

Vole Population Fluctuations: Why and When ?

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Abstract: In this paper I summarize the results and conclusions of a 25-year study of demography of the prairie vole (*Microtus ochrogaster*), and meadow vole (*M. pennsylvanicus*). The roles of survival and reproduction are evaluated in respect to why population fluctuations occur some years and not others, what initiates a population fluctuation, and what is responsible for the variation in the peak density among population fluctuations. Population fluctuations of both species were erratic in respect to annual occurrence, the time of the peak density of fluctuations within years, and the height of peak the density a given year. For both species, changes in survival appeared to be responsible for whether a fluctuation occurred a given year and the time of the peak density of a fluctuation. Population density at the beginning of the increase phase and length of the increase were most responsible for variation in peak densities of population fluctuations of both species. Stoppage of growth of populations of *M. ochrogaster* resulted from decreased survival, whereas stoppage of most population fluctuations of *M. pennsylvanicus* resulted from decreased reproduction. Variation in mortality associated with initiation of a population fluctuation is presumed to result primarily from the net effect of a consortium of generalist predators, populations of each which are controlled by factors other than vole densities. Accordingly, predation pressure on vole populations a given year is presumed to be unpredictable, resulting in the observed erratic nature of population fluctuations of *M. ochrogaster* and *M. pennsylvanicus*.

Key words: Meadow vole (*Microtus pennsylvanicus*); Prairie vole (*Microtus ochrogaster*); Population cycles, Population fluctuations; Voles

田鼠种群波动的原因和时间

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摘要: 本文总结了橙腹田鼠 (*Microtus ochrogaster*) 和草原田鼠 (*M. pennsylvanicus*) 25 年的种群统计学研究结果和结论。探讨了田鼠种群波动周期性、诱发种群波动以及导致波动期间峰值变异的因素。并对种群存活值和繁殖活动的作用进行了分析和评价。根据两种田鼠种群波动周期性、波动峰值出现的时间以及特定年份峰值的高度等特征, 证明两物种波动均具有不稳定性。两种田鼠存活值的变化是由特定年份是否发生波动以及波动峰值出现的时间决定。增加初始阶段的种群密度及时间长度是造成两种动物种群波动峰值不同的主要原因。橙腹田鼠种群停止增长的原因是存活值降低, 而草原田鼠则是繁殖活动减少。据推测, 与种群波动初始密度相关的种群死亡率的差异是由捕食者的净效应 (Net effect) 决定的, 调控两种种群密度的因素均为非密度的其它生态学因子。由于特定年份田鼠种群捕食压力的不确定性, 导致了橙腹田鼠和草原田鼠种群波动的不稳定性。

关键词: 橙腹田鼠; 草原田鼠; 种群周期; 种群波动; 田鼠

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1 Introduction

Populations of most arvicoline (microtine) rodents have been observed to undergo high amplitude 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). The intervals between population fluctuations, whether short-term or encompassing 2 or more years, may be annual or erratic, or may occur at 2 - 5 year intervals, i. e., display population "cycles"

(Krebs *et al.*, 1969; Krebs and Myers, 1974; Taitt and Krebs, 1985; Krebs, 1996; Bjørnstad *et al.*, 1998). The reality of population cycles remains unresolved (Batzli, 1996). A species may display different patterns of fluctuation among sites and among years within sites (Marström *et al.*, 1990; Getz *et al.*, 2001). Neither is there convincing evidence that different species undergo synchronous fluctuations in the same site (Krebs *et al.*, 1969; Getz *et al.*, 2001).

Survival and reproduction are most responsible for temporal and habitat differences in population success of arvicoline rodents (Krebs and Myers, 1974; Batzli, 1992,

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1996; Lin and Batzli, 2001), while emigration and immigration do not appear to be important factors influencing population densities (Gaines and McClenaghan, 1980; Dueser *et al.*, 1981; Verner and Getz, 1985; Lin and Batzli, 2001; Getz *et al.*, 2005a). Immigrants may, however, be important in maintaining populations of voles in marginal habitats (Getz *et al.*, 2005a).

In this paper I summarize the general conclusions from a 25-year demographic study of two sympatric vole species (prairie vole, *Microtus ochrogaster*, and meadow vole, *M. pennsylvanicus*) in three habitats in east-central Illinois, USA. Specifically, I evaluate the role of survival and reproduction on population fluctuations, including whether a fluctuation occurs a given year, initiation of a population fluctuation, timing of the beginning of the increase phase, stoppage of population growth and triggering of the population decline, variation in peak densities of population fluctuations, and variation in intervals between population peaks. I summarize the analyses of a total of 40 population fluctuations of *M. ochrogaster* and 21 of *M. pennsylvanicus*. Some of the results and conclusions summarized in this paper have not yet been published elsewhere.

2 Methods

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 trapped voles in two restored tallgrass prairies (a mixture of big bluestem, *Andropogon gerardii*; Indian grass, *Sorghastrum nutans*; and switch grass, *Panicum spp.*), one located in Trelease Prairie, the other in Phillips Tract, from March 1972 through May 1997 (Getz *et al.*, 2001). Study sites established within a former bluegrass (*Poa pratensis*) pasture located in Phillips Tract that had been released from grazing in spring 1971 were trapped January 1972 - May 1997 (Getz *et al.*, 2001). Two adjacent sites in Phillips Tract planted with alfalfa (*Medicago sativa*) were trapped May 1972 - May 1997. Voles were trapped at a site until invading forbs and grasses began to crowd out the alfalfa. One year before trapping was terminated at one site, alfalfa was planted at the other site so that the plants would be fully developed when trapping commenced in that site. In addition to the sites used in the main study, data from additional study sites in bluegrass and tallgrass were also included in some of the analyses. Follow-up 3-day trapping sessions were also conducted during October and November of 1997 and 1998. Table 1 lists the specific study sites in each habitat, along with schedule of usage and time of the peak of each population fluctuation. The study sites are described in detail by Getz *et al.* (1979, 1987, 2001).

A grid system with 10-m intervals was established on all study sites. One wooden multiple-capture live-trap (Burt, 1940) was placed at each station. Each month a 2-day prebaiting period was followed by a 3-day trapping session; traps were checked at 08:00 h and 15:00 h each day (Getz *et al.*, 2001). At first capture, we toe-clipped all animals (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 (1998). At each capture we recorded species, grid station, individual identification, sex, reproductive condition (males: testes abdominal or scrotal; females: vagina open or closed, pregnant, as determined by palpation, or lactating), and body mass to the nearest 1 g. For analysis, we grouped individuals as adult when ≥ 30 g and as young when < 29 g.

Monthly survival was calculated as the proportion of the total animals present at the beginning of the month that survived to the next month. Since many animals were present at least two months, for survival analyses, we utilized data from every other month so as to increase the probability of independency of the data. Seasonal analyses were based on the following categories: spring, March - May; summer, June - August; autumn, September - November; winter, December - February. Population fluctuations used for our analyses were identified from Getz *et al.* (2001).

All population fluctuations of both species were less than one year in duration. For *M. ochrogaster*, the average time from onset of the increase to peak density was 4.3 ± 0.4 months; an entire fluctuation, from beginning of the increase to the end of the decline was 8.3 ± 0.6 months. For *M. pennsylvanicus* the average time from onset of the increase to the peak density was 3.8 ± 0.5 months, with 8.6 ± 0.7 months for an entire fluctuation, from increase through the decline. Thus, we were able to categorize years during which a population fluctuation occurred, and years when a population fluctuation did not occur. For phase analyses, we arbitrarily designated the following phases, based on changes in population density: increase, peak (typically only one month in duration), decline, and trough (the low-density period between populations, from the end of the decline to the beginning of the next increase phase).

Population fluctuations of *M. ochrogaster* with at least the following peak densities were used in the analyses: alfalfa, 75 voles/ha; bluegrass, 25 voles/ha; tallgrass, 20 voles/ha. Population fluctuations with peak densities of ≥ 30 voles/ha were used for the *M. pennsylvanicus* analyses in both alfalfa and bluegrass. These peak densities were lower than those from other studies reported by Taitt and Krebs (1985). *M. pennsylvanicus* popula-

tion densities were erratically high in tallgrass with no distinct high-amplitude fluctuation. Population fluctuations in this study were so defined because they stood out as conspicuous events upon examination of the 25 years of data in the three habitats. Differences in peak densities among the three habitats reflected differences in habitat quality (Getz , 2005b) . All original capture data and explanatory files from the 25-year study are available to anyone wishing to make use of them at web page : [http : // www.life.uiuc.edu/getz/](http://www.life.uiuc.edu/getz/)

Table 1 Study sites utilized in the 25 year study , including area , dates trapped , and time of population peaks of *Microtus ochrogaster* and *M. pennsylvanicus* in each. There were no distinct population fluctuations of *M. pennsylvanicus* in tallgrass. Sites with an asterisk (*) were utilized in the main study. The others were used in related studies (Getz et al. , 1987) .

Habitat/ " site "	Area (ha)	Dates trapped	Years/months of peak densities
<i>M. ochrogaster</i>			
Alfalfa 1 *	1.4	Mar 1972 - Jun 1977	1977/10; 1975/11; 1976/06
2 *	1.0	Jul 1977 - Sep 1983	1981/11; 1983/02
3 *	1.0	Oct 1983 - Dec 1989	1985/01; 1985/11; 1986/12; 1987/09
4 *	1.0	Jan 1990 - Jun 1993	1990/01; 1990/10
5 *	1.0	Jul 1993 - May 1997	1993/11; 1994/12; 1998/11
Bluegrass 6 *	2.0	Jan 1972 - Jun 1977	1973/01; 1973/12; 1975/10; 1977/04
7 *	0.9	Jul 1977 - Jun 1987	1981/11; 1985/02; 1985/10
11 *	1.0	Jul 1987 - May 1997	1987/11; 1990/01; 1990/11; 1993/11
9	1.0	Jul 1977 - May 1997	1983/11; 1985/01; 1985/11; 1987/09; 1989/11; 1990/11
Tallgrass 12 *	2.0	Mar 1972 - Jun 1977	1973/01
15 *	0.5	Sep 1977 - May 1984	1983/04
13 *	0.7	Sep 1984 - Apr 1987	1985/06
16 *	0.5	Sep 1987 - May 1997	1988/01; 1989/12
14	0.7	Jan 1981 - Nov 1983	1983/06
19	0.5	Sep 1984 - May 1997	1985/06; 1989/12
<i>M. pennsylvanicus</i>			
Alfalfa 1 *	1.4	Mar 1972 - Jun 1977	none
2 *	1.0	Jul 1977 - Sep 1983	1977/11; 1978/09; 1979/08; 1980/05
3 *	1.0	Oct 1983 - Dec 1989	none
4 *	1.0	Jan 1990 - Jun 1993	none
5 *	1.0	Jul 1993 - May 1997	1995/08
Bluegrass 6 *	2.0	Jan 1972 - Jun 1977	1976/07
7 *	0.9	Jul 1977 - Jun 1987	1977/08; 1978/09; 1979/07; 1980/07; 1981/11; 1982/06; 1986/02
11 *	1.0	Jul 1987 - May 1997	1995/11; 1998/11
8	0.5	Jun 1977 - Dec 1983	1977/12; 1978/06; 1979/09
10	1.0	Jul 1977 - May 1987	1977/12; 1979/06; 1980/01

3 Demography

3.1 Population densities and fluctuations

Population fluctuations of the two species in the main study sites in the three habitats are given in Figs. 1 and 2. Mean population densities of *M. ochrogaster* in these sites over the 25 years of the study were 50 voles/ha in alfalfa , 18 voles/ha in bluegrass , and 7 voles/ha in tallgrass (*P* < 0.05 ; Getz et al. , 2001) . Mean peak density of 13 population fluctuations in alfalfa was 202 voles/ha (range , 77 - 638/ha) , for the 11 fluctuations in bluegrass , 67 voles/ha (25 - 156/ha) , and for the 5

in tallgrass , 59 voles/ha (34 - 92/ha) . There also was a population fluctuation in alfalfa , with a peak of 85 voles/ha in November 1998.

Mean population densities of *M. pennsylvanicus* in the main study sites were highest in tallgrass (30 voles/ha) , intermediate in bluegrass (14 voles/ha) , and lowest in alfalfa (7 voles/ha ; *P* < 0.05 ; Getz et al. , 2001) . Mean peak density of the 5 population fluctuations in alfalfa was 53 voles/ha (range , 29 - 79/ha) and of the 9 in bluegrass , 56 voles/ha (35 - 91/ha) . *M. pennsylvanicus* also displayed a population fluctuation , with a peak of 38 voles/ha , in bluegrass in November 1998. There were extensive periods when *M. pennsylvanicus*

was absent or present in very low population densities in both alfalfa and bluegrass.

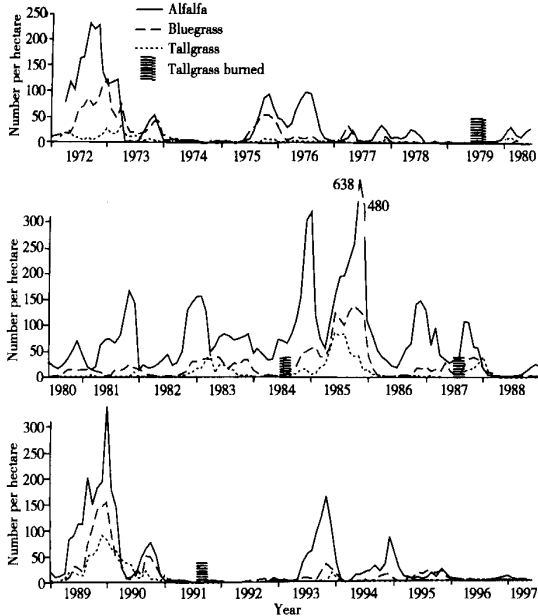


Fig. 1 Densities of *Microtus ochrogaster* in 3 habitats in east-central Illinois; populations were monitored at monthly intervals

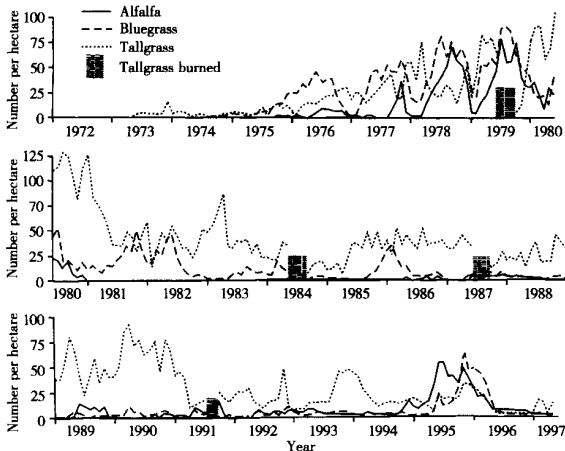


Fig. 2 Densities of *Microtus pennsylvanicus* in 3 habitats in east-central Illinois. Populations were monitored at monthly intervals

3.2 Timing of fluctuations

Most (30 of 39) increase phases of *M. ochrogaster* fluctuations began in spring-early autumn, with the greatest number beginning in September (Table 2). Peak densities of the population fluctuations occurred mainly (32 of 39) in late autumn-winter, with the greatest number peaking in November. Thus, most declines of *M. ochrogaster* population fluctuations occurred during winter. Beginning of increase phases and peak densities of *M. pennsylvanicus* fluctuations occurred throughout the year, with no distinct seasonal pattern (Table 2). Most population fluctuations of *M. pennsylvanicus* peaked June-Sep-

tember. Accordingly, few (7 of 20) decline phases occurred during winter.

Table 2 Months of beginning of the increase phase and month of the peak phase of population fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus*. Data for all three habitats combined

Month	<i>M. ochrogaster</i>		<i>M. pennsylvanicus</i>	
	Increase	Peak	Increase	Peak
January	0	9	0	1
February	1	2	1	1
March	3	2	5	0
April	3	0	3	0
May	6	1	2	1
June	2	1	1	3
July	4	2	1	3
August	2	0	0	3
September	10	1	4	3
October	3	5	1	0
November	4	10	2	3
December	1	6	0	2

3.3 Whether a population fluctuation a given year

The proportion of adult female *M. ochrogaster* that were reproductively active (vagina open, pregnant, or lactating) did not differ during winters preceding years with a population fluctuation and those preceding years with no fluctuation (Alfalfa: 0.37 ± 0.05 and 0.45 ± 0.05 , respectively; $t = 1.15$, $df = 55$, $P = 0.25$. Bluegrass: 0.57 ± 0.07 and 0.42 ± 0.08 , respectively; $t = 1.55$, $df = 47$, $P = 0.13$. Tallgrass: 0.52 ± 0.11 and 0.55 ± 0.11 , respectively; $t = 0.07$, $df = 28.8$, $P = 0.95$). Of the 30 population cycles recorded for *M. ochrogaster* in the three habitats during the main study, only three were preceded by winters with higher than average proportion reproductively active females. Three of the years when there was no population fluctuation were preceded by winters with higher than normal proportion reproductively active females.

Neither did the proportion of adult female *M. pennsylvanicus* that were reproductively active differ during the winters preceding years with a fluctuation and years with no fluctuation (Alfalfa: 0.38 ± 0.13 and 0.62 ± 0.15 , respectively; $t = 1.184$, $df = 16$, $P = 0.25$. Bluegrass: 0.31 ± 0.07 and 0.18 ± 0.08 , respectively; $t = 1.55$, $df = 39$, $P = 0.13$). Only two of the 14 population fluctuations were preceded by winters with higher than average reproductively active females; none of the years when there was no population fluctuation was preceded by a winter with higher than average reproductively active females.

Survival of *M. ochrogaster* was significantly greater in both alfalfa and bluegrass during summer-autumn (typical period of population growth) of years with population fluctuations, as contrasted to years when there was no fluctuation (Alfalfa: 0.76 ± 0.02 and 0.44 ± 0.04 , re-

spectively; $t = 6.96$, $df = 82.8$, $P < 0.01$. Bluegrass: 0.47 ± 0.01 and 0.36 ± 0.02 , respectively; $t = 2.12$, $df = 117$, $P < 0.04$. The proportion of reproductively active adult females did not differ significantly during summer-autumn of years with and without population fluctuations (Alfalfa: 0.88 ± 0.04 and 0.87 ± 0.02 , respectively; $t = 0.21$, $df = 50.2$, $P = 0.83$. Bluegrass: 0.88 ± 0.04 and 0.85 ± 0.02 , respectively; $t = 0.49$, $df = 96$, $P = 0.63$). There were too few data from tallgrass for comparable analyses.

Because there was no seasonal pattern to initiation of population fluctuations of *M. pennsylvanicus*, survival and proportion reproductively active adult females were compared during the entire year for years with and without population fluctuations. Survival was greater during years when there was a population fluctuation in contrast to years when there was no fluctuations in alfalfa, but not bluegrass (Alfalfa: 0.56 ± 0.03 and 0.35 ± 0.04 , respectively; $t = 3.28$, $df = 126$, $P < 0.01$. Bluegrass:

0.56 ± 0.03 and 0.41 ± 0.04 , respectively; $t = 2.45$, $df = 107.2$, $P = 0.15$). The proportion of reproductively active adult females was less during years when there was a population fluctuation than years when there was no fluctuation in alfalfa, while there was no difference in bluegrass (Alfalfa: 0.64 ± 0.05 and 0.84 ± 0.04 , respectively; $t = 3.94$, $df = 91$, $P < 0.01$. Bluegrass: 0.60 ± 0.03 and 0.60 ± 0.04 , respectively; $t = 0.85$, $df = 175.7$, $P = 0.40$). There were too few data from tallgrass for comparable analyses.

Monthly survival of both species was significantly greater during the increase phase than during the preceding low-density trough phase (Table 3). Only a significantly greater proportion of adult female *M. ochrogaster* in alfalfa were reproductively active during the increase than the preceding trough. The proportion of reproductively active adult female *M. pennsylvanicus* was significantly greater during the increase than the trough in bluegrass, but not alfalfa (Table 3).

Table 3 Comparison of survival (proportion [mean \pm SE] of individuals surviving to next month) and proportion (mean \pm SE) of adult females reproductively active during the trough, increase, and decline phases of *Microtus ochrogaster* and *M. pennsylvanicus* population fluctuations. Sample sizes (number of months of data included in each sample) are in parentheses. Two sample *t*-tests were used to test for differences in each variable between trough and increase and the decline and increase phase. Asterisks are used to indicate difference of Trough and Decline from the Increase (*t*-tests); values with a single asterisk (*) indicate significant difference at $P < 0.05$; those with double asterisks (**) indicate significant difference at $P < 0.01$.

	Phase		
	Decline	Trough	Increase
<i>M. ochrogaster</i>			
Alfalfa			
Survival	0.513 \pm 0.025 ** (127)	0.686 \pm 0.016 (65)	0.419 \pm 0.025 * (54)
Reproductive	0.778 \pm 0.028 * (117)	0.821 \pm 0.023 (68)	0.551 \pm 0.045 ** (51)
Bluegrass			
Survival	0.387 \pm 0.030 ** (128)	0.594 \pm 0.025 (49)	0.369 \pm 0.027 * (40)
Reproductive	0.800 \pm 0.033 (90)	0.759 \pm 0.035 (49)	0.457 \pm 0.059 ** (37)
Tallgrass			
Survival	0.309 \pm 0.034 ** (83)	0.612 \pm 0.038 (20)	0.420 \pm 0.035 ** (27)
Reproductive	0.799 \pm 0.040 (68)	0.621 \pm 0.082 (21)	0.521 \pm 0.081 (25)
<i>M. pennsylvanicus</i>			
Alfalfa			
Survival	0.421 \pm 0.033 ** (85)	0.546 \pm 0.034 (20)	0.396 \pm 0.042 * (25)
Reproduction	0.810 \pm 0.043 (47)	0.787 \pm 0.035 (20)	0.516 \pm 0.082 * (22)
Bluegrass			
Survival	0.437 \pm 0.034 ** (107)	0.588 \pm 0.020 * (44)	0.520 \pm 0.039 * (30)
Reproduction	0.625 \pm 0.050 * (71)	0.650 \pm 0.045 (43)	0.435 \pm 0.066 * (29)

3.4 Peak densities of population fluctuations

Peak densities of population fluctuations of *M. ochrogaster* were erratic in all three habitats [Fig. 1 and as indicated by the Standard Deviations in comparison to peak densities (Alfalfa: mean peak density, 202 voles/ha; SD, ± 151.8 . Bluegrass: mean peak density, 67 voles/ha; SD, ± 48.3 . Tallgrass: mean peak density, 59 voles/ha; SD, ± 30.9)]. Peak densities of *M.*

pennsylvanicus were less erratic than those of *M. ochrogaster* (Alfalfa: mean peak density, 53 voles/ha; SD, ± 21.4 . Bluegrass: mean peak density, 56 voles/ha; SD, ± 18.9).

Another indication of the erratic nature of peak densities is the Standard Deviation in the differences in peak densities of successive population fluctuations. By this indicator, peak densities of population fluctuations of *M.*

ochrogaster were most erratic in alfalfa and more so than those of *M. pennsylvanicus* (*M. ochrogaster*: alfalfa, SD ± 143.5 voles/ha; bluegrass, SD ± 45.5 voles/ha; tallgrass, SD ± 12.8 voles/ha. *M. pennsylvanicus*: alfalfa, SD ± 17.1 voles/ha; bluegrass, SD ± 14.5 voles/ha).

Multiple linear regression analyses were conducted on the effects of the following variables on peak densities of population fluctuations of the two species: time (month) of the beginning of the increase period, beginning density, length of the increase phase, length of the reproductive period, survival rates during the increase, proportion adult females reproductively active during the increase, population growth rates, and body mass of adult males. Of these variables, beginning density and length of the increase phase were most closely related to peak densities of the two species.

3.5 Stoppage of population growth

When data for all population fluctuations were combined for analysis, both monthly survival and the proportion of reproductively active adult females of both species were less during the decline phase than during the increase (Table 3). However, the proportion of reproductively active adult females of both species was lower during the winter than other seasons (Table 4). Data from *M. ochrogaster* population fluctuations that peaked in spring-summer were used to test the role of decreased reproduction on generating a population decline. Survival was significantly higher during the increase than during the decline (0.69 ± 0.03 and 0.48 ± 0.06 , respectively; $t = 3.329$, $df = 34$, $P < 0.01$). There was, however, no difference in the proportion of reproductively active adult females during the increase and decline (0.40 ± 0.08 and 0.51 ± 0.05 , respectively; $t = 0.655$, $df = 32$, $P = 0.37$).

Table 4 Seasonal comparisons (mean \pm SE) of monthly survival and proportion of adult females reproductively active for *Microtus ochrogaster* and *M. pennsylvanicus* in the three habitats over the 25 years of the study. See text for definition of variables and seasons. For each habitat, values within a column with different superscripts differ significantly at the 0.05 level (Tukey's HSD test).

	<i>Microtus ochrogaster</i>		<i>Microtus pennsylvanicus</i>	
	Survival	% Reproductive	Survival	% Reproductive
Alfalfa				
Spring	0.544 \pm 0.035 ^a	0.817 \pm 0.033 ^a	0.524 \pm 0.061 ^a	0.728 \pm 0.064 ^{ab}
Summer	0.530 \pm 0.031 ^a	0.909 \pm 0.019 ^a	0.461 \pm 0.051 ^a	0.797 \pm 0.021 ^b
Autumn	0.530 \pm 0.030 ^a	0.843 \pm 0.024 ^a	0.421 \pm 0.049 ^a	0.830 \pm 0.042 ^b
Winter	0.509 \pm 0.030 ^a	0.400 \pm 0.036 ^b	0.356 \pm 0.051 ^a	0.452 \pm 0.100 ^a
F (ANOVA); df	0.394; 3, 267	59.789; 3, 236	1.563; 3, 124	5.083; 3, 88
P	0.758	<0.001	0.202	0.003
Bluegrass				
Spring	0.409 \pm 0.042 ^a	0.673 \pm 0.043 ^a	0.572 \pm 0.041 ^a	0.665 \pm 0.052 ^a
Summer	0.391 \pm 0.042 ^a	0.851 \pm 0.035 ^b	0.507 \pm 0.040 ^a	0.691 \pm 0.050 ^a
Autumn	0.478 \pm 0.035 ^a	0.875 \pm 0.025 ^b	0.481 \pm 0.043 ^a	0.787 \pm 0.040 ^a
Winter	0.456 \pm 0.038 ^a	0.496 \pm 0.054 ^c	0.460 \pm 0.042 ^a	0.243 \pm 0.052 ^b
F (ANOVA); df	1.284; 3, 229	17.286; 3, 187	1.414; 3, 191	27.249; 3, 158
P	0.281	<0.001	0.239	<0.001
Tallgrass				
Spring	0.401 \pm 0.058 ^a	0.677 \pm 0.069 ^{ab}	0.541 \pm 0.030 ^a	0.624 \pm 0.042 ^a
Summer	0.416 \pm 0.050 ^a	0.863 \pm 0.050 ^a	0.724 \pm 0.025 ^a	0.431 \pm 0.055 ^b
Autumn	0.442 \pm 0.052 ^a	0.787 \pm 0.050 ^a	0.606 \pm 0.024 ^a	0.697 \pm 0.036 ^a
Winter	0.433 \pm 0.040 ^a	0.537 \pm 0.076 ^b	0.601 \pm 0.025 ^a	0.186 \pm 0.036 ^c
F (ANOVA); df	1.126; 3, 132	5.348; 3, 117	7.377; 3, 244	33.590; 3, 225
P	0.341	0.002	<0.001	<0.001

When *M. pennsylvanicus* population fluctuations that peaked during winter were removed from the analyses, survival during the increase phase was greater than that during the decline in alfalfa (0.58 ± 0.03 and 0.41 ± 0.05 , respectively; $t = 2.71$, $df = 27.9$, $P = 0.01$), but not in bluegrass (0.60 ± 0.02 and 0.52 ± 0.04 ; $t = 1.25$, $df = 56$, $P = 0.22$). The greater proportion of reproductively

active adult females during the increase in comparison to the decline approached significance in alfalfa (0.79 ± 0.04 and 0.52 ± 0.05 ; $t = 1.98$, $df = 31.2$, $P = 0.06$), and was insignificant in bluegrass (0.60 ± 0.05 and 0.47 ± 0.08 ; $t = 0.92$, $df = 54$, $P = 0.36$). When individual population fluctuations of *M. pennsylvanicus* were analyzed separately, however, a decline in the proportion of repro-

ductively active adult females was associated with stoppage of growth of 15 of 20 fluctuations, in 11 of which there was no decline in survival. During only 4 of the 20 population declines was there decreased survival, with no associated decrease in the proportion of reproductively active adult females.

There was no correlation between peak densities of population fluctuation and survival rates during the subsequent decline (*M. ochrogaster*: alfalfa, $r = -0.04$, $P = 0.89$; bluegrass, $r = 0.11$, $P = 0.74$; tallgrass, $r = 0.62$, $P = 0.27$. *M. pennsylvanicus*: alfalfa, $r = 0.48$, $P = 0.41$; bluegrass, $r = -0.02$, $P = 0.95$)

3.6 Intervals between fluctuations

Length of time until the next population fluctuation (beginning of the increase phase) was not correlated with peak density of population fluctuations of either species (*M. ochrogaster*: alfalfa, $r = -0.39$, $P = 0.21$; bluegrass, $r = 0.31$, $P = 0.36$. *M. pennsylvanicus*: bluegrass, $r = -0.04$, $P = 0.94$). There were too few fluctuations of *M. ochrogaster* in tallgrass and of *M. pennsylvanicus* in alfalfa for analysis.

Although the mean interval between peaks of population fluctuations of *M. ochrogaster* in alfalfa and bluegrass and *M. pennsylvanicus* in bluegrass was approximately 24 months, the Standard Deviation for *M. ochrogaster* in alfalfa and bluegrass and for *M. pennsylvanicus* in bluegrass (too few data were available for *M. ochrogaster* in tallgrass and *M. pennsylvanicus* in alfalfa for comparable analyses) was very high [(mean \pm SD) *M. ochrogaster*: alfalfa, 24.1 ± 17.8 months; bluegrass, 23.8 ± 12.4 months. *M. pennsylvanicus*: bluegrass, 29.8 ± 35.0 months].

4 Seasonal effects

There was no seasonal difference in monthly survival of either species in any of the three habitats (Table 4). Proportions of reproductively active adult females of both species were lower during winter than other seasons.

5 Overall correlations

Partial correlation analysis of survival (compensating for proportion reproductively active adult females) and proportion of reproductively active adult females (compensating for survival) of *M. ochrogaster* over the 25 years of the study indicated that population density was significantly correlated with survival (alfalfa: $r = 0.37$, $P < 0.01$; bluegrass: $r = 0.57$, $P < 0.01$; and tallgrass: $r = 0.61$, $P < 0.01$). Proportion of reproductively active adult females was not correlated with population density (alfalfa: $r = 0.02$, $P = 0.78$; bluegrass: $r = 0.06$, $P = 0.49$; tallgrass: $r = -0.12$, $P = 0.36$). Population density of *M. pennsylvanicus* in alfalfa was significantly

correlated with survival ($r = 0.55$, $P < 0.01$), but not with the proportion of reproductively active adult females ($r = 0.06$, $P = 0.67$). In bluegrass both survival ($r = 0.38$, $P < 0.01$) and the proportion of reproductively active adult females ($r = 0.23$, $P = 0.02$) were significantly correlated with population density.

6 Discussion

Distinct large fluctuations in population density of both *Microtus ochrogaster* and *M. pennsylvanicus* occurred erratically over the 25 years of the present study. The timing of initiation of population increases and the month of peak densities of population fluctuations of both species were not consistent among population fluctuations, occurring erratically from one fluctuation to the other. Increases in population density associated with population fluctuations of *M. ochrogaster* and *M. pennsylvanicus* appeared to be triggered by increased survival; there was no consistent increase in the proportion of reproductively active adult females associated with initiation of population increases. Thus, whether a population fluctuation of either species occurred a given year was the result of survival that year. Those years survival was low there was no large population fluctuation, whereas those years when survival was unusually high a population fluctuation occurred.

Peak densities of population fluctuations both species were correlated most closely with population density at the beginning of the increase and length of the increase phase. Peak density of population fluctuations was unrelated to differential survival or reproduction during the increase phase, but was mainly a result of how long population growth continued. This suggests that timing of stoppage of population growth was the primary determinant of peak densities achieved during a given population fluctuation.

Increased mortality appeared to be the primary factor responsible for stoppage of population growth and triggering of a decline phase of *M. ochrogaster*. Low reproduction during winter may have enhanced population declines of *M. ochrogaster* that occurred in winter, but did not appear to trigger such declines. Population declines of population fluctuations that reached a peak in spring-summer did not involve reduced reproduction; the proportion of reproductively active adult females remained high during the decline phase, whereas survival was lower during the decline than during the increase. Stoppage of population growth of 15 of 20 *M. pennsylvanicus* population fluctuations was most closely related to a decline in the proportion of reproductively active adult females. A decline in survival alone was associated with stoppage of growth and initiation of a decline phase in only 4 of the 20

population fluctuations. The reason for the decline in reproduction was not apparent. A decline in the proportion of reproductively active adult females was associated with population fluctuations that declined in spring-summer as well as those declining during the winter.

Predation is presumed to be the primary factor responsible for variation in survival associated with changes in population density, including initiation of population fluctuations (Getz *et al.*, 2005b). I propose that variation in predation pressure influences whether a population fluctuation occurs during a given year and in turn the length of the interval between population fluctuations. I further suggest that variation in predation pressure is the primary factor responsible for cessation of population growth and thus the amplitude of population fluctuations of *M. ochrogaster*.

Delayed density-dependent effects of predator-prey interactions, may result in high amplitude fluctuations in population density (May, 1976; Saucey, 1984; Hanski *et al.*, 1993; Hornfeldt, 1994; Ostfeld *et al.*, 1995). Resident generalist predators tend to dampen population fluctuations and reduce the probability of population fluctuations, whereas resident specialists may deepen and prolong population lows and generate multi-annual fluctuations (Hanski *et al.*, 1991; Korpimäki and Norrdhal, 1991; Graham and Lambin, 2002). Nomadic specialists, on the other hand, dampen fluctuations by rapidly responding to sites with high population densities. We found no correlation between peak densities of population fluctuations and subsequent survival rates during the decline. This suggests predation effects on survival may not have been entirely density dependent.

Lin and Batzli (1995) listed 21 potential predators of voles in our study sites; only the least weasel (*Mustela nivalis*) is considered a resident specialist predator on voles (Pearson, 1985). Although we did not monitor *M. nivalis* populations, we frequently caught individuals in our vole live-traps, providing an indication of weasel presence in our study sites. These captures were almost always during times when vole population densities were high. If *M. nivalis* were the primary predator on voles and displayed delayed density-dependent effects on vole populations (Getz *et al.*, 2004), we should have observed synchrony among the vole populations. Most of our study sites were contiguous; individual *M. nivalis* would easily have moved among the sites. However, populations of neither species displayed synchrony among the three habitats. Getz *et al.* (2001) suggested synchrony among population fluctuations of *M. ochrogaster*, but on further evaluation, they do not appear to be synchronous. Nor was there synchrony between population fluctuations of the two species. Thus, *M. nivalis* does not appear to be the primary factor responsible for periods of low densities or

stoppage of population growth of either species.

Whereas feral cats (*Felis silvestris*) utilize a variety of prey during spring-early autumn, voles most likely constitute the predominant prey during late autumn-winter (Lin and Batzli, 1995). *F. silvestris* may be nomadic in their hunting, but their abundance is not entirely density-dependent in respect to vole populations. Numbers in a given area at a given time most likely reflect more closely the varying numbers of *F. silvestris* maintained at nearby houses or farmsteads, not the numbers of feral animals in the area in response to vole densities. *F. silvestris* would spend much of the time feeding in vole habitats near their shelter, whether it be homesteads or forest stands, even when population densities were low (George, 1974; Warner, 1985). Thus, *F. silvestris* may or may not hold down vole population densities during the low phase, depending upon location of the site in relation to nearby farmsteads and abundance of *F. silvestris* at these farmsteads.

Of eight raptors common in the area, only one, the migratory rough-legged hawk (*Buteo lagopus*), is a nomadic specialist predator on voles. Although *B. lagopus* may be involved in stopping population growth and in initiating a decline phase of *M. ochrogaster*, it would not play a role in maintaining lengthy low-density periods. *B. lagopus* begin arriving in east-central Illinois in November, about the time of most peaks of *M. ochrogaster* population fluctuations, and remain until early spring. By the time *B. lagopus* migrated north in spring, the decline phase normally has run its course. These hawks, therefore, migrate north before a population increase phase would be initiated and arrive back after an increase either had been suppressed that year by other predators or had already been initiated with the population having achieved a relatively high density. *B. lagopus* could, therefore, have contributed to stoppage of population growth of most *M. ochrogaster* fluctuations. We did not maintain records of sightings on our study areas, but at least a few individuals were observed in and around the study sites most winters. Christmas bird count data for our region indicate that numbers of *B. lagopus* vary at least 12-fold among winters (summarized in American Birds for years 1972 - 1996). Thus, effects of *B. lagopus* on stoppage of population growth would be erratic from year to year. Further, *B. lagopus* were not present in the study areas during the course of most *M. pennsylvanicus* population fluctuations.

Resident generalist predators are the most likely primary source of mortality maintaining low population densities of voles (Hanski *et al.*, 1991). Lin and Batzli (1995) listed five species of generalist snakes (western fox snake, *Elaphe vulpina*; black rat snake, *E. obsoleta*; eastern yellow-bellied racer, *Coluber constrictor*; eastern milk snake, *Lampropeltis triangulum*; prairie king

snake, *L. calligaster*) as potential predators on voles in our study sites. These snakes feed on voles, but would have hibernated at least a month prior to the cessation of growth of population fluctuations with peak densities in autumn-winter. Lin and Batzli (1995) and Getz *et al.* (2000) further concluded that snake predation on adult voles was a minor source of mortality in vole populations. Thus, it is most likely that snakes would not be major contributors even to cessation of increases of population fluctuations that peaked in spring-summer. While snakes are not a major predator on adult voles, Getz *et al.* (1990, 2000) suggested snakes play a major role in suppressing population increases in *M. ochrogaster* through predation on nestlings.

Differential density-dependent effects of the remaining six resident generalist mammalian predators (raccoon, *Procyon lotor*; red fox, *Vulpes vulpes*; gray fox, *Urocyon cinereoargenteus*; coyote, *Canis latrans*; long-tailed weasel, *Mustela frenata*; mink, *M. vison*) and seven resident generalist raptors (American kestrel, *Falco sparverius*; northern harrier, *Circus cyaneus*; red-tailed hawk, *Buteo jamaicensis*; barn owl, *Tyto alba*; eastern screech owl, *Otus asio*; short-eared owl, *Asio flammeus*; great-horned owl, *Bubo virginianus*) may be involved in cessation of population growth of *M. ochrogaster* fluctuations.

Resident and migrant specialist and generalist predators would exert varying predation pressure on vole populations during spring-autumn. Depending upon the net effect of such combined predation pressure, population densities would remain low some years, while other years population fluctuations would occur. Variable response-time of the array of predators to population increases of voles would result in different peak densities among years. Further, predator-prey interactions of the various species would vary among habitats (Getz *et al.*, 2005b). Predation effectiveness varies with hunting ability and habitat conditions (cover) and ability of prey to avoid predators (variable prey risk; Glickman and Morrison, 1969; Muller-Schwarze and Muller-Schwarze, 1971; Spiegel *et al.*, 1974; Derting and Crawford, 1989).

The impact of individual species of predators would vary from year to year since population densities of each are controlled by different factors. Some years one or more species may be responsible for suppressing population growth of voles, while other species would be involved other years. Given the erratic nature of such events, population fluctuations would be expected to be erratic in nature, with no typical predator-prey cycle, and thus no distinct predictable interval between population fluctuations. This is what we observed with respect to population fluctuations of both species of voles over the 25 years of our study. Although the role of predation in population fluctuations of arvicoline rodents has been controversial

(e.g., Korpimäki and Norrdahl, 1998; Graham and Lambin, 2002; Arpat *et al.*, 2004), our results suggest that predation plays an important role in the dynamics of our study populations.

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References:

- American Society of Mammalogists. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *J Mammal*, **79**: 1416 - 1431.
- Arpat O, Getz L L, Oli M K. 2004. Demography of fluctuating populations: temporal and phase-related changes in vital rates of *Microtus ochrogaster*. *J An Ecol*, **73**: 201 - 215.
- Batzli G O. 1992. Dynamics of small mammal populations: a review. In: McCullough D R, Barrett R H eds, *Wildlife 2001: populations*. New York: Elsevier Applied Science, 831 - 850.
- Batzli G O. 1996. Population Batzli cycles revisited. *Trends Ecol Evol*, **11**: 448 - 449.
- Bjornstad O N, Stenseth N C, Saitoh T, Lingjaerde O C. 1998. Mapping the regional transition to cyclicity in *Clethrionomys rufocanus*: special densities and functional data analysis. *Res Pop Ecol*, **40**: 77 - 84.
- Burt W H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. *Univ Mich Mus Zool Misc Publ*, **45**: 1 - 58.
- Derting T, Cranford J A. 1989. Physical and behavioral correlates of prey vulnerability to barn owl (*Tyto alba*) predation. *Am Midl Nat*, **121**: 11 - 20.
- Dueser R D, Wilson M L, Rose R K. 1981. Attributes of dispersing meadow voles in open-grid populations. *Acta Theriol*, **26**: 139 - 162.
- Gaines M S, McClenaghan L R, Jr. 1980. Dispersal in small mammals. *An Rev Ecol Syst*, **11**: 163 - 196.
- George W G. 1974. Domestic cats as predators and factors in winter shortages of raptor prey. *Willson Bull*, **86**: 384 - 396.
- Getz L L, Cole F R, Verner L, Hofmann J E, Avalos D. 1979. Comparisons of population demography of *Microtus ochrogaster* and *M. pennsylvanicus*. *Acta Theriol*, **24**: 319 - 349.
- Getz L L, Hofmann J E, Klatt B J, Verner L, Cole F R, Lindroth R L. 1987. Fourteen years of population fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus* in east central Illinois. *Can J Zool*, **65**: 1317 - 1325.
- Getz L L, Solomon N, Pizzuto T. 1990. Effects of predation of snakes on social organization of the prairie vole, *Microtus ochrogaster*. *Amer Midl Nat*, **123**: 365 - 371.
- Getz L L, Simms L E, McGuire B. 2000. Nestling survival and population cycles in the prairie vole, *Microtus ochrogaster*. *Can J Zool*, **78**: 1723 - 1731.
- Getz L L, Hofmann J E, McGuire B, Dolan T W, III. 2001. Twenty-five years of population fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus* in three habitats in east-central Illinois. *J Mammal*, **82**: 22 - 34.
- Getz L L, Simms L E, Hofmann J E, McGuire B. 2004. Delayed density-dependent effects and population fluctuations in the prairie vole *Microtus ochrogaster*. *Acta Zool Sinica*, **50**: 1 - 8.

- Getz L L, Oli M K, Hofmann J E, McGuire B. 2005a. The influence of immigration on demography of sympatric voles. *Acta Theriol*, In Press.
- Getz L L, Oli M K, Hofmann J E, McGuire B. 2005b. Habitat specific demography of sympatric vole populations over 25 years. *J Mammal*, In Press.
- Glickman S E, Morrison B J. 1969. Some behavioral and neural correlates of predation susceptibility in mice. *Comm Behav Biol*, **4**: 261 - 267.
- Graham M I, Lambin X. 2002. The impact of weasel predation on cyclic field-vole survival: the specialist predator hypothesis contradicted. *J An Ecol*, **71**: 946 - 956.
- Hanski I, Hansson L, Henttonen H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *J An Ecol*, **60**: 353 - 367.
- Hanski I, Turchin P, Korpimäki E, Henttonen H. 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature*, London, **364**: 232 - 235.
- Hornfeldt B. 1994. Delayed density dependence as a determinant of vole cycles. *Ecology*, **75**: 791 - 806.
- Korpimäki E, Norrdahl K. 1991. Do breeding nomadic avian predators dampen population fluctuations of small mammals? *Oikos*, **62**: 195 - 208.
- Korpimäki E, Norrdahl K. 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. *Ecology*, **79**: 2448 - 2455.
- Krebs C J, Keller B, Tamarin R H. 1969. *Microtus* population demography: demographic changes in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus* in southern Indiana. *Ecology*, **50**: 587 - 607.
- Krebs C, Myers J H. 1974. Population cycles in small mammals. *Adv Ecol Res*, **8**: 267 - 399.
- Krebs C J. 1996. Population cycles revisited. *J Mammal*, **77**: 8 - 24.
- Lin Y K, Batzli G O. 1995. Predation on voles: an experimental approach. *J Mammal*, **76**: 1003 - 1012.
- Lin Y K, Batzli G O. 2001. The influence of habitat quality on dispersal, demography and population dynamics of voles. *Ecol Monogr*, **71**: 245 - 275.
- Marström V, Höglund N, Krebs C J. 1990. Periodic fluctuations in small mammals at Boda, Sweden from 1961 - 1988. *J An Ecol*, **59**: 753 - 761.
- May R M. 1976. Models for single populations. In: May R M ed. *Theoretical ecology: principles and applications*. Philadelphia, PA., W. B. Saunders, 5 - 29.
- Müller-Schwarze D, Müller-Schwarze C. 1971. Responses of chipmunks to models of aerial predators. *J Mammal*, **52**: 456 - 458.
- Oksanen T, Henttonen H. 1996. Dynamics of voles and small mustelids in the taiga landscape of northern Fennoscandia in relation to habitat quality. *Ecography*, **19**: 432 - 443.
- Ostfeld R S, Canham C D. 1995. Density-dependent processes in meadow voles: an experimental approach. *Ecology*, **76**: 521 - 532.
- Pearson O P. 1985. Predation. In: Tamarin R H ed. *Biology of New World Microtus*. Spec Publ No. 8, Am Soc Mammal, 535 - 566.
- Saucey F. 1984. Density dependence in time series of the fossorial form of the water vole, *Arvicola terrestris*. *Oikos*, **71**: 381 - 392.
- Spiegel R, Price E, Huck U W. 1974. Differential vulnerability of wild, domestic and hybrid Norway rats to predation by great horned owls. *J Mammal*, **55**: 386 - 392.
- Taitt M J, Krebs C J. 1985. Population dynamics and cycles. In: Tamarin R H ed. *Biology of New World Microtus*. Spec Publ No. 8, Am Soc Mammal, 535 - 566.
- Verner L, Getz L L. 1985. Significance of dispersal in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus*. *J Mammal*, **66**: 338 - 347.
- Warner R E. 1985. Demography and movements of free-ranging domestic cats in rural Illinois. *J Wildl Manag*, **49**: 340 - 346.