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Vole population dynamics: factors affecting peak densities and amplitudes of annual population fluctuations of *Microtus pennsylvanicus*

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We studied factors affecting peak densities and amplitudes of fluctuation during 20 annual population fluctuations of *Microtus pennsylvanicus* Ord, 1815 in alfalfa and bluegrass habitats over a 25-year period. Survival was correlated with population density over the 25 years and was the most consistent variable associated with stoppage of population growth. Although not correlated with population density over the 25 years, a decline in the proportion of reproductively active adult females contributed to cessation of growth of population fluctuations that peaked in late autumn-winter, and to cessation of growth of eight of eleven population fluctuations that peaked during summer-early autumn. We conclude variation in survival to be the primary factor affecting peak densities and amplitudes of population fluctuation of *M. pennsylvanicus*.

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Introduction

Populations of many arvicoline rodents have been observed to undergo large fluctuations in numbers. Some population fluctuations are short-term, completing a fluctuation within a few months (Krebs and Myers 1974, Taitt and Krebs 1985), whereas others may take 2–3 years to run their course (Oksanen and Henttonen 1996). Intervals between population fluctuations may be annual, erratic, or occur periodically at 2-5 year intervals, in which case they are referred to as "population cycles" (Krebs *et al.* 1969, Krebs and Myers 1974, Taitt and Krebs 1985, Krebs 1996, Bjørnstad *et al.* 1998, Klemola *et al.* 2002, Lambin *et al.* 2006). Population fluctuations of arvicolines vary greatly in absolute peak densities (highest density achieved during a fluctuation) and ampli-

tudes of fluctuation (difference between density at the beginning of a fluctuation and the peak density of the fluctuation) across years. Fluctuations attributed to cyclic phenomena typically achieve peak densities in excess of 500/ha (Korpimäki *et al.* 2004). Such high densities often are found in relatively simple ecosystems or where specialist predator-prey systems are involved (Hudson and Bjørnstad 2003). In other situations, lower amplitude population fluctuations may display distinct episodes of fluctuation, even if not population cycles *per se* (Taitt and Krebs 1985, Getz *et al*. 2001). High mortality from predation or low habitat quality may depress amplitudes of fluctuation (Meserve 1971, Oksanen *et al.* 1999).

Survival and reproduction are assumed to be the important demographic variables responsible for temporal and spatial differences in population fluctuations of arvicoline rodents. Variables proposed as being associated with differences in peak densities and amplitudes of fluctuation include: litter size, proportion of females pregnant, age at sexual maturity, proportion of females in the population, length of the reproductive period, survival rate, rate of realized population growth (summation of effects of reproductive and survival variables), and the length of time environmental conditions favor population growth (Krebs and Myers 1974, Gaines and McClenaghan 1980, Dueser *et al.* 1981, Verner and Getz 1985, Batzli 1992, 1996, Oli and Dobson 1999, 2001, Lin and Batzli 2001, Getz *et al.* 2005a, 2005b, Hörnfeldt *et al*. 2005).

During the course of a 25-year study of demography of the meadow vole, *Microtus pennsylvanicus* Ord, 1815, (Getz *et al.* 2001) we obtained data relevant to the evaluation of factors influencing peak densities and amplitudes of fluctuation, as well as cessation of population growth. We here present results of our analyses of data for 20 population fluctuations of *M. pennsylvanicus*. Specifically, we tested the hypotheses that 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 (ie, higher population density when the increase phase began), (3) greater survival during the increase phase, (4) greater proportion of reproductively active adult females during the increase phase, (5) higher rate of population increase, (6) longer reproductive period (number of months the proportion of reproductively active females > 0.50), (7) longer increase phase; and for stoppage of population growth: (1) lesser survival during the decline phase than during the increase phase or the first month after the peak than at the peak and (2) smaller proportion of reproductively actively adult females during the decline phase than during the increase phase or the first month after the peak than at the peak.

Material and methods

Study sites

The study sites were located in the University of Illinois Biological Research Area ("Phillips Tract") 6 km NE of Urbana, Illinois (40°15'N, 88°28'W). We monitored populations of *M. pennsylvanicus* from May 1972 – May 1997 in 0.8–2.0 ha bluegrass *Poa pratensis* sites and in 1.0–1.4 ha alfalfa *Medicago sativa* sites. Specific bluegrass sites trapped for the basic long-term demography study (sites 6, 7, 11; Table 1) depended upon requirements for associated manipulative studies (Getz *et al.* 1987, 2005). In addition to the long-term bluegrass sites, we trapped concurrently 2 other bluegrass sites as part of manipulative studies, 1 for 7 years (site 8; Table 1), the other for 10 years (site 10; Table 1). All bluegrass sites had been released from grazing in spring 1971. We trapped alternately 2 alfalfa sites in the 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*. 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.

The study sites were contiguous within a 6 ha area surrounded by a 4 m wide macadam county road, cultivated fields, a 24 ha mature deciduous forest, and a 25 ha area that underwent succession from an agricultural field to a young deciduous forest during the study. Most sites either had boundaries of unsuitable vole habitat, or the adjacent site was also trapped, to account for individuals whose home ranges extended into an adjacent site (Getz *et al.* 2001). Further details of the study sites are described in Getz *et al.* (1979, 1987, 2001).

Trapping procedures

We established a grid system with 10-m intervals in all study sites, and placed one locally made wooden multi-

Table 1. Study sites from which *Microtus pennsylvanicus* data were used in the current study: area, dates trapped, timing of the peak population density (month of highest density) and peak density (in parentheses) for each fluctuation. See Getz *et al*. (2001) for map of the study area showing location of study sites.

Habitat/"site"		Area (ha)	Dates trapped	Years/months (*n*/ha) of peak densities
Alfalfa	2	1.0	July 1977 – September 1983	77/11 (36), 78/9 (70), 79/7 (79), 80/5 (29)
	3	1.0	October 1983 – December 1989	None
	4	1.0	January 1990 – June 1993	None
	5	1.0	July 1993 – May 1997	95/7 (52)
Bluegrass	6	2.0	January 1972 – June 1977	76/6 (48)
	7	0.9	July 1977 – January 1987	77/8 (54), 78/7 (81), 79/8 (91), 80/7 (52), 81/11 (50), 82/6 (35), 86/2 (35)
	11	1.0	July 1987 – May 1997	95/11 (62)
	8	0.5	May 1977 – November 1983	77/12 (34), 78/8 (80), 79/9 (110)
	10	1.0	May 1977 – May 1987	77/12 (31), 79/6 (69), 80/1 (69)

ple-capture live-trap (Burt 1940) at each station. Each month we pre-baited traps for 2 days and then trapped for 3 days; cracked corn was used for pre-baiting and as bait in the traps. We set traps in the afternoon and checked them at approximately 08:00 h and 15:00 h for the following 3 days. At first capture, we toe clipped all animals ($\leq$ 2 toes on each foot) for individual identification. All procedures were approved by the University of Illinois Laboratory Animal Care Committee and meet the guidelines recommended by the American Society of Mammalogists (Animal Care and Use Committee 1998).

At each capture we recorded grid station, individual identification, sex, reproductive condition (males: testes abdominal or scrotal; females: vagina open or closed, pregnant as determined by palpation, or lactation), and body mass to the nearest 1 g. We considered animals that weighed $\leq$ 29 g as young and those weighing $\geq$ 30 g as adult (Hasler 1975).

Data analysis

Population fluctuations

Voles were either absent or present in small numbers ($<$ 10/ha) for prolonged periods during our study; this precluded use of capture-mark-recapture (CMR) analyses (Boonstra 1985, Pollock *et al.* 1990, Lebreton *et al.* 1992) for estimating abundance or demographic parameters. Survival during periods of low density is essential for testing the proposed hypotheses. In addition, CMR parameters were inestimable in Program MARK (White and Burnham 1999), even when using the relatively simple Cormak-Jolly-Seber model. Further, our data sets exceeded the input capacity of MARK. Thus, we used estimates of abundance reported by Getz *et al.* (2001), who employed the minimum number known to be alive (MNA) model (Krebs 1999) to estimate population densities and survival. Trappability, ie, the proportion of individuals known to be present on the study site (captured that month, or the month[s] before and month[s] after) that were captured a given month was estimated to be approximately 90%, in part because of use of multiple-capture live traps.

We combined data from synchronous fluctuations for some of our analyses, as described below. For seasonal analyses we allocated all observations to spring (March–May), summer (June–August), autumn (September–November), or winter (December–February). For some analyses, we further subdivided autumn into early (September–October) and late (November) autumn.

We estimated survival as the proportion of animals (total population, adults, and young) that survived from one month to the next. Although mortality, the complement of survival, as here defined, included both *in situ* death and emigration, death is presumed to be the most prevalent cause of disappearance (Verner and Getz 1985). Because females more accurately determined when reproduction starts or ends, we used the proportion of the adult females that were reproductively active as an index of reproductive activity of the population.

Peak densities and amplitudes of fluctuation

We used multiple linear regression analyses to examine the influence of total monthly survival, proportion of the adult females that were reproductively active each month, length (in months) of the reproductive period (proportion of reproductively active females greater than 0.50), population density at the beginning of the increase phase, length (in months) of the increase phase, and realized population growth (total increase in numbers/ha divided by the number of months of the increase) on peak densities and amplitudes of population fluctuations. Because of small numbers of population fluctuations in each habitat, we pooled data from all fluctuations in both habitats for regression analyses.

We also ran partial correlation analyses to test for correlations between population density and overall monthly total population survival and proportion reproductively active females in each habitat throughout the entire 25-year period and for only the periods of population fluctuations. Although correlations do not establish causes and effects, these analyses allowed us to estimate which variable was most closely associated with changes in population density. Because the mean persistence time of individuals on the

study site was approximately two months (Getz *et al*. 1979), we used data from every second month to minimize temporal autocorrelation of the data.

Cessation of growth

We analyzed effects of changes in survival (adults and young voles, considered separately) and the proportion of reproductively active females on cessation of population growth by comparing differences in these 2 variables during the 3 months before the peak (Pk -3 to Pk -1), the peak month (Pk), and the 3 months after the peak (Pk +1 to Pk +3). We analyzed separately the data for population fluctuations peaking in spring-early autumn and late autumn-winter. For this specific analysis, we used the proportion of adult females that were pregnant during a given month; pregnancy is the best indicator of reproductive activity. For statistical analysis of pre-peak survival and proportion of females pregnant, we used data from months Pk -3 and Pk- 1 as pre-peak, and Pk +1 and Pk +3 as post-peak periods. This increased independence of the data since there was a 2-month interval between the months used in each period and the pre- and post-peak periods. When there were synchronous population fluctuations among the study sites, we averaged the data to obtain one value for each month of each fluctuation.

Frequently, the major decline in survival and proportion of reproductively active females occurred the month following the peak. We therefore analyzed each fluctuation individually to compare total survival and the proportion of reproductively active females the month of the peak with values for the month after the peak. These analyses provided another means of estimating which of these 2 variables was most closely associated with stoppage of growth of each fluctuation.

To examine the potential negative feedback of population density on survival and reproduction associated with stoppage of population growth, we tested the correlation between total survival and the proportion of reproductively active females with population density during a complete fluctuation, with a lags of 0–3 months. All fluctuations were grouped for these analyses.

All original capture data and explanatory files from the 25-year study are available to anyone wishing to make use of them at web pages: http://www.life.uiuc.edu/getz/ and http://ideals.uiuc.edu/handle/2142/161.

Statistical analyses

We log-transformed all variables before analyses (Zar 1999); after log-transformation, all variables were either normally distributed or approached normality. Besides multiple-linear regression analyses, we used one-way ANOVA, independent-sample *t*-test, or Pearson's correlation analysis, where appropriate. Degrees of freedom (df) for *t*-tests are given in whole numbers; all variances were equal (Levene's test for equality of variances). We used SAS (1999) and SPSS 10.0.7 for Macintosh (SPSS, Inc. 2001) for all statistical analyses.

Results

Population fluctuations

We defined individual population fluctuations as those with peak densities exceeding 25 voles/ha. There were 14 population fluctuations of *M. pennsylvanicus* in the main study sites (Fig. 1, Table 1); another 6 fluctuations were observed in the 2 additional bluegrass sites (Table 1). The fluctuations stood out as conspicuous events: alfalfa, mean peak density, 52 voles/ha, (range 29–79), was 7.6 times greater than the mean high density for years without a fluctuation, 6.8 ± 0.4 voles/ha; bluegrass, mean peak density, 56 voles/ha (range, 31-110), was 8.5 times the mean high density of non-fluctuation years, 6.6 ± 0.5 voles/ha).

All fluctuations, but one, were < 1 year in duration. The mean (± SE) time from onset of the increase to peak density was 3.8 ± 0.5 months; the mean duration of a complete fluctuation, from beginning of the increase to the end of the decline, was 8.6 ± 0.7 months. Thus, we were able to categorize calendar years during which a population fluctuation did or did not occur. Population fluctuations occurred at irregular intervals in the two habitats; there were only 5 synchronous fluctuations among the alfalfa and bluegrass sites (Getz *et al*. 2001). Movement of animals among sites did not appear to be involved in synchrony of population fluctuations. Only 601 *M. pennsylvanicus* that were marked in 1 site emigrated to another site during the 25 years of the study. Most such dispersal occurred at high densities, rather than prior to beginning of population fluctuations (Getz *et al*. 2005a).

Peak densities of population fluctuations of *M. pennsylvanicus* were not correlated with the time from establishment of a new alfalfa study site ($r = 0.39$, $n = 5$, $p = 0.52$). Neither was the peak density of population fluctuations correlated with length of time from release of the bluegrass sites from grazing ($r = -0.18$, $n = 15$, $p = 0.68$). Population fluctuations of *M. pennsylvanicus* were not uniformly or predictably seasonal. Ten increases began in spring, three in summer, six in autumn, and one in winter. One fluctuation peaked in spring, 12 in sum-

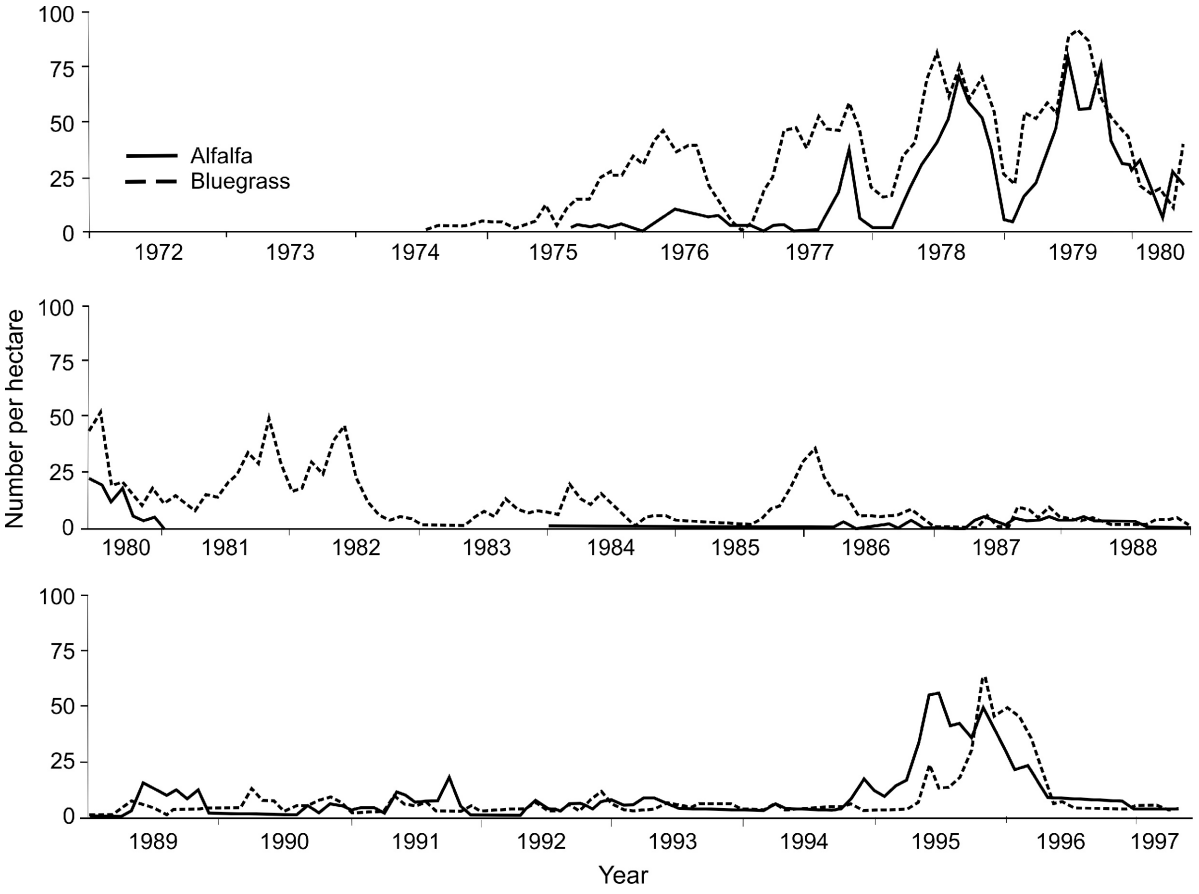

Fig. 1. Population densities of *Microtus pennsylvanicus* in alfalfa and bluegrass habitats in east-central Illinois. Populations were monitored at monthly intervals.

mer-early autumn, and 7 in late autumn-winter (Table 1); 9 declines occurred during summer-early autumn and 11 during late autumn-winter (Getz *et al.* 2001).

Population fluctuations occurred erratically across years. In alfalfa there were 4 annual fluctuations, 1977–1980, and then none until 1995. In the main bluegrass study sites, there were 7 annual fluctuations from 1976–1982, another fluctuation in 1986, and the last in 1995 (Fig. 1, Table 1). There were 3 annual fluctuations (1977–1979, but none through 1983) in 1 of the additional bluegrass sites; in the other, fluctuations occurred in 1977, 1979, and 1980, but no more through 1986.

Peak densities and amplitudes of fluctuation

Regression analysis indicated none of the variables was a significant predictor of peak density or amplitude of fluctuation. A multiple linear regression model including all variables was insignificant and explained only 45% of the variation in peak densities (Table 2) and 25% of the variation in amplitudes of fluctuations (Table 3). Although there was no correlation between length of the increase and either peak density or amplitude of fluctuation, the later in the year an increase phase started, the lower were the peak densities ($r = -0.56$, $n = 19$, $p = 0.01$) and amplitudes of the fluctuation ($r = -0.57$, $n = 19$, $p = 0.01$).

Over the entire 25 years of the study, population density was significantly correlated with to-

Table 2. Results of multiple linear regression analysis examining the effects of variables hypothesized to influence peak densities of *M. pennsylvanicus* population fluctuations. The regression model was insignificant and explained a small proportion of variation in peak densities ($F_{6,12} = 1.66$, $p = 0.21$, $R^2 = 0.454$).

Variable	Parameter estimate	SE	*t*	*p*
Intercept	3.64483	0.54266	6.72	< 0.01
Survival	0.58300	0.03683	1.58	0.14
Reproductive females	–0.17605	0.29107	–0.60	0.56
Beginning density	0.16254	0.10189	1.60	0.14
Length of increase	–0.03834	0.24746	–0.15	0.88
Length of reproduction	0.33032	0.23373	1.41	0.18
Population growth rate	–0.13201	0.13615	–0.97	0.35

Table 3. Results of multiple linear regression analysis examining the effects of variables hypothesized to influence amplitudes of *M. pennsylvanicus* population fluctuations. The regression model was insignificant and explained a small proportion of variation in peak densities ($F_{6,12} = 0.67$, $p = 0.68$, $R^2 = 0.250$).

Variable	Parameter estimate	SE	*t*	*p*
Intercept	3.67217	0.69156	5.31	< 0.01
Survival	0.60551	0.46936	1.29	0.22
Reproductive females	–0.06596	0.37093	–0.18	0.86
Beginning density	–0.00055	0.12985	–0.00	0.99
Length of increase	0.07323	0.31536	0.23	0.82
Length of reproduction	0.29713	0.29786	1.00	0.34
Population growth rate	–0.09880	0.17351	–0.57	0.58

tal survival in both habitats (alfalfa: $r = 0.48$, $n = 38$, $p < 0.01$; bluegrass: $r = 0.29$, $n = 69$, $p = 0.02$). Population density was not significantly correlated with the proportion of reproductively active females in alfalfa ($r = 0.08$, $n = 38$, $p = 0.64$) and only marginally correlated in bluegrass ($r = 0.23$, $n = 69$, $p = 0.05$). Total survival (alfalfa and bluegrass, combined) was correlated with population density during a fluctuation (no lag: $r = 0.32$, $n = 155$, $p < 0.01$; l-mon lag: $r = 0.50$, $n = 146$, $p < 0.01$; 2-mon lag: $r = 0.61$, $n = 136$, $p < 0.01$; 3-mon lag: $r = 0.38$, $n = 125$, $p < 0.01$). The proportion reproductively active females (alfalfa and bluegrass, combined) was not correlated with population density during a fluctuation (no lag: $r = 0.14$, $n = 155$, $p = 0.08$; l-mon lag: $r = 0.03$, $n = 146$, $p = 0.68$; 2-mon lag: $r = -0.02$, $n = 136$, $p = 0.86$; 3-mon lag: $r = 0.12$, $n = 125$, $p = 0.17$).

Cessation of population growth

Total survival during winter did not differ from other seasons, irrespective of whether a population fluctuation occurred ($F = 0.090$, df = 3,73, $p = 0.96$) or did not occur ($F = 0.242$, df = 3,95, $p = 0.86$; Fig. 2). The proportion of reproductively active females was significantly lower during winter than during other seasons for years with ($F = 9.521$, df = 3,67, $p < 0.01$) and marginally so for years without a fluctuation ($F = 2.972$, df = 3,78, $p = 0.04$) population fluctuations (Fig. 3). The proportion of reproductively active adult females did not differ during summer ($t = 0.53$, df = 41, $p = 0.60$) or autumn ($t = 1.30$, df = 46, $p = 0.20$) of years with and without population fluctuations (Fig. 3).

When data for population fluctuations peaking in spring-early autumn were grouped as

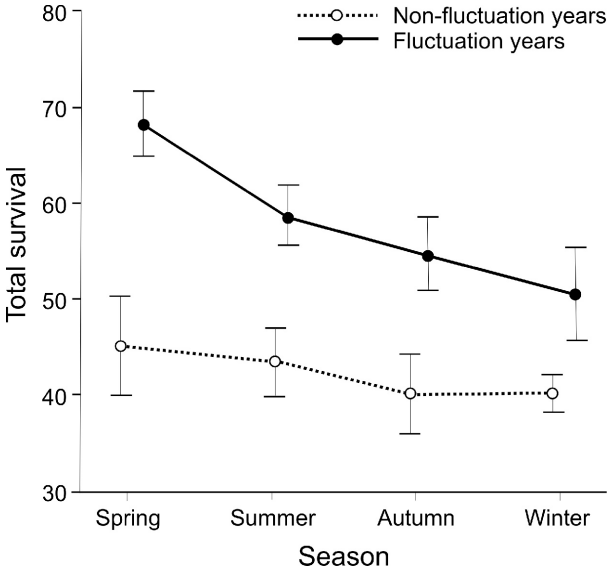

Fig. 2. Seasonal pattern in the mean (± SE) seasonal monthly survival (proportion of the total population that survived to the next month) of *Microtus pennsylvanicus* in combined alfalfa and bluegrass habitats during years with population fluctuations (n = 20) and years with no fluctuation (n = 47).

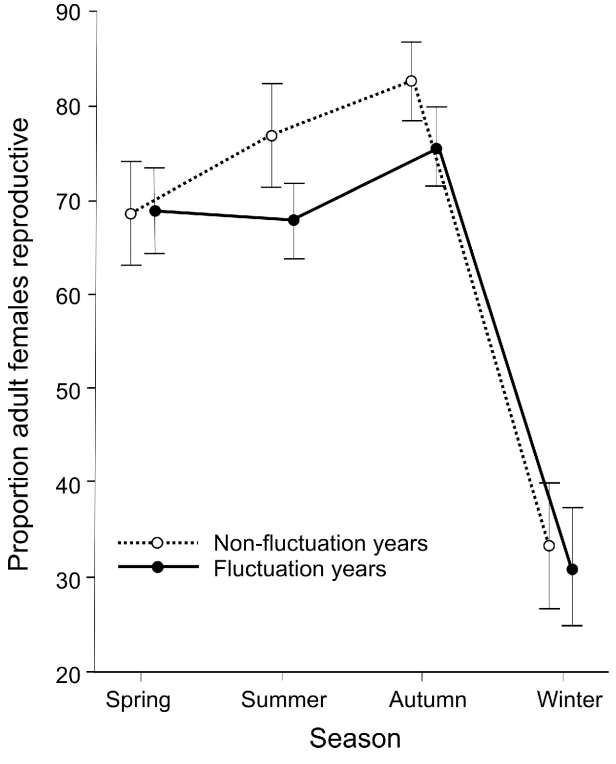

Fig. 3. Seasonal pattern in the mean (± SE) seasonal proportion of adult female *Microtus pennsylvanicus* that were reproductively active in combined alfalfa and bluegrass habitats during years with population fluctuations (n = 20) and years with no fluctuation (n = 47).

pre-peak (Pk–3 and Pk–1) and post-peak (Pk+1 and Pk+3) periods (Tables 4 and 5), survival of adults (t = 0.53, df = 30, p = 0.60) and young (t = 0.43, df = 25, p = 0.67) and proportion of adult females pregnant (t = 0.83, df = 34, p = 0.41) did not differ before and after the peak. During fluctuations peaking in early autumn-winter, adult survival was significantly greater before than after the peak (t = 3.48, df = 14, $p < 0.01$), but not survival of young (t = 0.16, df = 11, p = 0.88). The proportion of pregnant females was also greater before than after the peak (t = 3.25, df = 38, $p <$ 0.01).

Comparison of the peak month with the first month after the peak showed that either total population survival declined > 10% or the proportion of reproductively active adult females declined > 20% after cessation of population growth in 18 of 20 fluctuations. Survival and proportion of reproductively active females changed erratically after two peak fluctuations. Survival remained the same the first 2 months and then declined by 14% the third month after the peak, whereas the proportion of reproductively active females increased for 3 months after the peak in bluegrass in August 1978. Survival remained the same the first month after the September 1979 peak in bluegrass and declined by 15% the second peak; the proportion of reproductively active females increased 23% the first 2 months after the peak and then declined 24% the third month.

In respect to the other ll population fluctuations that peaked during spring-early autumn, the proportion of reproductively active females declined > 20% or survival declined > 10% the first month after the peak. There was a decline in only survival or in the proportion of females reproductively active the month after three peaks, each; both survival and proportion reproductively active females declined the month after 5 peaks. A > 20% reduction in the proportion of adult females that were reproductively active the first month after the peak was associated with all 7 population fluctuations that peaked during late autumn-winter. Survival declined > 10% the first month after 2 of the late autumn-winter peaks.

Table 4. Survival (mean ± SE) of *Microtus pennsylvanicus* the 3 months before the peak (P-3 to P-1), peak month, and 3 months after the peak (P+1 to P+3) during population fluctuations with peaks during either late autumn-winter or spring-early autumn. Adults ≥ 30 g, young < 29 g.

Month	Late autumn-winter peaks		Spring-early autumn peaks	
	Adult	Young	Adults	Young
Peak –3	0.37 ± 0.10	0.63 ± 0.15	0.54 ± 0.09	0.60 ± 0.12
Peak –2	0.44 ± 0.10	0.25 ± 0.14	0.64 ± 0.07	0.49 ± 0.07
Peak –1	0.42 ± 0.10	0.30 ± 0.09	0.56 ± 0.06	0.414 ± 0.08
Peak	0.42 ± 0.04	0.30 ± 0.07	0.57 ± 0.06	0.46 ± 0.12
Peak +1	0.33 ± 0.09	0.55 ± 0.05	0.54 ± 0.06	0.52 ± 0.17
Peak +2	0.44 ± 0.10	0.46 ± 0.03	0.58 ± 0.09	0.29 ± 0.10
Peak +3	0.37 ± 0.03	0.44 ± 0.04	0.41 ± 0.07	0.24 ± 0.07

Table 5. Proportion (± SE) of adult female *Microtus pennsylvanicus* reproductively active the 3 months before the peak (P-3 to P-1), peak month, and 3 months after the peak (P+1 to P+3) during population fluctuations with peaks during either late autumn-winter or spring-early autumn.

Month	Late autumn-winter peaks	Spring-early autumn peaks
Peak –3	0.73 ± 0.07	0.75 ± 0.12
Peak –2	0.68 ± 0.05	0.75 ± 0.06
Peak –1	0.70 ± 0.10	0.66 ± 0.09
Peak	0.69 ± 0.12	0.74 ± 0.04
Peak +1	0.44 ± 0.11	0.67 ± 0.08
Peak +2	0.31 ± 0.11	0.75 ± 0.10
Peak +3	0.27 ± 0.12	0.76 ± 0.07

Discussion

Temporal variation in habitat quality has been suggested to influence peak densities and amplitudes of fluctuation of arvicoline rodents (Batzli 1992, Lin and Batzli 2001, Schmidt *et al.* 2005). Although we did not measure annual variation in vegetation composition, there was no conspicuous change from year to year in the vegetation in any of the sites. Furthermore, there was no correlation between the time a site was first established (providing time for vegetative changes, and thus habitat quality) and peak densities of subsequent population fluctuations. We conclude, therefore, that variation in vegetation was not a major factor influencing peak densities and amplitudes among population fluctuations of *Microtus pennsylvanicus* across years in our study sites.

Annual population fluctuations of *M. pennsylvanicus* were most common in our sites (4 of 5 fluctuations in alfalfa and 12 of 15 in bluegrass). There was, however, no distinct seasonal pattern, ie, season in which the peak density occurred, to the population fluctuations; 13 fluctuations had peaks during spring-early autumn and seven during late autumn-winter.

The peak densities were somewhat lower than those reported for *M. pennsylvanicus* by Taitt and Krebs (1985) from published short-term studies, and were much lower than those recorded for this species by Boonstra (1985) and Ostfeld and Canham (1995). Peak densities and amplitudes of fluctuation were also lower than those typically associated with multi-annual population fluctuations of other arvicoline rodents (Huitu *et al.* 2003, Zhang *et al.* 2003, Korpimäki *et al.* 2004, Bryja *et al.* 2005). On a landscape scale, however, the fluctuations stood out as conspicuous episodes of relatively high density among extensive periods of very low density. Perhaps only unusually high-density fluctuations have been reported in the literature.

Getz *et al.* (2005b) concluded that variation in beginning density and length of the increase phase were the most important factors influencing peak densities and amplitudes of population fluctuations of *M. ochrogaster*. Variation in sur-

vival, presumably from summation of independent effects of multiple predators, was proposed to be the primary factor associated with cessation of population growth and thus variation in amplitude of population fluctuations of *M. ochrogaster*. Reduction in reproduction was not associated with cessation of population growth.

For *M. pennsylvanicus*, none of the variables tested was correlated with either peak densities or amplitudes of fluctuation. Neither survival rates nor proportion of the adult females that were reproductively active *during* the increase phase was correlated with either peak densities or amplitude of population fluctuations. We conclude, however, that, as for *M. ochrogaster*, differential timing of factors stopping population growth was the most important determinant of variation in the peak densities and amplitudes of fluctuation achieved by *M. pennsylvanicus* across years.

Cessation of population growth and the start of a decline result mainly from increased mortality and decreased reproduction; emigration does not appear to be an important factor (Krebs and Myers 1974, Gaines and McClenaghan 1980, Verner and Getz 1985, Lidicker and Stenseth 1992). Increased mortality and decreased reproduction may result from effects of density-dependent factors (eg, quality of the animals, predation; Christian 1971, 1980, Saucy 1984, Krebs 1996, Norrdhal and Korpimäki 2000, Lima *et al.* 2006) or density-independent factors (eg, adverse weather conditions, as during winter; Aars and Ims 2002, Stenseth *et al*. 2003).

On first analysis, a decline in reproduction, rather than reduced survival, appeared to be the most important variable responsible for cessation of population growth and variation in peak densities of most population fluctuations of *M. pennsylvanicus*. A reduction in the proportion of reproductively active females was associated with 15 of 20 population declines, including all 7 that peaked during late autumn-winter. The proportion of reproductively active females declined in winter irrespective of whether there was a population fluctuation, whereas survival did not display a seasonal pattern. Comparisons of the 3 months before the peak with the 3 months after the peak for fluctuations peaking in late autumn-winter revealed a significant decline in adult survival as well as in the proportion of the females that were reproductively active. It would appear, therefore, that growth of population fluctuations that peaked in late autumn or winter were not necessarily stopped solely by the winter decline in reproduction, the pattern seen in most populations of temperate small mammals. A decline in survival was also involved in cessation of population growth during late autumn-winter.

For population fluctuations that peaked in spring-early autumn, there was no difference in either survival or the proportion of females reproductively active when compared for the three months before and after the peaks. When the peak month was compared with the first after the peak, there was a marked decline in either survival or the proportion of the females that were reproductively active the first month after 11 of the 13 peaks. Both variables declined after 5 peaks, whereas declines in only 1 variable occurred after 3, each, peaks.

Survival was significantly correlated population density in both the alfalfa and bluegrass, when data from the 2 habitats for all 25 years were considered, as well as when analyses were restricted to periods of population fluctuations. The proportion of adult females that were reproductively active was not correlated with population density in either habitat over the 25 years of the study nor when the analyses were limited to periods of population fluctuation.

Extreme weather episodes did not appear to be a primary factor in cessation of population growth. An unusually dry period of 1–3 months (43.3%–84.2% lower precipitation than the 30-year mean for those months; unpublished records of the Illinois State Water Survey) preceded four of the eight reductions in the proportion of reproductively active adult females associated with population declines during spring-early autumn. During extreme droughts, however, there is ample free water in the green vegetation for individual *M. pennsylvanicus* to meet their water requirements from normal daily food consumption (Getz 2006), even when considering the additional water requirements for lactation (Oswald

et al. 1993). Other stresses associated with drought conditions may have adversely affected reproduction (Louch 1958). Reduced survival was not associated with these episodes of low precipitation. Neither were extreme weather episodes associated with declines in survival or in the proportion of reproductively active females during winter.

From the above evidence, we conclude that a decline in survival was the most consistent variable associated with cessation of population growth of *M. pennsylvanicus*. A decline in reproduction was either the primary variable or a contributory variable to reduced survival in respect to cessation of growth of 15 of the 20 population fluctuations. Thus, changes in survival and reproduction were complexly associated with cessation of population growth and magnitudes of peak densities and amplitudes of fluctuation.

Increased survival, presumably from the net effect of relaxation of pressure from generalist predators, was presumed to be responsible for initiation of population fluctuations of *M. pennsylvanicus* across years (Getz *et al*. 2006). Experimental studies by Desy and Batzli (1989) and Lin and Batzli (1995, 2001) demonstrated predation effects were a major factor in survival of voles and depression of population densities in our study area. *M. pennsylvanicus* was especially susceptible to predation in low cover habitats (Lin and Batzli 2001). We propose, therefore, that not only relaxation of predation pressure determined when a population fluctuation occurred, but that increased predation pressure was a major factor influencing peak densities and amplitudes of population fluctuation of *M. pennsylvanicus*.

Although survival, presumably from variation in predation pressure, appears to be a major factor driving population fluctuations across years and affecting amplitudes of fluctuation within years of both *M. ochrogaster* and *M. pennsylvanicus* in our study sites, multi-annual population cycles were not evident (Getz *et al*. 2001, Turchin 2003). These observations agree with other studies showing that predation plays a major role in population fluctuations of arvicoline rodents whether resulting in annual or erratic fluctuations (Hörnfeldt *et al*. 2005) or population cycles (Korpimäki *et al*. 2004, 2005). Lambin *et al*. (2006) concluded, however, that regular high-amplitude population cycles observed in south-west France were not readily explained by predation effects.

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