and Krebs 1985, Getz et al. 1987, Marcström et al. 1990). It is small wonder that simple explanations of population fluctuations of arvicoline rodents have been elusive. In excess of 22 hypotheses have been proposed to explain cyclic phenomena in arvicoline rodents, but still no consensus has been reached yet concerning the causes of population cycles (Batzli 1992, 1996, Oli and Dobson 1999, 2001).

The fact remains, however, that some species do undergo high amplitude fluctuations in numbers. At a minimum, we are left with explaining what drives such large-scale fluctuations in abundance, irrespective of the type of fluctuations involved. Changes in population size are consequences of changes in demographic variables. Thus, a complete understanding of causes of population fluctuations necessitates understanding demographic changes that underlie changes in population size (Oli and Dobson 1999, 2001, Dobson and Oli 2001). In general, two basic demographic processes potentially are involved in changes in numbers necessary for population cycles: losses from the population (mortality and emigration) and additions to the population (reproduction and immigration). We need to know how demographic characteristics change as the population goes through various phases of a cycle. In this way, we may understand what demographic features characterize the trough, increase, peak, and decline phases of the cycle.

We also need to test for differences in demographic variables: (1) within phases among cycles within a habitat, (2) within phases of the cycles among habitats, and (3) within phases among species in the same habitat. The first analysis will test for consistency of demographic factors driving population cycles, while the second will test whether phase-specific demographic features differ among habitats. The third analysis will test for differences in demographic mechanisms of population cycles between species. Because abiotic environmental factors can influence demographic variables as well as population sizes, we also need to examine seasonal influences on cyclic phenomena. We show elsewhere (Getz et al. In Review a) that seasonal effects may be important in generation of population cycles of *M. ochrogaster*.

To address the above questions, long-term data are needed from a species occupying different habitats in the same region, and from different species occupying the same habitats. Given the stochastic vagaries of weather and other extrinsic factors, a large number of cycles must be studied to arrive at even an approximation of the importance of given demographic variables on population cycles. Unfortunately, most previous studies of arvicoline rodents have been of short duration (average of 3.5 years; Taitt and Krebs 1985) and few have followed a population for more than 2-3 cycles. Further, most studies have involved either one species in one or two habitats or two species in one habitat.

The present study addresses some of the shortcomings of previous studies. Our study was conducted in three habitats located within a radius of 500 m. Two species of voles (prairie vole, *Microtus ochrogaster*, and meadow vole, *M. pennsylvanicus*) with different habitat requirements inhabited the three habitats. Monthly live-trapping sessions were conducted year-round in all three habitats for 25 years (1972-1997). Thus, our data were ideal for addressing the questions posed above.

Methods

Species

Microtus ochrogaster

M. ochrogaster is characteristic of graminoid habitats and monocots are a component of its diet; however, forbs are required for maximum population success (Zimmerman 1965, Meserve 1971, Cole and Batzli 1978, 1979, Haken and Batzli 1996). Although *M. ochrogaster* populations achieve high population densities in habitats with dense cover (Birney et al. 1976), this species is successful in habitats with relatively sparse vegetative cover (Klatt 1986, Klatt and Getz 1987, Getz and Hofmann 1999, Lin and Batzli 2001). High kidney efficiency of *M. ochrogaster* results in relatively low water requirements (Getz 1963), allowing the species to occupy dry grasslands.

Microtus pennsylvanicus

Although *M. pennsylvanicus* prefers succulent forbs (Thompson 1965, Lindroth and Batzli 1984), it is successful when feeding on a diet consisting mainly of graminoids (Cole and Batzli 1978, 1979, Haken and Batzli 1996). *M. pennsylvanicus*, therefore, may be abundant in primarily graminoid habitats (Getz and Hofmann 1999). *M. pennsylvanicus* is most abundant in habitats providing dense vegetative cover throughout the year (Getz 1970, Birney et al. 1976, Klatt 1986, Klatt and Getz 1987, Lin and Batzli 2001). Because of low kidney efficiency (Getz 1963), the species is characteristic of moist situations (Miller 1969). *M. pennsylvanicus* did not occur in the study region prior to 1972 (Getz et al. 1978); the species first appeared in the study sites in May 1973.

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* and *M. pennsylvanicus* in three habitats: restored tallgrass prairie (March 1972--May 1997), bluegrass, *Poa pratensis*, (January 1972--May 1997) and alfalfa, *Medicago sativa*, (May 1972--May 1997). Tallgrass prairie was the original habitat of both species in Illinois, while bluegrass, an introduced species, represents one of the more common habitats in which the two species can be found today in Illinois. Alfalfa is an atypical habitat that provides exceptionally high-quality food for both species (Cole and Batzli 1979, Lindroth and Batzli 1984). 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 two restored tallgrass prairies: one located in Trelease Prairie and the other in Phillips Tract. Relative abundance of the predominant plant species in Trelease Prairie were as follows: big bluestem, *Andropogon gerardii* (17%); bush clover, *Lespedeza cuneata* (16%); ironweed, *Vernonia* (12%); Indian grass, *Sorghastrum nutans* (10%); about 15 other 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 site: *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. We trapped sites in one or both of the 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).

The bluegrass study sites were established within a former bluegrass pasture located in Phillips Tract. Relative abundances of plants were: *P. pratensis* (70%); dandelion, *Taraxacum officinale* (14%); about 25 other species with relative abundances of ≤ 10% (Getz et al. 1979). To reduce successional changes, especially invading forbs, shrubs and trees, bluegrass sites were mowed 25 cm above the surface during late summer every 2-3 years. All bluegrass sites were mowed at the same time.

Two alfalfa sites in Phillips Tract were trapped during the study. A site was trapped until invading forbs and grasses began to crowd out the alfalfa. One year before trapping was terminated in that site, the other was planted with alfalfa so that the alfalfa would be fully developed when trapping subsequently commenced in that site. Sites were separated by a 10-m closely mown strip. Animals moved between the two sites, however, so we presumed we were monitoring a single population

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*. A series of 3-m wide strips were mowed 25 cm above the surface periodically each June-September to control invading weedy forbs and to promote new growth of alfalfa. Mowing of the strips was timed so that at least two-thirds of the field had dense vegetative cover at all times.

Habitat quality

The alfalfa habitat provided high quality and quantity food for both species. Quantity and quality of food available in bluegrass was relatively high, but less than that in alfalfa, for both *M. ochrogaster* and *M. pennsylvanicus*. Availability of preferred food in tallgrass was low for both species. However, *M. pennsylvanicus* is able to utilize graminoid vegetation present in bluegrass and tallgrass more effectively than is *M. ochrogaster*.

Vegetative cover was adequate for *M. ochrogaster* throughout the year in alfalfa, but was inadequate during most winters for *M. pennsylvanicus* (Getz et al. In Review a). Vegetative cover was sufficient in both bluegrass and tallgrass throughout the year for both species (Getz et al. In Review a).

Free water in the vegetation, even at the end of an extreme drought period, was sufficient to meet the water requirements of both species in all study sites (Getz et al. In Review a).

Procedures

All study sites were organized on a grid system with 10-m intervals. One wooden multiple-capture live-trap (Burt 1940) was placed at a 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, and thus we did not provide nesting material 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 (≤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, individual identification, grid station, 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

We estimated the density of voles for each trapping session using the minimum number 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 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 the animals estimated to be present, 92% of the *M. ochrogaster* and 91% of the *M. pennsylvanicus* were actually 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. As described below, the peak period of most population cycles of both species was only one month in duration. In effect, most of our study populations increased to a peak density one month and then declined rapidly the following month (Figs. 1 and 2). Thus, "peaks" represent only a high point in the fluctuations rather than a true "phase". Nevertheless, we have included the peak period as a separate phase in our analyses to provide a comparison with results of other studies. Beginning and termination of each phase for each cycle was based on major inflections in population change for that phase and cycle.

We performed seasonal analyses of the data to determine the relative importance of seasonal and phase effects on population cycles. We used the following categories in our seasonal analyses: spring (March-May); summer (June-August); autumn (September-November); winter (December-February).

Demographic variables

For each species-habitat combination, we estimated monthly survival, reproduction, persistence of young, proportion of young in the population, and proportion of immigrants. We defined monthly survival as the proportion of the animals present one month that survived to the next month. Survival was estimated for all animals in the population (total population survival), and separately for adults (>30 g; adult survival) and young animals ($\leq$29 g; young survival). We estimated persistence of young animals, presumed to have been born on the study site since the last trapping session, as the time between first and last capture. Animals caught one month were assumed to have been born two weeks prior to being captured and to have disappeared from the sites two weeks following the date of last capture. We calculated the proportions of adult males and females recorded as reproductive for each month. We also calculated for each month the proportion of the total population comprised of young animals, presumed to have been born into the population since the previous trapping session. Unmarked animals $\geq$30 g caught in a given month were presumed to have been born elsewhere and immigrated into the study site since the previous trapping session. The proportion of the total population comprised of new immigrants was estimated for each month, as was the proportion of new animals (those first caught a given month) that were immigrants.

Body mass

Body mass is an indirect indicator of quality of the animals, in that individuals in good condition would be expected to have higher body mass than those in poor condition. We limited our examination of body mass to adult males ($\geq$30 g). In this way, we avoided bias from variation in the proportion of the population comprised of young animals and from variation in the reproductive status of females (i.e., changes in body mass due to pregnancy and parturition). 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.

Sex ratio

We compared sex ratio of the adult population among phases to determine any possible relationship with population cycling. The proportion of the adult ($\geq$30 g) population composed of males was utilized in the analysis of sex ratios among phases of population cycles.

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), we log-transformed all variables. Variables that included “zeros” were log (X+1)-transformed because logarithm of zero is not defined. We used 2-sample t-tests, and one-way ANOVAs followed by Tukey’s honestly significant difference (HSD) post-hoc multiple comparison tests. Degrees of freedom (df) for “persistence of young” are actual numbers of individuals involved; all other df values represent the 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, df is given to one decimal place. All statistical analyses were performed using SPSS 10.0.7 for Macintosh (SPSS, Inc. 2001).

Results

Population densities

Microtus ochrogaster

Mean population density over the 25 years of the study in alfalfa (50/ha) was higher than that in bluegrass (18/ha) which, in turn, was higher than that in tallgrass (7/ha; Getz et al. 2001). There were 13 population cycles in alfalfa (Fig. 1), with a mean peak density of 202/ha (range, 77-638/ha), 12 in bluegrass with a mean peak density of 67/ha (range, 25-156/ha) and five in tallgrass with a mean peak density of 59/ha (range, 34-92/ha). Peak densities differed among habitats ($F = 11.7846$, df = 2,26, $P = 0.0002$), with mean peak density in alfalfa being significantly higher than those in bluegrass and tallgrass ($P < 0.05$). There was no difference between mean peak densities in bluegrass and tallgrass ($P > 0.05$). Amplitudes of fluctuations also differed among habitats ($F = 9.486$, df = 2,25, $P = 0.001$), with significantly higher amplitudes in alfalfa (175/ha) than in bluegrass and tallgrass (57 and 53/ha, respectively; $P < 0.05$). Amplitudes of fluctuation did not differ in bluegrass and tallgrass ($P > 0.05$).

Mean length of the low (trough) phases did not differ between alfalfa and bluegrass (11.8 and 14.2 months, respectively; $t = 1.424$, df = 17.6, $P = 0.172$). However, in tallgrass there were extensive periods when *M. ochrogaster* was either absent or in very low population densities (Fig. 1).

Microtus pennsylvanicus

Mean population density in tallgrass (30/ha) was higher than that in bluegrass (14/ha) which, in turn, was higher than that in alfalfa (7/ha) (Getz et al. 2001).

Microtus pennsylvanicus was acyclic in tallgrass, with a maximum density of 128/ha (Fig. 2; Getz et al. 2001). There were five population fluctuations in alfalfa with a mean peak density of 53/ha (range, 29-79/ha) and nine fluctuations in bluegrass, with a mean peak density of 56/ha (range, 35-91/ha). Peak densities (t = 0.45, df = 12, P = 0.658) and amplitudes of fluctuation in alfalfa and bluegrass did not differ (47/ha and 44/ha, respectively; t = 0.135, df = 12; P = 0.895). *M. pennsylvanicus* was either absent or in very low population densities for longer periods in alfalfa than in bluegrass (Fig 2).

Demographic variables

Microtus ochrogaster

Mean monthly survival (total population, adult and young) generally was greater during the increase phase than during other phases of the cycle in alfalfa and bluegrass; the differences were greater in alfalfa (Table 1) than in bluegrass (Table 2). Except for adults in alfalfa, survival was next highest during the peak. Survival was lowest during the decline and trough. Few differences in survival were recorded in tallgrass (Table 3); survival of the total population was greater during the increase and peak, as compared with the trough, and survival of young was greater during the increase than during the trough.

As was observed for monthly survival rates, persistence of young was greatest for those animals born during the increase phase in all three habitats (Tables 1, 2, 3). There was no other significant difference concerning persistence of young.

The proportions of reproductive adult males and females were significantly lower during the decline than during the increase phase in alfalfa (Table 1) and all other phases in bluegrass (Table 2). There was no difference in the proportion of either sex reproductive during the peak and decline in alfalfa (Table 1). The only difference in proportion of reproductive adults between the trough and increase in all three habitats was a greater proportion of reproductive males during the increase in alfalfa (Table 1). Fewer females were reproductive during the decline than during the trough in alfalfa (Table 1) and tallgrass (Table 3), as were both sexes in bluegrass (Table 2). There was no difference in the proportion of males reproductive among the four phases in tallgrass (Table 3).

We found no difference regarding the proportions of the population comprised of young born into the population in either alfalfa (Table 1) or bluegrass (Table 2). However, the proportion of the population comprised of young was greater during the trough than during the increase in tallgrass (Table 3). Also, in tallgrass, immigrants made up a significantly smaller proportion of the total population, as well as of the new animals, during the decline than during the increase (Table 3).

Microtus pennsylvanicus

There were only four significant differences among the 32 comparisons of survival and persistence of young with phase of the population cycle of *M. pennsylvaanicus*. Mean monthly adult survival rates were higher during the peak than during the decline and trough in alfalfa (Table 4). In bluegrass, total population survival was greater during the increase and peak than during the trough (Table 5). Persistence of young in alfalfa did not differ with respect to phase of the cycle in which they were born (Table 4). Survival of young during the trough in bluegrass was lower than during the other 3 phases (Table 5). Young born during the increase in bluegrass persisted longer than did those born during the trough and decline (Table 5).

The proportions of males and females that were reproductive were lowest during the decline in alfalfa (Table 4). Although a similar pattern emerged in bluegrass, the differences were not significant (Table 6). Proportions of the population comprised of young animals did not differ among the four phases in alfalfa (Table 4); the proportion of the population comprised of young animals was less during the trough than during the decline in bluegrass (Table 5). Proportions of immigrants did not differ among phases in either alfalfa (Table 4) or bluegrass (Table 5). However, the proportions of new animals that were immigrants were greater during the trough and peak than during the increase and decline in bluegrass (Table 5).

Comparison of demographic variables among phases

The data were analyzed to test for differences of demographic variables with respect to (1) within phases among cycles within each habitat, (2) within phases of cycles among habitats and (3) within phases of cycles between the two species in alfalfa and bluegrass. These comparisons were made to determine whether variables associated with phases of the population cycle were characteristic of the species, irrespective of habitat, and explain demographic differences among habitats and between species.

Within phases among cycles within each habitat

With the exception of the trough, individual phases of each population cycle were only a few months in duration. As a result, there were few data regarding several demographic variables for most cycles. Sufficient data were available for analysis of total population survival and proportion of females reproductive for the trough, increase and decline phases of most cycles within each habitat. Comparisons of peak phases were not possible because peaks typically were only one month in duration.

Microtus ochrogaster.--Total survival during the 1991-1993 trough (Fig. 1) in alfalfa was lower than that of the other cycles (F = 3.400, df = 7,130, P = 0.002). When this cycle was removed from the analysis, there was no difference among the other cycles (F = 1.897, df = 6,121, P = 0.087). During the decline of 1975-1976, total population survival was exceptionally high. There was no difference in survival among the declines of the remaining cycles (F = 1.375, df = 11,37, P = 0.225). A significant difference (F = 2.183, df = 11,37, P = 0.038) in proportion of females reproductive among the decline phases in alfalfa resulted from a higher proportion of reproductive females during the 1987 decline; when this cycle was removed from analysis, the difference disappeared (F = 1.954, df = 10,32, P = 0.074).

Survival during four of the increase phases varied significantly among the cycles in bluegrass (two unusually high, 1982, 1987; two unusually low, 1991, 1993; F = 5.161, df = 11,35, P <0.001). Only one specific cycle, each, in the trough

(1991-1993) and decline (1982) was responsible for the significant differences with respect to proportion of the females reproductive among these phases in bluegrass ($F = 2.615$, df = 11,79, $P = 0.007$ and $F = 2.811$, df = 10,35, $P = 0.011$, respectively). When these cycles were removed from the analyses, the proportion of reproductive females did not differ among phases of the remaining cycles (trough: $F = 1.866$, df = 10,66, $P = 0.066$; decline: $F = 1.091$, df = 9,32, $P = 0.396$).

Monthly survival and proportion of females reproductive did not differ among phases of the five cycles in tallgrass.

Microtus pennsylvanicus.--There were only two significant demographic differences within each phase among the various population cycles in alfalfa and bluegrass, both involving proportion of females that were reproductive. In alfalfa, the only difference in the proportion of females reproductive during the decline was between the declines of 1980-1981 and 1995-1996 ($F = 4.894$, df = 3,17, $P = 0.012$). In bluegrass, a significant difference among cycles in the proportion of females reproductive during the increase ($F = 3.081$, df = 8,34, $P = 0.010$) was attributed to very low reproduction during the 1985-1986 cycle. When this cycle was removed from the analysis, the difference disappeared ($F = 2.201$, df = 7,30, $P = 0.063$). Total population survival during the trough, increase and decline phases did not differ among the cycles in either habitat.

Phases within cycles among habitats

All demographic variables associated with the four phases of the population cycle were compared among the three habitats for *M. ochrogaster* and between alfalfa and bluegrass for *M. pennsylvanicus*. These comparisons tested whether the variables were characteristic of the species, irrespective of habitat, or were habitat specific. If the latter, did the differences account for demographic differences among the habitats?

Microtus ochrogaster.--There were 12 instances in which demographic variables differed significantly for given phases among the habitats. Seven of these involved differences that were consistent with differences in demography among the habitats, including five involving survival and two reproduction: (1) higher total population survival during the trough in alfalfa than in either bluegrass or tallgrass (F = 13.140, df = 2,355, $P < 0.001$); (2) higher total survival during the increase in alfalfa than in bluegrass (F = 5.053, df = 2,131, P = 0.007); (3) longer persistence of young born during the peak in bluegrass than in tallgrass (F = 5.278, df = 2,906, P = 0.005); (4) lower survival of young during the increase in tallgrass than in either alfalfa or bluegrass (F = 5.828, df = 2,106, P = 0.004); (5) shorter persistence of young born during the trough in tallgrass than in either bluegrass or alfalfa (F =

5.802, df = 2,660, *P* = 0.003); (6) greater proportion of reproductive males during the increase in alfalfa than in either bluegrass or tallgrass (*F* = 4.627, df = 2,133, *P* = 0.016); (7) lesser proportion of reproductive females during the increase in tallgrass than in either alfalfa or bluegrass (F = 6.297, df = 2,135, *P* = 0.002).

The remaining differences in the demographic variables, all involving reproduction or immigration, were not consistent with among-habitat differences in population densities: (1) greater proportion of young during the trough in tallgrass than in either alfalfa or bluegrass (*F* = 18.505, df = 2,365, *P* < 0.001; (2) lesser proportion of new animals consisting of immigrants during the trough in tallgrass than in either bluegrass or alfalfa (*F* = 10.929, df = 2,240, *P* = 0.001); (3) greater percentage of new animals that were immigrants during the increase in tallgrass than in bluegrass (*F* = 3.808, df = 2,71, *P* = 0.027) (4) greater proportion of young during the decline in tallgrass than in alfalfa (F = 3.668, df = 2,117, *P* = 0.028); (5) lesser proportion of reproductive males during the decline in bluegrass than in either alfalfa or tallgrass (*F* = 4.089, df = 2,111, *P* = 0.019).

Microtus pennsylvanicus.--Four significant differences in demographic variables, involving survival and persistence of young within given phases of the two habitats, all resulted from higher values in bluegrass than in alfalfa and were consistent with higher population densities in bluegrass as compared to alfalfa: (1) greater total population survival during the decline: *t* = 2.20, df = 53, *P* = 0.032; (2) greater adult survival during the decline: *t* = 2.17, df = 43, *P* = 0.036; (3) longer persistence of young during the increase: *t* = 2.26, df = 131.1, *P* = 0.009; (4) longer persistence of young during the peak: *t* = 2.73, df = 48.4, *P* = 0.009. Three instances of differences in proportions of reproductive adults, none of which agreed with higher population densities in bluegrass than in alfalfa, were: (1) greater proportion of reproductive females during the trough in alfalfa (*t* = 2.93, df = 116, *P* = 0.004; (2) greater proportion of reproductive males during the trough in alfalfa; *t* = 2.015, df = 125.9, *P* = 0.046; and (3) greater proportion of reproductive males during the increase in alfalfa; *t* = 3.113, df = 44.0, *P* = 0.003. Two of the remaining four significant differences involved greater proportions of immigrants in alfalfa during the increase (*t* = 2.57, df = 53, *P* = 0.013) and a greater proportion of immigrants during the decline in bluegrass than in alfalfa (*t* = 2.52, df = 34.6, *P* = 0.017); only the latter difference was consistent with differences in population densities between the two habitats. The remaining two demographic differences involved greater proportion of young in alfalfa during the trough (t = 2.76, df =

129.5, *P* = 0.011) and increase (*t* = 2.53, df = 59.7, *P* = 0.014); these differences were inconsistent with higher densities in bluegrass.

Interspecific comparisons among phases

Demographic comparisons were made between phases of *M. ochrogaster* and *M. pennsylvanicus* in alfalfa and bluegrass. Comparisons were not possible for tallgrass because *M. pennsylvanicus* did not exhibit distinct population fluctuations in this habitat.

Alfalfa.--Most differences between the two species in alfalfa involved the increase and peak phases. Five differences involved greater survival of *M. ochrogaster* than *M. pennsylvanicus* and reflected higher population densities of the former species in alfalfa: (1) total population survival during the trough (*t* = 3.55, df = 151.4, *P* = 0.001), (2) total population survival during the increase (*t* = 4.067, df = 83, *P* < 0.001); (3) adult survival during the increase (*t* = 2.026, df = 82, *P* = 0.046); (4) adult survival during the peak (*t* = 2.20, df = 16.8, *P* = 0.042; and (5) young survival during the peak (*t* = 3.32, df = 21, *P* = 0.003). Only two differences involved reproduction: young comprised a greater proportion of the population of *M. ochrogaster* than *M. pennsylvanicus* during the increase (*t* = 3.167, df = 86, *P* = 0.002) and peak phases (*t* =

4.019, df = 27, *P* = 0.001). These, too, were consistent with differences in densities of the two species in alfalfa.

Other comparisons of the increase and peak phases were not consistent with differences in population densities of the two species in alfalfa. The proportion of reproductive male *M. pennsylvanicus* was greater than that of *M. ochrogaster* during the trough (*t* = 2.709, df = 166.1, *P* = 0.007) and increase (*t* = 2.783, df = 85, *P* = 0.007), while there was no difference in the proportion of females reproductive between the two species during these phases. Proportion of immigrants in the population generally was greater for *M. pennsylvanicus* than *M. ochrogaster* during the increase (proportion of the population and of new animals; *t* = 2.549, df = 37, *P* = 0.015 and *t* = 2.455, df = 37, *P* = 0.019) and the proportion of new animals that were immigrant was greater during the peaks (*t* = 3.362, df = 14, *P* = 0.005). Demographic variables did not differ between the two species during the decline phase.

Bluegrass.--There were few differences between *M. ochrogaster* and *M. pennsylvanicus* with respect to most demographic variables during all four phases of the population cycle in bluegrass. Survival of adult *M. pennsylvanicus* was greater than that of *M. ochrogaster* during the trough (*t* = 2.887, df = 138.1, *P* = 0.005), and total population survival of *M. pennsylvanicus* was also greater during the decline (*t* =

3.119, df = 68, P = 0.003). The proportion of young animals during the trough (t = 2.824, df = 242.9, *P* = 0.005) and the proportion of new animals that were immigrants during the decline (*t* = 2.55, df = 52, *P* = 0.014) were greater for *M. ochrogaster* than for *M. pennsylvanicus*. The proportion of *M. ochrogaster* females reproductive was greater than that of *M. pennsylvanicus* during the trough (*t* = 2.985, df = 122.8, *P* = 0.003) and increase phases (*t* = 3.77, df = 76, *P* < 0.001).

Seasonal effects on demographic variables

Detailed analysis of seasonal differences in demographic variables have been presented elsewhere (Getz et al. In Review a). There we addressed the relationship of habitat to seasonal differences in population variables. Here we look for seasonal effects in relation to increase and decline phase differences in demographic variables. These analyses will allow us to estimate seasonal influences on population growth and decline which are important in bringing about changes in numbers during a population cycle. In order to determine seasonal effects, we compared seasons during which population growth and declines typically occur for years with population cycles and years without population cycles.

Microtus ochrogaster population cycles typically peaked during autumn or winter in both alfalfa and bluegrass, while those in tallgrass generally peaked in spring or summer (Figs. 1 and 2; Getz et al. In Review b). For alfalfa and bluegrass populations, we analyzed data for summer and autumn with respect to the increase phases and winter for the decline phases. Timing of peaks in tallgrass was too erratic and peaks were too few in number to permit seasonal comparisons.

Most cycles of *M. pennsylvanicus* peaked during spring-summer. Thus, for *M. pennsylvanicus*, we used spring-summer data as representative of the increase phase and autumn data for the decline phase. Because of the few population cycles, we combined data from alfalfa and bluegrass for analysis for this species.

Microtus ochrogaster

In alfalfa, total population monthly survival during summers of cycle years was greater than that for non-cycle years (0.606 ± 0.030 and 0.433 ± 0.056, respectively; t = 2.899, df = 43.1, P = 0.006). Survival during autumn of cycle years was also greater than during non-cycle years (0.654 ± 0.021 and 0.426 ± 0.057, respectively; t = 3.9, df = 31.5, P < 0.001). Survival during the winter of population declines did not differ from that during years without winter declines (0.504 ± 0.039 and 0.515 ± 0.056, respectively; t = 0.037, df = 67, P = 0.971).

In bluegrass, there also was greater survival during the summer and autumn of cycle years as compared to non-cycle years (Summer: 0.487 ± 0.048 and 0.307 ± 0.063, respectively; t = 2.559, df = 54.1, P = 0.013. Autumn: 0.566 ± 0.026 and 0.401 ± 0.058, respectively; t = 2.987, df = 39.9, P = 0.005). As in alfalfa, there was no difference in survival in bluegrass during winters with a population decline and winters without a decline (0.503 ± 0.044 and 0.420 ± 0.058, respectively; t = 1.449, df = 58.2, P = 0.153).

In alfalfa, there was no difference in the proportion of females reproductive in summers when the population was increasing in numbers as contrasted to summers without an increase phase (0.913 ± 0.21 and 0.901 ± 0.038, respectively; t = 0.358, df = 56, P = 0.722). Similarly, there was no difference in the proportion of females reproductive in autumns with population increases as compared to autumns without increases (0.867 ± 0.019 and 0.815 ± 0.054, respectively; t = 1.106, df = 30.3, P = 0.277). Finally, there was no difference in the proportion of females reproductive during winters with population declines and winters without declines (0.378 ± 0.044 and 0.436 ± 0.061, respectively; t = 0.756, df = 56, P = 0.453).

Similar results for the increase phase were observed regarding the bluegrass populations. Proportion of females reproductive during summer (0.825 ± 0.044 and 0.887 ± 0.056, respectively; *t* = 0.665, df = 41, *P* = 0.510) or autumn (0.842 ± 0.024 and 0.905 ± 0.043, respectively; *t* = 0.830, df = 54, *P* = 0.410) did not differ between cycle and non cycle years. During the winter, more females were reproductive when there was no population decline than when the population was in a decline phase (0.672 ± 0.077 and 0.328 ± 0.058, respectively; *t* = 3.327, df = 47, *P* = 0.002).

Microtus pennsylvanicus

Survival of the total population of *M. pennsylvanicus* was greater during the spring of cycle than for non-cycle years (0.678 ± 0.038 and 0.464 ± 0.047, respectively; *t* = 3.810, df = 68.2, *P* < 0.001), summer (0.590 ± 0.029 and 0.436 ± 0.044; *t* = 3.44, df = 76.4, *P* = 0.001) and autumn (0.552 ± 0.042 and 0.407 ± 0.042; *t* = 2.597, df = 71.1, *P* = 0.011).

There was no difference in the proportion of females reproductive during the spring of cycle and non-cycle years (0.686 ± 0.048 and 0.688 ± 0.062, respectively; *t* = 0.249, df = 55.5, *P* = 0.805), summer (0.683 ± 0.042 and 0.770 ± 0.060; *t* = 0.788, df = 50.6, *P* = 0.434) and autumn (0.760 ± 0.039 and 0.827 ± 0.039; *t* = 0.680, df = 77, *P* = 0.498).

Body mass

For *Microtus ochrogaster*, adult male body mass was higher during the increase and peak than during the trough and decline in alfalfa and bluegrass (Table 6). When body mass differences between increase/peak and decline/trough were compared for only those cycles that peaked during spring/summer (alfalfa, 1; bluegrass, 3) the difference approached significance (increase/peak, 40.1 ± 0.3g; decline/trough, 39.2 ± 0.3g; t = 1.764, df = 578.9, P = 0.078). There was no difference between the increase/peak and decline/trough in tallgrass. However, adult male body mass during the decline was higher than during the trough than the peak in tallgrass (Table 6). For *M. pennsylvanicus*, adult male body mass did not vary significantly among the four phases of the population cycle in either alfalfa or bluegrass (Table 6).

Body mass of adult males is significantly lower during the winter than during other seasons (Getz et al. In Review a). Since most population cycles of *M. ochrogaster* declined during winter, we compared differences in body mass during the winter of cycle and non cycle years. Differences were significantly lower during cycle years (Alfalfa: F = 13.193, df = 3,2889, P < 0.001. Bluegrass: F = 14.187, df = 3, 1263, P < 0.001), but not during non cycle years (Alfalfa: F = 0.682, df = 3,878, P = 0.563. Bluegrass: F = 2.333, df = 3,171, P = 0.076).

Sex ratio

There was no difference in sex ratios among the four phases of the population cycles of either species in any habitat (Table 7).

Discussion

Changes in numbers associated with generation of a population cycle are the net result of population losses from mortality and emigration, and additions from reproduction and immigration. Demographic variables are involved in four aspects of population cycles: (1) initiation of population growth, (2) continued growth to a high amplitude peak, (3) stoppage of population growth at the peak, and (4) decline to low numbers. For large-scale fluctuations in abundance to occur, one or more demographic variables must change (Oli and Dobson 1999, 2001). There is no lack of evidence for the involvement of demographic variables in generating population cycles (Hoffman 1958, Krebs et al. 1969, Keller and Krebs 1970, Krebs et al. 1973, Krebs and Myers 1974, Gaines and Rose 1976, Boonstra 1977, Getz et al. 1979, Verner and Getz 1985, Batzli 1992, 1996, Krebs 1996, Oli and Dobson 1999, Getz et al. 2000). However, there is no consensus about which variables are most important among temporally and spatially different population cycles of even one species, let alone across species. The present study involved analysis of demographic variables obtained during a 25-year study of demography of *Microtus ochrogaster* and *M. pennsylvanicus* in three habitats in east-central Illinois.

Elsewhere we show increased survival to be the primary factor associated with initiation of a population cycle in both *M. ochrogaster* and *M. pennsylvanicus* (Getz et al. 2000, In Review b). Results of the present analysis support these conclusions. Survival rates of *M. ochrogaster* were approximately 22% higher and those of *M. pennsylvanicus* 16% higher during the increase phase as contrasted to the trough. Further, except for *M. pennsylvanicus* in alfalfa, young born during the increase phase persisted 2-3 weeks longer on the study sites than did those born during the trough. We found no change in reproduction associated with the increase phase of a population cycle; this was true whether reproduction was measured as the proportion of adult males and females reproductive or as the proportion of the population comprised of recruited young. There also was no relationship between immigration and the increase phase of a population cycle in either species.

The change from an increase to a decline phase defines a population cycle. The peak is merely a pivotal point at which the population stops growing, followed by a decline in numbers to form fluctuations of varying amplitudes. Thus, comparisons of the increase and decline phases are important in understanding the role of changing demographic variables in the switch from population growth to population decline, which is necessary to generate population cycles.

Survival rates (total population, adult and young) and persistence of young *M. ochrogaster* were significantly lower during the decline than during the increase in alfalfa and bluegrass, but not in tallgrass. Proportions of the adult males and females that were reproductive were lower during the decline than the increase in alfalfa and bluegrass, but not in tallgrass.

Differences in demographic variables between the increase and decline phases of *M. pennsylvanicus* populations were less distinct. Survival, persistence of young and proportions of reproductive males and females all were lower during the decline than during the increase. However, differences were significant only for reproductive adults in alfalfa and persistence of young in bluegrass.

The only consistent seasonal effect on demographic variables was a lower proportion of reproductive females of both species during the winter in all three habitats. Because the decline phase of most (22 of 30) cycles of *M. ochrogaster* occurred during the winter (Getz et al. In Review c), density-independent seasonal reduction in reproduction may have contributed to winter population declines, but not to declines in populations peaking in spring-summer (Getz et al. In Review a). Although reproduction in *M. pennsylvanicus* declined during the winter, most (10 of 14) declines began prior to winter. Thus, seasonal influence on reproduction was not a primary factor in generating most declines in this species.

With a single exception (increase phase of *M. ochrogaster* in bluegrass), when demographic variables differed within phases among population cycles of either species of voles in alfalfa and bluegrass, only one cycle was unique. These results are consistent with earlier suggestions that phase-specific demographic changes drive the dynamics of fluctuating vole populations (Krebs 1996, Oli and Dobson 1999, 2001).

There was considerable variation in demographic variables associated with given phases among the three habitats. For both species, most differences involved survival and persistence of young and were consistent with demographic differences among the habitats. Five of the seven differences among phases of *M. ochrogaster* that explained demographic differences between alfalfa and bluegrass involved survival; only two involved reproduction. Three of the four differences that were inconsistent with demography in the two habitats involved reproduction. Similarly, for *M. pennsylvanicus*, all four differences in survival within phases between alfalfa and bluegrass populations were consistent with demographic differences between the two habitats. Only two of the five differences in reproductive variables explained demographic differences between the two habitats. None of the other differences was consistent with demographic differences between alfalfa and bluegrass.

Five of the 11 within-phase differences in demographic variables between *M. ochrogaster* and *M. pennsylvanicus* cycles in alfalfa involved greater survival for *M. ochrogaster* and were consistent with higher densities of the former species in this habitat. None of the four differences in reproduction or the two differences involving immigrants explained higher numbers of *M. ochrogaster* than *M. pennsylvanicus* in alfalfa. In bluegrass, where the two species displayed similar changes in numbers, demographic variables associated with phases of population cycles of the two species were generally similar.

Adult male body mass of *M. ochrogaster* was significantly greater during the increase/peak than during the decline/trough in alfalfa and bluegrass populations peaking in autumn-winter. Further, a winter decline in body mass was observed only during years in which a population decline occurred during winter. Lesser body mass during the decline/trough than during the increase/peak of those populations peaking in spring/summer approached significance. Taken together, these results suggest that variation in individual quality, at least for males, may be involved in population cycling in *M. ochrogaster*. However, we conclude elsewhere that decreased quality of animals is not a primary factor responsible for population declines (Getz et al. In Review c). There was no indication of a relationship between population density and quality of animals of *M. pennsylvanicus*. There were no phase-specific differences in adult male body mass in either alfalfa or bluegrass for this species.

Variation in sex ratio was not a factor in population fluctuations of either species in any habitat.

Thus, survival was the most consistent demographic variable associated with spatio-temporal differences in population density of *M. ochrogaster*. A seasonal decline (during winter) in reproduction tends to accentuate population cycles that peak in autumn-winter. In contrast, changes in survival and reproduction could not be so readily associated with population fluctuations in *M. pennsylvanicus*. In this species, increased survival and persistence of young were associated with the increase phase only in bluegrass; there was no decrease in survival or persistence of young during the decline in either alfalfa or bluegrass. Decreased reproduction was associated with declines only in alfalfa. The inconsistent relationship between changes in numbers and survival and reproduction reflect the more erratic nature of population fluctuations of *M.*

pennsylvanicus in all three habitats over the 25 years of the study.

Elsewhere we suggest that improvement in survival due to relaxation of predation pressure is responsible for population growth and high amplitude fluctuations in *M. ochrogaster* and *M. pennsylvanicus* in our study sites (Getz et al. In Review b). Density-dependent mortality caused by a resident specialist predator (least weasel, *Mustela nivalis*), a seasonal specialist predator (feral cat, *Felis silvestris*) and a migratory specialist raptor (rough-legged hawk, *Buteo lagopus*), as well as a number of generalist predators appears to be responsible for cessation of population growth. Density-dependent intrinsic factors affecting mortality may also play a role in stoppage of population growth (Getz et al. In Review c). Predation pressure from an array of resident generalist predators appears to be the most likely reason for periods of low densities (Boonstra et al. 1998, Getz et al. In Review b).

While results of the present analyses are consistent with these presumptions, we acknowledge that our results do not allow conclusive rejection of alternative explanations (Boonstra 1994, Oli and Dobson 1999, 2001). For example, phase-related changes in age at first reproduction have been suggested to be an important demographic determinant of the dynamics of cyclic populations of small mammals (Oli and Dobson 1999, 2001), but our data did not permit a rigorous test of this idea. Nevertheless, our data do allow us to conclude that, among the many demographic variables we considered, changes in survival rates, presumably a consequence of variation in predation pressure, contribute substantially to the numerical dynamics of our study populations. We speculate that density-dependent predation stops growth and triggers the decline phase. When peak densities occur in autumn-winter (most populations of *M. ochrogaster* and some of *M. pennsylvanicus* in alfalfa and bluegrass), density-independent winter reduction in reproduction may contribute to the initiation of the decline phase. For *M. ochrogaster* and *M. pennsylvanicus* populations peaking in spring-summer, decreased survival, presumably a result of predation by generalist predators, appears to trigger the decline in densities.

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Table 1. Demographic variables associated with various phases of the *Microtus ochrogaster* population cycle in alfalfa habitat. Survival, proportion (mean + SE) of individuals surviving to next month; Persistence, number of months (mean + SE) voles first captured as young animals remained on the study site; % Reproductive, proportion (mean ± SE) of adults reproductive; % Immigrants, proportion (mean ± SE) of population composed of immigrants; % New/Imm, proportion (mean ± SE) of new animals that are immigrants. See text for definition of variables and statistics. Values within a row with different superscripts differ significantly at the 0.05 level (Tukey's HSD test).

Variables	Phase of population cycle				*F*; df	*P*
	Trough	Increase	Peak	Decline		
Survival						
Total	$0.513 \pm .025^{a}$	$0.686 \pm .016^{b}$	$0.656 \pm .028^{b}$	$0.421 \pm .028^{a}$	13.868;3,277	<0.0009
Adults	$0.445 \pm .028^{a}$	$0.638 \pm .018^{b}$	$0.470 \pm .032^{a}$	$0.345 \pm .032^{a}$	13.966; 3,262	<0.0001
Young	$0.235 \pm .033^{a}$	$0.538 \pm .030^{b}$	$0.530 \pm .053^{b}$	$0.322 \pm .033^{a}$	15.664; 3,205	<0.0001

Table 1 (Cont.)

Persistence	1.96 ± 08^{a}	$2.15 \pm .05^{b}$	$1.68 \pm .05^{a}$	$1.65 \pm .07^{a}$	20.425; 3,3009	<0.001
% Reproductive						
Males	$0.801 \pm .062^{a}$	$0.910 \pm .020^{b}$	$0.857 \pm .050^{ab}$	$0.679 \pm .046^{a}$	5.656; 3,255	0.0009
Females	$0.775 \pm .028^{a}$	$0.818 \pm .023^{a}$	$0.726 \pm .062^{ab}$	$0.547 \pm .046^{b}$	10.118; 3,245	<0.0001
% Young	$0.158 \pm .017^{a}$	$0.174 \pm .012^{a}$	$0.184 \pm .021^{a}$	$0.124 \pm .014^{a}$	1.488; 3,287	0.2181
% Immigrants	$0.249 \pm .029^{a}$	$0.255 \pm .030^{a}$	$0.261 \pm .063^{a}$	$0.164 \pm .027^{a}$	0.659; 3,134	0.5788
% New/Imm	$0.619 \pm .039^{a}$	$0.609 \pm .045^{a}$	$0.502 \pm .084^{a}$	$0.489 \pm .085^{a}$	0.804; 3,110	0.4943

Table 2. Demographic variables associated with different phases of the population cycle of *Microtus ochrogaster* in bluegrass habitat. See Table 1 and text for definition of variables and statistics

Variables	Phase of population cycle				F; df	P
	Trough	Increase	Peak	Decline		
Survival						
Total	$0.387 \pm .030^{a}$	$0.594 \pm .025^{b}$	$0.544 \pm .031^{b}$	$0.369 \pm .027^{a}$	9.940; 3,236	<0.0001
Adults	$0.428 \pm .036^{a}$	$0.571 \pm .029^{b}$	$0.462 \pm .042^{ab}$	$0.353 \pm .046^{a}$	5.022; 3,192	0.0023
Young	$0.199 \pm .034^{a}$	$0.384 \pm .044^{b}$	$0.354 \pm .053^{b}$	$0.333 \pm .034^{b}$	5.9898; 3,164	0.0007
Persistence	$1.66 \pm .10^{a}$	$2.19 \pm .06^{b}$	$1.87 \pm .10^{ab}$	$1.70 \pm .09^{a}$	10.7241; 3,1320	<0.0001

Table 2 (cont.)

% Reproductive						
Males	0.793 ± .034^{a}	0.868 ± .031^{a}	0.781 ± .060^{a}	0.521 ± .055^{b}	8.4951; 3,212	<0.0001
Females	0.800 ± .033^{a}	0.766 ± .035^{a}	0.784 ± .052^{a}	0.457 ± .059^{b}	12.0808; 3,194	<0.0001
% Young	0.208 ± .026^{a}	0.205 ± .013^{a}	0.204 ± .025^{a}	0.162 ± .019^{a}	0.4538; 3,243	0.7148
% Immigrants	0.319 ± .039^{a}	0.246 ± .024^{a}	0.246 ± .028^{a}	0.322 ± .152^{a}	0.4039; 3,150	0.7504
% New/Imm	0.637 ± .035^{a}	0.518 ± .035^{a}	0.562 ± .051^{a}	0.511 ± .065^{a}	1.3357; 3,187	0.2641

Table 3. Demographic variables associated with different phases of the population cycle of *Microtus ochrogaster* in tallgrass habitat. See Table 1 and text for definition of variables and statistics.

Variables	Phase of population cycle				*F*; df	*P*
	Trough	Increase	Peak	Decline		
Survival						
Total	0.309 ± .034^{a}	0.612 ± .038^{b}	0.574 ± .053^{b}	0.420 ± .035^{ab}	10.5932; 3,129	<0.0001
Adults	0.485 ± .046^{a}	0.596 ± .045^{a}	0.522 ± .084^{a}	0.420 ± .042^{a}	1.5282; 3,76	0.2140
Young	0.253 ± .060^{a}	0.616 ± .118^{b}	0.451 ± .108^{ab}	0.463 ± .087^{ab}	3.7750; 3,62	0.0149
Persistence	1.43 ± .10^{a}	2.34 ± .21^{b}	1.45 ± .12^{a}	1.60 ± .14^{a}	9.8487; 3,367	<0.0001

Table 3 (Cont.)

% Reproductive						
Males	0.777 ± .046^{a}	0.760 ± .068^{a}	0.721 ± .096^{a}	0.781 ± .074^{a}	0.0607; 3, 114	0.9803
Females	0.799 ± .040^{a}	0.621 ± .082^{ab}	0.673 ± .105^{ab}	0.521 ± .081^{b}	3.9200; 3,123	0.0103
% Young	0.396 ± .041^{a}	0.168 ± .034^{b}	0.171 ± .030^{ab}	0.218 ± .040^{ab}	4.8718; 3,138	0.0030
% Immigrants	0.252 ± .036^{ab}	0.304 ± .058^{b}	0.211 ± .080^{ab}	0.114 ± .027^{a}	3.4243; 3,120	0.0195
% New/Imm	0.396 ± .048^{a}	0.697 ± .061^{b}	0.485 ± .124^{ab}	0.356 ± .073^{a}	4.0590; 3,106	0.0090

Table 4. Demographic variables associated with different phases of the *Microtus pennsylvanicus* population cycle in alfalfa habitat. See Table 1 and text for definition of variables and statistics.

Variables	Phase of population cycle				*F*; df	*P*
	Trough	Increase	Peak	Decline		
Survival						
Total	0.421 ± .033^{a}	0.546 ± .034^{a}	0.533 ± .050^{a}	0.396 ± .042^{a}	2.3543; 3,139	0.0747
Adults	0.348 ± .043^{a}	0.478 ± .054^{ab}	0.581 ± .022^{b}	0.302 ± .042^{a}	4.7350’ 3,102	0.0039
Young	0.390 ± .172^{a}	0.410 ± .078^{a}	0.224 ± .089^{a}	0.274 ± .057^{a}	0.8994; 3,41	0.4498
Persistence	1.78 ± .24^{a}	1.89 ± .18^{a}	1.53 ± .26^{a}	1.49 ± .12^{a}	1,7970; 3,245	0.1483

Table 4 (Cont.)

% Reproductive						
Males	0.921 ±.030^{a}	0.975 ± .012^{a}	0.977 ± .012^{a}	0.717 ± .092^{b}	4.7056; 3,108	0.0040
Females	0.810 ± .043^{a}	0.787 ± .035^{a}	0.782 ± .048^{a}	0.516 ± .082^{b}	6.0373; 3,98	0.0008
% Young	0.244 ± .041^{a}	0.101 ± .019^{a}	0.066 ± .021^{a}	0.339 ± .163^{a}	1.335; 3,137	0.1630
% Immigrants	0.342 ± .043^{a}	0.368 ± .038^{a}	0.216 ± .045^{a}	0.202 ± .036^{a}	1.9463; 3,121	0.1257
% New/Imm	0.702 ± .053^{a}	0.773 ± .042^{a}	0.804 ± .049^{a}	0.557 ± .080^{a}	2.1019; 3,92	0.1054

Table 5. Demographic variables associated with different phases of the *Microtus pennsylvanicus* population cycle in bluegrass habitat. See Table 1 and text for definition of variables and statistics.

Variables	Phase of population cycle				*F*; df	*P*
	Trough	Increase	Peak	Decline		
Survival						
Total	0.437 ± .034^{a}	0.588 ± .020^{b}	0.580 ± .032^{b}	0.520 ± .039^{ab}	5.6797; 3,193	0.0010
Adults	0.571 ± .039^{a}	0.535 ± .025^{a}	0.531 ± .030^{a}	0.422 ± .038^{a}	2.1575; 3,139	0.0958
Young	0.194 ± .052^{a}	0.462 ± .044^{b}	0.372 ± .053^{b}	0.365 ± .046^{b}	7.7639; 3,114	0.0001
Persistence	1.69 ± .18^{a}	2.55 ± .13^{b}	2.20 ± .13^{ab}	1.79 ± .12^{a}	7.7582; 3,737	<0.0001

Table 5 (Cont.)

% Reproductive						
Males	0.819 ±.042^{a}	0.838 ± .040^{a}	0.898 ± .049^{a}	0.666 ± .075^{a}	2.2221; 3,158	0.0877
Females	0.625 ± .050^{a}	0.650 ± .045^{a}	0.670 ± .054^{a}	0.435 ± .066^{a}	2.6692; 3,159	0.0495
% Young	0.118 ± .020^{a}	0.188 ± .028^{ab}	0.158 ± .039^{ab}	0.257 ± .043^{b}	5.0201; 3,202	0.0022
% Immigrants	0.311 ± .034^{a}	0.252 ± .028^{a}	0.196 ± .022^{a}	0.295 ± .060^{a}	0.7185; 3,179	0.7185
% New/Imm	0.677 ± .044^{a}	0.497 ± .042^{b}	0.572 ± .071^{a}	0.295 ± .060^{b}	7.5623; 3,163	0.0001

Table 6. Adult male body mass (mean ± SE, in grams) of *Microtus ochrogaster* and *M. pennsylvanicus* in relation to phase of the population cycle and habitat over the entire 25-year study. See text for definition of statistics.

	Phase of population cycle				*F*; df	*P*
	Trough	Increase	Peak	Decline		
M. ochrogaster						
Alfalfa	39.8 ± 0.2^{a}	40.9 ± 0.1^{b}	40.8 ± 0.2^{b}	38.8 ± 0.2^{c}	25.669; 3,4689	<0.001
Bluegrass	36.1 ± 0.4^{a}	38.9 ± 0.2^{b}	38.5 ± 0.3^{b}	37.1 ± 0.2^{a}	19.528; 3, 1600	<0.001
Tallgrass	36.6 ± 0.6^{a}	38.0 ± 0.5^{ab}	38.7 ± 0.5^{ab}	38.1 ± 0.6^{b}	3.889; 3,474	0.009
M. pennsylvanicus						
Alfalfa	41.3 ± 0.7^{a}	41.4 ± 0.5^{a}	42.9 ± 0.5^{a}	42.8 ± 0.7^{a}	2.339; 3,516	0.073
Bluegrass	40.7 ± 0.6^{a}	40.7 ± 0.4^{a}	40.3 ± 0.4^{a}	38.7 ± 0.6^{a}	2.345; 3,753	0.072

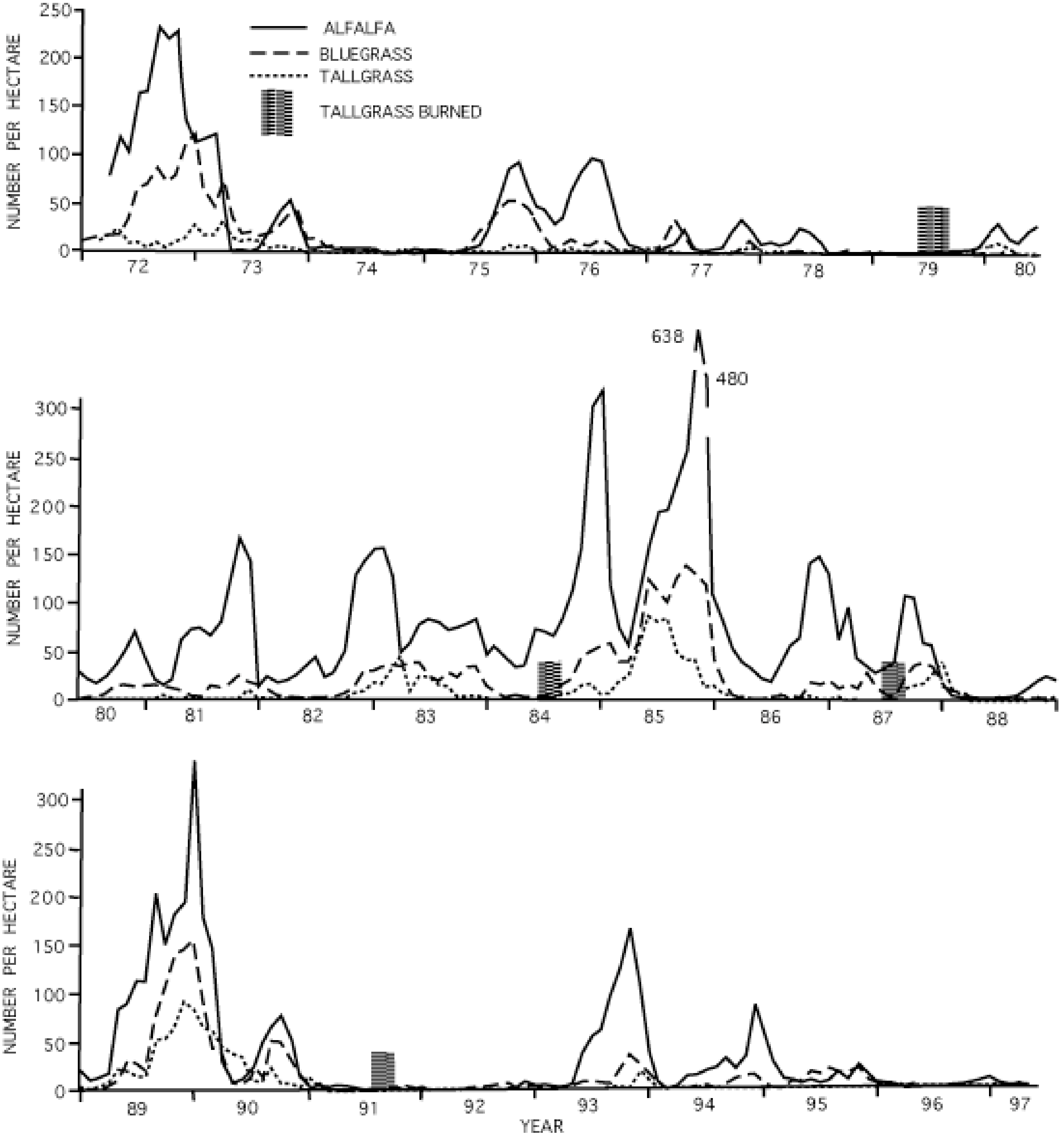
Table 7. Sex ratio (proportion of adults that were male ± SE) of *Microtus ochrogaster* and *M. pennsylvanicus* in relation to phase of the population cycle and habitat over the entire 25-year study. See text for definition of statistics.

	Phase of population cycle				*F*; df	*P*
	Trough	Increase	Peak	Decline		
M. ochrogaster						
Alfalfa	0.50 ± 0.02[a]	0.50 ± 0.01[a]	0.51 ± 0.01[a]	0.55 ± 0.08[a]	1.778; 3,282	0.151
Bluegrass	0.56 ± 0.03[a]	0.50 ± 0.01[a]	0.51 ± 0.02[a]	0.52 ± 0.04[a]	0.218; 3,232	0.884
Tallgrass	0.62 ± 0.03[a]	0.56 ± 0.03[a]	0.54 ± 0.02[a]	0.53 ± 0.03[a]	1.004; 3,144	0.393
M. pennsylvanicus						
Alfalfa	0.56 ± 0.03[a]	0.44 ± 0.03[a]	0.44 ± 0.03[a]	0.34 ± 0.04[a]	3.215; 3,130	0.025
Bluegrass	0.51 ± 0.03[a]	0.45 ± 0.02[a]	0.44 ± 0.02[a]	0.41 ± 0.03[a]	0.633; 3,204	0.594

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.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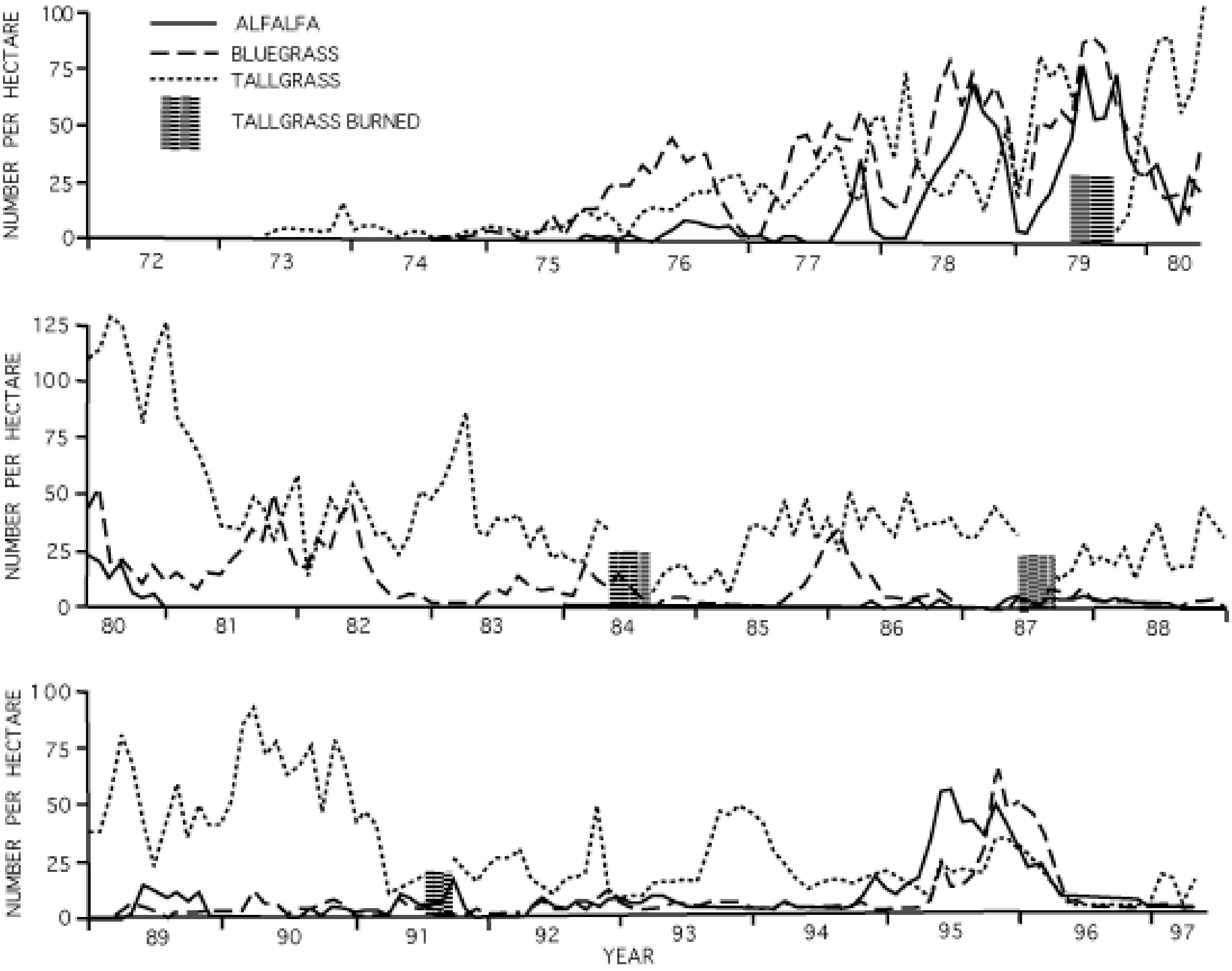
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Comments for reviewers:

This manuscript is one of six over-view papers that have resulted from the preliminary analyses of an intensive 25-year study of prairie and meadow voles here at the University of Illinois. As you might imagine we could not put all the results in a single paper. We broke down the basic results in what we felt were the most logical presentations. Unfortunately, by breaking up the presentation in this manner, the conclusions of each paper rely on the results/conclusions of the other papers. Accordingly, we have had to make reference to the results/conclusions in other papers when arriving at the conclusions for a given paper.

All six manuscripts have been submitted simultaneously with the hope (and I do understand the irrational implications of such a statement!!) that all can be accepted in time for proper referencing of all papers. For the drafts, we have referenced the other papers as "In Review", (which can easily be converted to "In Press", if have been accepted) so you can see what other evidence is used to support our conclusions. To facilitate your understanding of the conclusions from the other papers, I have included copies of the abstracts of the other five papers with the manuscript so you can evaluate our basic conclusions, if you so choose.

I realize this is not the conventional manner in which one submits manuscripts for evaluation. However, given the massive effort that went into the study, the magnitude of the data sets, the amount of time it took to enter, clean up and analyzed the data (and my age, 71+), I see no other way of moving the data in any sort of reasonable time frame. I hope this is not imposing too greatly on your review of the manuscript and that you understand the rationale for such an procedure.

Habitat-specific demography of sympatric vole populations

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

Abstract: We studied demographic variables affecting population densities and fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus* in alfalfa, bluegrass and tallgrass habitats for 25 years. Food availability was greatest for both species in alfalfa, intermediate in bluegrass and least in tallgrass. Vegetative cover was relatively sparse in alfalfa, especially in winter, and dense in bluegrass and tallgrass throughout the year. *M. ochrogaster* was most abundant in alfalfa, intermediate in bluegrass and least abundant in tallgrass. Population densities of *M. pennsylvanicus* were highest in tallgrass, intermediate in bluegrass and lowest in alfalfa. Population densities of *M. ochrogaster* were higher than those of *M. pennsylvanicus* in alfalfa, while the latter species was more abundant in tallgrass. Population densities of the two species were similar in bluegrass. Survival of *M. ochrogaster* was significantly greater in alfalfa than in bluegrass or tallgrass; survival of *M. pennsylvanicus* was higher in tallgrass than in alfalfa or bluegrass. Survival of *M. ochrogaster* was greater than that of *M. pennsylvanicus* in alfalfa, while that of *M. pennsylvanicus* was significantly greater in tallgrass. Differential survival among habitats and between species was influenced primarily by amount of vegetative cover; food availability was not a factor. There was no difference in survival of the two species in bluegrass where cover was dense. In alfalfa, survival of *M. ochrogaster* did not differ seasonally, while survival of *M. pennsylvanicus* tended to be lowest during the winter when cover was most sparse. Survival of *M. ochrogaster* was greater than that of *M. pennsylvanicus* during winter in alfalfa. We suggest that *M. pennsylvanicus* is more susceptible to predation from large mammalian and avian predators than is *M. ochrogaster*. Reproduction had little impact on temporal fluctuations in abundance of either species in all three habitats; differences in reproduction did not explain habitat-specific or inter-specific differences in population dynamics.

49 ms pages; 7 table; 3 figures

VOLE POPULATION FLUCTUATIONS:
FACTORS AFFECTING PEAK DENSITIES AND INTERVALS BETWEEN PEAKS

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

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.

31 ms page; 3 tales; 2 figures

Submitted: Journal of Mamamolgy

Vole population dynamics: factors affecting amplitudes of fluctuation

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

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. Only six of 39 winter peaks of *M. ochrogaster* were preceded by episodes of extreme weather that resulted in decreased survival. 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. Episodes of extreme weather were associated with stoppage of population growth of four *M. pennsylvanicus* cycles, three during winter and one during summer. Decreased survival was associated with only one such episode of weather extremes.

37 ms pages; 10 tables; 2 figures

Submitted: Oikos

HOME RANGE DYNAMICS OF SYMPATRIC VOLE POPULATIONS: INFLUENCE OF FOOD RESOURCES, POPULATION DENSITY, INTERSPECIFIC COMPETITION, AND MATING SYSTEM

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

We studied variation in home range size in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus* in alfalfa, bluegrass and tallgrass habitats over a 25-year period in east-central Illinois. The three habitats differed in food availability and vegetative cover. Home range indices of both species were complexly related to abundance of food resources. Home ranges of *M. ochrogaster* were smallest in the high food habitat (alfalfa), largest in the low food habitat (tallgrass) and intermediate in medium food habitat (bluegrass). *M. pennsylvanicus* home ranges were largest in the low food habitat, but did not differ between the high and intermediate food habitats. *M. ochrogaster* did not have smaller home ranges in supplementally fed medium and low food habitats; those of *M. pennsylvanicus* were smaller only in the low food habitat. Home ranges of *M. ochrogaster* were compressed only at population densities above 100/ha, irrespective of food levels; those of *M. pennsylvanicus* were smaller at high densities only in medium and low food habitats. Presence of the other species did not influence size of home ranges of either species. Within-habitat seasonal variation in home range indices indicated a confounding response to cover (prey risk) and food. Home ranges of all age classes of *M. pennsylvanicus* were larger than those of *M. ochrogaster* in all three habitats. There was no obvious relationship between home range sizes of adult males and females in relation to the mating system of each species. For both species in all three habitats, home ranges of adult males were larger than those of adult females.

35 ms pages; 4 tables

Submitted: Journal of Mammalogy

Dynamics of sympatric vole populations: influence of food resources and interspecific competition

Lowell L. Getz[*], Joyce E. Hofmann[⌖], Betty McGuire[**],
and Madan K. Oli[⌖⌖]

Summary

1. Abundance of food resources and interspecific competition can significantly influence the dynamics of arvicoline rodent populations.

2. We studied responses of *Microtus ochrogaster* and *M. pennsylvanicus* to supplemental food and interspecific competition in bluegrass (marginal food habitat) and tallgrass prairie (low food habitat). Removal experiments were conducted to study reciprocal interspecific interactions between the two species in bluegrass and the effects of *M. pennsylvanicus* on *M. ochrogaster* in tallgrass.

3. Mean population densities and patterns of fluctuation of *M. ochrogaster* did not differ between supplementally fed and control sites in either bluegrass or tallgrass habitats. However, amplitudes of fluctuation and proportion of reproductive females were higher in supplementally fed than in control bluegrass sites for this species. Mean population densities of *M. pennsylvanicus* were slightly higher in supplementally fed than in control tallgrass sites; the addition of food to bluegrass, however, did not result in higher population densities for this species.

4. Population densities of *M. ochrogaster* and M. *pennsylvanicus* in bluegrass were not suppressed by the presence of the other species. Although survival of *M. ochrogaster* was lower in the presence of *M. pennsylvanicus*, there was no negative effect on reproduction. Presence of *M. ochrogaster* did not adversely affect either survival or reproduction of *M. pennsylvanicus* in bluegrass. Although *M. pennsylvanicus* appeared to exert a strong suppressing effect on population densities of *M. ochrogaster* in tallgrass, neither survival nor reproduction of *M. ochrogaster* was lower when *M. pennsylvanicus* was present in this habitat. Similar results were observed from interspecific correlations between population densities, survival and reproduction of the two species during a 25-year demographic study in bluegrass and tallgrass.

5. We conclude that food resources and interspecific competition do not play a major role in driving the dynamics of M. *ochrogaster* and *M. pennsylvanicus* populations in our study sites.

28 ms pages; 3 tables; 9 figures

Submitted: Journal of Animal Ecology