Vole population dynamics: factors affecting peak densities and amplitudes of Microtus ochrogaster population fluctuations

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Abstract
We studied factors affecting peak density and amplitude of 39 population fluctuations of Microtus ochrogaster in alfalfa, bluegrass, and tallgrass habitats over a 25-year period. Thirty-two of the 39 fluctuations peaked in autumn or winter. Length of the increase period and initial population density appeared to have the greatest impact on variation in peak density and amplitude of fluctuation, but survival, proportion of females reproductive, and realized population growth rate also had significant effects. Cessation of growth of population fluctuations with peaks in autumn-winter resulted from a reduction in survival, enhanced by winter reduction in reproduction. Cessation of growth of populations with peaks during spring-summer resulted from reduction in survival; reproduction in these populations remained high from the increase through the peak and decline. We suggest that unpredictable density-dependent predation by generalist predators is the primary mortality factor stopping population growth, resulting in erratic peak densities and amplitudes of population fluctuation of M. ochrogaster.

Key words: Microtus ochrogaster, population fluctuation, prairie vole, predation, voles
Introduction

Two criteria have been proposed for population fluctuations of arvicoline (microtine) rodents to be classified as multi-annual: (1) amplitudes of fluctuation (difference between trough and peak densities) must be \( \geq 10 \)-fold and (2) intervals between population peaks must be \( \geq 2 \) yrs (Krebs & Myers 1974, Taitt & Krebs 1985, Krebs 1996). Some species appear to display high amplitude multi-annual fluctuations in population density (population cycles), while others fluctuate annually or erratically (Taitt & Krebs 1985, Getz et al. 1987; Lidicker 1988). An understanding of factors responsible for varying amplitudes of population fluctuation is necessary to characterize patterns of fluctuation of arvicoline populations.

The following variables have been proposed as being associated with increases in population density and resulting high amplitude population fluctuations of arvicoline rodents (Krebs & Myers 1974, Oli & Dobson 1999, 2001): increased litter size, increased proportion of pregnant females, earlier age at sexual maturity, increased proportion of females in the population, increased length of the reproductive period, increased survival, greater rate of population increase (summation of effects of reproductive and survival variables), and a longer period of time during which environmental conditions favor population growth.

We used data from a 25-yr study of populations of the prairie vole (Microtus ochrogaster) in east-central Illinois (Getz et al. 2001) to evaluate factors influencing peak densities and amplitudes of fluctuation, as well as cessation of population growth. Data were obtained from a total of 30 population fluctuations of M. ochrogaster in our main study sites; another nine fluctuations were recorded in
other sites monitored for shorter periods than the long-term study. Specifically, we tested whether the following factors were responsible for greater peak densities and higher amplitudes of fluctuation in some years rather than others: (1) earlier onset of population increase; (2) higher population density during the previous trough (i.e., higher beginning density of a population fluctuation); (3) greater survival during the increase; (4) greater proportion of reproductive females during the population increase; (5) higher rate of population increase; (6) longer reproductive period; (7) longer increase phase; and for stoppage of population growth: (1) lesser survival during the decline than during the increase, irrespective of season; and (2) smaller proportion of reproductive females during the decline than during the increase, irrespective of season.

Materials and methods

Study sites

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

We used two restored tallgrass prairie sites, one located in Trelease Prairie, the other in Phillips Tract (Getz et al. 2001). Both prairies were burned during the spring at 3-4-year intervals to retard invading shrubs and trees. All bluegrass study sites were within a former pasture located in Phillips Tract that had been released from grazing in spring 1971 (Getz et al. 2001). In addition to the long-
term sites, we trapped two other sites adjacent to long-term sites, each for 10 years. One of the sites was separated from the long-term site by a 0.5-m high aluminum fence, with several small portals, buried 0.5 m in the ground. Only 43 voles dispersed between the two sites. The other site had no barrier between it and the long-term site; we did not record movements of animals between these latter two sites. We trapped alternately two alfalfa sites in Phillips Tract that were separated by a 10-m closely mown strip of grass. We trapped at a site until invading forbs and grasses began to crowd out the *M. sativa*. The site under study was changed four times (Getz et al. 2001). One year before trapping was terminated in one site, the other was planted with *M. sativa* so that the plants would be fully developed when trapping commenced.

Trapping procedures

We established a grid system with 10-m intervals in all study sites, and placed one wooden multiple-capture live-trap at each station. Each month we pre-baited for two days and then trapped for three days; cracked corn was used for prebaiting and as bait in the traps. We set traps in the afternoon and checked them at approximately 0800 h and 1500 h for the following three days. At first capture, we toe-clipped all animals (*< 2 toes on each foot*) for individual identification. The field protocol was reviewed periodically by the University of Illinois Laboratory Animal Resource Committee throughout the study and approved, based on University and Federal guidelines, as well as those recommended by the American Society of Mammalogists, in effect at the time.

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

Data analysis

Population fluctuations

Population fluctuations used for our analyses were identified from Getz et al. (2001). The following peak densities defined population fluctuations of \textit{M. ochrogaster}: alfalfa, 75/ha; bluegrass, 25/ha; tallgrass, 20/ha. We excluded four fluctuations from some of the analyses because the increase phase was \( \leq 2 \) months or there was a \( > 5 \)-month fluctuating period of high density, with no distinct peak. There was partial synchrony of population fluctuations among the three habitats (Getz et al. 1987, 2001). However, population fluctuations were treated as independent observations because movement of individuals among sites does not appear to have caused synchrony of the fluctuations. Only 431 \textit{M. ochrogaster} that were marked in one site emigrated to another site during the 25 years of the study.

Peak densities and amplitudes of fluctuation

We used multiple linear regression analyses to examine the influence of survival, proportion of females reproductive, beginning population density, length of the increase phase, and realized population growth on peak densities and amplitudes of population fluctuations. First, we used stepwise variable selection procedure to select variables that had significant influence on peak densities or amplitudes of fluctuations. We then fitted the final regression models including only those variables identified as influential in the
stepwise regression analyses. Because of small numbers of population fluctuations in alfalfa and tallgrass, we could not fit regression models separately for each habitat. We also ran partial correlation analyses to test for correlations between population density and total population survival and proportion of females reproductively active throughout the entire 25-year period.

Cessation of growth

Because of marked demographic differences among populations of *M. ochrogaster* in the three habitats (Getz et al. 2001), and since sample sizes within habitats were sufficient for analyses, the roles of changing survival and reproduction on stoppage of population growth were run separately for each habitat. Density-independent seasonal impacts on survival and reproduction were examined by comparing monthly survival of adults and young and proportion of adult females reproductively active during September-February (the months within which autumn-winter populations typically occurred) for years of population fluctuations (when peaks occurred during autumn-winter) and for years when no population fluctuation occurred during autumn-winter. Effects of survival on population fluctuations peaking during spring-summer, were examined during April-September (months within which spring-summer population fluctuations typically occurred). Because of small monthly sample sizes, data to test seasonal effects on reproduction were combined as spring (March-May), summer (June-August), and autumn (September-November). Comparisons were made for years with and without population fluctuations.

Effects of changes in survival and reproduction on stoppage of population growth were analyzed by comparing differences in these two demographic variables for or during the three months prior to the peak
(P-3 to P-1), the peak month (Pk), and the three months following the peak (P+1 to P+3). Data for population fluctuations peaking in spring-summer and autumn-winter were analyzed separately.

For these analyses we estimated survival for adult and young voles separately to test for differential effects of survival of the two age classes. Survival rates were estimated as the proportion of animals that survived to the next month. Increased nestling survival has been identified as a major factor involved in initiation of population fluctuations of *M. ochrogaster* (Getz et al. 2000), but the role of changing nestling survival on the initiation or continuation of the decline phase has not been examined. An index of nestling survival was derived from the number of juveniles (< 20 g) present one month divided by the number of pregnant females present the previous month (Getz et al. 2000). We assumed that surviving young born to females pregnant in one trapping session would be out of the nest and trappable as juveniles during the following monthly trapping. Keller and Krebs (1970) observed that embryo counts of *M. ochrogaster* did not vary seasonally in southern Indiana, but were 25% lower at the peak than during the increase for multiparous females, although embryo counts of primiparous females did not differ between the peak and increase. We limited our estimates to months with at least five pregnant females. For these comparisons, we included the three months preceding the peak, the peak, and the first month of the decline. There were too few pregnant females during the second and third months of the decline for analysis. Population densities were too low during years with no population fluctuation to calculate estimates of nestling survival.

To estimate the proportion of reproductively active females for population fluctuations that peaked during the autumn and winter, we used the proportion of adult females that were pregnant during a given
month; pregnancy is the best indicator of reproductive activity.
Because few females were present in the population during spring and
summer of years without population fluctuations, we used the proportion
of females displaying any indication of reproductive activity (vulva
open, lactating, or pregnant) for analysis of differences in
reproduction associated with populations with peaks in spring-summer.

Statistical analyses

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), and thus we log-
transformed all variables. This allowed us to test for differences
using analysis of variance (ANOVA), independent-sample t-tests or
Pearson’s correlation analysis, where appropriate. Significant one-way
ANOVAs were followed by Tukey’s honestly significant difference (HSD)
post-hoc multiple comparisons. Sample sizes represent number of months
of data. When degrees of freedom (df) for t-tests are given in whole
numbers, variances were equal (Levene’s test for equality of
variances). When variances were not equal, df is given to one decimal
place. We used SPSS 10.0.7 for Macintosh (SPSS, Inc. 2001) for all
statistical analyses.

Results

Population fluctuations

Twenty-five M. ochrogaster population fluctuations in the main
study sites peaked during autumn-winter (October-February); three peaks
occurred in spring (one in bluegrass; two in tallgrass) and two in
summer (one in alfalfa; one in tallgrass). In the other study sites,
all six populations in bluegrass peaked during autumn or winter, while
one in tallgrass peaked in winter and two in summer. Thus, of 39 population fluctuations, 32 peaked from October to February. Five of the seven spring-summer peaks were in tallgrass and three of these peaked during the same month (June 1985). The average time from onset of the increase to peak density was $4.3 \pm 0.4$ months, with $8.3 \pm 0.6$ months for an entire fluctuation, from increase to subsequent trough.

There was no correlation between the time from establishment of a new alfalfa study site and peak densities of population fluctuations ($r = -0.275$, $n = 14$, $p = 0.34$). Likewise, length of time from release of bluegrass sites from grazing was not correlated with peak densities of population fluctuations ($r = -0.089$, $n = 11$, $p = 0.79$). Length of time following burning of tallgrass was not correlated with subsequent peak densities ($r = -0.531$, $n = 5$, $p = 0.36$).

Peak densities and amplitudes of fluctuation

Stepwise regression analysis indicated that five variables (beginning population density, length of the increase phase, survival, proportion of females reproductive, and realized population growth rate) significantly influenced both peak densities and amplitudes of fluctuation. Neither time of beginning of the increase nor length of the reproductive period significantly influenced either peak densities or amplitudes of fluctuation. Beginning population density and length of the increase appeared to have a greater effect on peak densities than did the other three variables. A multiple linear regression model with these five variables as predictors was significant and explained 83% of the variation in peak densities (Table 1) and 80% of the amplitudes of fluctuation (Table 2). Over the 25 years of the study, partial correlation analysis of survival and proportion of reproductive females indicated that population density was significantly correlated
with survival (alfalfa: \( r = 0.33, n = 228, p < 0.01 \); bluegrass: \( r = 0.490, n = 173, p < 0.01 \); and tallgrass: \( r = 0.635, n = 91, p < 0.01 \)). Proportion of females reproductively active was not significantly correlated with population density in alfalfa (\( r = 0.030, n = 228, p = 0.66 \)) or tallgrass (\( r = -0.121, n = 91, p = 0.25 \)) and only marginally so in bluegrass (\( r = 0.147, n = 173, p = 0.05 \)).

Cessation of population growth

Adult survival did not differ from September through February of years there was no population fluctuation during autumn-winter (Table 3). During years with population fluctuations that peaked in autumn-winter, adult survival of in alfalfa and bluegrass was high during September and October, began to decline in November, and dropped a total of 29% and 36%, respectively, by the end of February (Table 3). Survival in February was significantly less than during September and October for both habitats (Table 3). Survival of young did not differ during September-February irrespective of population fluctuations in either alfalfa or bluegrass (Table 4).

Adult survival during autumn-winter fluctuations in alfalfa was high during the three months prior to the peak (P-3 to P-1), began dropping at the peak (Pk), and was significantly lower the three months of the decline (P+1 to P+3) than during the increase (Table 5). A similar trend was observed in bluegrass, but the difference did not become significant until the second and third months of the decline (P+2 and P+3). Survival of young in alfalfa dropped markedly, following the peak, but was significantly lower than the increase only during P+1 (Table 5). Survival of young in bluegrass did not change from the increase through the decline (Table 5). When data were grouped as pre-peak (P-3 to P-1), peak (Pk), and post-peak (P+1 to P+3)
months for analysis, post-peak survival was significantly lower than
pre-peak and peak survival for adults in alfalfa ($F_{2,85} = 25.84, p <
0.01$) and bluegrass ($F_{2,102} = 13.33, p < 0.01$) and for young in alfalfa
($F_{2,82} = 8.32, p < 0.01$), but not in bluegrass ($F_{2,91} = 0.50, p = 0.61$).

August-December comparisons of nestling survival indices in
alfalfa and bluegrass, combined because of low sample sizes, indicated
nestling survival declined 23.4% from August to October, and 45.0% from
October to December ($1.07 \pm 0.25, 0.85 \pm 0.13, 0.82 \pm 0.16, 0.60 \pm
0.18$, and $0.45 \pm 0.16$, respectively); the differences approached
significance ($F_{4,109} = 2.32, p = 0.06$). Nestling survival indices were
higher during the three months preceding the peak ($1.07 \pm 0.20, 0.92 \pm
0.19$ and $0.79 \pm 0.14$, respectively) than at the peak ($0.32 \pm 0.07; F_{3,81}
= 3.914, p = 0.01$).

Survival of adults ($F_{5,70} = 0.493, p = 0.78$) and young ($F_{5,39} =
0.612, p = 0.69$) did not differ during April-September of years with no
spring-summer population fluctuation. Neither did adult survival
differ significantly during these months in years with spring-summer
population fluctuations ($F_{5,35} = 2.03, p = 0.09$; however, that of young
was significantly less in September than April-August ($F_{5,26} = 4.78, p <
0.01$).

Although survival of adults from P-3 through P+3 did not differ
significantly for population fluctuations that peaked in Spring-Summer
(Table 5), when the data were grouped as pre-peak (P-3 to P-1), peak
(Pk), and post-peak (P+1 to P+3), both adult and young survival was
significantly lower at and following the peak than prior to the peak
($F_{2,39} = 5.59, p < 0.01$ and $F_{2,30} = 9.08, p < 0.01$, adults and young,
respectively). Owing to small sample sizes for population fluctuations
peaking during spring-summer, we combined nestling survival indices
during the three pre-peak months and compared them to nestling survival
during the peak and first month of the decline, combined. Nestling survival indices were marginally significantly greater during the increase than the peak and decline (1.48 ± 0.40 and 0.63 ± 0.12, respectively; t = 2.124, df = 19, p = 0.05). Nestling survival during the first month of the decline was 57.4% lower than those prior to the peak.

Nestling survival indices for all fluctuations (spring-summer and autumn winter peaks), combined, were 0.85 ± .08 during three pre-peak months, 0.48 ± .08 at the peak, and 0.58 ± .21 during the first post-peak month (F_{2,91} = 4.050, p = 0.02). Post-peak nestling survival differed from that during the pre-peak (Tukey’s HSD test, < 0.05).

The proportion of females in the population that were pregnant declined sharply from November through February in alfalfa and bluegrass during years without population fluctuations as well as years when there were population fluctuations with autumn-winter peaks (Table 6). Population fluctuations that peaked in autumn-winter were characterized by a major decline in the proportion of adult females pregnant during the peak month and the three months following the peak (Table 7). When the data were combined as to pre-peak (P-3 to P-1), peak (Pk), and post-peak (P+1 to P+3) months, the proportion of females pregnant was less during the post-peak than during the pre-peak months in both alfalfa (F_{2,85} = 19.85, p < 0.01) and bluegrass (F_{2,97} = 33.77, p < 0.01).

The proportion of reproductively active females in the population remained high through autumn of years with spring-summer population fluctuations (0.74 ± .04, 0.88 ± .02, 0.85 ± .02, spring, summer, autumn, respectively; F_{2,192} = 5.640, p < 0.01; spring was significantly lower than summer and autumn, Tukey’s HSD test, < 0.05), as well as years when there was no population fluctuation (0.72 ± .05, 0.90 ± .04,
0.87 ± .04, spring, summer, autumn, respectively; \( F_{2,124} = 1.742, p = 0.179 \). The significance in differences in proportion females reproductive from P-3 to P+3 resulted primarily from low proportion reproductive in P-3 (Table 7). When data for populations that peaked in spring-summer were grouped as to the three months preceding the peak (P-3 to P-1), the peak (Pk), and the three months (P+1 to P+3) following the peak, there was no difference in the proportion of females pregnant \( (F_{2,37} = 1.01, p = 0.37) \).

Discussion

Batzli (1992) and Lin and Batzli (2001) concluded that factors responsible for variation in population growth in voles included variation in habitat quality (cover and food), predation pressure, and weather conditions. Our analyses suggest that temporal variation in habitat quality was not a factor affecting height of fluctuations within habitats. There was no correlation between the time a site was first established or manipulated (i.e., time for change in vegetation, and thus habitat, quality) and peak densities of subsequent population fluctuations.

In our study sites, population density at the beginning of a population increase and length of time during which the population was increasing appeared to be most important in determining peak densities and amplitudes of fluctuation. Higher survival and reproduction, and associated greater population growth rates also influenced peak densities and amplitudes. From these findings, we conclude that differential timing and magnitude of factors stopping population growth are the most important determinants of variation in the height of population fluctuations among years. Cessation of population growth and initiation of a decline result mainly from increased mortality and
decreased reproduction; emigration does not appear to be an important factor (Krebs & Myers 1974, Gaines & McClenaghan 1980, Verner & Getz 1985, Lidicker & Stenseth 1992, this study). Increased mortality and decreased reproduction may result from effects of density-independent factors (e.g., adverse weather conditions as during winter) or density-dependent factors (e.g., predation, quality of the animals; Christian 1971, 1980; Saucey 1984; Krebs 1996).

There was no indication of a seasonal change in survival associated with stoppage of population growth. Survival of adults and young did not differ from September through February (months within which autumn-winter population fluctuations typically occurred) of years with no autumn-winter population fluctuation. The proportion of females that were reproductively active typically was significantly lower during January and February than during September and October, irrespective of population fluctuations. Neither survival of adult and young during April-September nor proportion reproductive females during March-November (months within which spring-summer populations fluctuations typically occurred) differed during years when there was no population fluctuation.

Decreased survival, including nestling survival, was associated with the stoppage of population growth and the decline of population fluctuations that peaked in autumn-winter or spring-summer (with the exception of survival of young in bluegrass during autumn-winter peaks). A decline in proportion of reproductively active females occurred only in conjunction with the decline of population fluctuations that peaked in autumn-winter. Proportion reproductive females remained high through the peak and decline of spring-summer population fluctuations. Further, survival, but not proportion of females reproductively active, was significantly correlated with
population density in all three habitats over the 25 years of the study. The latter provides additional evidence for the greater importance of survival than reproduction on height of population fluctuations of *M. ochrogaster*.

From these results, we conclude that increased mortality is the most likely cause of cessation of population growth and decline in numbers of *M. ochrogaster*. Stoppage of growth of populations peaking in autumn-winter, however, may be enhanced by a density-independent winter reduction in reproduction.

Our observations regarding increased mortality as the primary reason for stoppage of population growth are in agreement with the results of predator-exclusion studies concerning the influence of predation on vole population fluctuations. In Fennoscandia, exclusion of mammalian and avian predators resulted in continued growth to exceptionally high densities and reversal of the decline in vole numbers until atypically high vole densities resulted in food shortage and subsequence population crash (Korpimäki & Norrdahl 1998, Kemola et al. 2000, Korpimäki et al. 2002). Presence of generalist predators led to annual (Korpimäki et al. 2002), or irregular fluctuations (Oksanen & Henttonen 1996), or population stability (Klemola et al. 2002). Predation by specialist predators appears to result in cyclic fluctuations (Hanski et al. 1991, Korpimäki & Norrdahl 1998).

Lin and Batzli (1995) concluded from experimental enclosure studies adjacent to our study sites that generalist predators could respond rapidly to locally high population densities of voles. They listed 21 species of predators present in our study areas: eight raptors, five large carnivores, three small carnivores, and five snakes. Of these, only one (least weasel, *Mustela nivalis*) is a resident specialist predator on voles, while the other specialist on
voles (rough-legged hawk, *Buteo lagopus*) is a winter migrant present during November-March. Thus, generalist predators were the likely source of most mortality influencing height of population fluctuations of *M. ochrogaster*.

The contribution of individual predator species to overall mortality of voles would vary from year to year because numbers of given predators undoubtedly are controlled by factors other than vole densities. Some years one species alone may be a major factor in stoppage of population growth, while other years several species acting in concert may stop population growth. Given the independent nature of population fluctuations of such diverse predator species as raptors, large and small mammals, and snakes and variation in mortality effects (numerical and functional responses; Pearson 1985) of each species, density-dependent predation effects may be greater at different times and vole densities in different years (Pearson 1985, Norrdahal & Korpimäki 2002, Gilg et al. 2003). Accordingly, population densities and amplitudes of fluctuation of voles would be expected to be erratic in nature, with no predictable peak densities or amplitudes of fluctuation. This is what we observed with respect to population fluctuations of *M. ochrogaster* over the 25 years of our study. We note, however, that the role of phase-related changes in maturation rate, and consequently, age at maturity (Ozgul et al. 2004) in influencing amplitudes of population fluctuations remains to be evaluated.

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References


SPSS, Inc. 2001. SPSS 10.0.7 for Macintosh. Chicago, Illinois


Table 1. Results of multiple linear regression analysis examining the effects of variables hypothesized to influence peak densities of *M. ochrogaster* population fluctuations. The regression model was significant, and explained a substantial proportion of variation in peak densities ($F_{5,31} = 30.04$, $p < 0.01$, $R^2 = 0.829$).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Parameter estimate</th>
<th>SE</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.79237</td>
<td>0.23968</td>
<td>3.31</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Survival</td>
<td>0.54865</td>
<td>0.23242</td>
<td>2.36</td>
<td>0.02</td>
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<td>Reproductive females</td>
<td>0.63349</td>
<td>0.27275</td>
<td>2.32</td>
<td>0.03</td>
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<td>Beginning density</td>
<td>0.44890</td>
<td>0.07910</td>
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<td>&lt;0.01</td>
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<tr>
<td>Length of increase</td>
<td>1.11045</td>
<td>0.18063</td>
<td>6.15</td>
<td>&lt;0.01</td>
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<tr>
<td>Growth rate</td>
<td>0.65408</td>
<td>0.27438</td>
<td>2.38</td>
<td>0.02</td>
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Table 2. Results of multiple linear regression analysis examining the effects of variables hypothesized to influence amplitudes of *M. ochrogaster* population fluctuations. The regression model was significant, and explained a substantial proportion of variation in peak densities ($F_{5,31} = 24.69$, $p < 0.01$, $R^2 = 0.799$).

<table>
<thead>
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<th>Variable</th>
<th>Parameter estimate</th>
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<th>P</th>
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<tr>
<td>Survival</td>
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<td>0.25721</td>
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<td>0.03</td>
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<tr>
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<td>Beginning density</td>
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<td>1.33457</td>
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<td>6.68</td>
<td>&lt;0.01</td>
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<tr>
<td>Growth rate</td>
<td>0.94687</td>
<td>0.30364</td>
<td>3.12</td>
<td>&lt;0.01</td>
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Table 3. Survival rates (mean ± SE) of adult *Microtus ochrogaster* during autumn (September–November) and winter (December–February). Survival rate was estimated as the proportion surviving to the next month. Values of F-statistic, degrees of freedom (number of months included in sample), and observed significance level (p) for one-way ANOVA comparing survival among the months are also given. Values within a column with different superscripts differ significantly at the 0.05 level (Tukey’s HSD test).

<table>
<thead>
<tr>
<th>Month</th>
<th>Alfalfa Fluctuation years</th>
<th>Alfalfa Nonfluctuation years</th>
<th>Bluegrass Fluctuation years</th>
<th>Bluegrass Nonfluctuation years</th>
<th>F; df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>September</td>
<td>0.638 ± 0.037&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.474 ± 0.107</td>
<td>0.542 ± 0.066&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.296 ± 0.048</td>
<td>4.23; 5.69</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>October</td>
<td>0.611 ± 0.055&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.535 ± 0.127</td>
<td>0.615 ± 0.042&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.380 ± 0.062</td>
<td>1.55; 5.51</td>
<td>0.19</td>
</tr>
<tr>
<td>November</td>
<td>0.525 ± 0.052&lt;sup&gt;abc&lt;/sup&gt;</td>
<td>0.575 ± 0.091</td>
<td>0.457 ± 0.048&lt;sup&gt;abc&lt;/sup&gt;</td>
<td>0.546 ± 0.062</td>
<td>5.01; 5.84</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>December</td>
<td>0.431 ± 0.078&lt;sup&gt;abc&lt;/sup&gt;</td>
<td>0.287 ± 0.107</td>
<td>0.380 ± 0.062&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>0.380 ± 0.048</td>
<td>1.67; 6.11</td>
<td>0.14</td>
</tr>
<tr>
<td>January</td>
<td>0.382 ± 0.075&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>0.358 ± 0.120</td>
<td>0.386 ± 0.056&lt;sup&gt;abc&lt;/sup&gt;</td>
<td>0.293 ± 0.062</td>
<td></td>
<td></td>
</tr>
<tr>
<td>February</td>
<td>0.347 ± 0.052&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.250 ± 0.078</td>
<td>0.257 ± 0.072&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.225 ± 0.062</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4. Survival rates (mean ± SE) of young *Microtus ochrogaster* during autumn (September-November) and winter (December-February). See Table 3 for statistics.

<table>
<thead>
<tr>
<th>Month</th>
<th>Alfalfa Fluctuation years</th>
<th>Alfalfa Nonfluctuation years</th>
<th>Bluegrass Fluctuation years</th>
<th>Bluegrass Nonfluctuation years</th>
</tr>
</thead>
<tbody>
<tr>
<td>September</td>
<td>0.478 ± 0.078</td>
<td>0.160 ± 0.096</td>
<td>0.310 ± 0.091(^{ab})</td>
<td>0.349 ± 0.141</td>
</tr>
<tr>
<td>October</td>
<td>0.527 ± 0.071</td>
<td>0.254 ± 0.062</td>
<td>0.371 ± 0.062(^{ab})</td>
<td>0.364 ± 0.136</td>
</tr>
<tr>
<td>November</td>
<td>0.484 ± 0.060</td>
<td>0.325 ± 0.064</td>
<td>0.460 ± 0.038(^{a})</td>
<td>0.351 ± 0.092</td>
</tr>
<tr>
<td>December</td>
<td>0.321 ± 0.059</td>
<td>0.306 ± 0.137</td>
<td>0.397 ± 0.063(^{ab})</td>
<td>0.302 ± 0.078</td>
</tr>
<tr>
<td>January</td>
<td>0.304 ± 0.052</td>
<td>0.434 ± 0.156</td>
<td>0.386 ± 0.056(^{ab})</td>
<td>0.338 ± 0.085</td>
</tr>
<tr>
<td>February</td>
<td>0.372 ± 0.084</td>
<td>0.333 ± 0.118</td>
<td>0.186 ± 0.056(^{b})</td>
<td>0.228 ± 0.083</td>
</tr>
<tr>
<td>F; df</td>
<td>1.83; 5,67</td>
<td>0.50; 5,32</td>
<td>2.23; 5,79</td>
<td>0.16; 5,78</td>
</tr>
<tr>
<td>p</td>
<td>0.12</td>
<td>0.78</td>
<td>0.06</td>
<td>0.98</td>
</tr>
</tbody>
</table>
Table 5. Survival (mean ± SE) of *Microtus ochrogaster* during the three months prior to the peak (P-3 to P-1), peak, and three months following the peak (P+1 to P+3) for cycles that peaked during autumn–winter and spring-summer. See Table 3 for statistics.

<table>
<thead>
<tr>
<th></th>
<th>Alfalfa</th>
<th></th>
<th>Bluegrass</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult survival</td>
<td>Young survival</td>
<td>Adult survival</td>
<td>Young survival</td>
<td></td>
</tr>
<tr>
<td>Peak -3</td>
<td>0.673 ± 0.043&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.485 ± 0.064&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.571 ± 0.069&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.410 ± 0.124</td>
</tr>
<tr>
<td>Peak -2</td>
<td>0.682 ± 0.033&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.562 ± 0.075&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.589 ± 0.069&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.324 ± 0.078</td>
</tr>
<tr>
<td>Peak -1</td>
<td>0.661 ± 0.035&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.550 ± 0.064&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.605 ± 0.044&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.421 ± 0.057</td>
</tr>
<tr>
<td>Peak</td>
<td>0.495 ± 0.037&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.400 ± 0.031&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.411 ± 0.045&lt;sup&gt;abc&lt;/sup&gt;</td>
<td>0.406 ± 0.045</td>
</tr>
<tr>
<td>Peak +1</td>
<td>0.301 ± 0.048&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.251 ± 0.033&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.378 ± 0.046&lt;sup&gt;abc&lt;/sup&gt;</td>
<td>0.343 ± 0.048</td>
</tr>
<tr>
<td>Peak +2</td>
<td>0.301 ± 0.060&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.356 ± 0.093&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.332 ± 0.055&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>0.462 ± 0.072</td>
</tr>
<tr>
<td>Peak +3</td>
<td>0.504 ± 0.074&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.373 ± 0.085&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.308 ± 0.078&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.192 ± 0.063</td>
</tr>
<tr>
<td>F; df</td>
<td>11.35; 6,81</td>
<td>3.12; 6,78</td>
<td>4.59; 6,98</td>
<td>1.67; 6,87</td>
</tr>
<tr>
<td>p</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>0.14</td>
</tr>
</tbody>
</table>
Table 6. Proportion of adult female *Microtus ochrogaster* that were pregnant during September-February of years with and without population fluctuations. See Table 3 for statistics.

<table>
<thead>
<tr>
<th>Month</th>
<th>Alfalfa Fluctuation years</th>
<th>Alfalfa Nonfluctuation years</th>
<th>Bluegrass Fluctuation years</th>
<th>Bluegrass Nonfluctuation years</th>
</tr>
</thead>
<tbody>
<tr>
<td>September</td>
<td>0.551 ± 0.026&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.475 ± 0.138&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.445 ± 0.061&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.179 ± 0.065&lt;sup&gt;bc&lt;/sup&gt;</td>
</tr>
<tr>
<td>October</td>
<td>0.490 ± 0.039&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.620 ± 0.105&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.430 ± 0.034&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.590 ± 0.096&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>November</td>
<td>0.269 ± 0.035&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.478 ± 0.100&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.273 ± 0.044&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.388 ± 0.082&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td>December</td>
<td>0.154 ± 0.039&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>0.205 ± 0.052&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.095 ± 0.035&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.305 ± 0.090&lt;sup&gt;abc&lt;/sup&gt;</td>
</tr>
<tr>
<td>January</td>
<td>0.078 ± 0.027&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.184 ± 0.085&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.076 ± 0.037&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.137 ± 0.055&lt;sup&gt;bc&lt;/sup&gt;</td>
</tr>
<tr>
<td>February</td>
<td>0.096 ± 0.045&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.138 ± 0.087&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.015 ± 0.009&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.014 ± 0.014&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>F; df</td>
<td>28.70; 5,69</td>
<td>3.87; 5,44</td>
<td>24.58; 5,79</td>
<td>6.10; 5,82</td>
</tr>
<tr>
<td>p</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>
Table 7. Proportion of adult female *Microtus ochrogaster*
pregnant the three months prior to the peak (P-3 to P-1),
peak, and three months following the peak (P+1 to P+3) during
population fluctuations that peaked during autumn-winter and
spring-summer. See Table 3 for statistics.

<table>
<thead>
<tr>
<th>Month</th>
<th>Winter-autumn peaks</th>
<th>Spring-summer peaks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Alfalfa</td>
<td>Bluegrass</td>
</tr>
<tr>
<td>Peak –3</td>
<td>0.448 ± 0.046&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.451 ± 0.061&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Peak –2</td>
<td>0.426 ± 0.032&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.394 ± 0.056&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td>Peak –1</td>
<td>0.398 ± 0.055&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.365 ± 0.043&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td>Peak</td>
<td>0.245 ± 0.053&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.235 ± 0.050&lt;sup&gt;bc&lt;/sup&gt;</td>
</tr>
<tr>
<td>Peak +1</td>
<td>0.147 ± 0.052&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.125 ± 0.040&lt;sup&gt;cd&lt;/sup&gt;</td>
</tr>
<tr>
<td>Peak +2</td>
<td>0.122 ± 0.055&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.036 ± 0.019&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>Peak +3</td>
<td>0.222 ± 0.074&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>0.113 ± 0.052&lt;sup&gt;cd&lt;/sup&gt;</td>
</tr>
<tr>
<td>F; df</td>
<td>6.84; 6,81</td>
<td>11.82; 6,91</td>
</tr>
<tr>
<td>p</td>
<td>&lt; 0.01</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>